Representing Actions in Memory

Neural Correlates and a Cross-Cultural Approach

Dissertation

zur Erlangung des akademischen Grades eines

Doktors der Philosophie

der Philosophischen Fakultät III

der Universität des Saarlandes

vorgelegt von

Katja Umla-Runge

aus Saarbrücken

Saarbrücken, 2012

OVERVIEW

LIST OF FIGURES

LIST OF TABLES

This manuscript contains text passages, figures and tables out of scientific papers of which I am the first author that have been submitted for publication in peer reviewed journals at the time of writing my doctoral thesis. In order to keep the text easily comprehensible, these parts are not explicitly marked, even in case that larger passages are literally copied.

Please note, since submission of the dissertation, one paper has been accepted and is currently in press:

Umla-Runge, K., Zimmer, H.D., Fu, X., & Wang, L. (in press). An action videoclip database rated for familiarity in China and Germany. Behavior Research Methods.

Content of this paper is presented in this text in Chapter 7. Now the copyright is with Psychonomic Society, Inc.

"Never mistake motion for action" (Ernest Hemingway)

1. INTRODUCTION

Action information involves motion information. However, motion information is only part of the story and there is much more to actions. Actions can be object directed or they can be executed without objects being present. They can be meaningful or meaningless, familiar or unfamiliar, simple or complex. Actions involve specific movements of the actor. In the case of object directed actions, these movements are related to the manipulation of an object. Actions have physical consequences and actors usually have goals in mind that they want to achieve by executing the action. Actions constitute an information category that we constantly process during our waking hours. We are permanently busy perceiving, executing, imagining, retaining, recognizing, retrieving and understanding actions.

In order to act purposeful, it is necessary to represent actions in memory which have been executed by oneself or others. How do we represent such actions in memory? Can we focus on different action features when we retain actions in memory? Does action familiarity influence how we represent actions in memory? Which brain structures are involved in the representation of actions? Do we need to distinguish between action representations in working and long term memory?

These are some questions one might want to ask about actions in memory and which I have investigated in my doctoral project. I have focused on features of action representations in memory, on factors that might influence how we represent actions in memory and on the neural correlates of action representations.

In the theoretical part, I will start with a general introduction to working and long term memory and how they have been conceptualized. Then, I will continue with a section on action information processing and action representations. In the last part of the introduction section, I will give an outline of the three experiments that form the basis of my doctoral thesis.

1. INTRODUCTION

2. WORKING MEMORY AND LONG TERM MEMORY

2.1. WORKING MEMORY

Working memory has been defined as a memory system in which information is actively maintained for a short time in order to be able to work effectively on a current task. The technical term was characterized by Miller, Galanter and Pribram (1960). In addition to a short term storage function, the ability to manipulate and control the content of the store has been ascribed to working memory.

The notion of working memory has evolved from short term memory which has been traditionally separated from long term memory. Early memory models already distinguished between two memory systems. James (1890) defined primary memory to be temporally distinct from secondary memory. Whereas primary memory would contain conscious information within any given moment, secondary memory would encompass all the knowledge we have ever accumulated. According to Waugh and Norman (1965), a rehearsal mechanism would be necessary for information from short term memory to be transferred to long term memory. If rehearsal did not take place, information would be lost from short term memory either due to decay or interference by other items. Atkinson and Shiffrin (1968) further developed this model in introducing executive control processes and in allowing a bidirectional connection between short time and long term memory. Apart from a transfer of information from short term to long term memory, information could also enter short term memory from being stored in long term memory.

Until Baddeley and Hitch formulated their influential multimodal working memory model in 1974, models on working memory were mainly restricted to verbal information. In contrast, their multimodal working memory model postulated the existence of separate visuo-spatial and verbal subsystems. Evidence for the separability of the subsystems comes from studies

2. WORKING AND LONG TERM MEMORY

using the dual task interference paradigm (Baddeley, 1986). Furthermore, neurological patients with selective impairments in one or the other subsystem have been described (Della Sala & Logie, 1993). Both the visuo-spatial and the verbal subsystem have been characterized to contain passive and active components for storage and rehearsal. In the verbal subsystem, the phonological store would store verbal information and the phonological loop would refresh the contents of the phonological store by a rehearsal mechanism (Baddeley, 1986). In analogy, the visuo-spatial subsystem would contain a passive visual cache and an active inner scribe (Logie, 1995). According to Logie's model of the visuo-spatial subsystem, the visual cache and inner scribe are preferentially recruited during working memory retention of static object and dynamic spatial features, respectively.

The ideas of domain specificity and different active and passive components in working memory relying on separate resources were new to the working memory research community at that time. It was in contrast to other accounts that emphasized shared resources for processing and storage in memory (Daneman & Carpenter, 1980). In addition to the domain specific subsystems, the Baddeley model includes a central executive system which was assumed to supersede the verbal and visuo-spatial subsystem and to monitor their content. In a later version, the episodic buffer was added as a third sub-system (Baddeley, 2000). It is conceptualized to be a store for integrated episodes containing information of different domains.

The results of neurocognitive studies also corroborate the existence of separate domain specific subsystems in working memory. Domain specific brain regions during working memory tasks correspond to regions which also contribute to perception and action (D'Esposito, 2007; Postle, 2006; Slotnick, 2004; Zimmer, 2008). In event-related potential (ERP) studies, it has been observed that retention of spatial and object information in working memory is related to topographically different slow potentials (Bosch, Mecklinger, & Friederici, 2001; Mecklinger & Pfeifer, 1996). Neuroimaging evidence is in line with electrophysiological findings on object and spatial working memory. Courtney, Ungerleider, Keil, and Haxby (1996) found the fusiform cortex to be selectively involved in working memory for faces whereas regions in the

2. WORKING AND LONG TERM MEMORY

parietal cortex showed enhanced activation during working memory for location information. Similarly, contrasting working memory retention for a shape or position, left temporo-occipital and right parieto-occipital regions have been found to be involved, respectively (Ventre-Dominey et al., 2005). Apparently, the dorsal parieto-occipital and the ventral temporo-parietal path of perception (Ungerleider & Mishkin, 1982) show sustained involvement during working memory retention. Selective brain regions during working memory retention of verbal, object or spatial information have been described in detail in the reviews of Smith and Jonides (1997) and of Wager and Smith (2003). Features of spatial working memory retention have been further investigated in our lab. It has been suggested that working memory for spatial information is modality independent (Lehnert & Zimmer, 2008). Furthermore, working memory retention of dynamic-spatial (motion) and static-spatial (position) information has been distinguished (Umla-Runge, Zimmer, Krick, & Reith, 2011). Whereas area hMT/V5+, an extrastriate region involved in the perception of motion, and the superior temporal sulcus (STS) were selectively activated during retention of dynamic-spatial information in working memory, a region at the junction of temporal, parietal and occipital lobes showed selective activation during working memory retention of static-spatial information. Similar to spatial information in working memory, object information has also been further subdivided. Working memory encoding and maintenance of face or place information selectively activated subregions within the inferior temporal cortex (Ranganath, DeGutis, & D'Esposito, 2004). Whereas the fusiform face area was specifically activated during encoding and retention of faces, the parahippocampal place area showed specific enhanced activation during encoding and retention of place information. In addition, the involvement of early sensory areas during working memory retention has been demonstrated in non-human primates (Pasternak & Greenlee, 2005). Domain specific brain regions have also been described for object directed actions, kinesthetic information and grasp related target features in working memory (Fiehler et al., 2011; Fiehler, Burke, Engel, Bien, & Rösler, 2008; Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004). I will return to domain specificity in action working memory in Chapter 3.3.

2. WORKING AND LONG TERM MEMORY

It is widely acknowledged that domain specific posterior regions of perception show sustained activation during working memory retention of this information (D'Esposito, 2007; Postle, 2006; Slotnick, 2004; Zimmer, 2008). However, there is an ongoing debate as to the contribution of prefrontal regions to working memory. There is some evidence that the prefrontal cortex is also organized in a domain specific way with the dorsolateral part being involved with spatial and the ventrolateral part with object information processing (Goldman-Rakic, 1995; Levy & Goldman-Rakic, 2000). However, a competing model posits a process specific organization of the prefrontal cortex with different regions being involved with maintenance and manipulation (Owen, 1997; Petrides, 1995, 2000). In agreement with a domain general model of prefrontal cortex, dorsolateral prefrontal cortex has been found to correlate with memory load irrespective of item type (Ranganath, DeGutis, et al., 2004). In attempt to reconcile domain specific and process specific models of the prefrontal cortex, Suchan (2008) suggested a division of prefrontal visuo-spatial working memory areas into a ventrolateral passive subsystem and a dorsolateral active subsystem with spatial features being retained more actively as compared to object features. Ruchkin, Grafman, Cameron, and Berndt (2003) have conceptualized prefrontal brain regions as a domain general attentional pointer system with storage taking place in posterior domain specific regions of perception. Recently, it has been questioned whether we should really speak of posterior "storage modules" or whether working memory should be rather conceptualized as a by-product of perceptual processing (D'Esposito, 2007; Postle, 2006). For visual working memory, an interaction of domain general structures in the prefrontal cortex and medial temporal lobe and domain specific structures in the inferior temporal cortex has been proposed (Ranganath, 2006; Ranganath & D'Esposito, 2005).

Another influential working memory model, Cowan's Embedded Processes model, is more focused on different levels of activation or accessibility of representations rather than describing different domains of information in working memory (Cowan, 1995, 1999). Three levels of accessibility of representations are distinguished. The broadest category encompasses all knowledge one disposes of, i.e. representations stored in long term memory.

2. WORKING AND LONG TERM MEMORY

A subset of this information is activated and part of this active information is within the focus of attention. Although the model does not make claims about different information domains, it is compatible with the idea of domain specificity. The differences between models as to the relationship of working and long term memory will be dealt with in Chapter 2.3.

2.2. LONG TERM MEMORY

According to Squire's hierarchical model of long term memory (Squire, 2004), we need to distinguish between declarative and non-declarative long term memory. Declarative or explicit memory refers to information which can be consciously recalled as compared to non-declarative or implicit memory which is considered unconscious memory. Within declarative memory, a distinction between episodic and semantic memory has been made. The major difference between episodic and semantic memory is that episodic memory entries are bound to a (spatio-temporal) context whereas semantic memory entries are not.

Different to working memory where information is kept active for a prolonged interval after conscious perception (or after internal generation), episodic long term memory requires mechanisms for retrieval. For retrieval of an episode to occur, it is necessary to reinstantiate the respective memory trace. It has been found that reactivation of long term memory contents is easier if the information to be retrieved has been activated recently as compared to information that has not been in use for a long time (Kahana, Howard, & Polyn, 2008). Reactivation is initiated by suitable retrieval cues. According to the encoding specificity principle (Tulving & Thomson, 1973), it is the degree of overlap of processes at the time of encoding and at retrieval which determines the suitability of a stimulus as a retrieval cue. Similar to information to be retained in working memory, retrieval cues can be externally presented or internally generated (Mecklinger, 2010). It has been suggested that

2. WORKING AND LONG TERM MEMORY

reinstantiation of the previous episode by a retrieval cue takes places via binding mechanisms (Zimmer, Mecklinger, & Lindenberger, 2004).

An important brain region which has been extensively discussed regarding its function in episodic long term memory, especially as to binding processes, is the hippocampus and surrounding areas (areas of the medial temporal lobe, MTL). Scoville and Milner (1957) showed that bilateral lesions of the hippocampus are related to a syndrome with profound anterograde amnesia with preserved performance in short term memory tasks. It has been demonstrated that the MTL is activated both during the encoding and retrieval phases in episodic long term memory (Schacter & Wagner, 1999). The Binding and Item Context model posits a functional specialization of MTL regions. Whereas the perirhinal cortex is assumed to represent item information, the parahippocampal cortex processes contextual information and the hippocampus binds items to contexts (Diana, Yonelinas, & Ranganath, 2007). Evidence has accumulated supporting this model (Ranganath, 2010). Apart from the MTL, other brain regions which have been found active during episodic long term memory retrieval independent of the item type to be retrieved are the prefrontal cortex and the posterior parietal cortex (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Simons, 2009; Simons & Spiers, 2003; Wagner, Shannon, Kahn, & Buckner, 2005).

However, there is also domain specificity in episodic long term memory. These domain specific brain regions involved in long term memory tasks have been found to overlap with domain specific regions in working memory and perception (Slotnick, 2004). Visual and auditory cortex regions which are activated during perception have been found to be reactivated selectively during episodic long term memory retrieval of visual and auditory information (Wheeler, Petersen, & Buckner, 2000). Similarly, bilateral extrastriate visual cortex was selectively activated during recognition memory for words which had been presented as pictures at encoding as compared to words which had been presented as words (Vaidya, Zhao, Desmond, & Gabrieli, 2002). Analogous to the findings from working memory and perception studies, the dorsal and ventral path regions have been found to be selectively activated during long term memory retrieval of spatial and object infor-

2. WORKING AND LONG TERM MEMORY

mation, respectively. In an fMRI study requiring participants to associate an abstract word with either face or position information at encoding, Khader, Burke, Bien, Ranganath, and Rösler (2005) found dorsal path regions to be selectively activated at test when words which had been associated with positions were to be evaluated. Words which had been associated with faces selectively activated ventral path regions at test. The same pattern of results has been observed in an ERP study with topographically different negative slow waves being observed at retrieval depending on the information type the words had been associated with at encoding (Khader, Heil, & Rösler, 2005). The amplitude of the slow waves was also found to increase with the number of domain specific associations to be recalled suggesting a modulation by memory load. Using a free recall paradigm, Polyn, Natu, Cohen, and Norman (2005) identified domain specific activation patterns during encoding for three diffe-rent information categories (celebrities, landmarks, objects) which were later reactivated prior to recall of an item from the respective category. As successful retrieval was strongly related to reactivation of brain regions which had also been active in the encoding phase, this has been interpreted as a neural marker for the encoding specificity principle (Vaidya et al., 2002; for a review see also Polyn & Kahana, 2008). Action information in episodic long term memory will be dealt with in detail in Chapter 3.3.

Following from results on domain specificity in episodic long term memory, it has been suggested that long term memory is not based on a specialized processing module but rather a by-product of perceptual processing. Representations in visual item memory are assumed to be provided by a network of feature specific regions and object representations are constructed by binding of the object's features (Slotnick, 2004). Similarly, the emergent memory account postulates the existence of hierarchically organized distributed perceptual representations which are involved in episodic long term memory (Graham, Barense, & Lee, 2010). According to this account, the MTL is thought to be preferentially recruited for conjunctive perceptual representations.

2. WORKING AND LONG TERM MEMORY

2.3. THE RELATIONSHIP BETWEEN WORKING AND LONG TERM MEMORY

Traditionally, in multistore models, working and long term memory have been considered separate memory systems, each one relying on its separate set of representations (Baddeley & Logie, 1999). According to this view, working and long term memory interact by means of bidirectional information transfer. Long term memory can influence working memory both implicitly and explicitly (Baddeley, 2010). Still, working and long term memory are considered separate cognitive systems. In contrast, unitary store models posit the existence of a single set of representations that can be used both in working and long term memory tasks (Cowan, 1999; Fuster, 1997; Jonides et al., 2008; Ranganath & Blumenfeld, 2005; Ruchkin, et al., 2003; Slotnick, 2004; Zimmer, 2008). From this point of view, working and long term memory can be considered different processes acting upon the same representations. According to Cowan's model, activated long term memory representations constitute the content of working memory.

Neurocognitive findings seem to support the unitary store view on working and long term memory. Category specific regions in inferior temporal cortex have been identified which are activated both during working memory retention and during retrieval from long term memory (Ranganath, Cohen, Dam, and D'Esposito, 2004). In this functional magnetic resonance imaging (fMRI) study, participants either performed a delayed matching-to-sample task or a delayed paired associate task using photographs of faces and places as stimulus material. Two inferior temporal regions were defined as regions of interest: the fusiform face area (FFA) which is involved in face perception and the parahippocampal place area (PPA) active during perception of places. Both regions exhibited similar domain specific activations in the two memory tasks. During working memory retention and associative long term memory retrieval of face information, the FFA showed enhanced activation. An analogous pattern emerged for the PPA if it was place information which was to be retained in working memory or retrieved from long term

memory. Similarly, pattern classifiers that were trained in classifying judgments on people, locations, and objects could identify retention in working memory of these types of information (Lewis-Peacock & Postle, 2008). Brain structures which were specifically involved were the fusiform gyrus for people, the parahippocampal gyrus for locations and the middle temporal and lateral occipital cortices for objects.

Other neuroimaging studies have focused on the relationship of working memory processing and encoding into long term memory. Schon, Hasselmo, LoPresti, Tricarico, and Stern (2004) found a correlation between the activation in the parahippocampal cortex during short term retention of indoor and outdoor scenes and subsequent recognition memory. Using novel objects as stimulus material, Ranganath, Cohen, and Brozinsky (2005) observed an analogous correlation for regions in the dorsolateral prefrontal cortex and the hippocampus. It has been suggested that the dorsolateral prefrontal cortex strengthens associations between items in working memory which is beneficial for long term memory retrieval of these items (Blumenfeld & Ranganath, 2006). The involvement of domain specific brain regions in both working and long term memory has also been informed by electrophysiological results. Khader, Ranganath, Seemüller, and Rösler (2007) found topographically distinct slow potentials during working memory retention of objects and letter strings. Amplitudes of slow potentials exhibited a domain specific enhancement for items which were successfully remembered as compared to items which were forgotten in a later long term memory test.

Based on these results, it is likely that working and long term memory are not two separate systems but highly interrelated. According to Slotnick (2004), representational formats can be differentiated at different levels of analysis: Modality specific representations refer to differences due to sensory modality (e.g. auditory vs. visual), domain specific representations distinguish between different information categories within a given modality (e.g. spatial vs. object within the visual modality) and feature specific representations make even more fine-grained distinctions between different aspects that define a domain (e.g. color vs. shape which are both necessary bits of information that define objects). Interestingly, the same modality, domain and fea-

2. WORKING AND LONG TERM MEMORY

ture specific brain regions have been found to be involved in perceptual, working and long term memory tasks (Slotnick, 2004).

These results are in good agreement with one set of modality, domain and feature specific representations which is commonly used in both working memory and episodic long term memory tasks. Memory representations seem to be hierarchically organized and implemented by the very neural structures that we also employ during perception and action execution (Fuster, 1997; Jonides et al., 2008; Slotnick, 2004; Zimmer, 2008).

2. WORKING AND LONG TERM MEMORY

3. ACTION INFORMATION PROCESSING

3.1. GENERAL ISSUES - REPRESENTATION AND PROCESSING OF ACTION INFORMATION

In this chapter, I would like to elaborate on one specific informational domain and its characteristics - the domain of actions. How do we define an action? Actions are movements executed by individuals. They can be automatic, i.e. triggered by a stimulus in the environment or they can be volitional, i.e. self-generated with the intention to achieve a specific goal (Haggard, 2008). Usually, volitional actions are also not stimulus-independent. Consider the example of object directed actions. Whereas the intention to perform an object directed action might be self-generated, object features also need to be taken into account in order to execute the action successfully. Volitional actions generally include an intention or action goal and a specific motor program of how to achieve this goal (Zimmer, Helstrup, & Nilsson, 2007).

In ideomotor theories, the importance of the action goal has been emphasized. It has been postulated that specification of an action's goal precedes specification of the motor program and that ends are superior to means both during action perception and execution (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Humphreys, Forde, & Riddoch, 2001; Prinz, 1997). According to the common coding theory, the same representational basis is used for action execution and perception and actions are represented in terms of their physical consequences or perceivable effects (Herwig, Prinz, & Waszak, 2007). Perceivable effects are defined as the distal attributes of an action, i.e. an action's consequences, as opposed to proximal sensory or motor innervations effects (Prinz, 1992). This holds for volitional actions but is not true for automatic externally driven actions which work by simple stimulus-response relations (Herwig et al., 2007). Haruno, Wolpert, and Kawato (2001) have proposed a computational model of action

control based on ideomotor principles. According to this model, an intended goal state is defined and its physical consequences are described. Then, possible motor commands are generated. The expected physical consequences of these motor commands are evaluated as to their similarity to the desired physical consequences and the actual motor command will be a similarity weighted sum.

A primacy of goals has also been demonstrated in imitation studies with children (Bekkering, Wohlschlager, & Gattis, 2000; Carpenter, Call, & Tomasello, 2005). In the Bekkering study, preschool children were asked to imitate actions of an experimenter who either touched his left or right ear with his right or left hand. It was found that, if there are two competing goals as well as two competing means, it is the goals which are preferentially imitated. Children made more means imitation errors as compared to end imitation errors. However, if there was only one goal or goals were de-emphasized, the number of means imitation errors decreased. This suggests a flexible hierarchical organization of goals and means with the possibility of a specific means to become a goal in itself.

If we learn how to perform an action, this is often accomplished in a sequence of action observation, imitation and extended practice (Zimmer, et al., 2007). If the means of the action matters, we will also build up a motor schema of this action. Motor schemata have been defined as abstract plans or representations which include the prototypical movements which are required in order to perform an action (Schmidt, 1975). They lack the exact motor parameters of how to perform an action in a specific situation. These parameters are specified during action planning and can also circumvent conscious awareness (Neumann, 1990).

Granted that action goals are central to volitional action, motor parameters are also important in action information processing. Action information has been suggested to be hierarchically organized (Grafton & Hamilton, 2007; Humphreys et al., 2001). Based on the results of fMRI repetition suppression studies with video clips of object directed actions, three different representational levels have been distinguished (Grafton & Hamilton, 2007).

3. ACTION INFORMATION PROCESSING

On the lowest level, information about the kinematics of an action is represented. This level includes information about movement trajectory, grasp and the dynamic interaction of effector and object (i.e. the means of object manipulation). On the medium level, the goal object of the action is represented and the highest level deals with the action's consequences or ends. Distinct brain regions have been shown to exhibit selective repetition suppression effects for action features from the three levels suggesting their representational separability (Grafton & Hamilton, 2007; Hamilton & Grafton, 2006, 2008; Tunik, Rice, Hamilton, & Grafton, 2007). I will refer to the details of the respective brain regions in Chapter 3.2.

The idea of different levels of action representations is corroborated by findings from apraxic patients. Apraxia generally describes a disorder of skilled movement and different subtypes have been distinguished (Heilman & Gonzalez-Rothi, 2003). Two of these subtypes are ideomotor and ideational apraxia. Whereas the former can be primarily identified by spatial errors when acting (like postural errors, errors of orientation and movement), the latter corresponds to a failure to use objects in a correct way (e.g. hammering with a screwdriver). Using an experimental approach with ideomotor and ideational apraxic patients, Platz and Mauritz (1995) assessed the patients' improvements by sensorimotor training. Patients with ideomotor apraxia were identified to be specifically impaired in motor programming, i.e. in spatial and temporal parameters of movement segments, and improved with sensorimotor training. In contrast, patients with ideational apraxia did not benefit from this kind of training. They were specifically impaired during motor planning which was defined as the content of the movement when considering the movement as a whole.

The importance of motor information in the representation of actions has also been stressed in the simulation account by Jeannerod (2001). According to this theoretical framework, S states can be defined which are mental states involving an action content. During S states, real actions are simulated. Consequentially, brain regions that are involved in action execution should also be involved in action simulation processes like action imagery or retention of actions in memory.

3. ACTION INFORMATION PROCESSING

Concerning the domain of action information, a specific category of neurons, the mirror neurons, have been discovered. These neurons discharge both during action execution and during action observation. They have been first demonstrated by means of single cell recordings in region F5 of the monkey inferior frontal cortex (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996).

In humans, the existence of a mirror neuron system has been suggested by neurophysiological and neuroimaging data (Buccino et al., 2001; Buccino, Binkofski, & Riggio, 2004; Iacoboni et al., 1999; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). It encompasses an anterior and a posterior cortical region: the inferior frontal cortex extending into the ventral premotor cortex and the inferior parietal lobe. The inferior parietal lobe contains the anterior intraparietal sulcus (aIPS) and the supramarginal gyrus. The mirror neuron system is assumed to enable a direct mapping of observed actions onto corresponding motor representations of these actions (Iacoboni et al., 1999). As evidence for the existence of mirror neurons in humans is mainly indirect, it is often referred to as the putative human mirror neuron system. Both its anterior and posterior region exhibit a somatotopic organization with different subregions being activated during observation of hand, foot and mouth actions (Buccino, et al., 2001). Observation of intransitive actions, i.e. actions that do not involve objects, activates solely the anterior region in a somatotopic fashion. During observation of transitive actions, i.e. object directed actions, both the anterior and posterior region exhibit a somatotopic organization.

The ventral premotor/inferior frontal cortex and the inferior parietal lobe have also been discussed as being part of a grasp circuit which is involved in transforming the spatial properties of objects into motor programs for grasping in both monkeys and humans (Binkofski et al., 1999; Fogassi et al., 2001; Frey, Vinton, Norlund, & Grafton, 2005; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). Comparing reaching and grasping movements,

3. ACTION INFORMATION PROCESSING

the aIPS has been found to be more activated during grasping (Binkofski et al., 1998; Frey, et al., 2005) suggesting that this region is especially important for sensorimotor integration. Apart from being active during execution of grasp movements, some studies have found the putative anterior and posterior human mirror neuron regions to be involved during grasp planning and action imagery (Binkofski et al., 2000; Jacobs, Danielmeier, & Frey, 2010). Others found that the role of the aIPS is restricted to grasp execution and not the planning phase (Rice, Tunik, & Grafton, 2006; Tunik, Frey, & Grafton, 2005) and that the supramarginal gyrus within the inferior parietal lobe is specifically involved in planning of goal directed actions (Tunik, Lo, & Adamovich, 2008).

In addition to the mirror neuron areas, there are other brain regions which have been shown to be involved in action information processing. Actions involve biological motion, i.e. motion of human beings. A structure which has been shown to be selectively activated during biological motion perception is the posterior portion of the superior temporal sulcus, also referred to as the STS (Grossman et al., 2000; Pelphrey et al., 2003; Puce, Allison, Bentin, Gore, & McCarthy, 1998; for a review see Allison, Puce, & McCarthy, 2000). An activation gradient has been demonstrated in the posterior STS with the highest activation during perception of upright biological motion, medium activation during perception of inverted biological motion and lowest activation during perception of scrambled motion (Grossman & Blake, 2001). The region has been shown to be sensitive to the intention of actions with stronger activation during observation of intended as compared to unintended biological motion (Morris, Pelphrey, & McCarthy, 2008; Pelphrey, Morris, & McCarthy, 2004). The STS needs to be distinguished from an adjacent temporal region in the middle temporal gyrus extending into inferior temporal gyrus (Beauchamp, Lee, Haxby, & Martin, 2002, 2003). This region has been shown to be selectively activated during observation of tool motion. The STS provides visual input to the anterior and posterior putative human mirror neuron areas (Iacoboni & Dapretto, 2006). The corresponding network is depicted in Figure 1.

3. ACTION INFORMATION PROCESSING
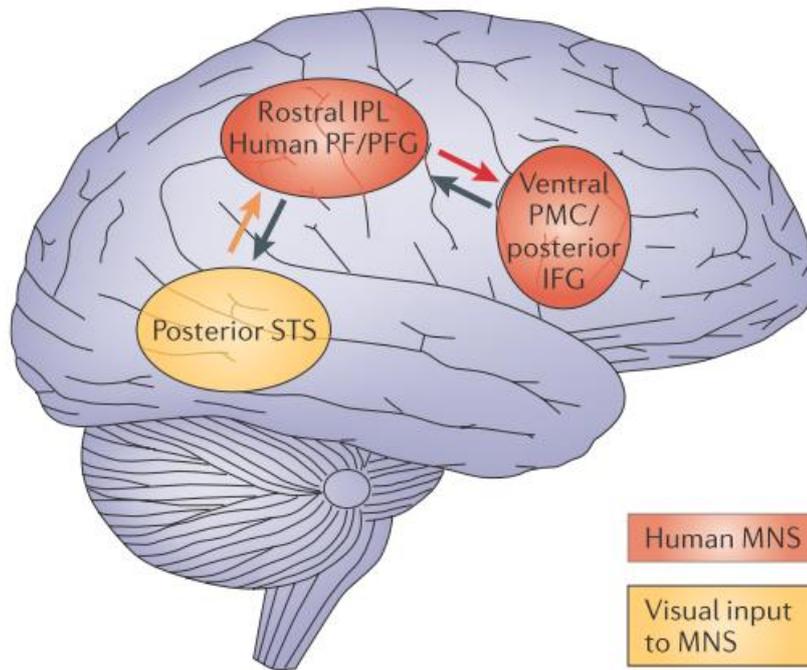
Figure 1. Key brain regions for action information processing. This Figure corresponds to Figure 1 in Iacoboni and Dapretto (2006). Permission for re-using it in my doctoral thesis has been obtained from Nature Publishing Group. IPL = inferior parietal lobe; PF/PFG = specific subregions of monkey inferior parietal cortex; PMC = premotor cortex; IFG = inferior frontal gyrus; MNS = mirror neuron system.

Another cortical region being strongly involved in action information processing is medial Brodmann Area (BA) 6, being composed of the anterior pre-supplementary motor area (pre-SMA) and the adjacent posterior SMA (Picard & Strick, 1996). Both areas are involved in preparation of action but with information processing in the pre-SMA preceding the SMA (Cunnington, Windischberger, & Moser, 2005; Cunnington, Windischberger, Robinson, & Moser, 2006). The pre-SMA and SMA have also been shown to be activated during motor imagery (Amador & Fried, 2004; Malouin, Richards, Jackson, Dumas, & Doyon, 2003). Using single cell recordings with human partici-pants, Amador and Fried (2004) could show that SMA and pre-SMA dis-charges were selective to specific features of motor plans and modulated by sequence complexity. This selectivity was observed both during actual movements and motor imagery. Reviewing the role of the pre-SMA during action planning, Cunnington et al. (2006) have concluded that it might be in-volved in generating and encoding motor representations as well as their re-tention during a state of readiness for action.

3. ACTION INFORMATION PROCESSING

As pointed out in Chapter 3.1., there is evidence that action representations are organized hierarchically (Grafton & Hamilton, 2007; Humphreys et al., 2001). In order to identify brain regions which are involved in the representation of action features at different levels of the hierarchy, several experiments using a specific repetition suppression paradigm have been conducted (Grafton & Hamilton, 2007; Hamilton & Grafton, 2006, 2008; Tunik, et al., 2007). With this paradigm, video clips of object directed actions are presented to participants while they are instructed to observe them. Specific action features can be either repeated from trial to trial or they can be novel. During observation, participants are engaged in a task which is unrelated to these features. If a brain region represents specific features and these features are repeated, it has been shown to be less active during repetition as compared to the first presentation - a phenomenon known under the name of selective repetition suppression (Desimone, 1996; Wiggs & Martin, 1998). Selective repetition suppression effects for object goals (i.e. target objects of actions) have been consistently observed in the left aIPS (Grafton & Hamilton, 2007; Hamilton & Grafton, 2006). For trajectory information (i.e. direction of reaching), selective repetition suppression effects emerged in the lateral occipital sulcus and the superior precentral sulcus (Hamilton & Grafton, 2006). Repetition suppression effects for the type of grasp were observed in the left inferior and middle occipital cortex, the middle intraparietal sulcus and the inferior frontal gyrus (Grafton & Hamilton, 2007). These regions were partly overlapping with the regions showing selective repetition suppression effects for kinematic information (i.e. the dynamic interaction of an effector with an object; for instance, pulling or pushing a drawer). Kinematic repetition suppression effects were found in the left middle intraparietal sulcus, the lateral occipital complex and the STS (Hamilton & Grafton, 2008). However, these effects were weaker as compared to repetition suppression effects for physical consequences or outcomes in the right inferior parietal lobe and inferior frontal gyrus in the same study. The latter regions correspond to the putative human mirror neuron regions.

The involvement of mirror neurons in the representation of goals has also been suggested by others. Single cell recordings in the monkey ventral

3. ACTION INFORMATION PROCESSING

premotor cortex revealed that a subset of these neurons is equally activated if the consequence of an action is hidden from view and if the consequence is observable suggesting that mirror neurons can infer action goals (Umiltà et al., 2001). In humans, it has been suggested that the anterior mirror neuron region represents the object goal of an action (Koski et al., 2002). Stronger activation in the opercular part of the inferior frontal gyrus and in the dorsal premotor cortex emerged bilaterally if participants imitated actions with a goal as compared to actions lacking a goal.

However, the involvement of the mirror neuron system in the representation of goals has also been questioned. In an fMRI study by Hesse, Sparing, and Fink (2009), participants were required to make means or end judgments about object directed actions. In the end task, they were to decide whether a cube had been placed on a marked spot or not. In the means task, they should decide whether the cube had been turned or not. The putative human mirror neuron system, i.e. the ventral premotor cortex and the inferior parietal lobe, was found to be significantly more active during means judgments as compared to end judgments. During end judgments, regions in the left precuneus, superior frontal, angular and middle temporal gyrus showed enhanced activation. Similarly, a frontoparietal network consisting in dorsal premotor cortex and inferior parietal lobe, has been observed during motor-based action comparisons relative to functional context comparisons about actions (Canessa et al., 2008). In contrast, functional context comparisons yielded selective activations in the lateral anterior inferotemporal cortex and the retrosplenial cortex.

Other studies have also focused on the representation of means and end information yielding heterogeneous results. Bach, Peelen, and Tipper (2010) found the left premotor cortex and the supramarginal gyrus to be more strongly activated during a spatiomotor task as compared to a function task with both tasks requiring compatibility judgments about tool and target objects. The left middle frontal gyrus showed enhanced activation during the function task as compared to the spatiomotor task. Studies on semantic memory have also suggested a stronger involvement of the inferior parietal lobe in motor judgments as compared to function judgments (Boronat et al.,

3. ACTION INFORMATION PROCESSING

2005; Kellenbach, Brett, & Patterson, 2003). Interestingly, these studies have not found that the inferior frontal/ventral premotor region is differentially involved during manipulation and function judgments. It has been suggested that the insensitivity of the ventral premotor cortex to the retrieval task reflects the automatic activation of this region upon the visual depiction of tools (Kellenbach, et al., 2003). Concerning function knowledge, both studies have not identified brain areas which are selectively activated in function tasks as compared to manipulation tasks. Finally, neural correlates of the representation of means and end information have also been investigated in an imitation context (Chaminade, Meltzoff, & Decety, 2002). Here, the left premotor cortex was selectively activated during imitation of the action goal. For imitation of means, medial prefrontal regions were selectively involved.

3.3. ACTION MEMORY

In the preceding chapters, I have provided a general overview about action information processing and its neural correlates. In this chapter, I will cover action memory and refer to what we know about action information processing in working and episodic long term memory as well as the brain structures involved in representing action information in memory.

How do we represent actions in memory? It has been suggested that motor information constitutes an information category which should be separated from verbal information and information about visual appearance (Engelkamp & Zimmer, 1985; von Essen & Nilsson, 2003). The first studies on action memory were behavioral experiments using the subject performed task (SPT) paradigm. This paradigm involves a learning phase were participants are required to study action phrases like "to peel the banana" or "to cut paper" either by enactment (SPT) or verbally (verbal task; VT). After encoding, they will be asked to take a memory test. A robust enactment or SPT effect has been observed in free recall and recognition memory tests with superior memory performance for items which had been encoded by enact-

ment relative to verbally encoded items (Cohen, 1981; Engelkamp & Cohen, 1991; Engelkamp & Krumnacker, 1980; Engelkamp & Zimmer, 1989). However, enacting does not improve performance in cued recall tests (Engelkamp, 1986). It has been suggested that though enactment provides good item specific information, it hinders relational integration between items. If subjects were required to observe an experimenter performing the actions (EPT; experimenter performed task), their memory accuracy was also superior to the verbal encoding condition, though not as high as when they performed the actions themselves (Engelkamp & Zimmer, 1997).

Neural correlates of action information in memory have also been investigated using the SPT paradigm. A positron emission tomography (PET) study by Nyberg et al. (2001) focused on episodic long term memory for action phrases which had been encoded either by enactment, imagery or verbally. Bilateral regions in motor and somatosensory cortex, the left aIPS and the left premotor cortex were commonly activated during encoding and retrieval of items which had been encoded by enactment or motor imagery. These regions were not activated if the phrases had been encoded verbally. The results have been interpreted as selective reactivation of motor information processing areas during retrieval of motorically encoded items. Results corroborating the interpretation of reactivation of motor information during retrieval have been obtained in a study by Masumoto et al. (2006) using magnetoencephalography (MEG). In a recognition memory test with action phrases which had been either encoded by enactment or verbally, the left primary motor cortex was significantly activated shortly after the onset of a recognition stimulus only for the enacted items but not for the verbally encoded items. Subsequently, the left parietal cortex showed enhanced activation for the enacted target items. Another fMRI study on the neural correlates of the enactment effect (Russ, Mack, Grama, Lanfermann, & Knopf, 2003) did not find selective activation in motor and premotor brain regions. In this study, the left supramarginal gyrus and the middle temporal gyrus were found to be selectively activated during long term memory retrieval of action phrases that had been enacted during encoding as compared to action phrases which had been studied verbally.

3. ACTION INFORMATION PROCESSING

Other studies have used visual action stimuli to investigate neural correlates of action memory. A study by Mecklinger et al. (2004) focused on working memory retention of action information about manipulable objects. Action retention was contrasted with retention of size information. The left ventral premotor/inferior frontal cortex and the left intraparietal sulcus were found to be selectively involved in the retention of action information in working memory. Furthermore, the left middle temporal gyrus showed enhanced activation in the action task as compared to the size task. Other working memory studies on the retention of action information involve real actions rather than imagined actions. In a study on kinesthetic working memory, blindfolded participants performed a delayed match to sample task with hand movements (Fiehler et al., 2008). During the delay, the aIPS and the superior parietal lobe showed memory load dependent activation. In a later study, Fiehler et al. (2011) investigated fMRI correlates of working memory retention of to be grasped targets. Participants were presented with target objects differing in size and orientation and were required to grasp the objects either immediately or after a variable delay interval. The right inferior parietal lobe was found to be commonly engaged during target encoding and retention prior to action.

3.4. ACTION FAMILIARITY

Action familiarity influences action information processing at various stages. Using a visual discrimination task with intransitive actions (dance moves), Calvo-Merino, Ehrenberg, Leung, and Haggard (2010) found that perception is modulated by visual and motor familiarity of the action. Visual discrimination performance for dance moves presented in an upright orientation was significantly better for professional dancers as compared to non-experts, whereas no significant difference in performance was observed between professional dancers and non-experts with inverted stimuli.

3. ACTION INFORMATION PROCESSING

In the memory domain, it has been shown that familiarity has an effect on both free recall and recognition memory performance with action phrases (Knopf, 1991; Knopf & Neidhardt, 1989). Whereas free recall was better for familiar actions as compared to unfamiliar actions, the reverse pattern was observed in a recognition memory task. Other studies on memory for action phrases speak of action familiarity in terms of bizarreness. Engelkamp, Zimmer, and Biegelmann (1993) have described differential effects of action bizarreness in a recognition memory test and a cued recall test. Whereas cued recall performance was generally better for normal as compared to bizarre action phrases, recognition memory was better for bizarre relative to normal action phrases. This latter effect was restricted to a verbal encoding condition and did not occur if participants had encoded the items by enactment. A modulation of recognition memory performance by action bizarreness in a verbal encoding condition has also been demonstrated by Mohr, Engelkamp, and Zimmer (1989). It is unclear whether bizarreness effects on memory are equivalent to effects of action familiarity or whether they should be considered effects of uncommon lexical combinations.

Furthermore, action familiarity has been shown to influence outcome prediction within a paradigm requiring a means-end analysis of actions. While ordinary children performed better if required to predict the outcome of a familiar action as compared to an unfamiliar action, this was not true for children with autistic spectrum disorder (Zalla, Labruyère, Clément, & Georgieff, 2010). In contrast, Wang, Fu, Aschersleben, and Zimmer (in press) found that preschool children make significantly more imitation errors related to the end as compared to the means of an action when they were asked to imitate familiar actions. For unfamiliar actions, however, there was no such difference between the error numbers from each category. Generally, it has been found that familiar/meaningful actions yield better imitation performance as compared to unfamiliar/non-meaningful actions (Rumiati & Tessari, 2002; Wang et al., in press).

The behavioral effects of action familiarity on different aspects of information processing have been corroborated by the findings of brain imaging studies comparing brain activation during observation of familiar and un-

3. ACTION INFORMATION PROCESSING

familiar actions. Brain regions within the putative human mirror neuron system have been shown to be stronger activated for familiar actions as compared to unfamiliar actions (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). In these studies, dance moves were used as action stimuli with either professional dancers (Calvo-Merino et al., 2005; Calvo-Merino et al., 2006) or ordinary students (Cross, Hamilton et al., 2009; Cross, Kraemer et al., 2009) as participants. In a first study with professional ballet and capoeira performers, Calvo-Merino et al. (2005) found enhanced human mirror neuron system activation when professional dancers observed dance moves from their own dance style as compared to dance moves from the other dance style. In an attempt to identify the respective contribution of visual and motor familiarity, Calvo-Merino et al. (2006) found stronger activation in premotor and parietal cortex for dance moves of the dancers' own motor repertoire as compared to dance moves which were equally visually familiar but which they never performed themselves. The ventral premotor cortex has also been found active during observation of trained as compared to untrained dance sequences (Cross, Hamilton et al., 2009) in a study with non-dancers. However, the involvement of the premotor and inferior parietal regions is not exclusively related to motor familiarity. Common activations have emerged in these regions for the observation of actions which were either familiar due to observational learning or due to physical learning when compared with unfamiliar actions (Cross, Kraemer et al., 2009). Consequentially, both visually and motorically familiar actions activate the putative human mirror neuron system more than unfamiliar actions.

The effects of action familiarity on brain activation described so far are based on intransitive actions, i.e. actions which have a specific sequential configuration of movements as their goal. Transitive actions, on the other hand, are a different category of action stimuli as achievement of the action goal requires manipulation of tools in a specific way in order to produce specific physical consequence. Though transitive and intransitive actions are quite different, it has been demonstrated that activation in the inferior parietal

3. ACTION INFORMATION PROCESSING

cortex is also modulated by the familiarity of tools for transitive actions. In these studies, tool familiarity has been defined as knowledge about tool function. The inferior parietal cortex showed enhanced activation for familiar as compared to unfamiliar tools both during observation (Vingerhoets, 2008) and during imagery of functional tool use (Vingerhoets, Acke, Vandemaele, & Achten, 2009). However, planning and execution of pantomime actions related to visually presented tools yielded highly overlapping networks including the aIPS irrespective of tool familiarity (Vingerhoets, Vandekerckhove, Honoré, Vandemaele, & Achten, 2011).

3. ACTION INFORMATION PROCESSING

4. OUTLINE OF THE PROJECT

My doctoral thesis is based on three experiments that aimed at elucidating action memory and its neural correlates.

Experiment 1 is an event-related fMRI study. We extended the debate on the relationship of working and long term memory to the domain of action stimuli and asked whether we can find domain specific overlap during retention in working memory and retrieval from episodic long term memory. Whereas previous studies have investigated this for perceptual rather than action information (Lewis-Peacock & Postle, 2008; Ranganath, Cohen, Dam, & D'Esposito, 2004) or have focused on action information in working or long term memory separately (Masumoto et al., 2006; Mecklinger et al., 2004; Nyberg et al., 2001; Russ et al., 2003), we integrated these lines of research into one experiment. In this experiment, participants took part in a working memory session first where they either retained a manipulable object's prototypical action or its size. We focused on the retention aspect of working memory rather than the manipulation aspect. In a later phase of the experiment, participants were required to recall whether they had previously performed an action/size working memory task with a given item or not. If human mirror neuron areas represent action information and if these representations are shared by working and long term memory processes, we should find the inferior frontal/ventral premotor cortex and the inferior parietal lobe to be commonly involved in both working memory retention and long term memory retrieval of action information.

In this study, we did not distinguish between different actions features. In the action working memory task, participants were to compare the movements that an actor would make in order to accomplish the prototypical actions associated with an encoding and a target object. In the long term memory task, they were to retrieve whether they had retained the respective movements before in working memory or not. It has been shown that we need to distinguish between action features at different levels (Grafton &

Hamilton, 2007). In particular, means and end information about actions have qualified as different information categories (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Bach et al., 2010; Boronat et al., 2005; Canessa et al., 2008; Hamilton & Grafton, 2008; Hesse et al., 2009; Kellenbach et al., 2003). Though previous studies have identified different neural structures for means and end information processing, there is no consensus on the role of the putative human mirror neuron system. Means and end information processing has been investigated in tasks requiring observation or semantic judgments. As to our knowledge, there are no previous studies that have investigated short term retention of means and end information.

In Experiment 2, also an event-related fMRI study, we investigated brain regions which are selectively activated during the retention of means and end information in working memory. We presented action video clips to participants and instructed them either to retain the means or the end of the action in working memory in order to decide whether a target stimulus matched the encoding stimulus in the respective information category or not. Motor similarity of encoding and target stimuli was manipulated. If specific brain regions selectively retain the means of an action, they should also be especially sensitive to the motor similarity manipulation. Regions related to the retention of end information should not be sensitive to motor similarity.

As participants in Experiment 2 were explicitly instructed to retain either means or end information in working memory, it is impossible to answer the question whether people have preferences to represent one or the other action feature based on these data. In Experiment 3, a behavioral study, we investigated in a cross-cultural context whether the familiarity of an action influences the type of action representation in memory. It has been shown that action familiarity affects information processing (Calvo-Merino et al., 2010; Engelkamp et al., 1993; Knopf, 1991; Mohr et al., 1989; Rumiati et al., 2005; Wang et al., in press; Zalla et al., 2010) and that familiar and unfamiliar actions yield different brain activations (Calvo-Merino et al., 2005, 2006; Cross, Hamilton et al., 2009; Cross, Kraemer et al., 2009; Vingerhoets et al., 2009). We hypothesized that action familiarity would have an effect on whether an action's means or end is represented in memory. In order to in-

4. OUTLINE OF THE PROJECT

vestigate this, we took advantage of familiarity differences in actions between Chinese and German young adults. Presenting action video clips of differential familiarity during an encoding phase, we focused on recognition accuracy for means and end information. We expected familiar actions to be more likely represented in terms of their ends as compared to unfamiliar actions which would be more likely represented in terms of their means. As actions can be considered a very basic information category, we did not expect cultural differences in action information processing. The mediating factor should be action familiarity which can differ between cultures.

4. OUTLINE OF THE PROJECT

5. EXPERIMENT 1 - WORKING AND LONG TERM MEMORY[1]

5.1. RESEARCH QUESTION AND HYPOTHESES

Both retention of everyday actions in working memory and their retrieval from long term memory are necessary for a successful interaction with one's environment. How do we represent this kind of action information in memory? Are the representations involved the same or different for working and long term memory? Different conceptualizations can be distinguished. Traditional models have conceptualized working and long term memory as different systems with separate sets of representations (Baddeley & Logie, 1999). Others argue that regions which are involved in perception and action represent information both in working and long term memory (Cowan, 1999; Fuster, 1997; Slotnick, 2004; Zimmer, 2008). For regions involved in perception, this has been demonstrated in previous studies (Lewis-Peacock & Postle, 2008; Ranganath, Cohen et al., 2004), however, evidence on regions involved in action processing is lacking. Concerning working memory, one theoretical view is that it does not involve dedicated storage buffers but is an emergent property of the prefrontal cortex and brain regions which process a stimulus perceptually or which are needed during action execution (D'Esposito, 2007; Postle, 2006).

With this fMRI experiment we aimed at elucidating the overlap in domain specific brain regions during retention of action information in working memory and its retrieval from long term memory. We conducted an fMRI study in which we focused on neural activity during working memory retention of action information about manipulable objects and its retrieval from episodic

---

[1] This chapter corresponds mostly to a manuscript titled „Actions in Working and Long Term Memory Share Domain Specific Representations" of which I am the first author and which has been under revision at the time of writing my doctoral thesis.

long term memory within a single sample of participants. As a second information category, we focused on size information about manipulable objects in working and long term memory. We used the working memory paradigm of Mecklinger et al. (2004) as the incidental encoding phase for a long term memory test. The working memory task was a delayed match to sample task within the framework of an S1-cue-S2 paradigm. A cue being presented after the offset of the encoding stimulus (S1) instructed the participants which information to retain in working memory in order to compare the encoding and the test stimulus (S2) in the respective information category. The working memory task was the incidental encoding phase for a long term memory test which was a source memory task. Participants were required to retrieve whether they had previously encountered an item in an action/size working memory task or not.

We hypothesized that if the same set of action specific representations is used for both working and long term memory, there should be common activations during working memory retention and long term memory retrieval for actions in domain specific regions. Based on previous findings (Kellenbach et al., 2003; Masumoto et al., 2006; Mecklinger et al., 2004; Nyberg et al., 2001; Russ et al., 2003), we expected the left ventral premotor/inferior frontal gyrus and the left inferior parietal cortex (supramarginal gyrus and/or aIPS) as well as the left middle temporal/STS region to commonly represent action information in working and long term memory. As we expected this information to be domain specific, the activation pattern should be different for the other information category, size information. Based on previous studies on the representation of size information (Ebisch et al., 2007; Kellenbach, Brett, & Patterson, 2001; Mecklinger et al., 2004; Oliver & Thompson-Schill, 2003; Rossion et al., 2000), we expected medial parietal and occipital regions to be selectively activated during working memory retention and long term memory retrieval of size information.

To our knowledge, previous studies have either focused on working memory or long term memory processes concerning action information processing. The overlap of action specific regions during working and long term memory processing has not been dealt with yet within a single experiment.

5. EXPERIMENT 1

Investigating this question is also informative beyond the realm of action information as it will provide results which are relevant to the general relationship of working and long term memory and their respective representations. Are they two separate systems which rely on different (action) representations? Is the same (action) representation used both in a working me-mory and a long term memory task?

5.2. METHODS

5.2.1. PARTICIPANTS

Sixteen healthy right-handed participants took part in the study (7 male, 9 female). Their mean age was 24.4 years (standard deviation = SD = 4.2 years). All participants gave written informed consent prior to the experiment. They did not have a history of psychiatric or neurological illnesses.

5.2.2. MATERIALS AND EXPERIMENTAL PROCEDURE

The experiment was run on a PC controlled by E-Prime 1.7 (Psychology Software Tools, Pittsburgh, Pennsylvania, USA). In the first part of the experiment, each subject took part in an S1-cue-S2 matching task (working memory test). In this task, a picture of an object was presented as S1, a cue followed specifying the task, and then a name of another object was presented as S2 which was to be compared with S1 in the feature indicated by the cue. For that purpose, photographs of 128 everyday manipulable objects were collected. For each object, a second one was searched that either matched or mismatched in action and/or size. 128 photographs of these matching/mismatching objects were prepared. The resulting 128 pairs of ob-

5. EXPERIMENT 1

jects could be assigned to the four categories "similar action/similar size", "similar action/different size", "different action/similar size" and "different action/different size". Examples of the stimulus material are displayed in Figure 2.

	Similar action	Different action
Similar size	32 Kinderwagen	32 Schuh
Different size	32 Kleiderschrank	32 Stuhl

Figure 2. Examples of object pairs in the working memory block of Experiment 1. Pairs were composed of a picture and a (German) word both referring to manipulable objects. They were defined as to similarity or difference of the prototypical action to be performed with the objects and their prototypical size. There were 32 pairs of objects within each of the four categories "similar action/similar size", "similar action/different size", "different action/similar size" and "different action/different size". Within each trial, the first object of a pair was presented as a photograph and the second as a word. Photograph/word status of objects was counterbalanced between participants. Kinderwagen = stroller, Kleiderschrank = wardrobe, Schuh = shoe, Stuhl = chair.

Each category consisted of 32 pairs. Of each pair, one member was presented as S1 and the second one as S2 of the S1-cue-S2 matching task. A photograph of the object was presented as S1 and a familiar object name as S2. Across participants, each object was used equally often as S1 and S2. Effectors for the actions were either hand or mouth. The size of the photographs subtended 5.9° in visual angle either vertically or horizontally depending on the object shape. Photograph resolution was 72 dpi. Additionally, each photograph existed in an unrecognizable, scrambled version which was generated applying a distortion filter in Adobe Photoshop (Adobe Sytems, San Jose, California, USA).

5. EXPERIMENT 1

The stimuli were rear projected onto a screen located behind the scanner subtending a width of 23° and a height of 18° in visual angle with a resolution of 1024 × 768 pixels. Participants could see the screen through a mirror system mounted to the head coil. The trial structure in the working memory block is illustrated in Figure 3.
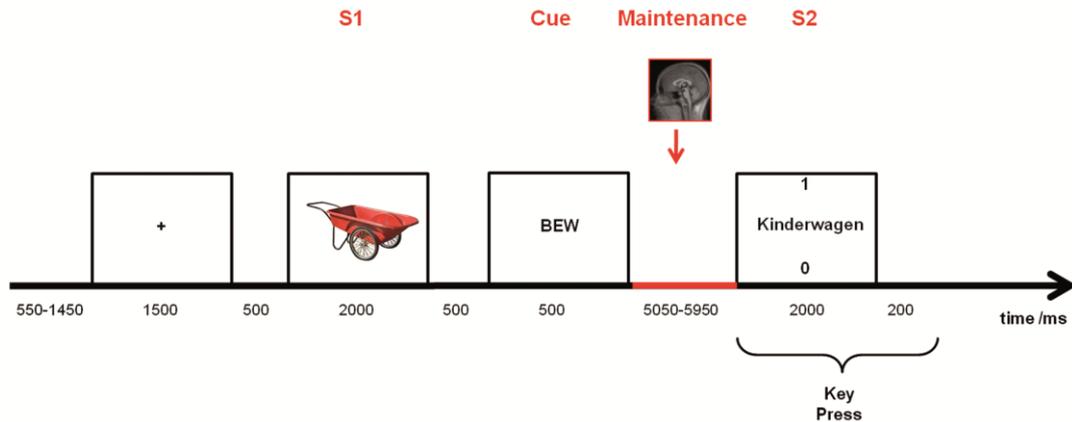
Figure 3. Trial structure in the working memory block of Experiment 1. The trial structure is exemplified by a movement (Bewegung; BEW) match trial. The duration of the inter-trial interval was jittered as was the duration of the retention interval. Analysis of brain activity was focused on the retention interval. Time is not drawn to scale. Kinderwagen = stroller.

Throughout the test, a white background was utilized. After a variable blank interval with an average duration of 1000 ms (25% 550 ms, 25% 850 ms, 25% 1150 ms, 25% 1450 ms), a black fixation cross was visible for 1500 ms. Another blank interval of 500 ms followed after which S1 was presented for 2000 ms. S1 was a photograph of an everyday manipulable object. After a blank interval of 500 ms, a visual cue was presented indicating which information of S1 would be tested later within the trial or that S1 would not have to be maintained in the control condition. Three different black three-letter-abbreviations were used as cues and were presented for 500 ms: BEW for "Bewegung" (movement) indicated that the movement that is performed with the object during the prototypical action should be made available in working memory whereas GRÖ for "Größe" (size) instructed the participants to make its prototypical size available. ZIF for "Ziffer" (digit) informed participants that it was not necessary to maintain anything about S1 for the upcoming task.

5. EXPERIMENT 1

With cue offset, the screen was blanked and a variable interval with an average duration of 5500 ms (25% 5050 ms, 25% 5350 ms, 25% 5650 ms, 25% 5950 ms) followed. This was the maintenance interval. Then S2 was presented which consisted of a centrally presented black word and two small black digits that were either presented to the left and right of the word or above and below it. S2 duration was 2000 ms. According to the three cue conditions, different tasks were required at this stage. In the action task (BEW), participants judged the similarity of the prototypical motor action that is performed with the two objects. In the size task (GRÖ), they made an analogous decision about the prototypical size of the two objects. Digit trials (ZIF) were used as control trials not requiring working memory (see also Bosch et al., 2001; Mecklinger et al., 2004; Umla-Runge et al., 2011). In this case, the task was to make a decision about the identity of the two digits presented together with the S2 word.

Match and non-match trials occurred with equal probability. Each participant worked on 32 action trials, 32 size trials and 32 digit trials. Within each condition, each of the four categories appeared equally often. Furthermore, we realized 32 scrambled trials without any memory demands. In these trials, S1 was a scrambled picture which could not be identified as an object and at S2, a digit identity judgment was required (ZIF). A random sequence of trials was accomplished for each participant. In all conditions, a response was possible during S2 presentation and the following 200 ms blank interval. Participants used their left and right thumbs to press the left and right button respectively on an MRI-compatible response pad which they held with both hands. Key assignment was counterbalanced between participants.

The working memory block was the incidental encoding phase for two long term memory tasks: an action source memory task and a size source memory task. The action and size long term memory tasks were blocked and the sequence of the two blocks was counterbalanced between participants. The trial structure of the long term memory tasks paralleled the one of the working memory tasks. In Figure 4, the trial structure of a long term memory trial is depicted.

5. EXPERIMENT 1

S1 object   Retrieval   Response cue
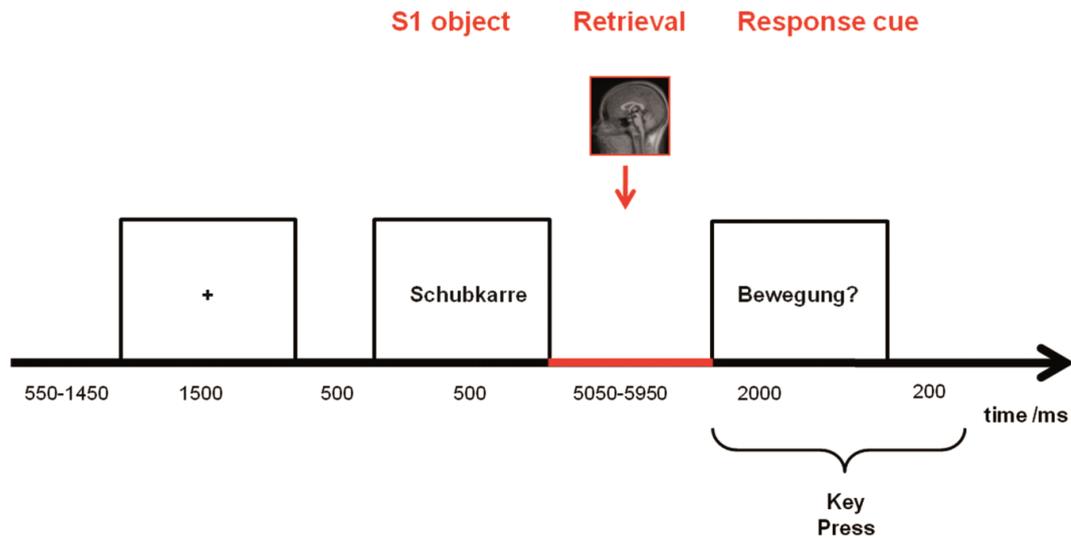
Figure 4. Trial structure in the long term memory block of Experiment 1. The trial structure is exemplified by an action source memory match trial (assuming that the trial illustrated in Figure 3 had been worked on in the working memory task). The duration of the inter-trial interval was jittered as was the duration of the retrieval interval. Analysis of brain activity was focused on the retrieval interval. Time is not drawn to scale. Schubkarre = wheelbarrow, Bewegung = movement.

Again a white background was utilized throughout the test. A trial in the action source memory task began with a variable blank interval with an average duration of 1000 ms (25% 550 ms, 25% 850 ms, 25% 1150 ms, 25% 1450 ms) after which a black fixation cross was presented centrally for 1500 ms. A blank interval of 500 ms was then followed by the presentation of a black word for 500 ms. The word referred to an object which had been presented before as S1 in the working memory task. During the subsequent retrieval interval with an average duration of 5500 ms (25% 5050 ms, 25% 5350 ms, 25% 5650 ms, 25% 5950 ms), participants were required to retrieve the former item episode in order to judge whether they had performed an action task with this object during the working memory phase or not. A visual response cue "Bewegung?" (= movement) was then displayed centrally for 2000 ms and participants were required to press the left or right button on the response pad according to their decision. Again, key assignment was counterbalanced between participants. Responses were recorded during the presentation of the response cue and a 200 ms blank interval that followed it.

The action source memory block consisted of 64 trials, half of them match trials (i.e. from action working memory trials) and the other half non-

5. EXPERIMENT 1

match trials (half of them came from ZIF trials with real objects and the other half from scrambled trials). The size source memory block consisted of 64 other trials, half of them match trials (i.e. from size working memory trials) and the other half non-match trials (again half from ZIF trials with real objects and half from scrambled trials). Trial structure in the size source memory block was identical, except for focusing on size. The visual response cue was "Größe?" (= size) in this case.

Participants were instructed for the working memory task before entering the scanner and took part in a practice session with twelve trials in which they received feedback after each trial. If their accuracy in the practice session was below .5, they were to repeat it once. The instructions for both long term memory blocks were read to them while they were lying inside the scanner. There was no practice session for the long term memory tasks.

5.2.3. FMRI ACQUISITION AND ANALYSIS

Functional imaging was performed with a 1.5 T MR scanner (Sonata, Siemens Magnetom Vision, Erlangen, Germany). Whole-brain images with 23 axial slices parallel to the AC/PC line were obtained using a T2*-weighted EPI sequence (TR: 2000 ms, TE: 50 ms, flip angle: 90°, FOV: 230/230 mm, interleaved slice acquisition, slice thickness: 4 mm, interslice gap: 1 mm, in-plain resolution: 3.6 × 3.6 mm) using a standard head coil. The functional sequence lasted 29.2 minutes for the working memory part and 12.5 minutes each for the two long term memory parts.

BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands) was used for preprocessing and statistical analysis. The first four scans within a session were discarded because of signal equilibration issues. Preprocessing included slice time correction, 3D motion correction, spatial smoothing with a Gaussian kernel (FWHM: 8 mm), linear trend removal and high-pass filtering with an individually calculated high pass filter for each participant and each

session (maximal distance between subsequent trials of one condition × 2 in Hz). Functional data were coregistered with individual high-resolution anatomical images (voxel size: 1 mm^3). Anatomical images were normalized into Talairach space (Talairach & Tournoux, 1988) and the respective normalization parameters were then applied to the functional data.

A whole-brain statistical analysis was performed applying a general linear model. For each participant, neural activity was modeled by convolving a stimulus function with a two gamma hemodynamic response function. In the working memory task, the analysis was restricted to activations in the retention interval time locked to cue offset. In the long term memory task, the analysis was restricted to activations in the retrieval interval time locked to probe offset. Ten predictors were applied referring to four working memory conditions and six long term memory conditions of the experiment. The working memory predictors were the action task, the size task, the digit task with real objects and the digit task with scrambled objects. The long term memory predictors were hits to old and correct rejections to ZIF items from the real or scrambled version in the action and size block, respectively. Furthermore, six motion correction predictors were added as predictors of no interest (three referring to translation, three to rotation). For both working and long term memory, only trials yielding a correct response were included in the analysis.

For the working memory task, we contrasted short time retention of action and size information. For the long term memory task, contrasts were computed for action hits and correct rejections as well as size hits and correct rejections. Furthermore, conjunction analyses were calculated using a random-effects-of-conjunction approach. This method performs the conjunction for each participant before running a random effects analysis over all participants. Therefore it is possible to detect brain regions that show a within subject overlap in activation during working and long term memory while it also acknowledges variability between subjects of the brain regions involved. For action information, we investigated which brain regions exhibited overlapping activations in the individual t-contrasts (action working memory – size working memory) and (action long term memory hits – action long term memory correct rejections). For size information, overlapping activations in

5. EXPERIMENT 1

the individual t-contrasts (size working memory – action working memory) and (size long term memory hits – size long term memory correct rejections) were looked at. Long term memory correct rejections involved both previously recognizable and scrambled objects. As action and size long term memory were tested in separate blocks with different retrieval instructions, hits and correct rejections were contrasted within each block rather than action hits and size hits across blocks. We report activations that were significant with $p < .005$ (uncorrected for multiple comparisons) at voxel level and $p < .05$ (corrected for multiple comparisons) at cluster level. Anatomical labeling was then performed using the brain atlas of Talairach and Tournoux (1988) and the Talairach Daemon database (Lancaster et al., 2000).

5.3. RESULTS

5.3.1. BEHAVIORAL DATA

The mean response times for correct responses in the working memory block were 1288 ms (SD = 162 ms) in the action working memory task, 1298 ms (SD = 159 ms) in the size working memory task, 997 ms (SD = 159 ms) in the ZIF task with real objects and 973 ms (SD = 139 ms) in the scrambled trials. There was no significant difference in response times between the action and size working memory tasks, $t (15) < 1$, n.s.

For accuracy, we calculated the mean corrected recognition scores PR (PR = Hit Rate - False Alarms Rate) for both the action and size working memory tasks (Snodgrass & Corwin, 1988). PR in the action working memory task was .60 (SD = .15) and .34 (SD = .25) in the size working memory task. Accuracy differed significantly between the two tasks, $t (15) = 3.91$, $p < .01$. The hit rate in the ZIF task with real objects was .91 (SD = .12),

5. EXPERIMENT 1

the hit rate in the scrambled trials was .94 (SD = .07). False alarm rates in the latter tasks were .07 (SD = .05) and .05 (SD = .07), respectively.

In the long term memory tasks, mean response times were 436 ms (SD = 113 ms) for action hits, 440 ms (SD = 112 ms) for action correct rejections, 439 ms (SD = 109 ms) for size hits and 448 ms (SD = 131 ms) for size correct rejections. Neither response times for hits nor response times for correct rejections differed significantly between the action and size long term memory tasks. The mean PR in the action long term memory task was .69 (SD = .11) as compared to .62 (SD = .16) in the size long term memory task. There was no significant accuracy difference between the two tasks, t (15) = 1.44, p ≤ .18.

5.3.2. FMRI DATA

5.3.2.1. ACTION AND SIZE IN WORKING MEMORY

Domain specific activation clusters which were obtained in a contrast of action and size information in working memory are listed in Table 1. For action information in comparison to size, activations in the left hemisphere included the putative human mirror neuron areas, i.e. the inferior parietal lobe (BA 40) and the inferior frontal gyrus extending into ventral premotor cortex (BA 6, BA 44). In addition, the left middle temporal gyrus extending into the STS (BA 21) and the pre-SMA (medial BA 6) were selectively activated during working memory retention of action information. Furthermore, activation clusters in the right inferior frontal gyrus (BA 45, BA 47) and the right middle temporal gyrus (BA 37) emerged. Subcortically, the left caudate nucleus was more activated for action information as compared to size information in working memory.

For size information in working memory in comparison to action, an activation cluster peaking in the right precuneus (BA 31) was selectively acti-

5. EXPERIMENT 1

vated. This cluster extended into the cuneus and superior occipital gyrus (BA 18, BA 19). In addition, selective activations for size information were observed in the right lingual gyrus (BA 18), the right inferior parietal lobe bordering the intraparietal sulcus (BA 40) and the right anterior cingulate (BA 32). Furthermore, the right caudate nucleus and the posterior lobe of the left cerebellum showed significant activations.

Figure 5 illustrates domain specific regions for the retention of action and size information in working memory.

Table 1. Action and size specific brain regions during retention in working memory.

a) Brain regions which were significantly more activated during the retention of action as compared to size information in working memory.

Brain Region	BA	Hemisphere	x	Y	z	Cluster size	t score
Action Working Memory > Size Working Memory							
Inferior parietal lobe	40	L	-61	-32	27	218	9.23
Middle temporal gyrus	21	L	-61	-50	-6	320	8.33
	37	R	44	-59	3	13	5.00
Inferior frontal gyrus	45	R	35	25	6	14	6.03
	47	R	47	19	-9	64	5.17
	45	L	-52	28	9	510	5.50
Medial frontal gyrus	6	L	-4	16	45	27	4.37
Caudate nucleus		L	-10	1	9	34	5.97

5. EXPERIMENT 1

b) Brain regions which were significantly more activated during the retention of size as compared to action information in working memory.

Brain Region	BA	Hemisphere	x	Y	z	Cluster size	t score
Size Working Memory > Action Working Memory							
Precuneus	31	R	26	-74	30	115	-5.98
Anterior cingulate	32	R	20	43	9	37	-4.80
Inferior parietal lobe	40	R	44	-50	48	50	-4.41
Lingual gyrus[2]	18	R	6	-94	-18	22	-4.06
Cerebellum		L	-34	-74	27	16	-4.60
Caudate nucleus		R	11	22	0	25	-4.42

Brain regions were significant with p < .005 uncorrected for multiple comparisons at voxel level and p < .05 corrected for multiple comparisons at cluster level. Displayed are the name of the brain structure, the corresponding Brodmann Area, hemisphere, Talairach coordinates and t-score for the peak voxel within each cluster. BA = Brodmann Area, L = left, R = right. The number of functional voxels (one functional voxel = 27 mm^3) is listed to indicate cluster size.

---

[2] The information refers to the center of gravity of this activation cluster. The peak voxel coordinate was located outside of the Talairach brain.

5. EXPERIMENT 1
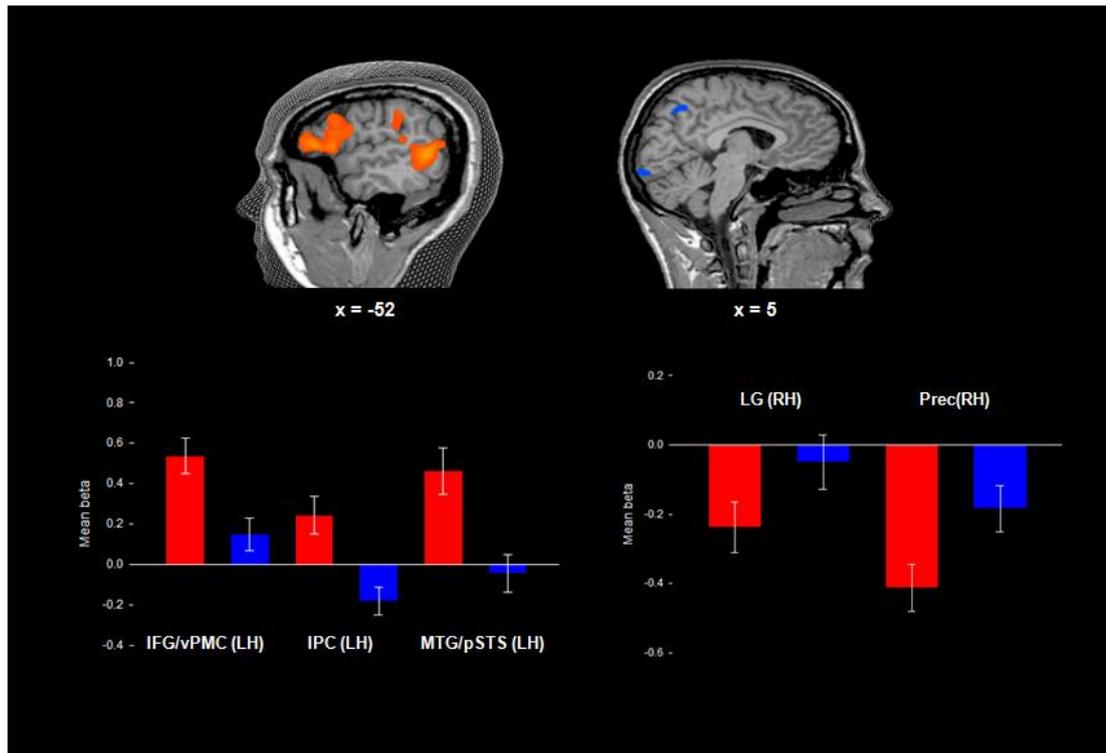
Figure 5. Brain activations for the retention of action and size information in working memory. Brain regions which were more active for action as compared to size information are displayed in red. Brain regions which were more active for the retention of size as compared to action information are displayed in blue. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level. Baseline-corrected mean parameter estimates are displayed for a subset of activation clusters. Red bars represent action retention, blue bars represent size retention. IFG/vPMC = inferior frontal gyrus/ventral premotor cortex; IPC = inferior parietal cortex; MTG/pSTS = middle temporal gyrus/posterior superior temporal sulcus; LG = lingual gyrus; Prec = precuneus; LH = left hemisphere; RH = right hemisphere.

5.3.2.2. ACTION AND SIZE IN LONG TERM MEMORY

When contrasting action hits with action correct rejections during the retrieval from long term memory, the strongest activation was obtained in the left ventral premotor cortex extending into inferior frontal gyrus (BA 44, BA 45). This structure corresponds to the anterior region of the putative human mirror neuron system. The posterior region in the left inferior parietal lobe (BA 40) was also activated as was the middle temporal gyrus (BA 21) at the lower bank of the superior temporal sulcus. Further activation clusters in the left hemisphere included the middle frontal gyrus (BA 10), cingulate gyrus (BA 23), precentral, medial and superior frontal gyri in the region of the SMA and pre-SMA (BA 6), cuneus (BA 19) and precuneus (BA 31). Right-

5. EXPERIMENT 1

hemispheric activation clusters were observed in the insula, precuneus (BA 7), middle temporal gyrus (BA 37), superior temporal gyrus (BA 39) and the middle frontal gyrus (BA 46). Both the cerebellum and the caudate nucleus in the right hemisphere were stronger activated for action hits as compared to action correct rejections. There were no brain regions that showed stronger activations for correct rejections as compared to hits in the action long term memory task.

Contrasting size hits and correct rejections, the strongest activation emerged in the left angular gyrus (BA 39) extending into precuneus and adjacent parieto-occipital regions (BA 18, BA 19, BA 31). Furthermore, activations in the right inferior and superior parietal lobe including the intraparietal sulcus were obtained (BA 7, BA 40). Other activation clusters were located in the posterior cingulate (BA 30, BA 31) and, left-hemispherically, in the precentral gyrus (BA 4, BA 6), middle temporal gyrus (BA 21), inferior frontal gyrus (BA 47) and posterior lobe of the cerebellum. There were no brain regions that showed stronger activations for correct rejections as compared to hits in the size long term memory task.

In Table 2, activation clusters for the retrieval of action and size information from long term memory are summarized. In Figure 6 the respective brain regions are depicted.

5. EXPERIMENT 1

Table 2. Action and size specific brain regions during retrieval from long term memory.

a) Brain regions which were significantly more activated during retrieval of action hits as compared to correct rejections from long term memory

Brain Region	BA	Hemisphere	x	Y	z	Cluster size	t score
Action: Hits > Correct Rejections							
Precentral gyrus	44	L	-46	10	12	180	6.37
	6	L	-37	-8	57	11	4.76
Medial frontal gyrus	6	L	-4	-17	66	22	4.27
Superior frontal gyrus	6	L	-19	4	54	9	4.06
Middle frontal gyrus	10	L	-34	46	3	30	6.28
	46	R	44	40	15	8	3.82
Inferior parietal lobe	40	L	-52	-53	36	106	5.83
Precuneus	7	R	20	-62	33	29	4.63
	31	L	-7	-65	18	25	4.27
Middle temporal gyrus	37	L	-58	-44	-6	16	4.24
	21	L	-61	-20	-6	10	4.23
	37	R	50	-50	-6	16	4.61
Superior temporal gyrus	39	R	41	-53	33	67	4.53
Cingulate gyrus	23	L	-7	-26	24	47	5.08
Cuneus	19	L	-4	-80	30	32	4.35
Insula		R	32	13	-3	64	5.23
Cerebellum		R	11	-77	-24	47	4.83
Caudate nucleus		R	8	4	3	12	4.22

5. EXPERIMENT 1

b) Brain regions which were significantly more activated during retrieval of size hits as com-
pared to correct rejections from long term memory

Brain Region	BA	Hemisphere	x	Y	z	Cluster size	t score
Size: Hits > Correct Rejections							
Angular gyrus	39	L	-49	-68	36	932	7.56
Inferior parietal lobe	40	R	59	-38	39	7	5.26
	40	R	47	-47	48	16	4.38
Superior parietal lobe	7	R	32	-53	57	6	4.03
Posterior cingulate	30	L	-16	-62	12	15	4.43
	30	L	-7	-47	24	18	4.37
Precentral gyrus	4	L	-40	-11	54	83	5.95
Inferior frontal gyrus	47	L	-31	28	-12	13	4.45
Middle temporal gyrus	21	L	-58	-29	-6	126	5.50
Cerebellum		L	-4	-80	-30	28	4.89

Significantly activated structures during long term memory retrieval of action information
(action hits > action correct rejections) and of size information (size hits > size correct rejec-
tions). Brain regions were significant with p < .005 uncorrected for multiple comparisons at
voxel level and p < .05 corrected for multiple comparisons at cluster level. Displayed are the
name of the brain structure, the corresponding Brodmann Area, hemisphere, Talairach coor-
dinates and t score for the peak voxel within each cluster. BA = Brodmann Area, L = left, R =
right. The number of functional voxels (one functional voxel = 27 mm^3) is listed to indicate
cluster size.

5. EXPERIMENT 1
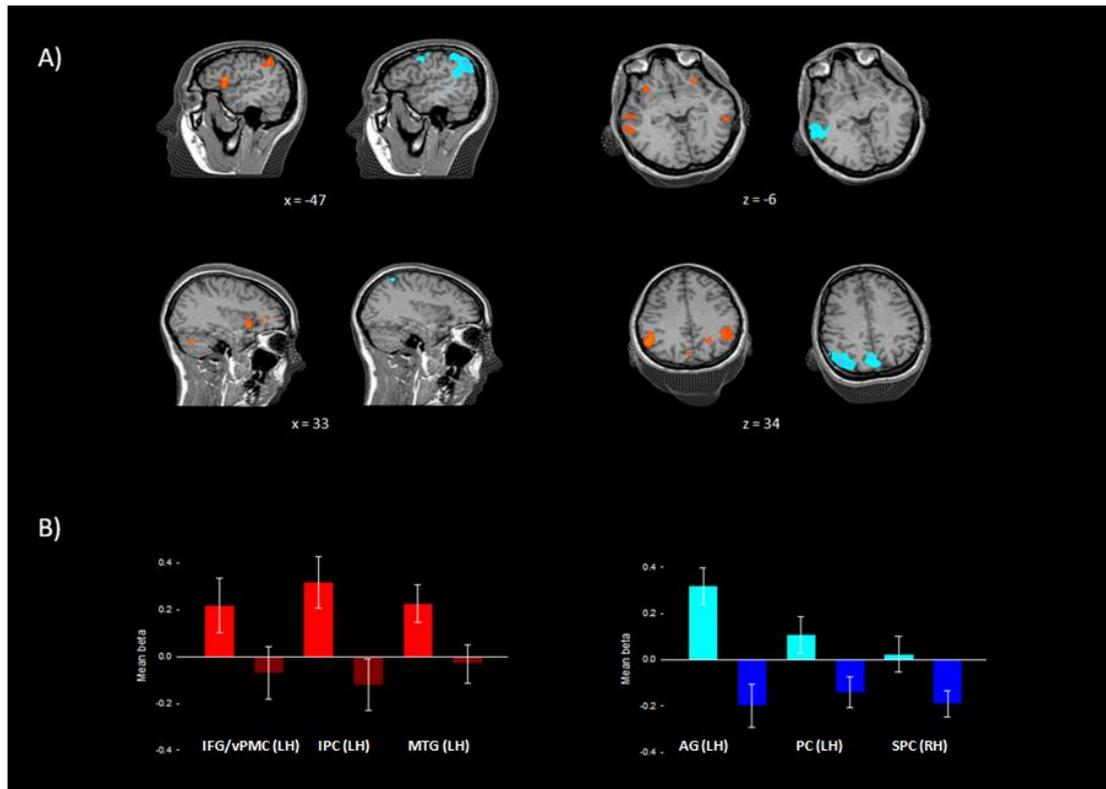
Figure 6. Brain activations for the retrieval of action and size information from long term memory. A) Brain regions which were more active for action hits as compared to correct rejections are displayed in red, brain regions which were more active for size hits as compared to correct rejections are displayed in blue. Significant activation clusters from each contrast are overlaid on two sagittal and two transversal slices. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level. B) The left diagram displays baseline-corrected mean parameter estimates for a subset of activation clusters resulting in the contrast of action hits and correct rejections. Light red bars represent action hits, dark red bars represent action correct rejections. In the right diagram, baseline-corrected mean parameter estimates for a subset of activation clusters resulting in the contrast of size hits and correct rejections are displayed. Light blue bars represent size hits, dark blue bars represent size correct rejections. IFG/vPMC = inferior frontal gyrus/ventral premotor cortex; IPC = inferior parietal cortex; MTG = middle temporal gyrus; AG = angular gyrus; PC = posterior cingulate; SPC = superior parietal cortex; LH = left hemisphere; RH = right hemisphere.

5.3.2.3. ACTION IN WORKING AND LONG TERM MEMORY

A conjunction analysis (random-effects-of-conjunction) was conducted to find action specific brain regions which show overlapping activation during retention of action information in working memory and its retrieval from long term memory. It focused on the contrasts between action and size working memory retention and between retrieval of action hits and correct rejections from long term memory. The resulting brain regions are depicted as red blobs in Figure 7.

5. EXPERIMENT 1

Seven out of eight activation clusters which emerged in this analysis were located in the left hemisphere. A cluster in the anterior part of the putative human mirror neuron system was commonly activated during retention of action information in working memory and its retrieval from long term memory. It comprised the left ventral premotor cortex and inferior frontal gyrus (BA 6, BA 44) and extended into BA 45 and BA 9 in the inferior frontal gyrus as well as the insula and the superior temporal lobe (BA 22). Posteriorly, the supramarginal gyrus (BA 40) in the inferior parietal lobe showed enhanced activation in both action working and long term memory. In the left temporal lobe, the analysis yielded activation clusters in the middle temporal gyrus (BA 19, BA 37, BA 39), the superior temporal gyrus (BA 22, BA 39) and at the border of the middle and inferior temporal gyri (BA 21). Two further activation clusters in the left hemisphere were found, one in inferior and middle frontal gyrus (BA 45, BA 46) and a second one subcortically in the caudate nucleus. In the right hemisphere, an activation cluster in inferior and middle frontal gyrus emerged (BA 45, BA 46).

5.3.2.4. SIZE IN WORKING AND LONG TERM MEMORY

For size information, an analogous conjunction analysis was conducted involving the contrasts between size and action working memory retention and between retrieval of size hits and correct rejections from long term memory. Brain regions that were commonly activated during retention of size information in working memory and its retrieval from long term memory are displayed as green blobs in Figure 7.

A medial structure in precuneus and cuneus (BA 7, BA 19) was involved in working and long term memory processing of size information. This activation cluster was bilateral, however, it extended more into the right hemisphere. Furthermore, the right inferior parietal lobe (BA 40) bordering the intraparietal sulcus was activated both for size working and long term

5. EXPERIMENT 1

memory. Table 3 includes details of the activation clusters found in the two conjunction analyses.

Table 3. Action and size specific brain regions commonly activated during working memory retention and long term memory retrieval.

Brain Region	BA	Hemisphere	x	Y	z	Cluster size	t score
Action Working Memory AND Action Long Term Memory							
Inferior frontal gyrus	45	L	-49	34	18	11	5.21
	47	R	38	28	3	10	4.07
Precentral gyrus	44	L	-46	10	12	70	4.85
Supramarginal gyrus	40	L	-55	-41	33	28	4.97
Middle temporal gyrus	39	L	-49	-65	12	37	4.65
	21	L	-61	-50	-6	33	4.19
Superior temporal gyrus	22	L	-55	-56	18	5	3.81
Caudate nucleus		L	-10	1	9	6	3.89
Size Working Memory AND Size Long Term Memory							
Precuneus	7	L	-1	-68	39	31	4.33
Inferior parietal lobe	40	R	41	-50	48	8	3.86

Significantly activated structures in a conjunction analysis of the contrasts (action working memory – size working memory) and (action long term memory hits – action long term memory correct rejections) and a conjunction analysis of the contrasts (size working memory – action working memory) and (size long term memory hits – size long term memory correct rejections). Brain regions were significant with p < .005 uncorrected for multiple comparisons at voxel level and p < .05 corrected for multiple comparisons at cluster level. Displayed are the name of the brain structure, the corresponding Brodmann Area, hemisphere, Talairach coordinates and t-score for the peak voxel within each cluster. BA = Brodmann Area, L = left, R = right. The number of functional voxels (one functional voxel = 27 mm³) is listed to indicate cluster size.

5. EXPERIMENT 1
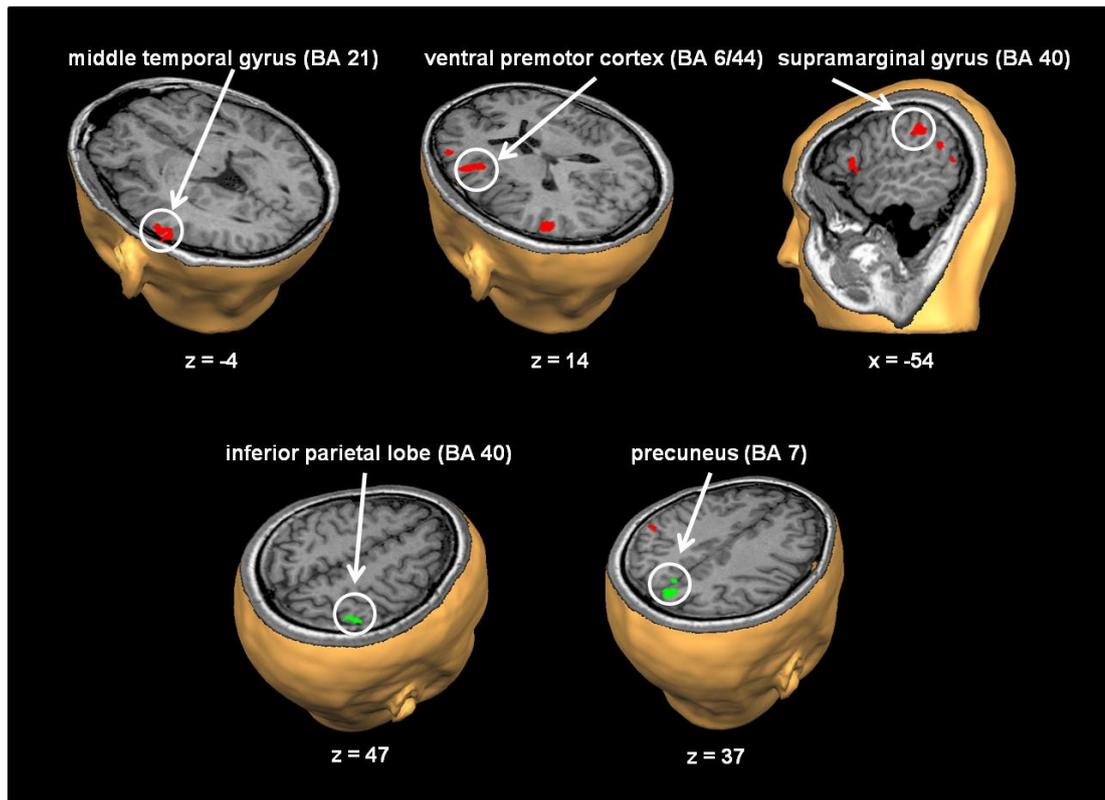
Figure 7. Domain specific activations for action and size information in working and long term memory. Two conjunction analyses using a random-effects-of-conjunction approach were conducted. Brain regions which were active both for the retention of action information in working memory and its retrieval from long term memory are displayed in red. Brain regions which were active both for the retention of size information in working memory and its retrieval from long term memory are displayed in green. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level.

5.4. DISCUSSION

In this study, we aimed at finding brain regions that show an overlap in activations during the retention of action information in working memory and its retrieval from long term memory. We expected the putative human mirror neuron system, i.e. inferior frontal/ventral premotor cortex and inferior parietal lobe, and the middle temporal/STS region to be involved in the representation of actions both in working and in long term memory. Furthermore, we expected these common regions to be domain specific. For a different information type in working or long term memory, it should be other brain regions showing overlapping activations. In this study, we chose size information as

5. EXPERIMENT 1

the other information type and expected medial parieto-occipital regions to be commonly activated.

For retention of action information in working memory and its retrieval from long term memory, we found the left ventral premotor and inferior frontal cortex to be commonly activated. This brain region corresponds to the putative anterior mirror neuron region in humans, an area which has been demonstrated to be involved both during action execution and action perception (Kilner et al., 2009). It has been shown that the ventral premotor cortex is activated during motor imagery and observation of movements (Binkofski et al., 2000; Buccino et al., 2001; Hanakawa et al., 2003; Jeannerod & Decety, 1995). Furthermore, Kellenbach et al. (2003) found the left ventral premotor cortex (BA 6, BA 44) to show enhanced activation in judgment tasks with manipulable objects (tools) as compared to non-manipulable objects. Functionally, the activation of this region could reflect the interaction of an effector with an object. The description of an effector-object relation would be involved in both the storage of movements and the retrieval of motor information about transitive actions. The activation peak was located in the frontal operculum, a brain structure that has been specifically linked to movement imagery (Binkofski et al., 2000) and planning of goal directed actions (Tunik et al., 2008).

Furthermore, we found a left-hemispheric cluster in the inferior parietal lobe to be commonly activated during action information processing in working and long term memory. This cluster was located in the supramarginal gyrus inferior to the intraparietal sulcus. The intraparietal sulcus has emerged in a considerable number of studies as a structure to be involved in the representation of action information (Binkofski et al., 2000; Jacobs et al., 2010; Kellenbach et al., 2003; Mecklinger et al., 2004; Nyberg et al., 2001). How-

5. EXPERIMENT 1

ever, transcranial magnetic stimulation (TMS) results suggest that there are two distinct regions within the left inferior parietal cortex which are related to action information processing, namely the aIPS and the supramarginal gyrus, and that these regions serve different functions (Rice et al., 2006; Tunik et al., 2005; Tunik et al., 2008). Whereas the aIPS is mainly involved in online processing during action execution, it is the supramarginal gyrus which is needed during action planning. If the supramarginal gyrus was inhibited during an action planning phase, a selective delay in planning goal directed actions resulted. There was no such effect if it was the aIPS that was inhibited. In a previous study by Russ et al. (2003), the supramarginal gyrus showed enhanced activation during recognition of actions which had been enacted during encoding as compared to actions that had been encoded with a verbal strategy. Their study focused on episodic long term memory. Our results show that the left supramarginal gyrus is activated both during working memory retention and episodic retrieval of action information.

Unlike some other neuroimaging studies on action processing (e.g. Kellenbach et al., 2003; Mecklinger et al., 2004; Nyberg et al., 2001), we did not find the intraparietal sulcus to be commonly activated during working and long term memory for actions. The conditions under which activations in the aIPS during tasks not involving overt execution of actions can be observed are unclear yet. Kellenbach et al. (2003) distinguished between action and function knowledge about manipulable objects. Using PET, they found the left intraparietal sulcus to be selectively involved in action judgments as compared to function judgments. Hesse et al. (2009) compared brain regions involved in a means and an end judgment task presenting video clips of manual actions. They found a bilateral inferior parietal region encompassing both the intraparietal sulcus and the supramarginal gyrus to be more active during the means task as compared to an end judgment task. In contrast, fMRI studies focusing on goal directed action perception attributed repetition suppression effects in the aIPS to the representation of object goals and action consequences (Hamilton & Grafton, 2006, 2008; Tunik et al., 2007). These results seem inconsistent. However, it is important to consider the differences in processes (perception with an unrelated task vs. judgment of the action

5. EXPERIMENT 1

features of interest) and analysis technique (repetition suppression approach vs. direct contrast between two tasks) that could have contributed to the diverging results. It is not possible to resolve this issue with the data of Experiment 1. What can be concluded at this point is that the distinction bet-ween the aIPS and the supramarginal gyrus has been corroborated by our data. The supramarginal gyrus but not the aIPS is commonly involved in the representation of actions in working and long term memory.

The left ventral premotor/inferior frontal and the inferior parietal cortex have been discussed as structures belonging to the human mirror neuron system. They are both active during action execution and action perception. The results of this experiment suggest that mirror neuron regions are required for the representation of actions in memory. Overlapping action related activations in the left inferior frontal and inferior parietal cortex during the retention of action information for a short time and their retrieval from long term memory is also in line with the simulation account formulated by Jeannerod (2001). Actions are represented through action simulation and these S states are the same in working and in long term memory.

5.4.2. ACTION REPRESENTATIONS IN WORKING AND LONG TERM MEMORY - THE STS REGION

Furthermore, the left middle temporal and superior temporal gyrus emerged as action related brain structures being activated both during working memory retention and long term memory retrieval. These structures of the lateral temporal cortex have emerged in other studies involving tool and biological motion. Beauchamp et al. (2002, 2003) presented their participants real and point-light video clips of tool motion and human motion. They found that two regions within the lateral temporal cortex need to be distinguished: the middle temporal gyrus extending to the inferior temporal sulcus was especially activated during observation of tool motion whereas the STS was more specifically activated during observation of biological motion (for the

5. EXPERIMENT 1

involvement of STS in biological motion processing also see Allison et al., 2000; Grossman et al., 2000; Pelphrey et al., 2003; Puce et al., 1998). The posterior middle temporal gyrus was also activated during action and function judgment tasks with manipulable objects as compared to function judgment tasks with non-manipulable objects (Kellenbach et al., 2003). This suggests that activations in the left middle and superior temporal gyrus during working memory retention and long term memory retrieval are related to the imagination and reinstatement of tool and biological motion information about actions.

5.4.3. SIZE REPRESENTATIONS IN WORKING AND LONG TERM MEMORY

The activations in the left hemispheric network consisting in inferior parietal cortex, inferior frontal/ventral premotor cortex and middle temporal gyrus are specific for the representation of action information. Different brain regions were commonly activated for size information processing in working and long term memory. In line with previous studies demonstrating the involvement of medial parietal and occipital brain regions during object size related tasks (Ebisch et al., 2007; Kellenbach et al., 2001; Mecklinger et al., 2004; Oliver & Thompson-Schill, 2003; Rossion et al., 2000), a medial cluster in the precuneus was selectively activated by size information. Interestingly, the right inferior parietal cortex adjacent to the intraparietal sulcus also emerged for size information in working and long term memory. Newman, Klatzky, Lederman, and Just (2005) compared brain activity during imagery of material and geometric features about objects. They found the intraparietal sulcus to be selectively engaged if participants were to evaluate objects as to their size or shape. Using tactile stimuli, Roland, O'Sullivan, and Kawashima (1998) also found the intraparietal sulcus to be selectively involved in both a length and a shape discrimination task but not a roughness discrimination task. The involvement of this brain region for the processing of macrogeometric object properties is further supported by others (Bodegård,

5. EXPERIMENT 1

Geyer, Grefkes, Zilles, & Roland, 2001; Jäncke, Kleinschmidt, Mirzazade, Shah, & Freund, 2001). In our study, the contribution of the right intraparietal sulcus area to size processing could be one reason why we did not find activations in the intraparietal sulcus for action processing.

5.4.4. WORKING AND LONG TERM MEMORY REPRESENTATIONS

In this fMRI experiment, action information referred to human actions with manipulable everyday objects. During the working memory task, participants were required to make the prototypical motor interaction with the object available by imagining the action. During retrieval from long term memory, they were instructed to retrieve whether they had performed an action task with an object before or not. If, for a subset of items, action representations are activated during working memory retention, action representations should be more accessible during long term memory retrieval for these items as compared to items with other sources. The long term memory task consisted in a source memory test. If we assume that representations differ in their accessibility corresponding to their level of activation (Cowan, 1999), recently activated domain specific representations should be reactivated more easily relative to domain specific representations that are activated for the first time during the course of the experiment. This would indicate that the same action representations would be involved in both working and long term memory tasks, however, within different processes. Making actions available in working memory requires mental enactment, whereas during long term memory retrieval, it is necessary to reinstate action information from previous episodes.

5. EXPERIMENT 1

Our results show overlapping activations for action retention in working memory and action retrieval from long term memory in the left ventral premotor/inferior frontal and inferior parietal cortex as well as the left middle and superior temporal gyri. For size information, overlapping activations occurred in the precuneus and right inferior parietal lobe. Overlapping activations in domain specific brain regions are in good agreement with an account that posits that both memory tasks share representations of the specific content. This suggests that the same action processing network, partly the mirror neuron system, contributes to retention in working memory and retrieval from long term memory.

5. EXPERIMENT 1

6. EXPERIMENT 2 - MEANS AND ENDS

6.1. RESEARCH QUESTION AND HYPOTHESES

In Experiment 1, we did not differentiate between action features. Action information processing was considered different from size information processing. The results show that domain specific action and perception related regions are selectively activated if the respective information category is to be retained in working memory or retrieved from long term memory. However, actions are not unitary and different action features have been distinguished (Hamilton & Grafton, 2007). In particular, the means and the end of an action have been defined as different levels of action analysis (Bach et al., 2009, 2010; Boronat et al., 2005; Canessa et al., 2008; Hamilton & Grafton, 2008; Hesse et al., 2009; Kellenbach et al., 2003).

Although there is consensus on the dissociability of means and end information about actions, it can be noticed that there is considerably less agreement as to the neural correlates of means and end information processing. On the one hand, the putative human mirror neuron areas in the inferior frontal/ventral premotor cortex and inferior parietal lobe have been linked to the representation of the end of an action (Hamilton & Grafton, 2008). On the other hand, the same regions have been discussed as being especially important for the representation of the means of an action (Bach et al., 2010; Hesse et al., 2009). Some studies have found only the anterior but not the posterior mirror neuron region to be involved in goal processing (Chaminade et al., 2002; Koski et al., 2002), others find the opposite pattern (Grafton & Hamilton, 2007; Hamilton & Grafton, 2006; Tunik et al., 2007), and still others do not find any brain region to be selectively involved in the processing of goals (Boronat et al., 2005; Kellenbach et al., 2003). Furthermore, the understanding of "goal" information is not consistent between these studies meaning either target object, end/consequences or function.

6. EXPERIMENT 2

In Experiment 2, we aimed at identifying neural correlates of working memory retention of means and end information. Motor information about the interaction of an effector and a target object was defined as means information, intended physical consequences of the action were defined as end information. If domain specific regions of perception and action are selectively activated during retention of that information type in working memory (e.g. Slotnick, 2004; Postle, 2006; Umla-Runge et al., 2011), we should find the human mirror neuron regions to be more strongly activated during retention of their preferred action feature. As pointed out, previous results are inconsistent in whether the putative mirror neuron regions preferentially process means or end information. Using an S1-cue-S2 paradigm like in Experiment 1 (see also Bosch et al., 2001; Mecklinger et al., 2004; Umla-Runge et al., 2011), we wanted to delineate the contribution of the putative human mirror neuron regions to selective retention of means and end information. Furthermore, previous studies have suggested an involvement of medial prefrontal regions in the SMA and pre-SMA during action imagery and action planning (Amador & Fried, 2004; Cunnington, et al., 2005, 2006; Malouin et al., 2003). As these regions have been strongly linked with actions' motor programs, we expected them to be preferentially activated during the retention of means information in working memory.

In Experiment 2, the focus of our analysis was on both the retention and the target phase. During target presentation in working memory tasks, it is match enhancement effects which have been typically observed. Single cell recordings in monkeys have revealed category selective brain regions in the prefrontal, inferior temporal and posterior parietal cortex which are more strongly activated for matching stimuli or matching stimulus features as compared to non-matching stimuli or stimulus features (Miller & Desimone, 1994; Miller, Erickson, & Desimone, 1996; Rawley & Constantinidis, 2010; Woloszyn & Sheinberg, 2009). Furthermore, it has been shown that neurons in these brain regions are also selectively activated during the delay period in a delayed match to sample task (Miller, et al., 1996; Woloszyn & Sheinberg, 2009). In humans, research on match enhancement effects has been mainly done within the context of recognition memory focusing on medial temporal

6. EXPERIMENT 2

lobe regions. In an fMRI study, Dudukovic, Preston, Archie, Glover, and Wagner (2011) investigated match enhancement effects in the hippocampus and parahippocampal cortex. They found effects in both regions which were differentially modulated by category specific attention. Whereas attentional modulation was not found for hippocampal match enhancement effects, parahippocampal match enhancement effects were significantly enhanced by attention to scenes. A neural circuit model for the computation of match and non-match judgments has been recently described by Engel and Wang (2011). It includes a passive repetition suppression process and an active match enhancement process. A match-/non-match judgment can be based on either of these processes. Two predictions have been derived from this model. First, match enhancement or repetition suppression effects in specific brain regions should correlate with the similarity of an encoding and target stimulus. Second, brain regions that show match enhancement effects should also show sustained activation during working memory retention.

We hypothesized that, if there are specific brain regions which represent an action's means and its end and they show enhanced activation during working memory retention, these very regions should also show match enhancement effects during target presentation. Furthermore, we manipulated the motor similarity of encoding and target stimuli. Motor similarity of two actions relates to similarity in the manner the actions are executed, i.e. to similarity in their means. If specific brain regions represent the means of an action in memory, it should be these very regions showing a graded match enhancement effect during target presentation depending on the degree of motor similarity of encoding and target stimulus. Consequently, in addition to a focus on selective retention in working memory, Experiment 2 aimed at identifying brain regions which are modulated by the degree of motor similarity of an encoding and a target stimulus. As our design involved a differential attentional focus to means or end information at the time of S2 presentation, it is also possible to investigate whether this modulation by motor similarity is dependent on the attentional focus of the subject, or whether motor similarity effects occur independent of the working memory task.

6. EXPERIMENT 2

6.2.1. PARTICIPANTS

Twenty-four healthy right-handed participants with normal or corrected to normal vision took part in the study. One of them was excluded from the analysis due to considerable movement artifacts. The mean age of the remaining twenty-three participants (7 male, 16 female) was 22.5 years (SD = 2.5 years). All participants gave written informed consent prior to the experiment.

6.2.2. MATERIALS AND EXPERIMENTAL PROCEDURE

6.2.2.1. FMRI SESSION

The experiment was run on a PC controlled by E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). The stimuli were rear projected on a screen located behind the scanner subtending a width of 23° and a height of 18° in visual angle in a resolution of 1024×768 pixels. Participants could see the screen through a mirror system mounted to the head coil. The task was an S1-cue-S2 matching task (working memory test). Video clips of transitive actions subtending a width of 16° and a height of 12° in visual angle were presented both as S1 and S2.

Throughout the test, a white background was utilized. Each trial began with a black fixation cross which was visible for 1500 ms. S1 was then presented centrally for a variable duration (average duration = 2477.5 ms, standard deviation = 549.8 ms, range = 1500 ms – 4000 ms). It was a video clip depicting a transitive action which was presented in a third-person per-

spective (from left, from right, from a position opposite of the observer). Video clips were visual stimuli only and did not contain sound. Each action was performed by one out of five actors (four females, one male). All actions were manual or feet actions. Video clips were centered on the effector(s). Other body parts of the actors or their clothes were not visible. After a blank interval of 500 ms, a visual cue was presented for 750 ms indicating which information of S1 was to be retained during the subsequent retention interval. The letter "M" instructed subjects to retain the means of the presented action in working memory. Means was defined as the dynamic interaction of the effector(s) with the action object. Alternatively, the letter "Z" required participants to retain the end of the action. End was defined as the physical consequences intended with the action. Means and end trials were intermixed and occurred with equal probabilities. After cue offset, a variable retention interval with only a blank screen visible followed with an average duration of 5500 ms (range = 5050-5950 ms). Then, S2 was presented which was another video clip of a transitive action. In each trial, the duration of S1 and S2, the perspective and the actor executing the action were equal. Objects in S1 and S2 were always different, the background could be the same or different. The action depicted in S2 could be the same or different in means and/or in end as compared to the action depicted in S1. During S2 presentation, participants were required to make an end or means match/non-match judgment in the action feature that had been cued before. If the cue had instructed them to retain the means of the action, a correct match judgment would mean that the means used to perform the action were the same in S1 and S2. If the means in the two video clips were different, a non-match judgment would be required. In analogy, if the cue had required participants to retain the action's end, a correct match judgment would mean that actions with the same end had been presented in S1 and S2. Actions with different ends would require a non-match judgment. Participants were instructed to make these judgments during target presentation without pressing a key. After a blank interval of 500 ms, a visual response cue was presented for 2000 ms. During this interval, they were required to press the response key reflecting their decision. The response cue consisted in a red and a green dot, each one subtending a visual angle of about 1°. In half of the trials, the red dot was presented in the

6. EXPERIMENT 2

left and the green dot in the right part of the screen, in the half of the trials the dots were arranged in the opposite manner. Participants were instructed that the green dot was a symbol for a match judgment and the red dot for a non-match judgment. Corresponding to the location of the dot reflecting their judgment, they should either press the left or the right key. By this method, target and response phase were separated in time and it was impossible to prepare the motor response corresponding to one's judgment in advance. This was important in order to ensure that motor preparatory processes and match enhancement effects do not occur at the same time as, for means match enhancement effects, we expected selective activation in motor control regions. Subjects made their response by pressing one out of two fMRI compatible keys held in one hand each with their right and left thumb, respectively. After response cue offset, a new trial began, again starting with a fixation cross. The trial structure is depicted in Figure 8.
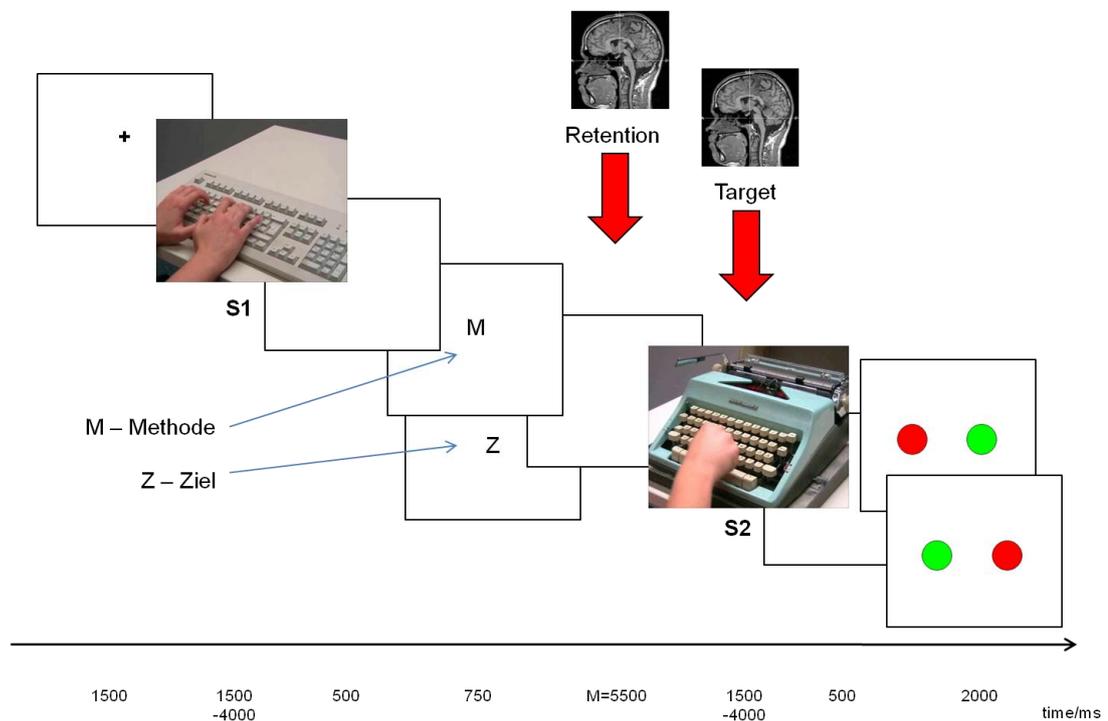
Figure 8. Trial structure of the means and end working memory task of Experiment 2. Each trial involved the presentation of action video clips as S1 and S2 with a duration between 1500 and 4000 ms of which one frame is depicted. Following S1, a cue instructing participants to retain the means of the action (M = Methode = means) or the end of the action (Z = Ziel = end) was presented. The focus of brain activation analysis was on the retention phase and the presentation of the target. The action video clips presented in this example matched in end but not in means. Time is not drawn to scale.

6. EXPERIMENT 2

Motor similarity of S1 and S2 was manipulated. Within one trial, S1 was considered the reference action. For a given S1, there were four different possibilities of S2: S2 could be equal in means and end (M^+E^+), it could be slightly different in means but equal in end (M^-E^+), it could be strongly different in means but equal in end ($M^{--}E^+$), or it could be different in both means and end ($M^{--}E^-$). The four categories of encoding-target relation are illustrated in Figure 9.
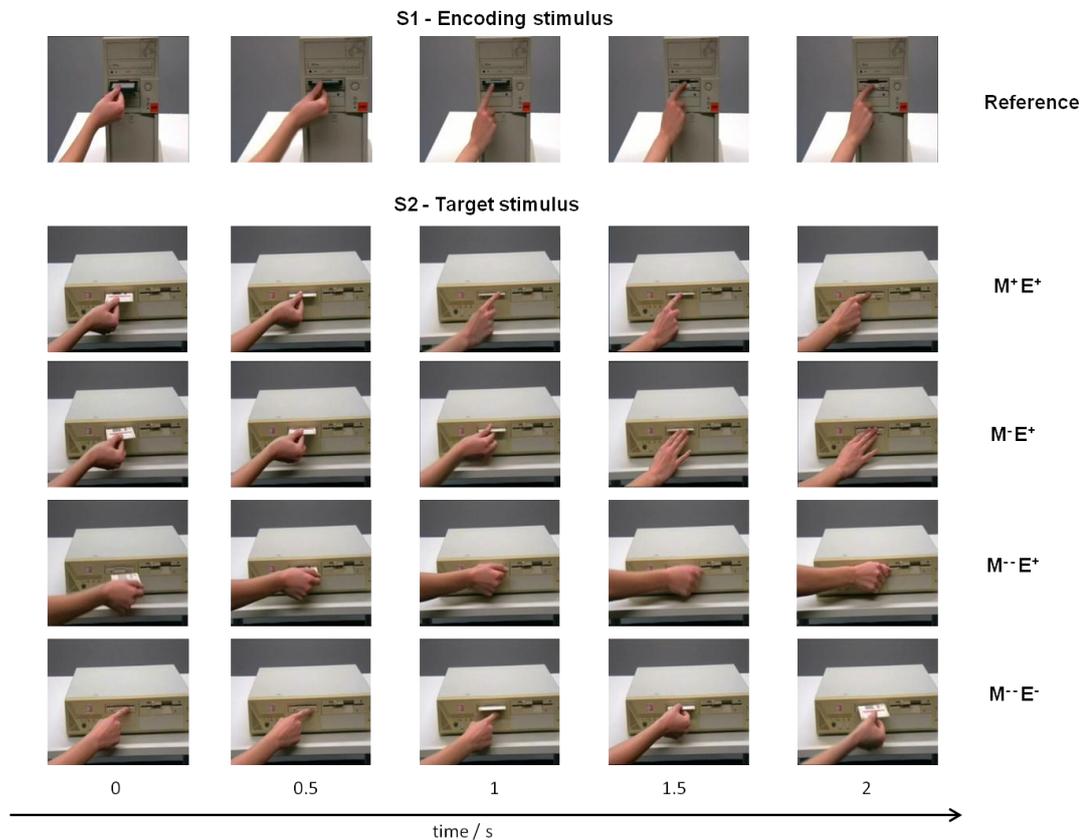
Figure 9. Manipulation of motor similarity of encoding and target stimulus. The upper row illustrates a reference action video clip which was depicted as S1 for half of the participants. Action video clips which were used as S2 for these subjects could be the same in means and end (M^+E^+), slightly different in means and the same in end (M^-E^+), strongly different in means and the same in end ($M^{--}E^+$) or different in means and end ($M^{--}E^-$). For the target action depicted as $M^{--}E^-$ a second video clip existed as it was used as a reference action for the other half of the participants. Further video clips (M^-E^+ and $M^{--}E^+$) existed as target stimuli for this reference action.

Perspective, actor and duration were the same across the eight video clips constructed for each of the 120 item groups. To illustrate this with the example from Figure 9, this item group would involve different manners of

6. EXPERIMENT 2

inserting and removing a floppy disk into/from a drive with eight video clips of 2000 ms in which the same actress performed the actions and her hand always entered the scene from left. The background in S1 and S2 could either be the same or variable. Either it was the same across the eight video clips (as in the example with the floppy disk) or it varied in all pairwise combinations of S1 and S2 that were being used in the experiment.

A means match judgment would be required for M^+E^+ target items, a means non-match judgment would be required for the other categories of target items. An end non-match judgment would be required for M^-E^- items, an end match judgment would be required for the other categories of target items. Within each task, twice as much items were used for the target item categories for which the required response deviated from the required response for the other item categories, i.e. for M^+E^+ items in the means task (match judgments) and for M^-E^- items in the end task (non-match judgments). By this method, we aimed at attenuating the unequal number of required match and non-match responses in each task. The number of trials for each task and target item category is summarized in Table 4.

Table 4. Number of trials and required response for each combination of task and target item category.

	M^+E^+		M^-E^+		M^-E^+		M^-E^-	
Means task	40	match	20	non-match	20	non-match	20	non-match
End task	20	match	20	match	20	match	40	non-match

Participants worked on 200 trials involving different action video clips, half of them means and half of them end working memory trials. They were separated into two blocks of 100 trials each where functional scans were recorded. Video clip usage in the two tasks and across the four conditions of motor similarity was counterbalanced between participants. After the first functional block, a structural scan lasting about ten minutes followed, allowing the participants to take a short break before the second functional block would begin. In each functional block, means and end trials occurred with equal probability. Furthermore, the number of trials in each combination of

6. EXPERIMENT 2

task and item category was half the number indicated in Table 4. Trials were presented in a pseudo-random sequence with all match items from the means task and all non-match items from the end task being presented within the first two thirds of each functional block. This procedure was used for the subjects not to notice that there were more non-match than match required responses in the means task and vice versa in the end task.

Subsequently, participants worked on a block with 32 control trials involving video clips which had not been presented in the experimental blocks. Usage of video clips in the working memory task and the control condition were counterbalanced between participants. A white background was also used throughout the block with control trials. Each trial began with a fixation cross which was presented centrally for 1500 ms. Then a video clip of an object directed action was presented with a variable duration between 1500 and 4000 ms. After a blank interval of 500 ms, a cue was presented centrally for 750 ms. The cue depicted the symbol "0" meaning that participants were not required to retain anything about the previously presented action in working memory. As control trials were summarized into a separate block, the cue was uninformative and it was only included to make control and working memory trials perceptually comparable. After cue offset, a variable blank interval followed with an average duration of 5500 ms (range: 5050-5950 ms). This interval corresponded to the retention interval in the working memory tasks and will be referred to as "retention control". Next, a video clip of the same length as the action video from this trial was presented containing three differently colored disks with a gradient of brightness along disk segments. They were rotating in front of a black background in a clockwise direction. This video clip subtended the same visual angle as the action video clips. After a blank interval of 500 ms, a red exclamation mark subtending a visual angle of about 1° would be presented either in the left or the right part of the screen and participants were required to press the key corresponding to its location. The trial structure of the control condition is depicted in Figure 10.

6. EXPERIMENT 2
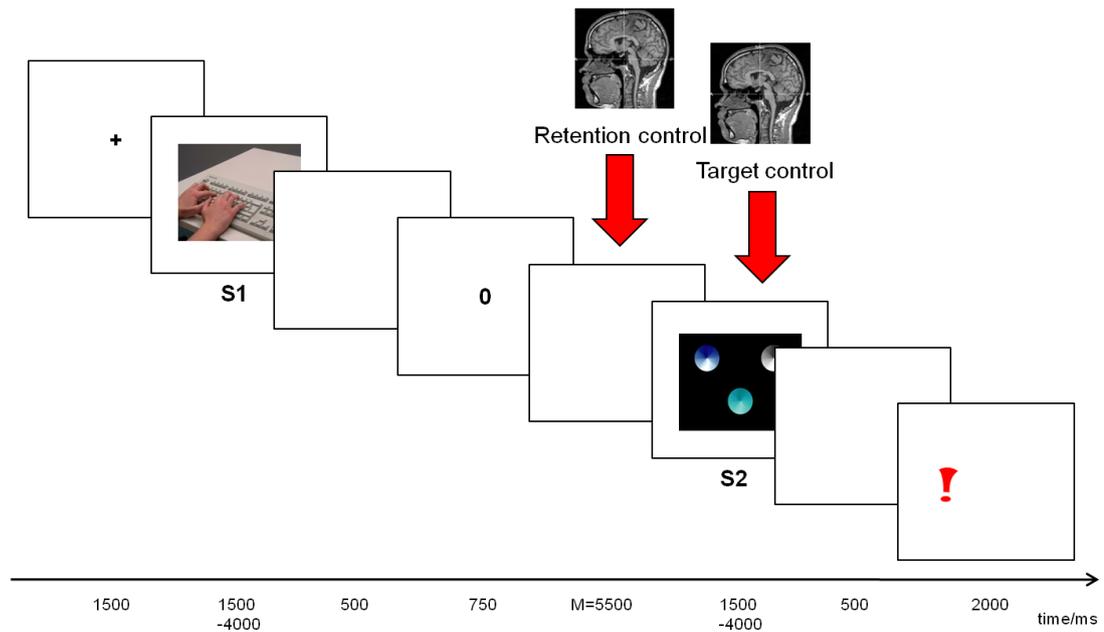
Figure 10. Trial structure of the control task of Experiment 2. Each trial involved the presentation of an action video clip as S1 and of a video clip with rotating disks as S2, both with an equal duration between 1500 and 4000 ms. For illustrative purposes, only one frame is depicted. The focus of brain activation analysis was on the retention and the target phase. Time is not drawn to scale.

Participants were instructed as to the means and end task and worked on twelve practice trials prior to entering the scanner room. After each practice trial, they received feedback about their performance in the individual trial and a summarized feedback about the percentage of correct answers until this trial. If their correctness was below 75%, they were required to repeat the practice phase. For the control trials, participants were instructed while lying in the scanner. They did not have practice trials for this phase.

In total, the fMRI session lasted about two hours for one participant including informing and instructing them, the practice phase, scan preparation and the recording of functional and structural scans.

6. EXPERIMENT 2

Following participation in the fMRI session, participants returned to our lab in the following week. In this session, they were presented with those pairs of action video clips they had been presented with as S1 and S2 in one trial of the means or end working memory task. They were instructed to rate the video clips' motor similarity. 200 pairs of action video clips were rated twice by each participant. During rating, a white background was utilized. A rating trial began with a black fixation cross being presented centrally for 500 ms. After a blank interval of 500 ms, an action video clip from the fMRI session was presented with a variable duration between 1500 and 4000 ms. A blank interval of 1000 ms followed. Then, the action video clip that had been presented in the same trial as the first one during the fMRI session of the individual was presented. Its duration was equal to the duration of the first video clip. Next, a blank interval of 500 ms followed before a sequence of the numbers 1 to 5 with the descriptions "motorisch unähnlich" (= motorically dissimilar) and "motorisch ähnlich" (= motorically similar) at the scale's ends (1 corresponding to dissimilar, 5 corresponding to similar) was presented. During a time interval of maximally 5000 ms, participants were required to press a key between 1 and 5 indicating the degree of motor similarity they attribute to the actions depicted in the two video clips. As soon as they gave their response, the next trial would start. The structure of trials in the rating session is depicted in Figure 11.
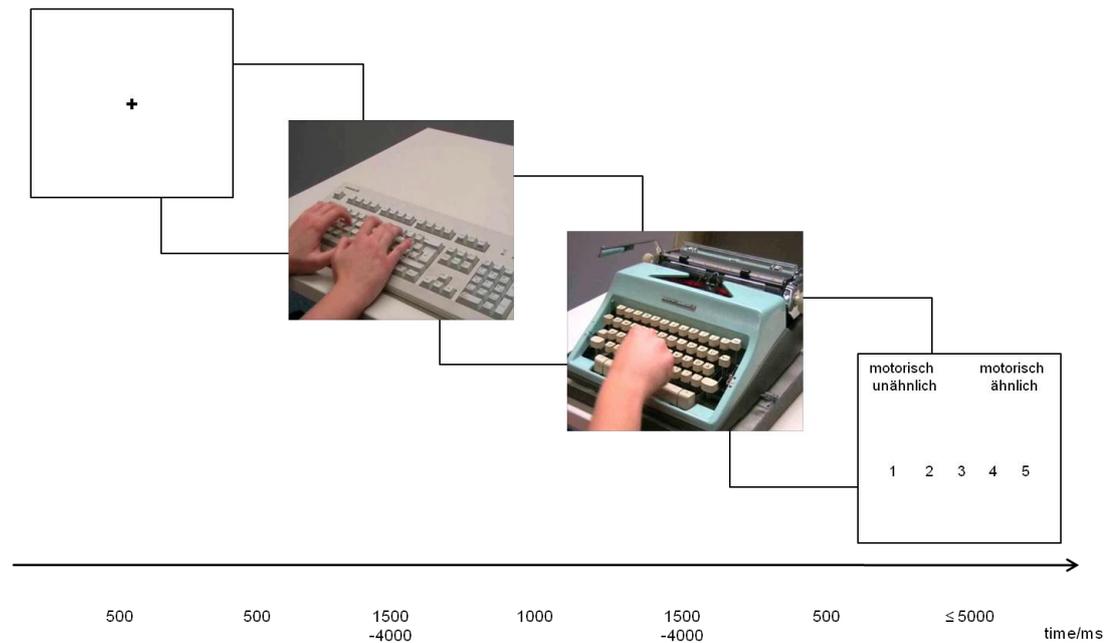
6. EXPERIMENT 2

Figure 11. Trial structure of the rating task of Experiment 2. Each trial involved the presentation of two action video clips with a duration between 1500 and 4000 ms of which one frame is depicted. As soon as participants pressed a key for the motor similarity rating, the next trial started. motorisch unähnlich = motorically dissimilar; motorisch ähnlich = motorically similar.

Each pair of action video clips was rated twice. In one rating, S1 was presented before S2, in the other case, S2 was presented before S1. The rating session was separated into three parts with 133, 133 and 134 trials, respectively. Breaks in between two parts were introduced which could be ended individually by participants pressing the space bar. On average, it took subjects 18 minutes to finish either part of the rating.

6.2.3. FMRI ACQUISITION AND ANALYSIS

Functional imaging parameters were the same as in Experiment 1 (cf. Chapter 5.2.3.). The functional sequences for the two working memory blocks lasted 26 minutes each, the one for the control condition lasted eight minutes. In between the working memory blocks, a structural scan with high-resolution images (voxel size: 1 mm^3) was obtained. The structural scan lasted approximately ten minutes.

6. EXPERIMENT 2

BrainVoyager QX (Brain Innovation, Maastricht, the Netherlands) was used for preprocessing and statistical analysis. The first four scans within a session were discarded because of signal equilibration issues. Preprocessing included slice time correction, 3D motion correction, spatial smoothing with a Gaussian kernel (FWHM: 8 mm) and high-pass filtering with a Fourier basis set at two cycles including linear detrending. Functional data were coregistered with individual high-resolution anatomical images (voxel size: 1 mm^3). Anatomical images were normalized into Talairach space (Talairach & Tournoux, 1988) and the respective normalization parameters were applied to the functional data.

A whole-brain statistical analysis was performed applying a general linear model. For each participant, neural activity was modeled by convolving a stimulus function with a two gamma hemodynamic response function. Both the retention interval and the target presentation phase were modeled. Twelve predictors were applied: means retention, end retention, retention control, M^+E^+ means task, M^+E^+ end task, M^-E^+ means task, M^-E^+ end task, $M^{--}E^+$ means task, $M^{--}E^+$ end task, $M^{--}E^-$ means task, $M^{--}E^-$ end task and target control. Temporal distance between retention and target phase was jittered. Correlations between retention and target phase predictors were checked at the single subject level before proceeding with a random effects group analysis. There were no significant correlations between predictors of interest. Furthermore, six motion predictors (three for translation, three for rotation) and one predictor for mean intensity were added to the analysis as predictors of no interest. Only trials yielding a correct response (hits, correct rejections) were analyzed.

Using a random effects approach, working memory retention of means and end information was contrasted directly and indirectly with the control condition. Furthermore, a 2 (task: means, end) × 4 (motor similarity: M^+E^+, M^-E^+, $M^{--}E^+$, $M^{--}E^-$) repeated measures ANOVA was computed focusing on the target phase. We report activations that at voxel level were significant with $p < .001$ (uncorrected for multiple comparisons, retention phase) or $p < .005$ (uncorrected for multiple comparisons, target phase) at voxel level and $p < .05$ (corrected for multiple comparisons, both retention and target phase) at

6. EXPERIMENT 2

cluster level. Anatomical labeling was performed using the brain atlas of Talairach and Tournoux (1988) and the Talairach Daemon database (Lancaster et al., 2000).

6.3. BEHAVIORAL DATA

6.3.1. RESULTS

Based on the data from the rating phase, mean motor similarity ratings were calculated for the 23 participants which were analyzed and the four categories of items (M^+E^+, M^-E^+, $M^{--}E^+$, $M^{--}E^-$). A repeated measures ANOVA with item category as the independent variable and mean motor similarity ratings as the dependent variable yielded a significant effect of item category on mean motor similarity ratings, $F(3, 66) = 662.77$, $\eta_p^2 = .97$, $p < .01$. As tested with planned comparisons, all item categories were significantly different from each other in their mean motor similarity ratings with M^+E^+ target items being most motorically similar to encoding items followed by M^-E^+, $M^{--}E^+$ and $M^{--}E^-$ items. Based on these findings, I will use the terms "item category" and "motor similarity" interchangeably from now on. Mean motor similarity ratings and standard deviations are summarized in Table 5.

6. EXPERIMENT 2

Table 5. Mean motor similarity ratings and standard deviations of encoding and target stimuli for the item categories M^+E^+, M^-E^+, $M^{--}E^+$ and $M^{--}E^-$.

	Mean motor similarity	Standard deviation
M+ E+	4.68	.17
M- E+	3.43	.38
M- - E+	2.27	.41
M- - E-	1.65	.33

A scale of 1 (= motorically dissimilar) to 5 (= motorically similar) was being used.

For working memory performance, a 2 (task: means, end) × 4 (motor similarity: M^+E^+, M^-E^+, $M^{--}E^+$, $M^{--}E^-$) repeated measures ANOVA was calculated with accuracy as the dependent variable (relative frequency of hits and correct rejections). The analysis yielded a main effect of task, $F(1, 22) = 81.92$, $\eta_p^2 = .79$, $p < .01$. There were significantly more correct answers in the end task (mean accuracy = .89) as compared to the means task (mean accuracy = .78). Furthermore, a main effect of motor similarity emerged, $F(3, 66) = 14.46$, $\eta_p^2 = .4$, $p < .01$. A post-hoc Tukey HSD test revealed that accuracy was significantly lower for M^-E^+ items as compared to the other target item categories with no other significant accuracy differences. Task and motor similarity also interacted significantly, $F(3, 66) = 35.7$, $\eta_p^2 = .62$, $p < .01$. A post-hoc Tukey HSD test showed that for M^+E^+ and M^-E^+ items, accuracy in the end task was significantly higher than in the means task, whereas for $M^{--}E^+$ and $M^{--}E^-$ items, there were no significant accuracy differences between tasks. Within the means task, accuracy was significantly lower for M^-E^+ items as compared to the other item categories. Furthermore, accuracy for M^+E^+ items was significantly lower relative to accuracy for $M^{--}E^-$ items. In the end task, accuracy for M^+E^+ items was significantly higher as compared to the item categories deviating strongly in means ($M^{--}E^+$ and $M^{--}E^-$ items). The interaction effect of task and motor similarity on accuracy is depicted in Figure 12.

6. EXPERIMENT 2
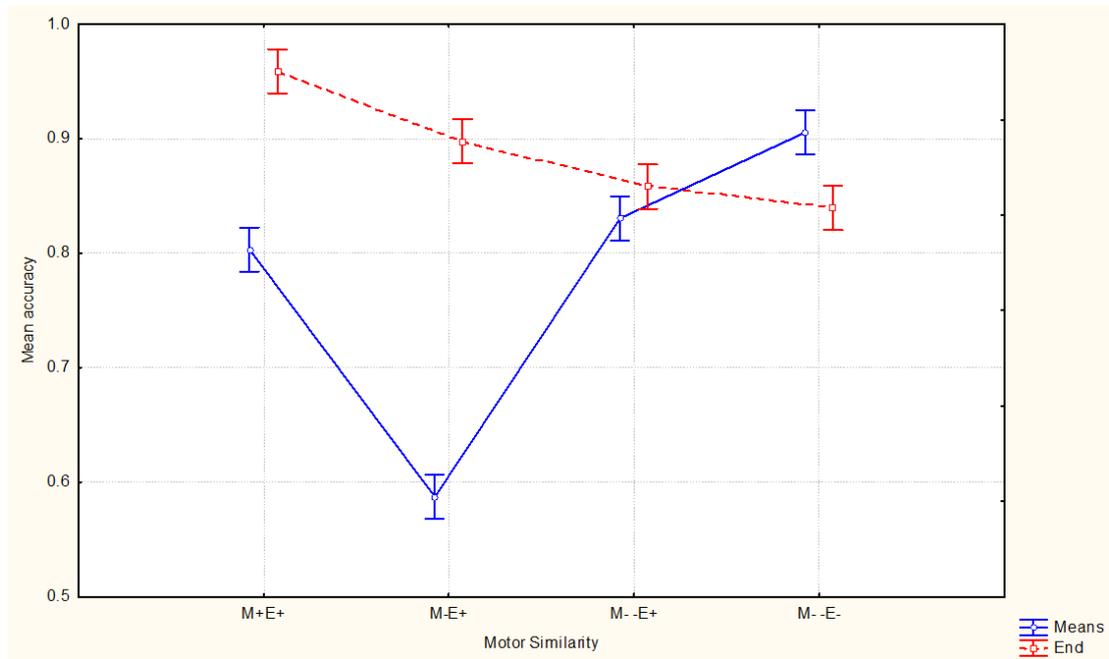
Figure 12. Interaction effect of task and motor similarity on mean accuracy. Bars denote standard errors for repeated measurement designs (Jarmasz & Hollands, 2009).

In a second analysis, accuracy comparisons were restricted to the conditions requiring the same response in the means and end task, i.e. M^+E^+ items requiring a match response and $M^{--}E^-$ items requiring a non-match response. Mean corrected recognition scores PR (PR = Hit Rate - False Alarms Rate) were calculated for the means and end working memory tasks (Snodgrass & Corwin, 1988), respectively. A paired t-test revealed that PR was significantly lower in the means task as compared to the end task, $t(22) = 2.28$, $p < .01$ (end task: mean PR = .80, SD = .11; means task: mean PR = .71, SD = .17).

The mean accuracy in the control task was .98 (SD = .03). Due to the temporal separation of target item presentation and response cue, response times were not analyzed for this experiment.

6. EXPERIMENT 2

The analysis of accuracy data reveals that participants performed significantly worse in the means working memory task as compared to the end working memory task. Across all item categories, the end task was significantly easier for the participants than the means task. However, there was also a significant interaction between task and motor similarity showing that these differences in difficulty between the means and end task were restricted to motorically similar and slightly dissimilar items. If the means of the encoding and target item deviated strongly, participants performed equally well in the means and the end task. This suggests that it was subtle discriminations in means which were especially difficult to make whereas strong deviations in means were readily detected. In comparison, accuracy variance in the end task across the four categories of motor similarity was much smaller. Target items which were the same in means and end ($M^+ E^+$ items) yielded almost perfect accuracy suggesting that identity of irrelevant action features (i.e. identity of means information) helped participants in their end match judgments.

Differences in task difficulty also became evident when the analysis was restricted to PR for the item categories requiring the same judgment in the means and end working memory tasks. $M^+ E^+$ items would require a match decision independent of the type of task. In analogy, $M^{--} E^-$ items would require a non-match decision independent of the type of task. A significant difference in the hit rate for $M^+ E^+$ items between the end and the means task was also reflected in a significant difference in PR.

One explanation for this accuracy pattern could be that end information is necessarily processed whereas means information is optionally processed. Given that accuracy levels were at the same level in the means and end task if the target items deviated strongly in means, this seems not very likely. Alternatively, means information could also be necessarily processed but not at the detailed level that was required in this experiment. That does not essentially mean that detailed means are not processed by our

6. EXPERIMENT 2

cognitive system. Rather it is possible that slight discriminations just do not become behaviorally relevant.

6.4. FMRI DATA - RETENTION PHASE

6.4.1. RESULTS

Contrasting the retention of means and end information in working memory, several domain specific activation clusters were found. Whereas regions selectively activated for means retention were located frontally, end selective regions were observed more posteriorly. There was also a hemispheric difference for the cortical activation clusters with the right hemisphere being more involved with the representation of means and the left hemisphere with the representation of ends in working memory.

If participants were required to retain the means of the observed action for a short time as compared to retention of its end, a bilateral region in the medial and superior frontal gyrus (BA 6, BA 8) corresponding to the pre-SMA was more strongly activated. Furthermore, a region in the right inferior frontal gyrus (BA 45, BA 47) extending into the insula showed enhanced activation for means information. This cluster overlaps with the right-hemispheric activation cluster that emerged as a selective region for action information as compared to size information in working memory (Experiment 1). In addition, a cluster in the right middle frontal gyrus extending into inferior frontal and precentral gyrus (BA 9) and a more anterior cluster in the right middle and superior frontal gyrus (BA 10) showed enhanced activation for the retention of means.

For the retention of end information, the strongest activation was observed in the left anterior middle and inferior temporal gyrus (BA 20, BA 21). Furthermore, the left hippocampus and parahippocampal gyrus (BA 19, BA

6. EXPERIMENT 2

28, BA 35, BA 36) were more strongly activated for the retention of end relative to means information. The cluster in BA 36 extended into the anterior cerebellum. The right caudate nucleus and an adjacent area in the anterior cingulate (BA 24, BA 32, BA 33) also showed enhanced activation for end information. Brain regions which were selective for the retention of means and end information about actions in working memory are characterized in Table 6 and depicted in Figure 13.

6. EXPERIMENT 2

Table 6. Means and end specific brain regions during retention in working memory.

Brain Region	BA	Hemisphere	x	y	z	Cluster size	t score
Means > End							
Inferior frontal gyrus	47	R	32	25	0	55	5.98
Middle frontal gyrus	9	R	38	16	30	42	5.11
Medial frontal gyrus	8	R	2	28	42	67	5.07
Middle frontal gyrus	10	R	29	46	9	72	4.91
End > Means							
Middle tempo-ral gyrus	21	L	-52	-8	-15	39	-7.75
Caudate nu-cleus		R	11	19	12	22	-5.81
Parahippo-campal gyrus	28	L	-22	-20	-9	27	-5.69
Parahippo-campal gyrus	19	L	-37	-47	0	31	-5.56
Parahippo-campal gyrus	36	L	-25	-29	-18	22	-4.89

Significantly activated structures contrasting working memory retention of means and end information in a repeated measurement design. Brain regions were significant with p < .001 uncorrected for multiple comparisons at voxel level and p < .05 corrected for multiple comparisons at cluster level. Displayed are the name of the brain structure, the corresponding Brodmann Area, hemisphere, Talairach coordinates and t-score for the peak voxel within each cluster. BA = Brodmann Area, L = left, R = right. The number of functional voxels (one functional voxel = 27 mm^3) is listed to indicate cluster size.

6. EXPERIMENT 2
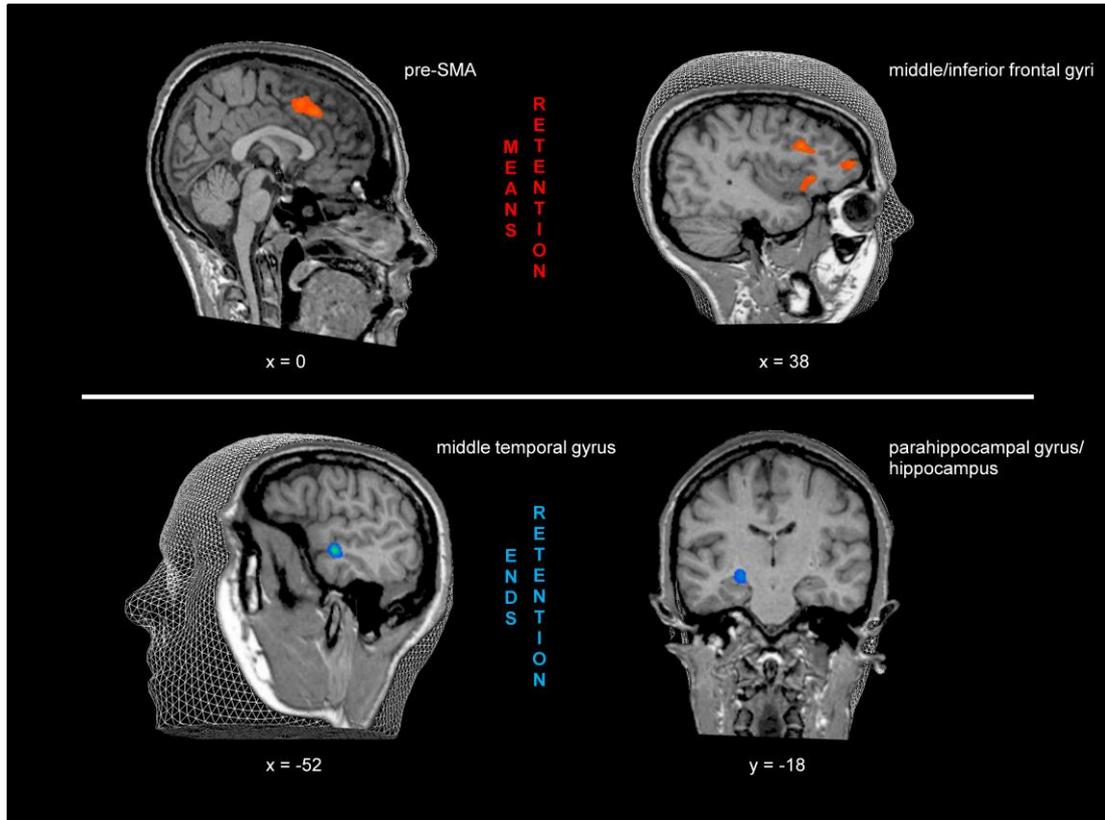
Figure 13. Selective activation clusters for the retention of means and end information in working memory. Brain regions which were more active for means as compared to end working memory retention are displayed in red. Brain regions which were more active for end as compared to means working memory retention are displayed in blue. Clusters were significant with p < .001 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level.

Contrasting each of the working memory tasks with the control condition yielded a very similar activation pattern for the means and end task. Extensive medial activation clusters spreading across primary visual cortex (BA 17, BA 18) to the cerebellum as well as bilateral striatal regions were more activated for both means and end information in working memory as compared to retention control. As the results were not very informative with respect to brain regions which are selectively recruited when means or end information is retained in working memory, they will not be dealt with here in more detail.

6. EXPERIMENT 2

6.4.2. DISCUSSION

One of our aims in Experiment 2 was to elucidate whether working memory retention of means and end information yield selective brain activations. Previous studies have suggested a distinction between means and end information processing about actions (Bach et al., 2009, 2010; Canessa et al., 2008; Chaminade et al., 2002; Hamilton & Grafton, 2008; Hesse et al., 2009; Kellenbach et al., 2003). However, results were inconsistent as to the role of the putative human mirror neuron regions. Furthermore, means and end processing have not been investigated within the context of working memory.

We obtained selective activations for means and end information processing during the retention phase. Whereas the pre-SMA and regions in the right middle and inferior frontal cortex were selectively activated during retention of means information in working memory, it was more posterior cortical regions in the left anterior inferior and middle temporal cortex as well as the parahippocampal cortex (including the hippocampus) which showed enhanced activations for end information in working memory.

The selective involvement of the pre-SMA during working memory for means information is in line with our expectations. The pre-SMA has been consistently found to be involved in motor planning and preparation for action (Cunnington et al., 2005, 2006). Furthermore, it is a structure which shows enhanced activation during sensorimotor integration. In tasks requiring action execution, it is more strongly activated if the action execution is contingent on the presentation of a stimulus (Kurata, Tsuji, Naraki, Seino, & Abe, 2000) in comparison to conditions in which it is independent of sensory input. In addition to its role in planning for action execution, the pre-SMA is engaged in motor imagery tasks (Deiber et al., 1998; Malouin, et al., 2003). This suggests that the region contributes to motor representations which are typically activated at the service of action planning prior to action execution. The involvement of the pre-SMA in working memory retention of means information fits with the interpretation that it is a region involved in representing motor information. A candidate mechanism to retaining the means of a just seen

6. EXPERIMENT 2

action in working memory is motor imagery. Similar regions within the pre-SMA have been found to be active during working memory retention of means as compared to end (Experiment 2) and working memory retention of action as compared to size information (Experiment 1).

Unexpectedly, we did not find the anterior or posterior human mirror neuron regions to be selectively involved during working memory retention of either means or end information suggesting that these brain regions do not preferentially process either action feature. We will get back to the role of the mirror neuron system in action working memory in Chapter 8.2.

However, we found other frontal regions to be selectively involved during working memory retention of means information. One means selective activation cluster was located in the right dorsolateral prefrontal cortex (BA 9). The dorsolateral prefrontal cortex has been shown to be involved during motor imagery (Malouin et al., 2003). In Parkinson's disease patients, i.e. patients who are impaired in voluntary movements, the right dorsolateral prefrontal cortex is significantly less activated during motor imagery as compared to healthy controls (Cunnington et al., 2001). Apart from the role of this region in the representation of motor information, it is also possible that the recruitment of the dorsolateral prefrontal cortex reflects differential working memory demands of the two tasks. Accuracy data suggest that the means working memory task was more demanding as compared to the end working memory task. It has been shown that dorsolateral prefrontal cortex activity increases with increasing working memory load during retention (Rypma, Berger, & D'Esposito, 2002). Furthermore, the dorsolateral prefrontal cortex is specifically recruited if a task requires manipulation and storage rather than storage only in working memory (Owen, 1997; Owen et al., 1999; Petrides, 2000). In our study, differential manipulation requirements of means and end information during retention in working memory are possible. Means information refers to the manner of manipulation of an object and it is a likely strategy that the means of an action is rehearsed using motor imagery. Information about an action's end, in contrast, lacks such a dynamic aspect which could be imaged.

6. EXPERIMENT 2

Another activation cluster specific for the retention of means information was found in the middle frontal gyrus (BA 10). Previously, the anterior middle frontal gyrus, though in the left hemisphere, has been described as being specifically involved during retrieval of perceptually detailed information in comparison to simple old-new judgments (Ranganath, Johnson, & D'Esposito, 2000). The right anterior prefrontal cortex has also been activated in working memory tasks involving monitoring (MacLeod et al., 1998). Concerning action information processing, it has been shown that the right anterior prefrontal cortex shows enhanced activation during motor imagery but not during action observation (Decety et al., 1994). It is unclear whether this region serves a specific function for action information processing or contributes to means working memory relative to end working memory in an action unspecific way. One can speculate whether enhanced anterior prefrontal activation reflects the higher need for detailed processing of previously perceived stimuli in the case of means retention as compared to end retention.

For the retention of means information, another frontal activation cluster was obtained in the right inferior frontal cortex (BA 47). This activation cluster was located in the same region which had been selectively activated during retention of action as compared to size information in working memory (Experiment 1) suggesting that this brain region could also be involved in the representation of motor information about actions. We will get back to the role of this region in Chapter 6.5.2.2.

For the retention of end information, a region in the left inferior and middle temporal gyrus was significantly more activated as compared to means information. This region was located in the anterior part of the inferior and middle temporal gyri in contrast to a more posterior area which has been typically found to be involved in the processing of object directed actions and tool motion in other studies (e.g. Beauchamp et al., 2002; 2003; also Experiment 1). It corresponds to an activation cluster which had been identified to be selective for end judgments in comparison to means judgments in Canessa et al. (2008) and Hesse et al. (2009). Whereas participants were required to judge whether two manipulable objects would be used in the same or different contexts in Canessa et al. (2008), participants decided

6. EXPERIMENT 2

whether a cube had been placed at one spatial location or another in Hesse et al. (2009). In our study, end information was defined as the intended physical consequences of an action. It is conceivable that the anterior temporal activation cluster is related to a search process for the intended physical consequences of the just observed action. The anterior temporal lobe has been found active in social cognition and theory of mind studies requiring the attribution of intentions to others (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Spunt, Satpute, & Lieberman, 2011). In addition, the anterior temporal lobe, especially the anterior inferior temporal gyrus, has been consistently found to show enhanced activation in tasks requiring semantic processing in general (Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Patterson, Nestor, & Rogers, 2007).

We also obtained several clusters in the left parahippocampal cortex including the hippocampus to be significantly activated during retention of end information in working memory. In previous studies, the parahippocampal cortex and the hippocampus have been found to be involved in context processing. Whereas the parahippocampal cortex processes context information independent of the objects in context, the hippocampus is sensitive to the binding of objects and contexts (Diana et al., 2007; Howard, Kumaran, Ólafsdóttir, & Spiers, 2011). It has been a matter of discussion whether it is spatial contextual information which is represented in the parahippocampal cortex (Burgess, Maguire, Spiers, & O'Keefe, 2001; Epstein & Ward, 2010) or associative contextual information in general (Bar, Aminoff, & Ishai, 2008). The parahippocampal cortex has been shown to be involved in contextual information processing both during encoding and retrieval of an episodic memory task (Hayes, Nadel, & Ryan, 2007). During working memory retention, this region was more strongly activated for bound as compared to unbound information suggesting that the parahippocampal cortex contributes to the retention of episodes rather than single features (Luck et al., 2010). It is conceivable that end information about actions also constitutes an integrative information type. In order to retain the end of an action in working memory, the sequentially presented visual features contained in the encoding action video clip need to be integrated into an action

6. EXPERIMENT 2

episode. For instance, the action video clip could contain a right hand approaching a bottle, grasping it on its lid and making a screwing movement in an anti-clockwise direction. If, after observing this video, a participant was asked to retain the end of an action for a later comparison with a test stimulus, he or she needed to integrate the presented information into the episode "the person opened a bottle". Retention of end information would require the association of an object (e.g., a bottle) and a context (e.g., open), though not necessarily in a spatial relationship.

The hippocampus and surrounding regions have also been highly associated with episodic long term memory encoding and retrieval (Schacter & Wagner, 1999; Scoville & Milner, 1957). The involvement of the parahippocampal cortex and the hippocampus in the representation of end information in working memory could also be based on differential reliance on perception and known episodes for means and end information, respectively. Means and end information differed with respect to their direct availability in the previously presented visual stimulus. Working memory retention of an action's means could be achieved by rehearsal of the observed stimulus but working memory retention of an action's end required participants to infer the intended physical consequences from what they had observed in the video clip. This might foster retrieval of similar episodes one has experienced before. In addition, hippocampal activity has also been observed in tasks requiring inference processes (Moses, Brown, Ryan, & McIntosh, 2010).

6. EXPERIMENT 2

6.5.1. RESULTS

In order to find selective means and end match enhancement effects during target presentation, the following contrasts were computed:

(1) M^+E^+ vs. M^-E^+, $M^{--}E^+$, $M^{--}E^-$ (means match enhancement)
(2) M^+E^+, M^-E^+; $M^{--}E^+$ vs. $M^{--}E^-$ (end match enhancement)

Two brain regions emerged to show means match enhancement effects. The right posterior SMA (BA 6) was more strongly activated during presentation of a target that matched the encoding stimulus in means in comparison to a target that deviated in means. Furthermore, a region in the left intraparietal sulcus at the junction with the postcentral sulcus was specifically activated for means matches in comparison to means non-matches. This region corresponds to the left aIPS.

No brain region was found to exhibit end match enhancement effects. The contrasts outlined above were aimed at identifying generalized match enhancement effects, i.e. match enhancement effects independent of the attentional focus of the participants. As it is possible that end match enhancement effects were modulated by the attentional focus, they were calculated separately for the end task and the means task. Significant end match enhancement effects restricted to the end task were found in the left parahippocampal cortex (BA 19, BA 30). This region was close to a parahippocampal region which had been found to be selectively activated during the retention of end relative to means information. No brain regions exhibited a significant end match enhancement effect restricted to the means task. Figure 14 depicts brain regions showing a significant means match enhancement effect which was independent of the subjects' attentional focus

and brain regions exhibi-ting a significant end match enhancement effect which was restricted to trials in which participants focused on ends.
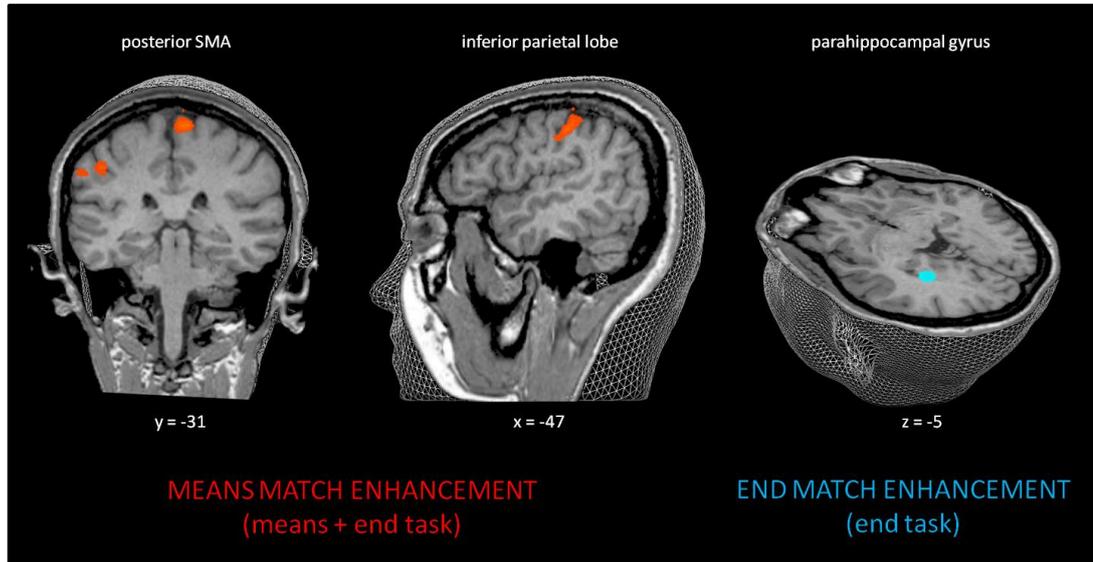
Figure 14. Selective activation clusters showing means or end match enhancement effects during target presentation. Means match enhancement occurred irrespective of attentional focus, end match enhancement occurred in the end task only. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level.

In order to get a clearer picture of the effects of motor similarity between encoding and target actions, a 2 (task: means, end) × 4 (motor similarity: $M^+ E^+$, $M^- E^+$, $M^{--} E^+$, $M^{--} E^-$) repeated measures ANOVA was calculated for the target presentation phase. Peak activation coordinates for regions exhibiting a main effect of task, of motor similarity or a significant interaction effect are summarized in Table 7.

6. EXPERIMENT 2

Table 7. Brain regions yielding significant main effects of task, motor similarity or a significant interaction effect during target presentation.

Brain Region	BA	Hemisphere	x	y	z	Cluster size	F-score
Task Main Effect							
Lingual gyrus	19	R	26	-74	0	18	23.54
Caudate nucleus	-	R	11	7	0	47	22.76
Superior frontal gyrus	8	L	-4	34	51	46	22.53
Globus pallidus	-	L	-10	4	0	25	22.42
Anterior cerebellum	-	R	14	-53	-27	19	21.6
Middle frontal gyrus	8	L	-25	-31	36	27	19.98
Inferior frontal gyrus	47	R	50	16	-6	41	14.68
Motor Similarity Main Effect							
Parahippocampal gyrus	35	R	26	-14	-24	32	10.33
Inferior parietal lobe	40	L	-49	-32	39	69	8.9
Precuneus	7	R	14	-77	45	66	8.36

6. EXPERIMENT 2

Task × Motor Similarity Interaction Effect							
Cerebellum, posterior lobe	-	R	44	-38	-33	28	10.32
Precentral gyrus	6	R	26	-17	57	35	8.96
Superior temporal gyrus[3]	41	L	-46	-26	9	19	7.34
Putamen	-	R	17	4	9	20	6.4

Significantly activated structures in a 2 (task: means, end) × 4 (motor similarity: M^+E^+, M^-E^+, M^-E^+, M^-E^-) repeated measures ANOVA focused on the target presentation phase. Brain regions are listed which exhibited a significant main effect of task, of motor similarity or an interaction effect of the two factors. They were significant with p < .005 uncorrected for multiple comparisons at voxel level and p < .05 corrected for multiple comparisons at cluster level. Displayed are the name of the brain structure, the corresponding Brodmann Area, hemisphere, Talairach coordinates and F-score for the peak voxel within each cluster. BA = Brodmann Area, L = left, R = right. The number of functional voxels (one functional voxel = 27 mm^3) is listed to indicate cluster size.

---

[3] The peak voxel in this region was located in the superior temporal gyrus (BA 41). However, the activation cluster corresponds to the left lateral sulcus cluster described in Frey et al. (2005).

6. EXPERIMENT 2

A main effect of task was observed in several activation clusters. Enhanced activation during presentation of a target in the means task relative to the end task was observed in the right lingual and middle occipital gyrus (BA 18, BA 19). Furthermore, the medial superior frontal cortex (BA 8) extending into the most anterior portion of the pre-SMA (BA 6) was selectively activated during target presentation in the means task relative to the end task. A more lateral and posterior activation cluster in BA 8 emerged which was also more strongly activated for the means task in comparison to the end task. In addition, a selective activation for the presentation of means targets in comparison to end targets was obtained in the right anterior cerebellum.

In contrast, the right inferior frontal cortex (BA 47) showed enhanced activation during target presentation in the end task relative to the means task. This activation cluster corresponds to the region which emerged as being more active for means in relation to end during the retention interval. In addition, the left and right striatum extending to the globus pallidus were significantly more active during end as compared to means trials.

A significant main effect of motor similarity emerged in the left aIPS. This was the same region which had been found to exhibit a significant match enhancement effect for means information. As revealed by a post-hoc Tukey HSD test, activation in this region was highest during presentation of target items which were motorically similar to encoding items (M^+E^+) and decreased with motor similarity: Activation for M^+E^+ items was significantly higher than activation for $M^{--}E^+$ and $M^{--}E^-$ items and activation for M^-E^+ items was significantly higher than activation for $M^{--}E^+$ items. Figure 15 displays the relationship of motor similarity and brain activation in the left aIPS.

6. EXPERIMENT 2
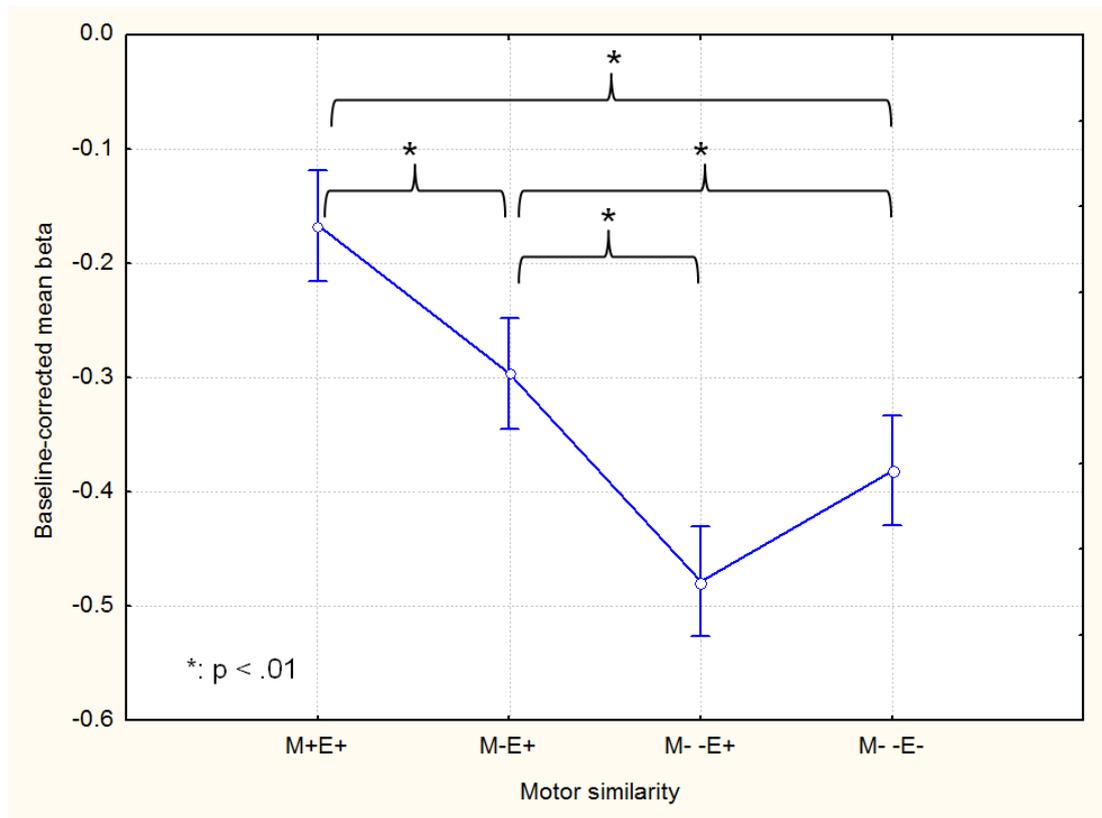
Figure 15. Modulation of brain activity by motor similarity in the left aIPS. Baseline-corrected mean betas and standard errors are depicted for the categories M^+E^+, M^-E^+, $M^{--}E^+$ and $M^{--}E^-$. Significant differences in left aIPS activation as revealed in a post-hoc Tukey HSD test are indicated by asterisks. Bars denote standard errors for repeated measurement designs (Jarmasz & Hollands, 2009).

Another region in which a significant main effect of motor similarity occurred was the right parahippocampal cortex (BA 28, BA 35) extending into the hippocampus and the fusiform gyrus (BA 20). A post-hoc Tukey HSD test revealed that, within this region, target items that deviated highly in means but were the same in ends ($M^{--}E^+$ items) yielded significantly lower activation as compared to both items that deviated slightly in means (M^-E^+ items) and items that were also different in ends ($M^{--}E^-$ items). There were no significant activation differences between other item categories.

The right precuneus (BA 7, BA 19) close to the parieto-occipital sulcus was also significantly modulated by motor similarity. In this region, M^+E^+ and $M^{--}E^+$ items showed significantly higher activation as compared to M^-E^+ and $M^{--}E^-$ items.

6. EXPERIMENT 2

Brain regions showing a significant modulation of activity by motor similarity are depicted in Figure 16.
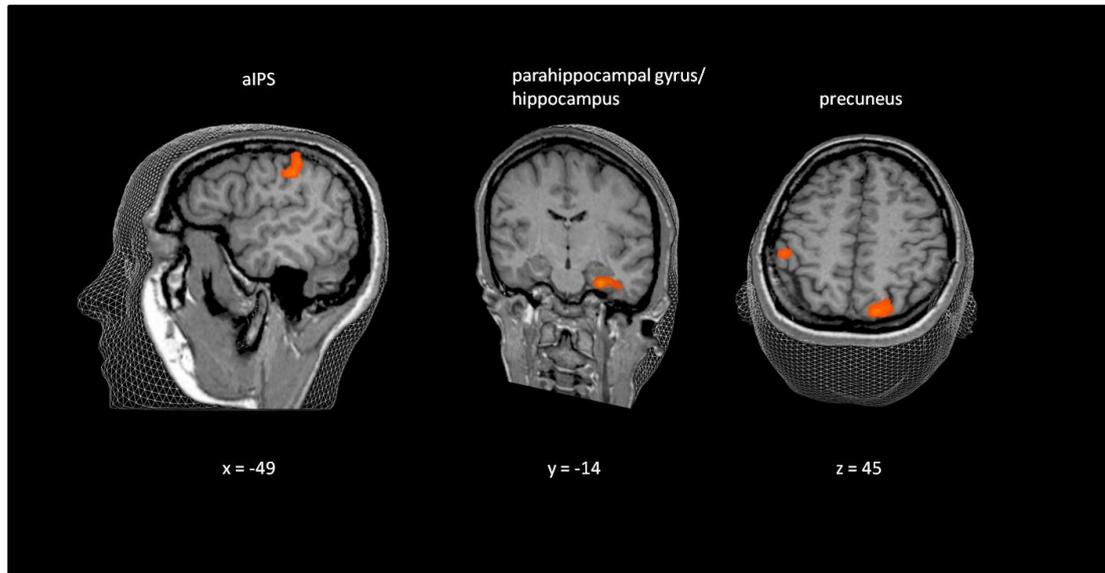
Figure 16. Activation clusters exhibiting a significant main effect of motor similarity during target presentation. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level.

Significant interaction effects of task and motor similarity during target presentation occurred in the right dorsal premotor cortex (BA 4, BA 6), the posterior lobe of the right cerebellum, the right striatum and the left lateral sulcus adjacent to the parietal operculum. The respective regions and base-line-corrected mean betas for the different conditions are depicted in Figure 17.

6. EXPERIMENT 2
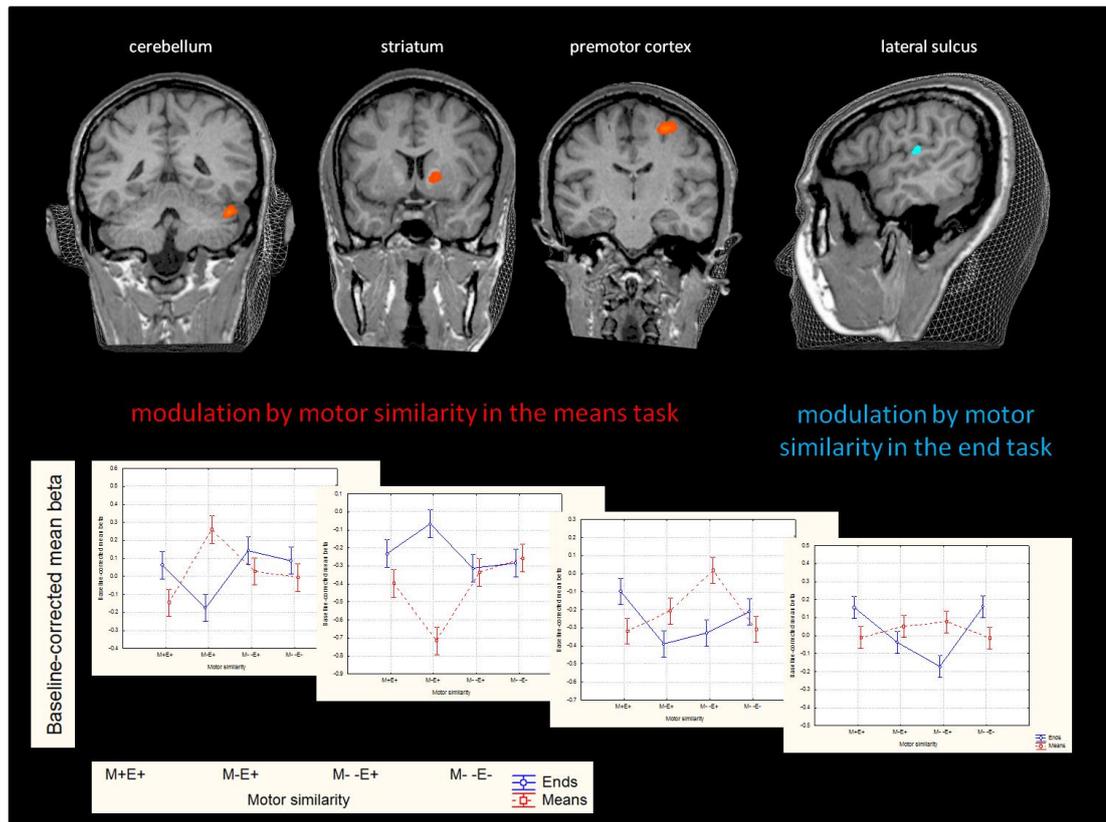
Figure 17. Brain regions exhibiting a significant interaction effect of motor similarity and task during target presentation. As revealed by post-hoc Tukey HSD tests, the right cerebellum, striatum and premotor cortex were significantly modulated by motor similarity in the means task but not in the end task. The left lateral sulcus was significantly modulated by motor similarity in the end task but not in the means task. Clusters were significant with p < .005 (uncorrected for multiple comparisons) at voxel level and p < .05 (corrected for multiple comparisons) at cluster level. Baseline-corrected mean betas and standard errors for repeated measurement designs (Jarmasz & Hollands, 2009) are depicted separately for each condition in each activation cluster.

As revealed by a post-hoc Tukey HSD test, motor similarity modulated activation in the right dorsal premotor cortex in the means task but not in the end task. Within the means task, activation in this region was largest for $M^{--}E^{+}$ items. In this condition, activation in the dorsal premotor cortex was significantly higher as compared to both $M^{+}E^{+}$ and $M^{--}E^{-}$ items. Numerically, activation increased with decreasing motor similarity. This effect did not include target items that additionally differed in end from the encoding stimulus.

A significant interaction effect of task and motor similarity was also observed in the posterior lobe of the right cerebellum and in the right striatum. Both regions were modulated by motor similarity only in the means task, not in the end task. Post-hoc Tukey HSD tests were computed in order to char-

6. EXPERIMENT 2

acterize the effects. The lowest activation in the cerebellum was obtained for target items with the same means as compared to encoding items ($M^+ E^+$ items). The activation for these items was significantly lower as compared to target items differing slightly in means ($M^- E^+$ items). Items differing in means ($M^- E^+$, $M^{- -} E^+$ and $M^{- -} E^-$ items) did not yield significantly different activation levels in the right cerebellum. In the striatum, there was also a modulation of activity by motor similarity in the means task only, however, in a different way. Striatal activation was significantly higher for target items deviating strongly in means ($M^{- -} E^+$ and $M^{- -} E^-$ items) as compared to items deviating slightly in means ($M^- E^+$ items). Activation between items deviating slightly in means ($M^- E^+$) and items with the same means ($M^+ E^+$) was not significantly different.

A significant interaction of task and motor similarity also occurred in the left lateral sulcus. As revealed by a post-hoc Tukey HSD test, activation in this region was modulated by motor similarity only in the end task but not the means task. Activation during presentation of target items in the extreme categories ($M^+ E^+$ and $M^{- -} E^-$ items) was significantly higher as compared to target items deviating strongly in means and being the same in ends ($M^{- -} E^+$ items). $M^{- -} E^+$ items differed not significantly in their activation from $M^- E^+$ items.

6.5.2. DISCUSSION

Apart from selective working memory retention which has been discussed in Chapter 6.4.2., Experiment 2 focused on selective means and end match enhancement effects and on the influence of motor similarity of an encoding and a target stimulus on brain activation levels during target presentation.

Domain specific match enhancement effects have been described in single cell recording studies with monkeys (Miller & Desimone, 1994; Miller et

6. EXPERIMENT 2

al., 1996) and these effects have been observed in the same neurons exhibiting sustained activity during working memory retention (Miller, et al., 1996; Woloszyn & Sheinberg, 2009). A recent computational model on possible mechanisms that allow us to make match and non-match decisions (Engel & Wang, 2011) predicts match enhancement effects to be correlated with the similarity of an encoding and a target stimulus. Consequentially, we expected sustained activation for the retention of means and end information and domain specific match enhancement effects for these action features to occur in the same brain regions. Furthermore, motor similarity of encoding and target stimulus should promote a graded match enhancement effect in brain regions representing the means of an action.

6.5.2.1. MEANS AND END MATCH ENHANCEMENT EFFECTS

Match enhancement effects have been found for means and end information in specific brain regions during target presentation. Means match enhancement effects were independent of the attentional focus of the participants, i.e. this effect emerged when both means and end trials were being considered. When a target item was presented which was performed by the same means as during the encoding phase, activation in medial posterior BA 6 and the left aIPS was significantly enhanced as compared to the presentation of a target which did not match the encoding stimulus in means.

Medial posterior BA 6 corresponds to the most posterior portion of the SMA. As has been discussed previously, the SMA is a brain region which is highly involved in motor planning and motor imagery (Amador & Fried, 2004; Cunnington et al., 2006). If the SMA represents motor information about actions in working memory, it is conceivable that it exhibits enhanced activation during presentation of a target stimulus which is motorically very similar to a previously presented encoding stimulus as compared to a motorically very dissimilar target stimulus. However, if we compare the location of the region within BA 6 exhibiting a means match enhancement effect and the location of

6. EXPERIMENT 2

the region within BA 6 being selectively activated during the retention of means information, we can see that they are not the same. Whereas pre-SMA was selectively activated during retention, it was posterior SMA which showed selective match enhancement effects during target presentation. These activation clusters did not overlap, also when using more liberal thresholds. How could that relate to what we already know about SMA and pre-SMA function? During means retention, it was required to imagine the speci-fic manner of interaction between an effector and an object. In this in-terval, no visual input was provided. In contrast, during target presentation, participants observed an action video clip and were required to make a deci-sion as to the identity or difference of the target action's means or end with regard to the encoding stimulus. Though both SMA and pre-SMA have been shown to be activated during preparation of action execution, it has been shown that the activation in the pre-SMA precedes activation in the SMA (Cunnington et al., 2005, 2006). Whereas activation in the pre-SMA is high-est prior to movement initiation, SMA activation peaks during action execu-tion. In our study, participants were neither required to execute actions during retention nor during target presentation. Motor imagery requirements were probably higher during the retention phase than during target presentation. It is possible that an anterior-posterior gradient in the medial BA 6, similar to the one that has been described during action planning and execution, also exists during processing of internally generated motor images and externally presented observed actions.

Another activation cluster exhibiting a significant match enhancement effect for means information was the left aIPS, a region which is part of the posterior putative human mirror neuron region. As the results from the re-peated measures ANOVA show, the left aIPS means match enhancement effect did not occur in an all-or-nothing fashion but was modulated by the de-gree of motor similarity between encoding and target stimulus. There was a significant main effect of motor similarity in the left aIPS but no interaction with the type of task. The left aIPS responded to motor similarity independent of the attentional focus during target presentation, i.e. independent of whe-ther the means of an action was relevant or irrelevant to the task. aIPS has

6. EXPERIMENT 2

been described as an integral part of a grasping circuit with significantly stronger activations in this region during grasping as compared to reaching movements (Binkofski et al., 1998; Frey et al., 2005). In addition, it has been demonstrated that the region shows suppressed activation if either the goal object of an action or the action's physical consequences are repeated (Hamilton & Grafton, 2006, 2008). These findings as to the role of the aIPS in the representation of action information are difficult to reconcile. Grasping characteristics, goal objects and physical consequences (ends) refer to different action features and it has been suggested that they are hierarchically organized (Grafton & Hamilton, 2007). The results of previous neurocognitive studies on the representation of means and end information are contradictory as to the role of the posterior putative human mirror neuron region. It has been argued by some that the region preferentially represents the end or the goal of an action (Hamilton & Grafton, 2006, 2008; Tunik et al., 2007). Others have found evidence that the inferior parietal lobe is more strongly activated during means processing as compared to end processing (Boronat et al., 2005; Hesse et al., 2009; Kellenbach et al., 2003). The observation of a graded match enhancement effect which is sensitive to the motor similarity of the target and encoding actions provides evidence that, first, the left aIPS is a region which is memory relevant and, second, it is a region which represents the detailed interaction of an effector with an object, i.e. an action's means. Interestingly, the aIPS exhibited this selectivity only during target presentation and was not selectively activated during working memory retention. This suggest that it is rather prefrontal regions together with the pre-SMA which are involved in motor simulation for the purpose of working memory retention in the absence of external input but that the aIPS is additionally recruited if sensory input requires a motor evaluation.

Whereas means match enhancement effects could be detected which were independent of the attentional focus, this was not the case for end match enhancement effects. End match enhancement effects were restricted to trials with an attentional focus on end information. The left parahippocampal cortex showed enhanced activation for target actions matching encoding actions in ends in comparison to target actions with dif-

6. EXPERIMENT 2

ferent ends. This region was adjacent to a parahippocampal cluster that had been selectively activated during retention of end information in working memory, and using more liberal thresholds, the retention and target phase clusters overlapped partly. A possible role of the parahippocampal cortex during working memory for end information is the binding of action goal objects to physical effects and has been discussed in Chapter 6.4.2. The activation overlap suggests that end specific brain regions that show sustained activation during the retention phase are also recruited during memory based end judgments about actions.

Means and end match enhancement effects were differentially modulated by attention. Whereas means match enhancement effects occurred independent of attention, end match enhancement effects could be observed only when participants focused on end information during target presentation. This suggests that, during observation of an action, means information is automatically processed independent of the task. It is important to acknowledge that means information and end information are action features which differ in their observability. Being presented with an action video clip, the means of the depicted action can be readily observed from the visual input. End information, in contrast, cannot be observed like means information. Rather, it needs to be inferred from visual input and this inference might require attentional control. One might want to conclude that, as means information is already provided by the visual stimulus without the need for inference, the means task would be easier to perform as compared to the end task. If there are brain regions which are automatically modulated by matching or non-matching means, this could map directly upon behavior. However, this is not the case. Accuracy was significantly higher in the end task as compared to the means task. This suggests that neural match enhancement effects are not necessarily reflected in our behavioral decisions.

6. EXPERIMENT 2

Whereas some brain areas were modulated by motor similarity independent of the type of task, in others, modulation by motor similarity was dependent on whether participants were engaged in the means or the end working memory task. We will discuss main effects of motor similarity (i.e. task independent effects) and interaction effects of motor similarity and task (i.e. task dependent effects) in succession.

Motor similarity modulated brain activity independent of working memory task in the left aIPS. The activation in this region was positively correlated to the degree of motor similarity between encoding and target stimulus and has been discussed in detail in Chapter 6.5.2.1.

In addition, motor similarity modulated activity in the right parahippocampal cortex and the right precuneus independent of the type of working memory task. These effects were more complex as they were not linearly correlated with the degree of motor similarity. Therefore, finding possible explanations for these motor similarity effects is not as straightforward. The activation cluster in the right parahippocampal cortex extended to the hippocampus. In this region, $M^{-}{}^{-}E^{+}$ target items yielded significantly lower activation as compared to the presentation of other target items. As $M^{-}{}^{-}E^{+}$ items were on the third position out of four categories of motor similarity, this cannot be a simple reflection of motor similarity influencing activation levels. Why should activation be both higher for items which have a higher degree of motor similarity ($M^{+}E^{+}$, $M^{-}E^{+}$) and for items which have a lesser degree of motor similarity ($M^{-}{}^{-}E^{-}$)? The hippocampus and surrounding areas have been found to be involved in contextual processing and binding (Diana et al., 2007). Could the differential involvement of the hippocampus and adjacent brain regions be related to the ease of relating a target item contextually to an encoding item? $M^{+}E^{+}$ and $M^{-}E^{+}$ target items share many features with encoding items. They depict an action performed with the same or an only slightly changed means as before in order to achieve the same end. Therefore, it should be relatively easy to recognize how $M^{+}E^{+}$ and $M^{-}E^{+}$ items re-

6. EXPERIMENT 2

late to the previously observed action. $M^-\ E^-$ items were different from the previously observed actions both in means and end. What was common between an $M^-\ E^-$ target item and the encoding item was the type of object involved. For example, a watering can could have been used to water plants in the encoding action video clip but in the target action video clip, it could have been filled with water from a tap. Relating an $M^-\ E^-$ target item to an encoding item could have been accomplished by the similarity of objects being involved. In addition, some $M^-\ E^-$ target items involved an "opposite end" as compared to the encoding item, e.g. inserting a floppy disk into a drive vs. removing it from a drive (cf. Figure 9). In contrast, $M^-\ E^+$ items depicted an action which was very different in means but the same in end as a previous item. Very different means could also involve very different manipulation tools, e.g. very different types of nutcracker in order to crack a nut. Following this reasoning, it could have been especially difficult to relate an $M^-\ E^+$ target item to an encoding item and this difficulty could have been reflected in lower activity in the hippocampus and surrounding areas during presentation of items from this category.

The third activation cluster being modulated by motor similarity in a task independent fashion was located in the right precuneus. In this region, activation was significantly higher during presentation of both $M^+\ E^+$ and M^- E^+ items as compared to $M^-\ E^+$ and $M^-\ E^-$ items. An activation pattern where motorically similar and motorically very dissimilar items with the same end yield higher activation as compared to motorically slightly dissimilar items and motorically very dissimilar items with a different end is probably not due to motor similarity. It is conceivable that this effect is either an artifact or based on other characteristics of the categories of target items.

Other brain regions were identified which showed task dependent effects of motor similarity during presentation of the target items. Motor similarity effects were restricted to the means task in three out of four clusters which showed task dependent effects.

The right dorsal premotor cortex, striatum and cerebellum were modulated by motor similarity only in the means working memory task. Though

6. EXPERIMENT 2

these regions were sensitive to motor similarity, this was not reflected in a graded match enhancement effect. A graded match enhancement effect for the relevant information would be reflected in a pattern with the strongest activation for the motorically most similar target items (M^+E^+ items) and the least activation for the motorically least similar items ($M^{--}E^-$ items). The regions exhibiting significant interaction effects of task and motor similarity yielded more complex activation patterns.

The right dorsal premotor cortex was more strongly activated for motor dissimilar items as compared to similar items. This is a pattern corresponding to repetition suppression effects rather than match enhancement effects. Both enhancement or repetition suppression have been discussed as processes contributing to the computation of match/non-match decisions and different cell populations respond in one or the other way (Duncan, Curtis, & Davachi, 2009; Engel & Wang, 2011). Motorically dissimilar items (M^-E^+ and $M^{--}E^+$ items) yielded higher activations than motorically similar items (M^+E^+ items). However, the activation level of motorically very dissimilar target items that also differed in ends ($M^{--}E^-$ items) deviates from this general pattern. Activation during presentation of $M^{--}E^-$ items was not significantly different from activation during presentation of motorically similar items (M^+E^+). The interaction effect suggests that the dorsal premotor cortex is engaged in match-/non-match computation for means information only if means information is relevant. One possible interpretation for the low activity during presentation of $M^{--}E^-$ items is that the detection of a deviating end occurred prior to means processing in the dorsal premotor cortex. In Experiment 2, detection of a deviating end implied that it was not necessary to further process means information. An action with a deviating end would always be deviating in means, too. Consequentially, it is possible the dorsal premotor cortex is involved in the detection of deviating means but does engage in this process only if it is task relevant. Alternatively, one can speculate whether the activation pattern in the premotor cortex could reflect the experience of conflict between means and end information. The lowest premotor activation occurred if relevant (means) and irrelevant (end) action features suggested the same response. For M^+E^+ items, both means and end information sug-

6. EXPERIMENT 2

gested a match response, for $M^{--}E^-$ items, both means and end information suggested a non-match response. If the irrelevant information (end) suggested a match response but the relevant information (means) required participants to give a non-match response, the highest activation levels were obtained in the dorsal premotor cortex. This could reflect processing of irrelevant end information in a motor planning region yielding higher responses in conflict situations. However, given that the dorsal premotor cortex has been found to be selectively involved in motor information processing as compared to function processing in other studies (Bach et al., 2010; Canessa et al., 2008), it is more likely that this region is involved in means match/non-match computations in appropriate situations.

The right cerebellum and the right striatum also showed enhanced activation during target presentation when the target was motorically dissimilar to the encoding stimulus as compared to motorically similar targets. However, there are also differences in the two structures' interaction effects. The cerebellum showed an activation pattern where items which showed a high degree of motor similarity (M^+E^+ items) yielded the lowest activation and all other items (M^-E^+, $M^{--}E^+$ and $M^{--}E^-$ items) came with a higher activation. In the striatum, the lowest activation was observed for items which were motorically highly similar or slightly dissimilar (M^+E^+ and M^-E^+ items) and higher activations were obtained for strongly dissimilar items ($M^{--}E^+$, $M^{--}E^-$). This suggests differential sensitivity to the motor similarity modulation in the right striatum and cerebellum with the cerebellum being more sensitive to slight motor variations in comparison to the striatum. Both the cerebellum and the basal ganglia have been discussed as brain structures involved in action information processing. There are projections from both regions to the SMA and pre-SMA (Akkal, Dum, & Strick, 2007). In motor learning, a cortico-striatal and cortico-cerebellar network have been distinguished (Doyon, Penhune, & Ungerleider, 2003). The motor functions of the cerebellum and striatum are not restricted to action execution. The striatum has been found to be involved in motor imagery and preparation for action (Lacourse, Orr, Cramer, & Cohen, 2005; Watanabe & Munoz, 2010), the cerebellum has been discussed as part of an extended action observation network (Calvo-

6. EXPERIMENT 2

Merino et al., 2006). Both regions have been described as substructures of the motor system involved in motor simulation during S-states (Jeannerod, 2001). It is interesting that both the striatum and the cerebellum exhibit motor similarity effects only when participants were engaged in the means task. This suggests that they are involved in means information processing only if means information is in the focus of attention. Whereas the aIPS has been found to be differentially activated according to the degree of motor similarity independent of the participants' attentional focus, graded repetition suppression effects in the cerebellum and striatum occur only if participants attend to motor information. This questions the characterization of repetition suppression effects being more automatic and match enhancement effects being more driven by attention (Engel & Wang, 2011).

Surprisingly, one brain region emerged which was significantly modulated by motor similarity only in the end task, i.e. when motor information was irrelevant to solve the task. This region was located in the left lateral sulcus at the border of the parietal operculum. This region has been described by Frey et al. (2005) to be a structure which, along with the left aIPS, is selectively activated during a grasping task as compared to a pointing task. In the means working memory task, the left lateral sulcus showed comparable activation over all item categories. However, if participants focused on the end of an action, this region showed a higher activation if both the relevant (end) and irrelevant (means) information category suggested the same response (M^+E^+ and $M^{--}E^-$ items). The activation was lower for M^-E^+ and $M^{--}E^+$ items, i.e. items requiring a match response in the ends task but being motorically dissimilar. It is possible that the left lateral sulcus is a region where means and end information are integrated in order to distinguish between actions. If both means and end information suggest that the present action is the same or different to an action one has encountered previously, the region responds with a higher signal as compared to a conflict situation in which different action features suggest different solutions. Note that this pattern is a mirror image of what we have observed in the means task in the right dorsal premotor cortex. If we consider the accuracy data of the participants, we can see that they were better to judge the ends of the encoding

6. EXPERIMENT 2

and target items correctly if these items were motorically similar ($M^+ E^+$ and $M^- E^+$) as compared to motorically dissimilar items ($M^{--} E^+$, $M^{--} E^-$). Although this accuracy pattern does not parallel the activation levels in the lateral sulcus, it shows that, being required to judge an action's end, they were sensitive to the irrelevant means information.

We will not elaborate on main effects of task during target presentation, with one exception. Both during working memory retention of means information in Experiment 2 and during retention of action information in Experiment 1, a right ventrolateral prefrontal region was found to be activated, suggesting that this region could be selectively involved in motor information processing. However, we found the same region to be selectively activated during target presentation if the attentional focus was on end information rather than means information. It is difficult to reconcile how the same region showing means selective effects during retention could be modulated by attentional focus in the target phase in the opposite direction. If the region represents motor information and selective attention is focused on this very information during target presentation, we should find enhanced activation for a focus on means relative to a focus on end. Therefore, it is likely that the activation in this brain region rather corresponds to an unspecific cognitive process rather than being involved in the representation of means information.

6.6. CONCLUSION

In Experiment 2, brain regions have been identified which are selectively activated during the retention of means and end information in working memory. Whereas the pre-SMA is selectively recruited during retention of means information, the left parahippocampal cortex selectively holds end information active for a short time. Selective means and end match enhancement effects have been shown in regions which are not identical but close to the brain regions which are selectively activated during retention.

6. EXPERIMENT 2

Means match enhancement effects have occurred independent of attentional focus, whereas end match enhancement effects have been observed only if participants were involved in an end match/non-match task. The left aIPS has been identified as an important memory relevant structure which is sensitive to the degree of motor similarity between encoding and target stimulus.

It can be concluded that means and end representations need to be distinguished in working memory. Whereas the putative anterior mirror neuron region was not selectively involved in working memory for means or end information, the left aIPS (part of the putative posterior human mirror neuron region) is a structure that is highly sensitive to the exact manner of action execution.

6. EXPERIMENT 2

7. EXPERIMENT 3 - ACTION FAMILIARITY[4]

7.1. RESEARCH QUESTION AND HYPOTHESES

In Experiment 2, we instructed participants to either retain means or end information about a transitive action in working memory. We found that being instructed to retain one or the other, different brain regions are active during retention. Furthermore, we found motor similarity of an encoding and a target stimulus to selectively modulate brain activity in some regions during target presentation. Participants were explicitly instructed to retain means or end information in this experiment. However, which aspect of an action do people represent in memory if they are not explicitly instructed to focus on a specific aspect of an action? Do they represent both the means and the end? Alternatively, do they prefer one information type above the other? Does it depend on the action which information type is represented in memory? In Experiment 3, we aimed at elucidating the circumstances under which means and end information about actions is represented.

It has been found that action familiarity influences different aspects of information processing like perception, imitation, memory performance and prediction. Furthermore, processing of familiar actions and tools seems to involve regions of the putative human mirror neuron system more than processing of unfamiliar actions and tools. The results of Wang et al. (in press) and Zalla et al. (2010) provide a first hint that action familiarity might influence the analysis of ends and/or means about actions in children. For familiar actions, healthy children were more accurate in predicting the action's outcome as compared to unfamiliar actions (Zalla et al., 2010). This suggests

---

[4] This chapter corresponds partly to a manuscript with the title „An Action Video Clip Database Rated for Familiarity in China and Germany" of which I am the first author and which had been submitted to Behavioral Research Methods for publication at the time of writing my doctoral thesis. The paper is currently in press.

that either end information is represented only for familiar actions but not for unfamiliar actions or that end information can be easier accessed for familiar relative to unfamiliar actions. Wang et al. (in press) categorized children's imitation errors into end or means error types. They found that children had more difficulty imitating with the correct end as compared to the correct means for familiar actions but there was no such difference for unfamiliar actions. This error pattern is at odds with the predictions of the dual route model of imitation by Rumiati and Tessari (2002). According to this model, imitation of meaningful actions can be accomplished either via an indirect semantic route or via a direct visual analysis route. Imitation of meaningless actions, in contrast, can only rely on the direct route. Consequentially, means errors should be more prevalent with familiar actions and end errors should be more prevalent with unfamiliar actions. Zalla's results on outcome prediction also suggest that ends are better represented for familiar actions as compared to unfamiliar actions.

Action familiarity might affect means and end information processing about actions differently. If we retain action information in memory, do we find a modulation of the represented action features by action familiarity? We hypothesized that the familiarity of an action would influence the type of information which is represented in memory. Familiar actions should be preferentially represented in terms of their ends, unfamiliar actions in terms of their means.

In Experiment 3, we aimed at investigating this question within a cross-cultural recognition memory paradigm setting. As action familiarity for a given sample is tied to specific action items which can easily lead to item effects being interpreted as familiarity effects, we took advantage of the observation that cultures differ partly in their action repertoire. Imagine a regular food intake situation in China and in Germany. Whereas as ordinary Chinese would use chopsticks in order to transport long noodles from a plate into their mouth, this would be a rather unusual manner for Germans. In contrast, ordinary Germans would wind the noodles up using fork and spoon, an action which would be exceptional for Chinese.

7. EXPERIMENT 3

The study involved action video clips which differed in familiarity both within culture and across cultures. With an extensive rating procedure, we identified sixty actions each which were familiar to both Chinese and Germans, familiar to Chinese and unfamiliar to Germans, familiar to Germans and unfamiliar to Chinese and unfamiliar to both Chinese and Germans.

In an incidental encoding phase, 120 familiar and 120 unfamiliar action video clips were presented to a sample of Chinese and a sample of German participants and they were required to respond to questions. A recognition test phase followed in which other target action video clips were presented. These video clips were never identical to the ones they had seen during the encoding phase. They always involved different object exemplars. Apart from that, the following possible relationships with the actions they had seen previously were possible and presented in an intermixed fashion: actions with the same means and ends ($M^+ E^+$), actions with different means and the same ends ($M^- E^+$) or actions with different means and different ends ($M^- E^-$). Half of the participants from each culture were required to make an old-/new-judgment as to the end and half of the participants were required to make an old-/new-judgment as to the means of the target action. Recognition accuracy was taken as the dependent variable.

We expected action familiarity to influence whether subjects represent the means or the end of the encoding item in memory. Consequently, target items with different means but the same ends were the critical item category. In order to judge these items correctly, it was necessary to represent the action's means in the means old-/new-judgment task and the action's end in the end old-/new-judgment task. For target items with the same means and ends or with different means and ends as compared to the encoding items, both action features suggested the same response ("old" with same means and ends, "new" with different means and ends) and therefore correct performance on these items was uninformative on the type of memory representation. For this reason, we defined $M^- E^+$ target items as experimental items and both $M^+ E^+$ and $M^- E^-$ target items as filler items.

7. EXPERIMENT 3

If action familiarity influences the type of action representation in memory, a significant interaction of familiarity and recognition memory task should be observed in the accuracy for experimental items. Based on previous studies (Rumiati & Tessari, 2002; Zalla et al., 2010), it was conceivable that end information would be better represented for familiar actions as compared to unfamiliar actions. In the case of unfamiliar actions, we reasoned that participants should represent these actions in terms of their means more than familiar actions. Given that these actions and correspondingly their ends are unfamiliar, participants should resort to a strategy where they represent what they can observe, i.e. the actions' means.

During incidental encoding, participants were presented with questions requiring them to make a decision about one aspect of the presented video clip. Questions could pertain to the action's end, its means or the appearance of an object. We hypothesized that questions pertaining to the action's end or its means during encoding could compensate for means or end representational advantages for unfamiliar and familiar actions, respectively. If familiar actions' ends are better represented relative to the ends of unfamiliar actions, asking an end related question during the encoding phase should emphasize the otherwise neglected information type and, consequently, attenuate accuracy differences for familiar and unfamiliar actions in the end old-/new-judgment task. In analogy, if unfamiliar actions' means are better represented relative to the means of familiar actions, asking a means related question during the encoding phase should attenuate accuracy differences for familiar and unfamiliar actions in the means old-/new-judgment task. As actions are so prevalent in the everyday lives of human beings and as working memory and speed of processing has been shown to be comparable between Easterners and Westerners (Hedden et al., 2002), we expected the same pattern of results to occur for Chinese and German participants, though based on partly differing stimuli.

7. EXPERIMENT 3

We started with 1754 object directed actions. In rating studies with action stimuli from other labs, real physical stimuli (line drawings, photographs, or video clips) are usually presented to the participants and their task is either to name them or to rate them with regard to some aspects like imageability or familiarity (Bonin, Boyer, Méot, Fayol, & Droit, 2004; Bonin, Roux, Méot, Ferrand, & Fayol, 2009; Cuetos & Alija, 2003; Fiez & Tranel, 1997; Masterson & Druks, 1998; Schwitter, Boyer, Méot, Bonin, & Laganardo, 2004; Szekely et al., 2005; Szekely et al., 2004). We adopted a different approach in order to identify object directed actions that differ in familiarity between Chinese and Germans. Presenting real actions bears the risk that the perceiver does not judge the familiarity of the action but the familiarity of the object exemplar that is being manipulated by the actor which would be a rating of object exemplar rather than action familiarity. In order to avoid this, we presented verbal action descriptions rather than visual action depictions. We constructed descriptions of actions in different languages (English, Mandarin and German). Action familiarity ratings were obtained in two waves, the first one yielding categorical familiarity ratings, the second one yielding numerical familiarity ratings.

In the categorical familiarity rating, English descriptions specifying means and ends were used for the 1754 object directed actions. One native Chinese speaker and one native German speaker both fluent in English made a familiarity judgment of the 1754 actions the descriptions referred to. Some examples of the action descriptions are given in Table 8.

7. EXPERIMENT 3

Table 8. Exemplary action descriptions specifying means and ends in English.

- to dial a telephone number pressing the keys of a telephone with the right thumb
- to stick an incense stick upright into an incense pot using the right hand
- to put a slice of toast into a toaster pulling the shifter down with the right thumb and index finger
- to remove garlic leftovers from a garlic press using a toothpick with the right hand

The familiarity judgment constituted in a judgment of what the raters think would be true for the majority of right-handed adults between 18 and 40 years of age from their home country. Action descriptions were listed in a table in an electronic document. Next to each item, raters filled in a letter corresponding to their familiarity judgment. Three categories were possible: "I think the action is mostly familiar" (F), "I think the action is mostly unfamiliar" (U), "I am not sure whether the action is mostly familiar or unfamiliar" (N). For the familiarity judgment, frequency of performing and/or observing the action was considered relevant. Both the action's means and end were to be taken into account.

From the 1754 action descriptions, 689 actions could be identified for which both the Chinese and the German rater claimed that this action would be either familiar or unfamiliar for the majority of right-handed young adults from their home country. Actions for which at least one of the raters claimed to be "not sure" were excluded from the set.

The 689 action descriptions were divided into three subsets of 172 items and one subset of 173 items. It was taken care that action descriptions referring to different means of performing an action with the same end were not included into the same subset in order to avoid familiarity comparisons between those items. Each subset was rated in the same way as described above by three additional native Chinese speakers and three additional native German speakers (in total: twelve additional native Chinese and German speakers each) fluent in English.

If for both Chinese and German raters, at least three out of the four raters within each country agreed on the action belonging to the category "F"

7. EXPERIMENT 3

and/or "U", this was taken as the criterion for an action being categorized as familiar/unfamiliar for right-handed young adults in the two countries.

439 actions could be categorized by this procedure and 135 actions out of these were chosen for the experiment. Video clips corresponding to the descriptions were generated with 60 actions being familiar in both countries, 30 actions being familiar in Germany and unfamiliar in China, 20 actions being familiar in China and unfamiliar in Germany and 25 actions being unfamiliar in both countries. Examples for actions from the four categories of familiarity are depicted in Table 9.

Table 9. Actions from different categories of familiarity.

| | | China | |
		familiar	unfamiliar
Germany	familiar	to dial a telephone number pressing the keys of a telephone with the right thumb	to roll through a slice of pizza moving a pizza wheel back and forth with the right hand
	unfamiliar	to sharpen a pencil holding it with the left hand and rotating the sharpener's crank handle with the right hand	to file the left fingernails using a pumice stone with the right hand
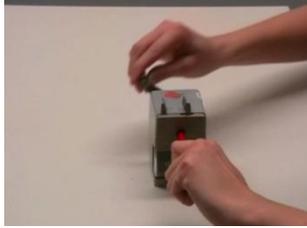
For each exemplary action, the action description and one frame from a video clip depicting the action are displayed.

As the categorical familiarity rating did not yield enough actions for the four categories of familiarity combinations in China and Germany, a second rating study was conducted where familiarity was judged numerically on a scale from 1 (= very unfamiliar) to 5 (= very familiar).

7. EXPERIMENT 3

Of the 1754 actions, 439 could be identified as either familiar or unfamiliar in both China and Germany. Consequentially, for 1315 actions, a categorization was not possible with the categorical method. These action descriptions were rated numerically in the second wave. English action descriptions were translated into Mandarin and German by one Chinese and one German native speaker and double-checked by one other Chinese and German native speaker. Translators were all fluent in English. The action descriptions were divided into five subsets of 219 items and one subset of 220 items. It was taken care that action descriptions referring to different means of performing an action with the same end were not included into the same subset in order to avoid familiarity comparisons between those items. Each subset was rated by 16 Chinese and 16 German native speakers, half of them males and half of them females. In total, 96 Chinese and 96 German native speakers participated in the rating. They were all right-handed and between 18 and 40 years old. Raters were paid for participation. For the familiarity judgment, frequency of performing and/or observing the action was considered relevant. Both the action's means and end were to be taken into account.

Unlike in the categorical familiarity rating, participants were instructed to judge the familiarity of each action for themselves rather than giving a judgment for the majority of young adults from their own country. Each action was rated on a scale from 1 (= very unfamiliar) to 5 (= very familiar). Each participant received an electronic questionnaire which contained the action descriptions in his/her native language from the respective subset. Subjects were required to rate each action's familiarity by ticking the box corresponding to their judgment out of boxes numbered 1 to 5 which were displayed below each action description.

Actions were considered familiar in a culture if mean familiarity ratings from the respective sample yielded a number equal or above 3.5, they were considered unfamiliar if mean familiarity ratings yielded a number equal or below 2.5. Based on the numerical familiarity rating, another 105 actions were chosen as items for the experiment and corresponding video clips were

7. EXPERIMENT 3

produced yielding 60 actions in each category of familiarity combinations in China and Germany.

Actions were chosen taking both high ratings for familiarity/unfamiliarity and practical considerations like the availability of objects and the ease/difficulty of producing corresponding video clips into account.

7.2.2. PARTICIPANTS

Forty-eight Chinese and forty-eight German native speakers took part in the experiment. Chinese participants were students from Beijing universities in the neighborhood of the Institute of Psychology at the Chinese Academy of Sciences. German participants were mostly students from Saarland University. All participants were right-handed and between 18 and 40 years old (China: mean age = 23.71 years, SD = 2.49 years; Germany: mean age = 22.95 years, SD = 3.29 years). Half of the participants within each culture were male and half female. They were paid for participation in the experiment. Five participants of the German sample were excluded because of performance at chance level. All participants gave written informed consent prior to the experiment.

7.2.3. MATERIALS AND EXPERIMENTAL PROCEDURE

The experiment was run on a PC controlled by E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA). Participants sat down facing a computer screen with a distance of approximately 50 cm. Screen resolution was 1024 × 768 pixels. A recognition memory paradigm was employed consisting in an incidental encoding phase and a test phase. In the encoding phase, participants worked on 240 trials with video clips of familiar and unfamiliar actions.

7. EXPERIMENT 3

60 actions each had been rated as familiar in both China and Germany, as familiar in China and unfamiliar in Germany, as familiar in Germany and unfamiliar in China and as unfamiliar in both China and Germany.

Throughout the experiment, a white background and was utilized. Numbers and words were displayed in black. Each trial began with a black fixation cross which was presented centrally for 250 ms. A blank interval of 250 ms followed before a video clip displaying an object directed manual action which had been rated to be either familiar or unfamiliar in the respective culture was being presented. Action video clip duration varied between 1500 and 4000 ms. Duration was comparable for familiar and unfamiliar actions (cf. Table 10). Clips were presented centrally across 640 × 480 pixels. Actions were presented in a third-person perspective (from left, from right, from a position opposite of the observer). Eight different actors were involved in performing the actions (two males, six females). Only the hands and arms of the actors were visible. The video clips were purely visual stimuli and did not contain sound.

Table 10. Mean video clip duration for items differing in familiarity.

		Mean duration	Standard deviation
China	**familiar**	2791.67 ms	732.37 ms
	unfamiliar	3000 ms	747.88 ms
Germany	**familiar**	2900 ms	763.58 ms
	unfamiliar	2891.67 ms	731.22 ms

Means and standard deviations of video clip duration are listed separately for familiar and unfamiliar items in China and Germany.

Participants were instructed to attend to the video clip as they would be required to answer a related question after stimulus offset. After a blank interval of 100 ms, a question and two possible answers were presented for maximally 5000 ms. Questions were presented centrally within the upper part of the screen, answers were presented to the left and right within the lower part of the screen. Mandarin was used for Chinese participants and German

7. EXPERIMENT 3

for German participants. Questions referred to an aspect of the video clip they had just seen. They could be either related to the action's end, its means or an object used in the video clip. Subjects were required to choose one out of the two possible answers by pressing a left or right key corresponding to the position of the correct answer as quickly as possible. Means, end and object questions occurred with equal probability for items from the four categories of familiarity combinations. It was taken care that action features conveyed in the incorrect response alternative would not overlap with means/end/object changes in the recognition phase. For each item, question types were counterbalanced between participants. Furthermore, the position of the correct answer was counterbalanced for all familiarity combinations and question types. Presentation of question and response alternatives was terminated with the key press. A blank interval of 100 ms was inserted before the next trial began with the presentation of a fixation cross. The trial structure during encoding is depicted in Figure 18.
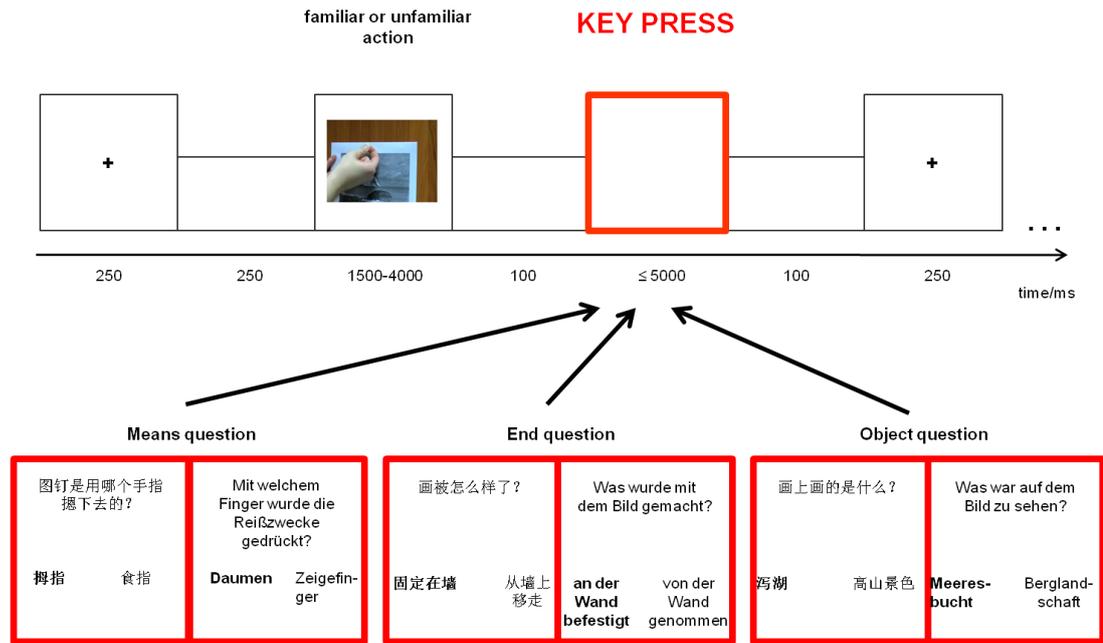
7. EXPERIMENT 3

Figure 18. Trial structure in the encoding phase of Experiment 3. Each trial involved the presentation of an action video clip with a duration between 1500 and 4000 ms of which one frame is depicted here. Following the video clip, one out of three forced choice question types would be presented requiring a response via key press. Questions and answers would be in Mandarin in the Chinese sample and in German in the German sample. For illustrative purposes, the bold response alternative corresponds to the correct response. In the experiment, both response alternatives were displayed using the same font. 图钉是用哪个手指摁下去的? = Mit welchem Finger wurde die Reißzwecke gedrückt? = With which finger was the thumbtack pushed?; 拇指 = Daumen = thumb; 食指 = Zeigefinger = index finger; 画被怎么样了? = Was wurde mit dem Bild gemacht? = What was done with the picture?; 固定在墙 = an der Wand befestigt = affixed to the wall; 从墙上移走 = von der Wand genommen = removed from the wall; 画上画的是什么？ = Was war auf dem Bild zu sehen? = What was presented on the picture?; 泻湖 = Meeresbucht = lagoon; 高山景色 = Berglandschaft = mountain scenery.

Up to three participants could work on the task in one experimental session in the same lab. They were read the instruction in Mandarin or German and started the experiment with a sequence of nine trials which were solely used in order to familiarize the participants with the task and were not analyzed. After those nine trials, the actual encoding phase with 240 trials followed in a randomized and counterbalanced fashion. 120 of these trials included experimental items, the remaining 120 filler items.

After encoding, half of the participants from each culture were instructed for an end old-/new-judgment task and half of the participants were instructed for a means old-/new-judgment task. It was ensured that all participants within one experimental session were in the same judgment task con-

7. EXPERIMENT 3

dition as the instruction for this part of the experiment was also read to them (again in Mandarin or German). In both testing conditions, action video clips were again presented to the participants. In comparison to the action video clips that had been presented during encoding, these video clips could either depict an action with the same means and end as before (M^+E^+), with a different means but the same end (M^-E^+) or with a different means and a different end (M^-E^-). Action video clips in this part of the experiment were never identical to the ones in the encoding phase and always involved different object exemplars. A trial in the test phase started with a black fixation cross being presented centrally in front of a white background for 250 ms. After a blank interval of 250 ms, an action video clip with variable duration (between 1500 ms and 4000 ms) was presented in the upper part of the screen simultaneously with the Mandarin or German words for "yes" and "no" to the right and left within the lower part of the screen. Action video clips during test bore one of the three relationships described above to action video clips during encoding (M^+E^+, M^-E^+, M^-E^-). Duration, perspective and actor were kept the same between encoding and test phase. Participants in the means old-/new-judgment task, were required to respond "yes" to items with the same means (M^+E^+) and "no" to items with a different means (M^-E^+, M^-E^-). Participants in the end old-/new-judgment task were instructed to respond "yes" to items with the same end (M^+E^+, M^-E^+) and "no" to items with a different end (M^-E^-). They were instructed to respond as quickly as possible while they should also avoid making mistakes. For "yes" or "no" answers, a right or left key on the keyboard should be pressed, respectively. Participants were allowed to press keys from video clip onset. As soon as they gave their response, the video clip terminated. If, during video clip presentation, they had not given a response, the Mandarin and German words for "yes" and "no" were displayed at the same position as before for maximally 5000 ms. During this time window, subjects were still allowed to give a response and it was terminated as soon as they pressed the left or right response key. Following the old-/new-judgment, a confidence question was presented in the upper part of the screen for 2000 ms at the longest. It read "How confident are you?" in Mandarin or German while, at the same time, the numbers "1", "2" and "3" were displayed in the lower part of the screen. Participants were instructed to

7. EXPERIMENT 3

press "1" if they had been unsure how to respond, "2" if they had some confidence in their response but still were not sure about it and "3" if they were sure that their answer was correct. As soon as they pressed one of the three rating alternatives, the presentation of the question ended. If, after 2000 ms, they had not responded to the confidence question, the question disappeared but the numbers were still visible at the same positions as before for up to another 3000 ms. As soon as they gave their response, the presentation stopped and the next trial came up, again starting with the presentation of a fixation cross. The trial structure during the recognition test phase is depicted in Figure 19.
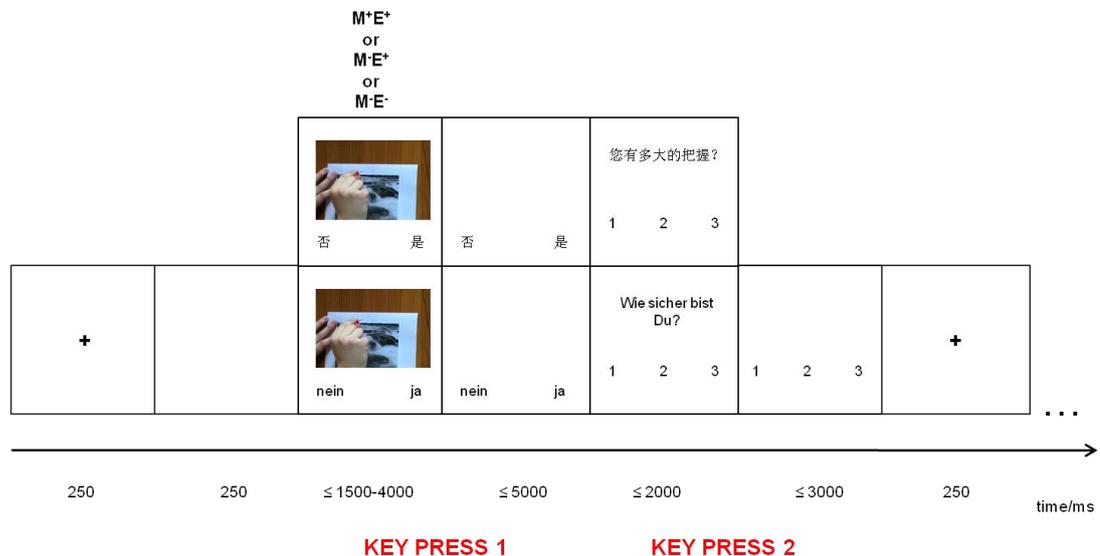

Figure 19. Trial structure in the recognition phase of Experiment 3. Each trial involved the presentation of an action video clip with a duration between 1500 and 4000 ms of which one frame is depicted. During one trial, participants were required to press keys twice. As soon as they pressed a key for the old-/new-judgment, the confidence question came up. As soon as they pressed a key for the confidence rating, the next trial started. Questions and words would be in Mandarin in the Chinese sample and in German in the German sample. $M^+ E^+$ = same means, same end; $M^- E^+$ = different means, same end; $M^- E^-$ = different means, different end. 否 = nein = no; 是 = ja = yes; 您有多大的把握？ = Wie sicher bist Du? = How confident are you?

For the 120 experimental items from the encoding part, action video clips during test involved $M^- E^+$ actions. Half of the 120 filler items from the encoding part were related to $M^+ E^+$ and half to $M^- E^-$ action video clips during test. The use of $M^+ E^+$ and $M^- E^-$ videos for filler items during test was coun-

7. EXPERIMENT 3

terbalanced between participants. In the means old-/new-judgment task, correct responses would be "yes" in 25% and "no" in 75% of the trials. In the end old-/new-judgment task, it would be "yes" in 75% and "no" in 25% of the trials. Prior to the test phase, participants were instructed that "yes" and "no" trials would not necessarily occur with equal proportions.

Except for the start of the test phase where action video clips related to the nine familiarization trials were presented, test trial sequence was randomized for each participant. Performance in the familiarization trials was excluded from analysis.

7.3. RESULTS

7.3.1. ENCODING PHASE

A 2 (culture: China, Germany) × 2 (familiarity: familiar, unfamiliar) × 3 (encoding question: end, means, object) mixed-model ANOVA was computed with culture as a between subjects variable and familiarity and enco-ding question as within subjects variables. Accuracy answering the encoding question was the dependent variable.

The analysis yielded a significant main effect of familiarity with more correct answers to the encoding question for familiar as compared to unfamiliar actions, $F (1, 89) = 9.31$, $\eta_p^2 = .09$, $p < .01$. In addition, culture influenced accuracy with German participants performing significantly better than Chinese participants, $F (1, 89) = 24.69$, $\eta_p^2 = .22$, $p < .01$. The type of encoding question also had a significant effect on accuracy, $F (2, 178) = 180.57$, $\eta_p^2 = .67$, $p < .01$. A post-hoc Tukey HSD test revealed that accuracies in the end, means and object encoding questions were significantly different from each other with end question accuracy being significantly higher than object ques-

7. EXPERIMENT 3

tion accuracy and object question accuracy being significantly higher than means question accuracy.

Furthermore, the type of encoding question interacted significantly with familiarity, F (2, 178) = 9.03, η_p^2 = .09, p < .01 and with culture, F (2, 178) = 17.26, η_p^2 = .16, p < .01. Post-hoc Tukey HSD tests revealed that accuracy was significantly higher for familiar actions as compared to unfamiliar actions in answering end questions. For the means and object encoding questions, there was no significant accuracy difference between familiar and unfamiliar actions. As to the effect with culture, it emerged that German participants accuracy pattern followed the overall accuracy pattern of the encoding question main effect (end > object > means). Chinese participants yielded significantly lower accuracy in the object encoding question than Germans. Consequently, Chinese participants' accuracy pattern deviated from the overall pattern: end > object = means.

Response times were not analyzed. They were not comparable between cultures because of encoding questions differing in length in the two languages.

7.3.2. RECOGNITION PHASE

A 2 (culture: China, Germany) × 2 (recognition task: end, means) × 2 (familiarity: familiar, unfamiliar) × 3 (encoding question: end, means, object) mixed-model ANOVA was computed with culture and recognition task as between-subjects variables and familiarity and encoding question as within-subjects variables. Accuracy for the experimental items ($M^- E^+$ items) was the dependent variable. The analysis yielded a significant interaction effect of familiarity and recognition task, F (1, 87) = 6.67, η_p^2 = .07, p < .05. Planned contrasts revealed that, for the end recognition task, there was no significant accuracy difference for familiar and unfamiliar actions, F (1, 87) = 1.03, n.s. However, for the means recognition task, participants performed significantly

7. EXPERIMENT 3

better for familiar as compared to unfamiliar actions, $F(1, 87) = 7.02$, $p < .01$. Furthermore, a significant interaction of encoding question and recognition task emerged, $F(2, 174) = 58.32$, $\eta_p^2 = .4$, $p < .01$. As revealed in a post-hoc Tukey HSD test, participants showed significantly higher accuracy with an end encoding question in the end recognition task as compared to the means recognition task as well as with a means encoding question in the means recognition task as compared to the end recognition task. With an object encoding question, there was no significant difference in recognition accuracy in the means and end task. The results of the significant two-way interactions must be evaluated in the light of a significant three-way interaction of the factors familiarity, encoding question and recognition task, $F(2, 174) = 3.5$, $\eta_p^2 = .04$, $p < .05$. Planned contrasts between recognition accuracy for familiar and unfamiliar actions separately for the types of recognition task and encoding question revealed that familiarity did not modulate recognition accuracy in the end recognition task (all p's > .05). For the means recognition task, a significant difference between accuracy for familiar and unfamiliar actions was observed with end encoding questions, $F(1, 87) = 10.22$, $p < .01$. In this case, recognition accuracy was significantly higher for familiar actions as compared to unfamiliar actions. With means and object encoding questions in the means recognition task, there was no significant difference in recognition accuracy between familiar and unfamiliar actions. In addition, a marginally significant main effect of culture was obtained with Chinese participants showing higher accuracy as compared to German participants, $F(1, 87) = 3.72$, $p \leq .06$. No other main or interaction effects were significant. The interaction of familiarity and recognition task and the interaction of familiarity, encoding question and recognition task are depicted in Figure 20.

7. EXPERIMENT 3
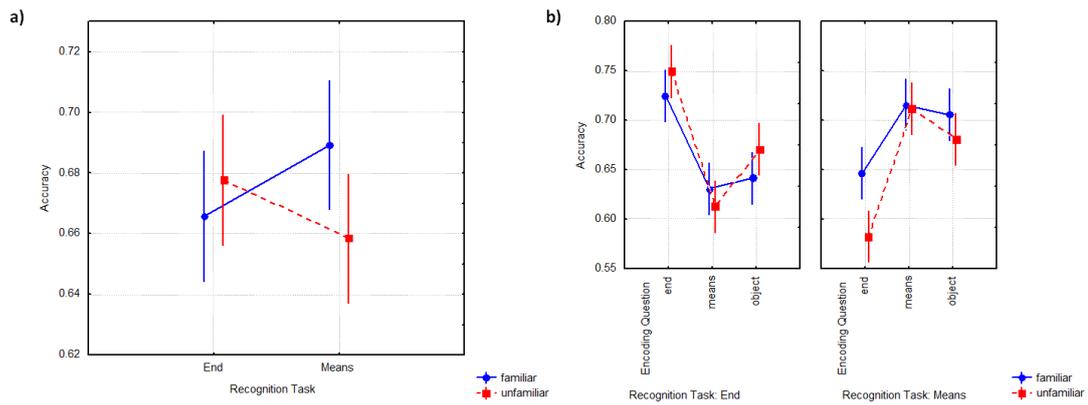
Figure 20. Significant interaction effects including familiarity. Displayed are significant inter-action effects a) of action familiarity and recognition task and b) action familiarity, encoding question and recognition task on recognition accuracy for M⁻E⁺ items. Bars depict the stand-ard error of the mean for interaction effects in mixed designs (Jarmasz & Hollands, 2009).

Accuracies for filler items were not informative as to the type of action feature represented in memory and will not be reported here. Similarly, we do not report response times as action video clips of different durations were used and relevant information was revealed at different points in time. Data from confidence ratings can be used for additional analyses and will also not be dealt with here.

7.4. DISCUSSION

With this cross-cultural study, we wanted to test whether the familiarity of an action influences how it is represented in memory. We hypothesized that an action's end should be better represented for familiar actions as com-pared to unfamiliar actions. In contrast, an action's means should be better represented for unfamiliar actions as compared to familiar actions. We rea-soned that encoding questions targeting the action feature to be judged du-ring recognition could compensate for such differences in the representation of familiar and unfamiliar actions. The effect of action familiarity on the action features which are represented in memory should be the same in the Chi-nese and German sample, though based on partly different stimuli.

7. EXPERIMENT 3

7.4.1. PRIMACY OF END OVER MEANS INFORMATION

We found a significant interaction effect of action familiarity, encoding question and recognition task on recognition accuracy. Planned contrasts revealed that there were no differences in recognition accuracy for familiar and unfamiliar actions if the task required an end old-/new-judgment. This was true both in the case of an end encoding question (i.e. a question targeting the action feature to be judged during recognition) and of means or object encoding questions (i.e. questions targeting the other action feature or non-action information). In the means old-/new-judgment task, we found a modulation of recognition accuracy by action familiarity. Participants performed better for familiar actions as compared to unfamiliar actions judging the means of a target action. This effect was restricted to the condition in which they had previously answered an end encoding question. For means and object encoding questions, there was no significant difference between familiar and unfamiliar actions in recognition accuracy.

Though the results show that action familiarity modulates representations in memory, the pattern is different to what we expected. Ends were equally well represented for familiar and unfamiliar actions. Means were better represented for familiar as compared to unfamiliar actions if participants were misled as to the relevant action feature. If participants were asked about an end related aspect about the action during the encoding phase but later on tested in a means recognition memory task, they performed significantly worse for unfamiliar as compared to familiar actions. Though recognition memory for means was modulated by the encoding action's familiarity, it was in the opposite direction as expected. It is not that unfamiliar actions are preferentially represented in terms of the actions' means but, in contrast, that means information can be better represented for familiar actions. An encoding question targeting means information could compensate for the processing advantage of familiar actions.

How can we explain this pattern of results? Let's first consider what happens during the first part of the experiment, i.e. the encoding phase, se-

parately in relation to what is to be judged during recognition. In the encoding phase, participants were required to attend to short action video clips. After video offset, a question about the clip would be presented together with two response alternatives of which they were required to choose the correct one. The question could relate to the action's end, its means or the appearance of an object present in the video. These results show that participants were significantly better responding to end encoding questions if actions were familiar as compared to actions which were unfamiliar. This suggests that the ends of familiar actions were more readily available for familiar actions as compared to unfamiliar actions (Rumiati & Tessari, 2002; Zalla et al., 2010). Still, in the recognition phase, the accuracy difference between familiar and unfamiliar actions during encoding was not paralleled. Recognition accuracy for end information was equally well for familiar and unfamiliar actions.

Generally, there was a strong effect of encoding question on recognition accuracy showing that elaborating on the relevant action information during the encoding phase helps. If participants were required to judge whether an action's end was old or new, they were significantly better if they had focused on end rather than means information during encoding. In analogy, if they were to judge whether the means of an action was old or new, they were significantly better if they had focused on means rather than end information during encoding.

Concerning familiarity, the data suggest that the end disadvantage for unfamiliar actions relative to familiar actions from the encoding phase has been compensated successfully from encoding to recognition. This could be an effect of the encoding question which required subjects to elaborate on the action's ends and which was presented simultaneously with two response alternatives, one of them being the solution to the "end puzzle". The presentation of the correct end as one of the response alternatives could have been especially helpful for unfamiliar actions as compared to familiar actions. In the case of unfamiliar actions which had been studied with means or object encoding questions, elaboration on possible ends was not required during encoding. Participants were to respond to questions about observable features of the video clips. Inferential processes were not necessary to answer

7. EXPERIMENT 3

means and object encoding questions. Still, there was also no significant difference between familiar and unfamiliar actions which had been studied with a means or an object encoding question in the end recognition task. Possibly, participants elaborated on possible ends of an action by default during observation of the actions at encoding. The presentation of a related item during recognition (i.e. an item with the same end but different means) could then function as a retrieval cue for the previous action episode and its end, thereby attenuating initial accuracy differences judging the ends of familiar and unfamiliar actions.

In the means recognition task, participants performed better for familiar actions as compared to unfamiliar actions if they were misled as to the relevant action feature at encoding, i.e. if they were to answer an end encoding question. This could be explained by a hierarchical model of action representations (Grafton & Hamilton, 2007) assuming a primacy of end information over means information (Haruno et al., 2001; Hommel et al., 2001; Zimmer et al., 2007). If end information is the default information which we elaborate on upon action observation, this is probably easier for familiar actions as compared to unfamiliar actions. In Experiment 3, the differential ease of answering end encoding questions for familiar and unfamiliar actions is reflected in a significant accuracy difference. Assuming that participants also tend to ruminate about a possible end of an unfamiliar action, finding the correct answer be more difficult for them. If means information is additional information which is optionally but not necessarily represented, it is more likely that participants skip or neglect this option for unfamiliar items as compared to familiar items. For familiar items, the end will be easier to infer. It is likely that the end of a familiar action is also linked to a known means. Familiar actions, i.e. actions which we frequently execute or observe, will not only be familiar in their end but also in their means. The known means of the familiar action will be activated and compared with the actual means of the observed action. Unfamiliar actions, by definition, will not have a known means as they are unfamiliar to the observer. Consequentially, a comparison of actual and known means will not be possible and thereby participants might not elaborate on means information. Related to this, it is also possible that participants

7. EXPERIMENT 3

are so engaged in ruminating about a possible end when confronted with an unfamiliar action, that they will not have sufficient capacity for an additional representation of the action's means. It follows that for unfamiliar items, processing means information will be impaired relative to familiar items. This effect resulted only for items which had been studied with an end encoding question. In contrast, means recognition accuracy differences would be attenuated or eliminated with items that had been studied with a means encoding question. Though processing of end information would be the superordinate goal by default, a question targeting means information and being presented together with the correct answer could be compensatory.

7.4.2. ENCODING EFFECTS OR REPRESENTATIONAL EFFECTS?

From this line of argument it is unclear at which point in time differential processing of familiar and unfamiliar actions occurs. Is it an effect of perception during the encoding phase or an effect of how information is represented in memory? At the time that a familiar or an unfamiliar action video clip is being presented to the participants, they do not know that a recognition memory test will follow where action features are to be judged. Accuracy differences for familiar and unfamiliar actions in answering encoding questions likely reflects differences in encoding specific aspects about the action. There were no significant differences for familiar and unfamiliar actions in answering means and object encoding questions. Means and object encoding questions referred to observable features of the video clip, e.g. whether it was the thumb and index finger or the whole hand being used to grasp a zip (means question) or whether the pants were blue or green (object question). However, for familiar actions as compared to unfamiliar actions, participants were significantly better to answer end encoding questions. End questions referred to action features which need to be inferred from the observable information (e.g. whether the pants were opened or closed). Although participants had more difficulties inferring ends of unfamiliar actions

than of familiar actions during encoding, recognizing that an action with a different means was performed in order to achieve the same end as before did not differentiate between familiar and unfamiliar actions. It seems that, after initial difficulties in processing the ends of unfamiliar items, all items irrespective of their familiarity status were finally represented with their actual or possible ends in memory and being presented with a related action in the recognition phase served as a retrieval cue for the action participants had seen during encoding.

Observable features like means or object information of familiar and unfamiliar actions were equally well processed during encoding. Accuracy in answering means or object encoding questions was not modulated by familiarity. However, a significant difference between familiar and unfamiliar items during means recognition restricted to items which had been studied with an end encoding question suggests that the major information which is represented about an action is its end. If, after perception, participants are asked a question referring to the action's means, they perform equally well for familiar and unfamiliar actions. This effect also transcends to the recognition phase where there were no significant differences between familiar and unfamiliar items being studied with a means encoding question if the task was an old-/new-means judgment. However, if, after perception, ends become relevant by an end encoding question which is harder to answer for unfamiliar as compared to familiar actions, a difference in the representation of means information will result for familiar and unfamiliar actions.

Consequentially, the accuracy pattern speaks in favor of an advantage in processing the ends of familiar actions as compared to unfamiliar actions. This effect occurred only after initial perception. In memory, all actions were represented by their actual or possible end. Means processing during perception was not modulated by familiarity but, in memory, means information about familiar and unfamiliar actions was differentially represented.

In this study, we employed encoding questions targeting different aspects of the video clips. We counterbalanced encoding question type for individual items in order to control for specific processing strategies that individ-

7. EXPERIMENT 3

ual items would favor. We hypothesized that elaboration on specific action features after observation which would be needed to answer encoding questions successfully could eliminate or attenuate processing biases for familiar and unfamiliar items. It can be argued that memory representations might be shaped by encoding questions in a way that would not have occurred had we simply presented action video clips during encoding without any further instructions. Especially, the presentation of the correct response as one response alternative could have promoted otherwise unnoticed information to be integrated into the memory representation about this action. It is possible that representational differences between familiar and unfamiliar actions had been obscured by encoding questions targeting the action feature which was tested later on. However, processing differences between familiar and unfamiliar actions should still be observable or even augmented in the conditions misleading the subject about feature relevance, i.e. the conditions where end encoding questions were coupled with a means recognition test and means encoding questions with an end recognition test. If we focus on these misleading conditions, our argument about a hierarchical organization of action representations with a primacy of end information over means information is being strengthened: Ends are equally well represented in memory for familiar and unfamiliar actions, means are better represented in memory for familiar actions as compared to unfamiliar actions.

It remains to have a closer look at the condition where subjects were to respond to a non-action feature during encoding. There was no significant accuracy difference for familiar and unfamiliar actions answering the encoding questions suggesting that object information as an observable information type was equally well processed during perception for familiar and unfamiliar actions. Restricted to items which had been encoded with an object encoding question, accuracy in both the means and end recognition task was not modulated by action familiarity. According to the model outlined above, ends should be equally well represented for familiar and unfamiliar actions but means should be better represented for familiar actions as compared to unfamiliar actions. Why don't we observe a modulation of means recognition accuracy by action familiarity if the initial focus is on a non-action

7. EXPERIMENT 3

feature? A common feature of means and object encoding questions is that they are focused on observable aspects of the action video clips. Object encoding questions are often related to the appearance of the tools used to accomplish the actions. Furthermore, tools are highly related to the means of the action. In contrast to that, an action's end would be an inferential rather than an observable feature and not related to the appearance of a specific tool. Therefore, it is possible that a focus on the object would also attenuate the representational advantage for means information that familiar actions exhibit relative to unfamiliar actions.

7.4.3. CULTURES DO NOT DIFFER IN ACTION INFORMATION PROCESSING

In a cross-cultural study with Chinese and German preschoolers, Wang et al. (in press) found that action familiarity had an effect on imitation performance and, especially, on the error types during imitation. For unfamiliar actions, there were no significant differences between the mean number of end and means errors. For familiar actions, participants made significantly more end errors as compared to means errors. Comparing the mean number of errors between actions with a different familiarity status, the data suggest that there were fewer means and fewer end imitation errors for familiar actions as compared to unfamiliar actions. This suggests that both means and ends were better represented for familiar as compared to unfamiliar actions. This effect was comparable in both Chinese and German samples suggesting that action imitation is uninfluenced by culture.

Whereas Wang et al. (in press) used action stimuli which were familiar and unfamiliar in both cultures, we adopted a different approach where half of the items which were familiar in one culture were unfamiliar in the other culture, respectively. Furthermore, we were interested in recognition memory in adult participants rather than imitation in children. We found action recognition memory for means information to be influenced by familiarity but no

7. EXPERIMENT 3

modulation of recognition memory for end information. This effect was comparable in the Chinese and the German sample.

Apart from a marginally significant main effect of culture suggesting that there was a trend for Chinese participants to perform better in both recognition memory tasks, we did not find significant interaction effects including culture on recognition accuracy[5]. This suggests two things: First, it indicates that our familiarity manipulation worked and that items being categorized as familiar/unfamiliar by the rating procedure, were in fact familiar and unfamiliar actions for the majority of right-handed young adults from the respective culture. Second, familiarity modulates action information processing in the same way in a Chinese and a German sample. For all actions, we focus on their ends when we represent them in memory. Means information becomes part of the memory representation if the action is familiar but not if it is unfamiliar. This could be due to comparison processes between the means in the action video clip and the known means. Alternatively, it could also be driven by capacity limitations with less capacity available for the representation of means information in the case of unfamiliar actions. A hierarchical organization of action representations with a primacy of end over means information seems to be shared across cultures. The results of Experiment 3 and the findings of Wang et al. (in press) suggest that action information is processed in a highly similar way across cultures. Though actions are diffe-rent across cultures, actions as such are ubiquitous in everyday life and, therefore, can be considered a very basic category of information.

---

[5] In the encoding phase, we also found a significant interaction effect of culture and encoding question. Chinese participants' accuracy in the object question was significantly lower as compared to German participants' accuracy. For the end and means questions, there were no such differences. This pattern is in line with differences in object processing between Easterners and Westerners which have been demonstrated in several studies (e.g. Goh et al., 2007; Nisbett & Miyamoto, 2005). Easterners tend to process scenes holistically, whereas Westerners focus on salient objects within scenes.

7. EXPERIMENT 3

In Experiment 3, we investigated in a cross-cultural context whether action familiarity influences the kind of action features which are represented in memory. Memory performance in an end recognition memory test was not differentially modulated by familiarity. However, the means of familiar actions were better represented for familiar actions as compared to unfamiliar actions. This suggests that actions are by default represented in terms of their ends. Even for unknown actions, we ruminate about possible ends for the purpose of representing the action in memory. Means information is secondary and can be additionally represented. It is more likely that we represent means information for familiar actions as compared to unfamiliar actions, probably resulting from comparison processes between the observed means and our prototypical means.

The same effects of action familiarity on recognition memory of individual action features were observed in both cultures. Identical items yielded opposite effects depending on their familiarity status within the German and Chinese sample. This suggests that action information processing is uninfluenced by culture.

7. EXPERIMENT 3

8. GENERAL DISCUSSION

I have described three experiments which were aimed at elucidating how action information is represented in memory. In this chapter, I would like to sum up our findings and finally introduce a model specifying the process from action perception to action representation in memory. The model will be linked with a network of brain regions that have been shown to be involved in the representation of action features in memory.

8.1. ACTION REPRESENTATIONS ARE SHARED IN WORKING AND LONG TERM MEMORY

In Experiment 1, action information was operationalized as information about prototypical movements which we perform when interacting with a specific object. We contrasted this action information with another information type about these objects, namely their prototypical size. The study focused on retention of this information in working memory and on its retrieval from long term memory. Domain specificity has been a topic in both working and long term memory research. Some studies have focused on the overlap in domain specific regions during working and long term memory processes (Lewis-Peacock & Postle, 2008; Ranganath, Cohen et al., 2004; Slotnick, 2004), however, the focus of these studies has been on perceptual attributes of visual objects rather than action information. With Experiment 1, we could show that domain specific regions for action information processing are also commonly recruited by working and long term memory. A left-hemispheric network consisting in inferior frontal/ventral premotor cortex, supramarginal gyrus and middle and superior temporal gyrus was commonly recruited if participants were to retain actions in working memory or to retrieve from long term memory. This network comprised areas of the putative human mirror

neuron system and areas which have been discussed within the context of tool motion and biological motion perception (Allison et al., 2000; Beauchamp et al., 2002, 2003). The inferior frontal/ventral premotor region and the inferior parietal lobe are brain regions which have been found to be activated both if we execute an action by ourselves and also if we observe another individual performing the action, suggesting a direct matching mechanism for action understanding (Buccino et al., 2001; Fadiga, Fogassi, Gallese, & Rizzolatti, 2000). It has been argued that we understand actions of others by matching them onto our own motor representations during observation. Our findings show that brain regions with these properties also play a role in memory for action information. Speaking of memory, we mean both working and long term memory and would like to suggest the existence of a shared representational basis not only for perceptual attributes but also for action information. Furthermore, regions which have been shown to be involved in the perception of biological motion and tool motion, namely the left middle and superior temporal gyrus, have been found to be commonly recruited by working and long term memory for actions. Our analysis of action information in memory was restricted to object directed actions, i.e. actions involving the manipulation of an object. A manipulable object was either depicted as a sta-tic photograph (in the working memory task) or as a word (in the long term memory task). It is likely that participants engaged in motor imagery in both tasks involving both biological motion (motion of the effector) and tool motion (motion of the object). Activation of these perceptual regions during working memory retention and long term memory retrieval of information about object directed actions shows that they serve a function beyond perception. Brain regions which are specialized for biological and tool motion perception also represent this information in memory.

It has been suggested that the STS provides perceptual input to the anterior and posterior putative human mirror neuron areas and that this network enables imitation (Iacoboni & Dapretto, 2006). We could show that the same network also enables memory with sustained selective activation in the network during working memory retention and long term memory retrieval. Furthermore, we have shown that activation of the action network is domain

8. GENERAL DISCUSSION

specific. Were participants to retain or to retrieve a different information type about the same objects, i.e. the objects' prototypical size, we found a different domain specific network to be involved. Retention of size information in working memory and its retrieval from long term memory involved the precuneus and the right inferior parietal cortex.

8.2. MEANS AND END SPECIFIC BRAIN REGIONS CAN BE IDENTIFIED DURING WORKING MEMORY RETENTION AND TARGET EVALUATION

It has been suggested that action information is hierarchically organized and that different levels of representations can be distinguished (Grafton & Hamilton, 2007). Consider the example of inserting a floppy disk into a drive which had been depicted as a reference action in Experiment 2 in Figure 9. This action has a specific end, namely inserting the floppy disk into the drive and a specific means, namely grasping it with the right thumb and index finger, orienting the disk horizontally and pushing it forward with the right index finger. When I referred to the example in the penultimate sentence, I used the action's end to describe it. This in line with the assumptions of the common coding theory which posits that actions are by default represented in terms of their physical consequences or ends (Hommel et al., 2001; Prinz, 1992). However, in addition to end information, as a rather conceptual action feature which is bare of motor information, actions do convey means information, i.e. motor information about the exact manner of interaction between an effector and an object. During perception of the exemplary action, we process how the disk was oriented, how it was grasped and how it was moved forward. Depending on the type of task, it can be necessary to retain both means and end information or either information type in working memory. To the best of our knowledge, means and end information about actions have not been researched within the framework of working memory. In addition, it is unclear whether the human mirror neuron system is selectively involved in the representation of means and end information and, if so,

8. GENERAL DISCUSSION

how. Furthermore, we wanted to find whether brain activation in means selective regions can be modulated by motor similarity of an encoding and a target stimulus.

We found that both means and end information can be retained in working memory. Still, there were significant accuracy differences between the tasks with the means task being more difficult than the end task. We could identify selective brain regions for both means and end information retention. Whereas right prefrontal regions and the pre-SMA were selectively recruited for the retention of means information, it was left parahippocampal and anterior temporal regions which showed selective activations during retention of end information. During target presentation, adjacent regions in the SMA and the parahippocampal cortex exhibited selective means and end match enhancement effects. This suggests that it is not the same but close-by regions which are involved during retention of means and end information in the absence of visual input and during match-/non-match judgments about these action features during presentation of a visual stimulus. Whereas regions of motor planning and control were selectively involved in means working memory, regions which process context and bind features into episodes were selectively involved in end working memory.

It is conceivable that this activation pattern reflects a difference in observability of means and end information. Whereas means information can be observed and matched upon motor representations, end information needs to be inferred from the visual stimulus. If one information type can be readily observed and the other needs to be inferred, observation probably takes place before inference. One could further argue that means information processing is automatic and end information processing is optional and takes place only if required for the task. This is in line with our finding that means match enhancement effects were independent of the working memory task but end match enhancement effects occurred only in the end working memory task. Possibly, the means of target actions could be observed and were therefore processed during both means and end trials. In contrast, the ends of target actions needed to be inferred from observable stimuli and were processed only during end trials. However, this is in contrast to the as-

8. GENERAL DISCUSSION

sumptions of the common coding theory which posits a primacy of end over means information. According to this theoretical approach, actions should be under-stood by end information and means information would be a surplus which can be but is not necessarily processed. This is also what the findings of Experiment 3 suggest. From the findings of Experiment 2, we can summarize that means information at S2 is processed independent of attention but end information processing at S2 needs an attentional focus on this information type. It is possible that this is specific to this kind of paradigm that we employed. After they had perceived an action at S1, participants were instructed to selectively retain the means or end of the action in working memory in order to make a match/non-match comparison of S1 and S2 later on within the trial. With this paradigm, it is possible to identify selective brain regions for the retention of means and end information in working memory, however, an artificial situation is created which is rarely encountered in everyday life. With some imagination, one can think of situations in which a person is required to judge the identity or difference of an action's means, e.g. a jury member evaluating two people who are engaged in synchronized swimming. However, most everyday life situations probably involve the evaluation of actions as to their ends rather than their means. Consequentially, priority of end over means information processing could be a result of the affordances of everyday life situations.

During retention of means and end information in working memory, regions of the putative human mirror neuron system were not selectively involved in processing of either action feature. However, during target presentation we found activation in the left aIPS, part of the posterior putative mirror neuron region, to be strongly modulated by motor similarity of encoding and target stimulus. In this region, a graded means match enhancement effect was observed with activation correlating positively with motor similarity. This suggests that the aIPS contributes to the memory representation of motor action features. Other studies, in contrast, have emphasized the involvement of the aIPS in the representation of object goals or ends of actions (Hamilton & Grafton, 2006, 2008; Tunik et al., 2007). In our study, selective aIPS activation for means working memory was observed only during evaluation of a

8. GENERAL DISCUSSION

target stimulus but not during the retention phase. The means related activations in the prefrontal cortex and the pre-SMA suggest that simulation of visuomotor information in the absence of visual input is more reliant on anterior brain regions rather than the aIPS. Interestingly, modulation of aIPS activation by motor similarity was independent of the attentional focus of the parti-cipant. It could be observed both during trials in which means information was relevant and trials in which means information was irrelevant for the required match/non-match judgment.

We did not find any evidence as to a selective involvement of the putative anterior human mirror neuron region in the representation of means or end information in working memory. However, this region was selectively involved in working memory retention and long term memory retrieval of motor information about actions when we compared it with a non-action feature (size information). It seems that the left ventral premotor/inferior frontal gyrus is involved in the retention of action information but it is not differentially involved in the representation of specific action features. It has been suggested that the inferior frontal/ventral premotor cortex is automatically recruited during action information processing (Kellenbach et al., 2003). However, comparison of the means and end working memory conditions with the control condition also did not yield activation in the putative anterior human mirror neuron region. This could be due to peculiarities of the control condition being presented in a separate block after two blocks of intermixed working memory trials.

When comparing specific brain activations during working memory retention in Experiment 1 and Experiment 2, it is important to acknowledge the differences in stimulus material and task requirements. In Experiment 2, action video clips were presented and participants were required to selectively retain either means or end information. In Experiment 1 (and also in Mecklinger et al., 2004), photographs of manipulable objects were presented and participants were required to retain the movement that is made during the prototypical object manipulation. This information about how to manipulate the object can also be considered means information. However, it is concei-vable that in these studies with static object stimuli, participants first

8. GENERAL DISCUSSION

needed to think of the prototypical action in conceptual terms before they could activate the corresponding motor program. It seems that the putative human mirror neuron regions are activated during retention in an action working memory task requiring both processing of means and end information but they are not activated in a study that requires selective retention of either action feature.

8.3. ACTION FAMILIARITY MEDIATES THE TYPE OF ACTION REPRESENTATION

We have shown that means and end information can be retained in working memory and that different brain regions are selectively recruited during their retention and target evaluation. The results on attentional modulation of means and end match enhancement effects could be explained by means information being automatically processed and end information processing requiring attentional control. This is at odds with the common co-ding account which posits a primacy of end over means information. The results pattern could have been influenced by peculiarities of our paradigm in which participants were required to selectively retain specific action features, a situation which is rarely encountered in everyday life. Following from Experiment 2, we wondered what would happen if participants are not instructed to retain specific aspects of an action. How do they preferentially represent actions in memory? Does representation of specific action features depend on whether they are familiar with the action or not?

We investigated this question within a cross-cultural context taking advantage of the observation that some actions which are familiar in China are unfamiliar in Germany and vice versa. We found that action familiarity influences memory representations. Immediately after encoding, participants were better in responding to end questions about actions for familiar actions as compared to unfamiliar actions. There were no significant differences in responding to means questions or questions about non-action related ob-

servable object features. This corroborates the distinction between observable and inferable action features. If presented with an action video clip, the action's means can be observed, no matter if the action is familiar or unfamiliar to the subject. However, the action's end needs to be inferred from the observable stimulus which might be more difficult for unfamiliar as compared to familiar actions. In fact, this finding is somewhat trivial as familiarity of an action is dependent on whether we know the action and its end or not. If we do not know the end, answering questions which target the end will be harder.

It is more informative to consider the representational effects of familiar and unfamiliar actions that are revealed in a recognition memory test following the encoding phase. Though participants were initially better in answering end related questions for familiar as compared to unfamiliar actions, there was no such difference between familiar and unfamiliar actions in an end recognition memory task. This was independent of the type of encoding question participants had worked on during the study phase. However, in a means recognition memory task, participants performed better for familiar as compared to unfamiliar actions. Had they been confronted with an encoding question focusing on an observable feature, this accuracy difference was attenuated. This suggests that for familiar actions, it was more likely that the means of the observed action became part of the subjects' memory representation as compared to unfamiliar actions. Alternatively, it would also be possible that participants reactivated the prototypical means of familiar actions. Independent of whether an action was familiar or unfamiliar, participants would preferentially represent the action's (actual or possible) end. Information about an action's end seems to be more central to its understanding as compared to information about its means. This is in line with the common coding account which posits a primacy of end over means information (Hommel et al., 2001; Prinz, 1992).

How can we reconcile fMRI findings which suggest attention independent processing of means information but attentionally controlled processing of end information with the findings from a cross-cultural behavioral study suggesting an ends-first-then-means processing strategy? This seem-

8. GENERAL DISCUSSION

ingly contradictory results will be dealt with in Chapter 8.4. where we will explain our model of action information processing. At this point, it remains to acknowledge that modulatory effects of action familiarity on how we represent action information in memory are independent of culture. Both the Chinese and the German sample were better in recognizing actions with deviating means if the actions were familiar to them as compared to actions which were unfamiliar. Recognizing that actions were aimed at the same end though was unrelated to the actions' familiarity status. This suggests that the representation of action information in memory is a very basic cognitive process which is unshaped by cultural experience.

8.4. ACTION FEATURE PROCESSING DURING PERCEPTION AND REPRESENTATION IN MEMORY

In my doctoral project, I was interested in how we represent action information in memory and, especially, how memory representations relate to the hierarchical organization of action features which have been formulated by others (Grafton & Hamilton, 2007). If means and end information can be dissociated both at the phenomenological level (Haggard, 2008; Humphreys et al., 2001; Zimmer et al., 2007) and at the neuronal level (Chaminade et al., 2002; Hesse et al., 2009), on which action level do we preferentially represent action information in memory? Do action representations always include end information and means information processing is optional? In contrast, isn't it means information which can be observed immediately and end information can only be inferred on the basis of observed features? In Figure 21, a model is sketched of how means and end information could possibly be processed during perception and representation in memory.

8. GENERAL DISCUSSION
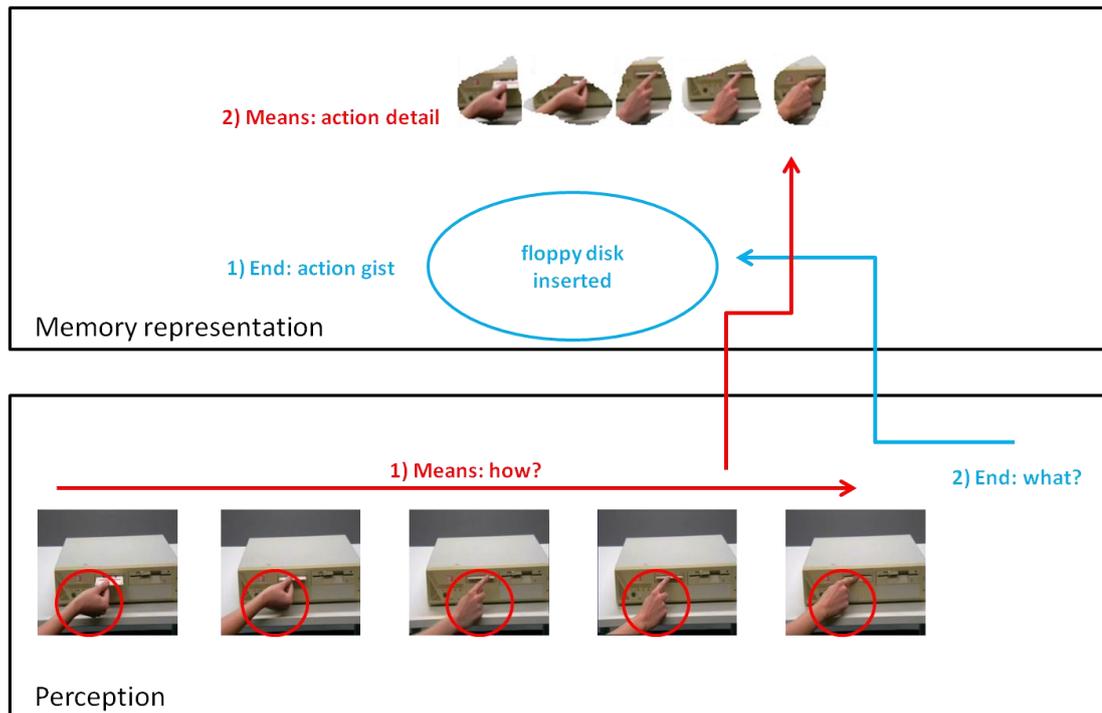
Figure 21. Relative emphasis of means and end information processing during action perception and action representation in memory. During perception, there is a primacy of means over end information. During representation in memory, end information is emphasized as compared to means information.

Typically, an action (unless very short) is not perceived at once but unfolds with time. From the onset of a visually presented object directed action, we can observe an effector interacting in a specific manner with an object. This dynamic visual input can be observed and mapped upon motor representations throughout the action observation process. This is the kind of information which we subsume under the label "means of the action". At some point during perception, the actual or a possible end of the action will become activated being inferred from the perceptual input. The time at which the actual or a possible "end of the action" becomes available can differ depending on whether the individual action is repetitive or sequential in nature, on its ambiguity, on its familiarity and on other mediating factors. If an action has been performed or observed frequently with a specific means used to achieve a specific end, an association between means and end will have built up which helps in the inference process. Still, means information will be prior to end information in perception as means can be observed from the outset whereas the end needs to be inferred from the visual input. Now, consider

8. GENERAL DISCUSSION

the phase of memory representation of action information. The visual input of the encoding phase has terminated. Means have been observed, ends have been inferred. Means information processing was prior to end information processing during perception but is this also true when we represent the action in memory? Probably not. Means information processing was intensely tied to the visual input during perception. It was present in the stimulus, independent of the observer's effort during encoding. In contrast, end information processing required the observer to engage in an inference process, going beyond the observable input. This would be a more active and elaborate process. Using the terminology of the levels of processing approach (Craik & Lockhart, 1972), one could also speak of deeper and shallower encoding which is encouraged for the action features of end and means information, respectively. Consequentially, the action feature which we preferentially represent in memory is its end. This information is the output of active inferential processing during perception. Means information can be additionally represented in memory, however, the gist of the action (i.e. the action's end) is superordinate to its details (i.e. the action's means). This is in line with the affordances of everyday life where it is usually more important that our action has led us to achieve some specific goal rather than that we have adhered to a specific manner of interacting with an object. Representation of actions in terms of their ends rather than their means is also the major claim of the common coding theory (Hommel et al., 2001).

Means and end information about actions can be distinguished both at the level of perception and during representation in memory. However, relative emphasis of means and end information during these two stages differs. Whereas during perception, there is a primacy of means over end information, it is a primacy of end over means information which is typically observed during representation in memory. It is important to notice that these relative contributions are not stable but can be adapted flexibly to the affordances of the current task.

Finally, I would like to tentatively sketch the contributions of specific cortical regions as to the representation of action information in memory. Figure 22 depicts the key brain regions that have emerged for the representa-

8. GENERAL DISCUSSION

tion of actions in memory in our fMRI studies and their possible functional roles. It is likely that these regions are equally recruited during working and long term memory processes as has been shown for a subset of the regions in Experiment 1.
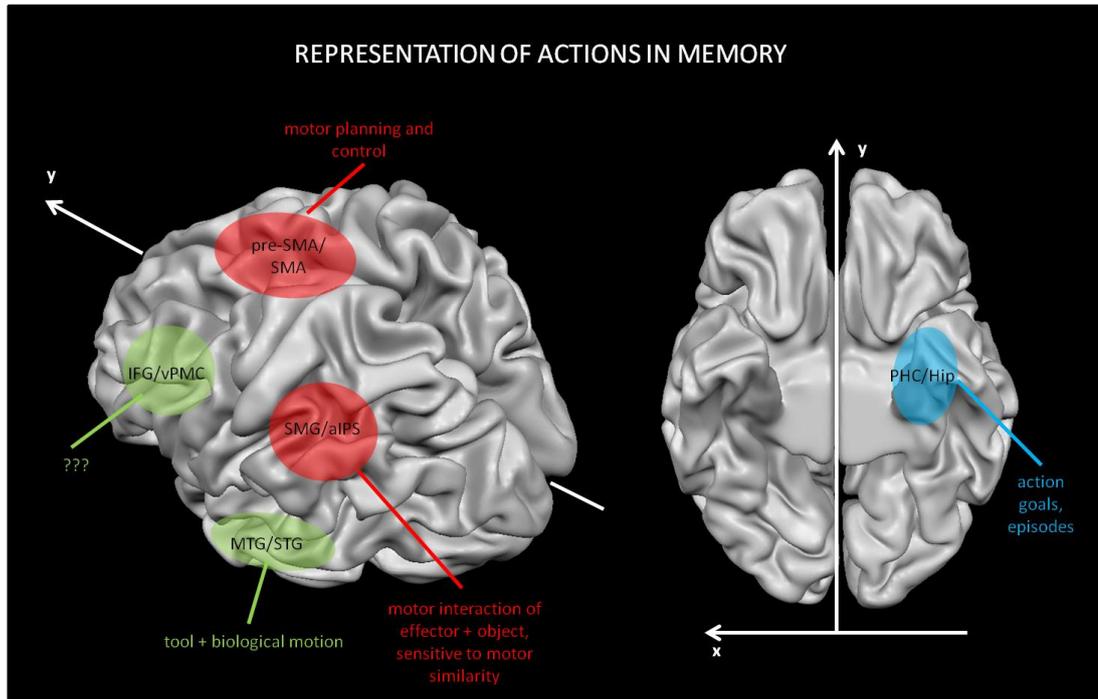

Figure 22. Brain regions involved in the representation of action information in memory. The blobs' colors correspond to the contribution of these regions to the representation of specific action features. Red = means; blue = ends; green = others. Future studies are needed to elucidate the roles of the individual regions in action memory, especially of the anterior putative human mirror neuron region. IFG/vPMC = inferior frontal gyrus/ventral premotor cortex; MTG/STG = middle temporal gyrus/superior temporal gyrus; pre-SMA/SMA = pre-supplementary motor area/supplementary motor area; SMG/aIPS = supramarginal gyrus/anterior intraparietal sulcus; PHC/Hip = parahippocampal cortex/hippocampus.

8. GENERAL DISCUSSION

Finally, I would like to discuss some peculiarities of the reported experiments and raise some possible research questions for future studies. One idea for a possible next experiment can be deducted from the findings of Experiment 2 and Experiment 3. In Experiment 3, we found that action familiarity modulated the representation of means but not the representation ends in memory. It would be interesting to investigate the neural correlates of means and end recognition memory and test whether means and end selective brain regions are differentially modulated by action familiarity. For this purpose, we could define the brain regions which had been identified as being selective for means and end information processing in Experiment 2 as regions of interest. By this method, one could also extend the findings on neural correlates of means and end processing from working memory to long term memory. Furthermore, one could also think of a repetition of Experiment 3 without the use of encoding questions. This would probably yield results that allow us to evaluate the influence of the encoding questions on the representation of means and end information in memory.

It would be interesting to run additional multivariate analyses on the fMRI data from Experiment 1. In the analysis I have reported here, we have computed conjunction analyses in order to investigate the overlap of domain specific brain regions during working memory retention and long term memory retrieval. Using a random-effects-of-conjunction approach, we calculated domain specific overlap in individual subjects and acknowledged variability of the overlapping regions across participants. Recently, a multivariate approach to analyze overlapping activations has gained popularity. Multivoxel pattern analysis (MVPA) has emerged as a powerful tool to investigate patterns of activation across either predefined areas of the brain or the whole brain (Mur, Bandettini, & Kriegeskorte, 2009; Norman, Polyn, Detre, & Haxby, 2006). The advantage of this method is a focus on differences in activation patterns for different informational domains rather than on differential activation levels in a single brain structure. From what we have learned from MVPA

and distributed memory representations (e.g., Lewis-Peacock & Postle, 2008), additional multivariate analyses on the fMRI data of Experiment 1 would be highly informative.

In Experiment 2 and 3, we have used action video clips as stimulus material. In these video clips, object directed actions were being depicted. Pairs of stimuli (S1 and S2 in Experiment 2; encoding and target stimuli in Experiment 3) always involved different objects. In Experiment 2, we also manipulated motor similarity between S1 and S2. This manipulation of motor similarity could be achieved in one of two ways: Either different ways of effector interaction with an unchanged target object were displayed (as in the example with inserting/removing floppy disk) or different means were linked to effector interaction with quite different target objects (as in the example with different types of nutcracker). As a large number of items was needed, we decided to include both types of means manipulation into the study. However, we need to acknowledge that motor similarity is probably correlated with object similarity for some items. This is important - especially regarding the graded means match enhancement effect which we have observed in the aIPS. In future studies, it will be necessary to disentangle the contribution of motor and object similarity in means information processing.

Another topic for future research is the role of the putative anterior mirror neuron region. The left inferior frontal/ventral premotor cortex has been identified in Experiment 1 as a region which is commonly involved in the retention of action information in working memory and its retrieval from long term memory. However, Experiment 2 revealed that this region is not preferentially activated during processing of means or end information in working memory. A major difference between the two fMRI studies was that in Experiment 1, photographs of manipulable objects were presented whereas the stimuli in Experiment 2 were videos of object directed actions. The pattern of results that we have observed in the putative anterior human mirror neuron region would be predicted if the region was automatically involved during action imagery and action observation. This interpretation remains to be tested in future studies. One could think of an experiment in which retention of means and end information is required with either photographs of manipula-

9. OUTLOOK

ble objects or action videos. When contrasted with control conditions involving the same stimuli, the putative anterior mirror neuron regions should be activated in the photograph condition but not in the video condition.

9. OUTLOOK

10. REFERENCES

Akkal, D., Dum, R. P., & Strick, P. L. (2007). Supplementary motor area and presupplementary motor area: Targets of basal ganglia and cerebellar output. *Journal of Neuroscience, 27*, 10659-10673.

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4*, 267-278.

Amador, N., & Fried, I. (2004). Single-neuron activity in the human supplementary motor area underlying preparation for action. *Journal Of Neurosurgery, 100*, 250-259.

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *The psychology of learning and motivation: II.* Oxford: Academic Press.

Bach, P., Gunter, T. C., Knoblich, G., Prinz, W., & Friederici, A. D. (2009). N400-like negativities in action perception reflect the activation of two components of an action representation. *Social Neuroscience, 4*, 212-232.

Bach, P., Peelen, M. V., & Tipper, S. P. (2010). On the role of object information in action observation: An fMRI study. *Cerebral Cortex, 20*, 2798-2809.

Baddeley, A. (1986). *Working memory*. New York: Clarendon Press/Oxford University Press.

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4*, 417-423.

Baddeley, A. (2010). Long-term and working memory: How do they interact? In L. Bäckman & L. Nyberg (Eds.), *Memory, aging and the brain: A Festschrift in honour of Lars-Göran Nilsson.* (pp. 7-23). New York: Psychology Press.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47-90). Hillsdale: Lawrence Erlbaum.

Baddeley, A. D., & Logie, R. H. (1999). Working memory: The multiple-component model. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 28-61). New York: Cambridge University Press.

Bar, M., Aminoff, E., & Ishai, A. (2008). Famous faces activate contextual associations in the parahippocampal cortex. *Cerebral Cortex, 18*, 1233-1238.

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2002). Parallel visual motion processing streams for manipulable objects and human movements. *Neuron, 34*, 149-159.

Beauchamp, M. S., Lee, K. E., Haxby, J. V., & Martin, A. (2003). fMRI responses to video and point-light displays of moving humans and manipulable objects. *Journal of Cognitive Neuroscience, 15*, 991-1001.

Bekkering, H., Wohlschlager, A., & Gattis, M. (2000). Imitation of Gestures in Children is Goal-directed. *Quarterly Journal of Experimental Psychology: Section A, 53*, 153-164.

Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H. J., . . . Seitz, R. J. (2000). Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Human Brain Mapping, 11*, 273-285.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: evidence from neuroimaging. *Experimental Brain Research, 128*, 210-213.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., & Freund, H. J. (1998). Human anterior intraparietal area subserves prehension: a combined lesion and functional MRI activation study. *Neurology, 50*, 1253-1259.

Binney, R. J., Embleton, K. V., Jefferies, E., Parker, G. J. M., & Ralph, M. A. L. (2010). The ventral and inferolateral aspects of the anterior temporal lobe are crucial in semantic memory: Evidence from a novel direct comparison of distortion-corrected fMRI, rTMS, and semantic dementia. *Cerebral Cortex, 20*, 2728-2738.

10. REFERENCES

Blumenfeld, R. S., & Ranganath, C. (2006). Dorsolateral prefrontal cortex promotes long-term memory formation through its role in working memory organization. *Journal Of Neuroscience, 26*, 916-925.

Bodegård, A., Geyer, S., Grefkes, C., Zilles, K., & Roland, P. E. (2001). Hierarchical processing of tactile shape in the human brain. *Neuron, 31*, 317-328.

Bonin, P., Boyer, B., Méot, A., Fayol, M., & Droit, S. (2004). Psycholinguistic norms for action photographs in French and their relationships with spoken and written latencies. *Behavior Research Methods, Instruments & Computers, 36*, 127-139.

Bonin, P., Roux, S., Méot, A., Ferrand, L., & Fayol, M. (2009). Normes pour des clips d'actions. *L'année psychologique, 109*, 271-293.

Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., & Detre, J. A. (2005). Distinctions between manipulation and function knowledge of objects: Evidence from functional magnetic resonance imaging. *Cognitive Brain Research, 23*, 361-373.

Bosch, V., Mecklinger, A., & Friederici, A. D. (2001). Slow cortical potentials during retention of object, spatial, and verbal information. *Cognitive Brain Research, 10*, 219-237.

Brunet, E., Sarfati, Y., Hardy-Baylé, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *NeuroImage, 11*, 157-166.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., . . . Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal Of Neuroscience, 13*, 400-404.

Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain & Language, 89*, 370-376.

Burgess, N., Maguire, E. A., Spiers, H. J., & O'Keefe, J. (2001). A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *NeuroImage, 14*, 439-453.

10. REFERENCES

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience, 9*, 613-625.

Calvo-Merino, B., Ehrenberg, S., Leung, D., & Haggard, P. (2010). Experts see it all: Configural effects in action observation. *Psychological Research, 74*, 400-406.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex, 15*, 1243-1249.

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*, 1905-1910.

Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., . . . Shallice, T. (2008). The different neural correlates of action and functional knowledge in semantic memory: An fMRI study. *Cerebral Cortex, 18*, 740-751.

Carpenter, M., Call, J., & Tomasello, M. (2005). Twelve- and 18-month-olds copy actions in terms of goals. *Developmental Science, 8*, F13-F20.

Chaminade, T., Meltzoff, A. N., & Decety, J. (2002). Does the end justify the means? A PET exploration of the mechanisms involved in human imitation. *NeuroImage, 15*, 318-328.

Cohen, R. L. (1981). On the generality of some memory laws. *Scandinavian Journal of Psychology, 22*, 267-281.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex, 6*, 39-49.

Cowan, N. (1995). *Attention and memory: An integrated framework*. New York: Oxford University Press.

Cowan, N. (1999). An Embedded-Processes Model of working memory. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control.* (pp. 62-101). New York: Cambridge University Press.

10. REFERENCES

Craik, F. I., & Lockhart, R. S. (1972). Levels of processing: A framework for memory research. *Journal of Verbal Learning & Verbal Behavior, 11*, 671-684.

Cross, E. S., Hamilton, A. F., Kraemer, D. J. M., Kelley, W. M., & Grafton, S. T. (2009). Dissociable substrates for body motion and physical experience in the human action observation network. *European Journal of Neuroscience, 30*, 1383-1392.

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral Cortex, 19*, 315-326.

Cuetos, F., & Alija, M. (2003). Normative data and naming times for action pictures. *Behavior Research Methods, Instruments & Computers, 35*, 168-177.

Cunnington, R., Egan, G. F., O'Sullivan, J. D., Hughes, A. J., Bradshaw, J. L., & Colebatch, J. G. (2001). Motor imagery in Parkinson's disease: a PET study. *Movement Disorders, 16*, 849-857.

Cunnington, R., Windischberger, C., & Moser, E. (2005). Premovement activity of the pre-supplementary motor area and the readiness for action: studies of time-resolved event-related functional MRI. *Human Movement Science, 24*, 644-656.

Cunnington, R., Windischberger, C., Robinson, S., & Moser, E. (2006). The selection of intended actions and the observation of others' actions: a time-resolved fMRI study. *NeuroImage, 29*, 1294-1302.

D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 362*, 761-772.

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. *Journal of Verbal Learning & Verbal Behavior, 19*, 450-466.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., . . . Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature, 371*, 600-602.

Deiber, M. P., Ibañez, V., Honda, M., Sadato, N., Raman, R., & Hallett, M. (1998). Cerebral processes related to visuomotor imagery and

10. REFERENCES

generation of simple finger movements studied with positron emission tomography. *NeuroImage, 7*, 73-85.

Della Sala, S., & Logie, R. H. (1993). When working memory does not work: The role of working memory in neuropsychology. In F. Boller & H. Spinnler (Eds.), *Handbook of neuropsychology* (Vol. 8, pp. 1-63). Amsterdam: Elsevier.

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences of the United States of America, 93*, 13494-13499.

Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences, 11*, 379-386.

Doyon, J., Penhune, V., & Ungerleider, L. G. (2003). Distinct contribution of the cortico-striatal and cortico-cerebellar systems to motor skill learning. *Neuropsychologia, 41*, 252-262.

Dudukovic, N. M., Preston, A. R., Archie, J. J., Glover, G. H., & Wagner, A. D. (2011). High-resolution fMRI reveals match enhancement and attentional modulation in the human medial temporal lobe. *Journal of Cognitive Neuroscience, 23*, 670-682.

Duncan, K., Curtis, C., & Davachi, L. (2009). Distinct memory signatures in the hippocampus: Intentional states distinguish match and mismatch enhancement signals. *Journal of Neuroscience, 29*, 131-139.

Ebisch, S. J. H., Babiloni, C., Del Gratta, C., Ferretti, A., Perrucci, M. G., Caulo, M., . . . Romani, G. L. (2007). Human neural systems for conceptual knowledge of proper object use: A functional magnetic resonance imaging study. *Cerebral Cortex, 17*, 2744-2751.

Engel, T. A., & Wang, X.-J. (2011). Same or different? A neural circuit mechanism of similarity-based pattern match decision making. *Journal of Neuroscience, 31*, 6982-6996.

Engelkamp, J. (1986). Nouns and verbs in paired-associate learning: Instructional effects. *Psychological Research, 48*, 153-159.

Engelkamp, J., & Cohen, R. L. (1991). Current issues in memory of action events. *Psychological Research, 53*, 175-182.

10. REFERENCES

Engelkamp, J., & Krumnacker, H. (1980). Imaginale und motorische Prozesse beim Behalten verbalen Materials. *Zeitschrift für experimentelle und angewandte Psychologie, 27*, 511-533.

Engelkamp, J., & Zimmer, H. D. (1985). Motor programs and their relation to semantic memory. *German Journal of Psychology, 9*, 239-254.

Engelkamp, J., & Zimmer, H. D. (1989). Memory for action events: A new field of research. *Psychological Research, 51*, 153-157.

Engelkamp, J., & Zimmer, H. D. (1997). Sensory factors in memory for subject-performed tasks. *Acta Psychologica, 96*, 43-60.

Engelkamp, J., Zimmer, H. D., & Biegelmann, U. E. (1993). Bizarreness effects in verbal tasks and subject-performed tasks. *European Journal of Cognitive Psychology, 5*, 393-415.

Epstein, R. A., & Ward, E. J. (2010). How reliable are visual context effects in the parahippocampal place area? *Cerebral Cortex, 20*, 294-303.

Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (2000). Visuomotor neurons: ambiguity of the discharge or 'motor' perception? *International Journal Of Psychophysiology, 35*, 165-177.

Fiehler, K., Bannert, M. M., Bischoff, M., Blecker, C., Stark, R., Vaitl, D., . . . Rösler, F. (2011). Working memory maintenance of grasp-target information in the human posterior parietal cortex. *NeuroImage, 54*, 2401-2411.

Fiehler, K., Burke, M., Engel, A., Bien, S., & Rösler, F. (2008). Kinesthetic working memory and action control within the dorsal stream. *Cerebral Cortex, 18*, 243-253.

Fiez, J. A., & Tranel, D. (1997). Standardized stimuli and procedures for investigating the retrieval of lexical and conceptual knowledge for actions. *Memory & Cognition, 25*, 543-569.

Fogassi, L., Gallese, V., Buccino, G., Craighero, L., Fadiga, L., & Rizzolatti, G. (2001). Cortical mechanism for the visual guidance of hand grasping movements in the monkey: A reversible inactivation study. *Brain, 124*, 571-586.

Frey, S. H., Vinton, D., Norlund, R., & Grafton, S. T. (2005). Cortical topography of human anterior intraparietal cortex active during visually guided grasping. *Cognitive Brain Research, 23*, 397-405.

10. REFERENCES

Fuster, J. M. (1997). Network memory. *Trends in Neurosciences, 20*, 451-459.

Goh, J. O., Chee, M. W., Tan, J. C., Venkatraman, V., Hebrank, A., Leshikar, E. D., . . . Park, D. C. (2007). Age and culture modulate object processing and object-science binding in the ventral visual area. *Cognitive, Affective & Behavioral Neuroscience, 7*, 44-52.

Goldman-Rakic, P. S. (1995). Architecture of the prefrontal cortex and the central executive. *Annals of the New York Academy of Sciences, 769*, 71-83.

Grafton, S. T., & Hamilton, A. F. (2007). Evidence for a distributed hierarchy of action representation in the brain. *Human Movement Science, 26*, 590-616.

Graham, K. S., Barense, M. D., & Lee, A. C. H. (2010). Going beyond LTM in the MTL: A synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia, 48*, 831-853.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience, 12*, 711-720.

Grossman, E. D., & Blake, R. (2001). Brain activity evoked by inverted and imagined biological motion. *Vision Research, 41*, 1475-1482.

Haggard, P. (2008). Human volition: Towards a neuroscience of will. *Nature Reviews Neuroscience, 9*, 934-946.

Hamilton, A. F., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *Journal of Neuroscience, 26*, 1133-1137.

Hamilton, A. F., & Grafton, S. T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex, 18*, 1160-1168.

Hanakawa, T., Immisch, I., Toma, K., Dimyan, M. A., van Gelderen, P., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology, 89*, 989-1002.

Haruno, M., Wolpert, D. M., & Kawato, M. (2001). MOSAIC model for sensorimotor learning and control. *Neural Computation, 13*, 2201-2220.

10. REFERENCES

Hayes, S. M., Nadel, L., & Ryan, L. (2007). The effect of scene context on episodic object recognition: Parahippocampal cortex mediates memory encoding and retrieval success. *Hippocampus, 17*, 873-889.

Hedden, T., Park, D. C., Nisbett, R., Ji, L.-J., Jing, Q., & Jiao, S. (2002). Cultural variation in verbal versus spatial neuropsychological function across the life span. *Neuropsychology, 16*, 65-73.

Heilman, K. M., & Gonzalez-Rothi, L. J. (2003). Apraxia. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4th ed., pp. 215-235). New York: Oxford University Press.

Herwig, A., Prinz, W., & Waszak, F. (2007). Two modes of sensorimotor integration in intention-based and stimulus-based actions. *Quarterly Journal of Experimental Psychology, 60*, 1540-1554.

Hesse, M. D., Sparing, R., & Fink, G. R. (2009). End or means—The "what" and "how" of observed intentional actions. *Journal of Cognitive Neuroscience, 21*, 776-790.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24*, 849-937.

Howard, L. R., Kumaran, D., Ólafsdóttir, H. F., & Spiers, H. J. (2011). Double dissociation between hippocampal and parahippocampal responses to object-background context and scene novelty. *Journal of Neuroscience, 31*, 5253-5261.

Humphreys, G. W., Forde, E. M. E., & Riddoch, M. J. (2001). The planning and execution of everyday actions. In B. Rapp (Ed.), *The handbook of cognitive neuropsychology: What deficits reveal about the human mind.* (pp. 565-589). New York: Psychology Press.

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nature Reviews Neuroscience, 7*, 942-951.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J.C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286*, 2526.

Jacobs, S., Danielmeier, C., & Frey, S. H. (2010). Human anterior intraparietal and ventral premotor cortices support representations of

10. REFERENCES

grasping with the hand or a novel tool. *Journal of Cognitive Neuroscience, 22*, 2594-2608.

James, W. (1890). Memory. In W. James (Ed.), *The principles of psychology,* (Vol I., pp. 643-689). New York: Henry Holt and Co.

Jäncke, L., Kleinschmidt, A., Mirzazade, S., Shah, N. J., & Freund, H. J. (2001). The role of the inferior parietal cortex in linking the tactile perception and manual construction of object shapes. *Cerebral Cortex, 11*, 114-121.

Jarmasz, J., & Hollands, J. G. (2009). Confidence intervals in repeated-measures designs: The number of observations principle. *Canadian Journal of Experimental Psychology, 63*, 124-138.

Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *NeuroImage, 14*, S103-109.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neurosciences, 18*, 314-320.

Jeannerod, M., & Decety, J. (1995). Mental motor imagery: a window into the representational stages of action. *Current Opinion in Neurobiology, 5*, 727-732.

Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annual Review of Psychology, 59*, 193-224.

Kahana, M. J., Howard, M. W., & Polyn, S. M. (2008). Associative retrieval processes in episodic memory. In H. L. Roediger III (Ed.), *Cognitive psychology of memory,* (Vol. 2). Oxford: Elsevier.

Kellenbach, M. L., Brett, M., & Patterson, K. (2001). Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective & Behavioral Neuroscience, 1*, 207-221.

Kellenbach, M. L., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: The importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience, 15*, 30-46.

10. REFERENCES

Khader, P., Burke, M., Bien, S., Ranganath, C., & Rösler, F. (2005). Content-specific activation during associative long-term memory retrieval. *NeuroImage, 27*, 805-816.

Khader, P., Heil, M., & Rösler, F. (2005). Material-specific long-term memory representations of faces and spatial positions: evidence from slow event-related brain potentials. *Neuropsychologia, 43*, 2109-2124.

Khader, P., Ranganath, C., Seemüller, A., & Rösler, F. (2007). Working memory maintenance contributes to long-term memory formation: Evidence from slow event-related brain potentials. *Cognitive, Affective & Behavioral Neuroscience, 7*, 212-224.

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience, 29*, 10153-10159.

Knopf, M. (1991). Having shaved a kiwi fruit: Memory of unfamiliar subject-performed actions. *Psychological Research, 53*, 203-211.

Knopf, M., & Neidhardt, E. (1989). Aging and memory for action events: The role of familiarity. *Developmental Psychology, 25*, 780-786.

Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., Dubeau, M.-C., Mazziotta, J. C., & Iacoboni, M. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex, 12*, 847-855.

Kurata, K., Tsuji, T., Naraki, S., Seino, M., & Abe, Y. (2000). Activation of the dorsal premotor cortex and pre-supplementary motor area of humans during an auditory conditional motor task. *Journal of Neurophysiology, 84*, 1667-1672.

Lacourse, M. G., Orr, E. L. R., Cramer, S. C., & Cohen, M. J. (2005). Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *NeuroImage, 27*, 505-519.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., . . . Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping, 10*, 120-131.

Lehnert, G., & Zimmer, H. D. (2008). Common coding of auditory and visual spatial information in working memory. *Brain Research, 1230*, 158-167.

10. REFERENCES

Levy, R., & Goldman-Rakic, P. S. (2000). Segregation of working memory functions within the dorsolateral prefrontal cortex. *Experimental Brain Research, 133*, 23-32.

Lewis-Peacock, J. A., & Postle, B. R. (2008). Temporary activation of long-term memory supports working memory. *Journal of Neuroscience, 28*, 8765-8771.

Logie, R. H. (1995). *Visuo-spatial working memory.* Hove: Lawrence Erlbaum Associates.

Luck, D., Danion, J.-M., Marrer, C., Pham, B.-T., Gounot, D., & Foucher, J. (2010). The right parahippocampal gyrus contributes to the formation and maintenance of bound information in working memory. *Brain and Cognition, 72*, 255-263.

Malouin, F., Richards, C. L., Jackson, P. L., Dumas, F., & Doyon, J. (2003). Brain activations during motor imagery of locomotor-related tasks: a PET study. *Human Brain Mapping, 19*, 47-62.

Masterson, J., & Druks, J. (1998). Description of a set of 164 nouns and 102 verbs matched for printed word and frequency, familiarity and age-of-acquisition. *Journal of Neurolinguistics, 11*, 331-354.

Masumoto, K., Yamaguchi, M., Sutani, K., Tsuneto, S., Fujita, A., & Tonoike, M. (2006). Reactivation of physical motor information in the memory of action events. *Brain Research, 1101*, 102-109.

Mecklinger, A. (2010). The control of long-term memory: brain systems and cognitive processes. *Neuroscience and Biobehavioral Reviews, 34*, 1055-1065.

Mecklinger, A., Gruenewald, C., Weiskopf, N., & Doeller, C. F. (2004). Motor affordance and its role for visual working memory: evidence from fMRI studies. *Experimental Psychology, 51*, 258-269.

Mecklinger, A., & Pfeifer, E. (1996). Event-related potentials reveal topographical and temporal distinct neuronal activation patterns for spatial and object working memory. *Cognitive Brain Research, 4*, 211-224.

Miller, E. K., & Desimone, R. (1994). Parallel neuronal mechanisms for short-term memory. *Science, 263*, 520-522.

10. REFERENCES

Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience, 16*, 5154-5167.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960). Plans for remembering. In G. A. Miller, E. Galanter & K. H. Pribram (Eds.), *Plans and the structure of behavior,* (pp. 125-138). New York: Henry Holt and Co.

Mohr, G., Engelkamp, J., & Zimmer, H. D. (1989). Recall and recognition of self-performed acts. *Psychological Research, 51*, 181-187.

Morris, J. P., Pelphrey, K. A., & McCarthy, G. (2008). Perceived causality influences brain activity evoked by biological motion. *Social Neuroscience, 3*, 16-25.

Moses, S. N., Brown, T. M., Ryan, J. D., & McIntosh, A. R. (2010). Neural system interactions underlying human transitive inference. *Hippocampus, 20*, 894-901.

Mur, M., Bandettini, P. A., & Kriegeskorte, N. (2009). Revealing representational content with pattern-information fMRI—An introductory guide. *Social Cognitive and Affective Neuroscience, 4*, 101-109.

Neumann, O. (1990). Direct parameter specification and the concept of perception. *Psychological Research, 52*, 207-215.

Newman, S. D., Klatzky, R. L., Lederman, S. J., & Just, M. A. (2005). Imagining material versus geometric properties of objects: an fMRI study. *Cognitive Brain Research, 23*, 235-246.

Nisbett, R. E., & Miyamoto, Y. (2005). The influence of culture: holistic versus analytic perception. *Trends in Cognitive Sciences, 9*, 467-473.

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences, 10*, 424-430.

Nyberg, L., Petersson, K. M., Nilsson, L. G., Sandblom, J., Aberg, C., & Ingvar, M. (2001). Reactivation of motor brain areas during explicit memory for actions. *NeuroImage, 14*, 521-528.

Oliver, R. T., & Thompson-Schill, S. L. (2003). Dorsal stream activation during retrieval of object size and shape. *Cognitive, Affective & Behavioral Neuroscience, 3*, 309-322.

10. REFERENCES

Owen, A. M. (1997). The functional organization of working memory processes within human lateral frontal cortex: The contribution of functional neuroimaging. *European Journal of Neuroscience, 9*, 1329-1339.

Owen, A. M., Herrod, N. J., Menon, D. K., Clark, J. C., Downey, S. P. M. J., Carpenter, T. A., . . . Pickard, J. D. (1999). Redefining the functional organization of working memory processes within human lateral prefrontal cortex. *European Journal of Neuroscience, 11*, 567-574.

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience, 6*, 97-107.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*, 976-987.

Pelphrey, K. A., Mitchell, T. V., McKeown, M. J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: Controlling for meaningful coherent motion. *Journal of Neuroscience, 23*, 6819-6825.

Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience, 16*, 1706-1716.

Petrides, M. (1995). Functional organization of the human frontal cortex for mnemonic processing. Evidence from neuroimaging studies. *Annals of the New York Academy of Sciences, 769*, 85-96.

Petrides, M. (2000). Dissociable roles of mid-dorsolateral prefrontal and anterior inferotemporal cortex in visual working memory. *Journal of Neuroscience, 20*, 7496-7503.

Picard, N., & Strick, P. L. (1996). Motor areas of the medial wall: a review of their location and functional activation. *Cerebral Cortex, 6*, 342-353.

Platz, T., & Mauritz, K. H. (1995). Human motor planning, motor programming, and use of new task-relevant information with different apraxic syndromes. *European Journal of Neuroscience, 7*, 1536-1547.

Polyn, S. M., & Kahana, M. J. (2008). Memory search and the neural representation of context. *Trends in Cognitive Sciences, 12*, 24-30.

10. REFERENCES

Polyn, S. M., Natu, V. S., Cohen, J. D., & Norman, K. A. (2005). Category-specific cortical activity precedes retrieval during memory search. *Science, 310*, 1963-1966.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience, 139*, 23-38.

Prinz, W. (1992). Why don't we perceive our brain states? *European Journal of Cognitive Psychology, 4*, 1-20.

Prinz, W. (1997). Perception and Action Planning. *European Journal of Cognitive Psychology, 9*(2), 129-154.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience, 18*, 2188-2199.

Ranganath, C. (2006). Working memory for visual objects: complementary roles of inferior temporal, medial temporal, and prefrontal cortex. *Neuroscience, 139*, 277-289.

Ranganath, C. (2010). A unified framework for the functional organization of the medial temporal lobes and the phenomenology of episodic memory. *Hippocampus, 20*, 1263-1290.

Ranganath, C., & Blumenfeld, R. S. (2005). Doubts about double dissociations between short- and long-term memory. *Trends in Cognitive Sciences, 9*, 374-380.

Ranganath, C., Cohen, M. X., & Brozinsky, C. J. (2005). Working memory maintenance contributes to long-term memory formation: neural and behavioral evidence. *Journal of Cognitive Neuroscience, 17*, 994-1010.

Ranganath, C., Cohen, M. X., Dam, C., & D'Esposito, M. (2004). Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *Journal of Neuroscience, 24*, 3917-3925.

Ranganath, C., & D'Esposito, M. (2005). Directing the mind's eye: prefrontal, inferior and medial temporal mechanisms for visual working memory. *Current Opinion in Neurobiology, 15*, 175-182.

10. REFERENCES

Ranganath, C., DeGutis, J., & D'Esposito, M. (2004). Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Cognitive Brain Research, 20*, 37-45.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *Journal of Neuroscience, 20*, RC108-RC108.

Rawley, J. B., & Constantinidis, C. (2010). Effects of task and coordinate frame of attention in area 7a of the primate posterior parietal cortex. *Journal of Vision, 12,* 1-16.

Rice, N. J., Tunik, E., & Grafton, S. T. (2006). The anterior intraparietal sulcus mediates grasp execution, independent of requirement to update: New insights from transcranial magnetic stimulation. *Journal of Neuroscience, 26*, 8176-8182.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131-141.

Roland, P. E., O'Sullivan, B., & Kawashima, R. (1998). Shape and roughness activate different somatosensory areas in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 3295-3300.

Rossion, B., Bodart, J.-M., Pourtois, G., Thioux, M., Bol, A., Cosnard, G., . . . De Volder, A. (2000). Functional imaging of visual semantic processing in the human brain. *Cortex, 36*, 579-591.

Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: a state of activated long-term memory. *Behavioral and Brain Sciences, 26*, 709-728.

Rumiati, R. I., & Tessari, A. (2002). Imitation of novel and well-known actions: The role of short-term memory. *Experimental Brain Research, 142*, 425-433.

Rumiati, R. I., Weiss, P. H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., & Fink, G. R. (2005). Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. *Journal of Cognitive Neuroscience, 17*, 1420-1431.

10. REFERENCES

Russ, M. O., Mack, W., Grama, C.-R., Lanfermann, H., & Knopf, M. (2003). Enactment effect in memory: evidence concerning the function of the supramarginal gyrus. *Experimental Brain Research, 149*, 497-504.

Rypma, B., Berger, J. S., & D'Esposito, M. (2002). The influence of working-memory demand and subject performance on prefrontal cortical activity. *Journal of Cognitive Neuroscience, 14*, 721-731.

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus, 9*, 7-24.

Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review, 82*, 225-260.

Schon, K., Hasselmo, M. E., LoPresti, M. L., Tricarico, M. D., & Stern, C. (2004). Persistence of parahippocampal representation in the absence of stimulus input enhances long-term encoding: A functional magnetic resonance imaging study of subsequent memory after a delayed match-to-sample task. *Journal of Neuroscience, 24*, 11088-11097.

Schwitter, V., Boyer, B., Méot, A., Bonin, P., & Laganardo, M. (2004). French normative data and naming times for action pictures. *Behavior Research Methods, Instruments & Computers, 36*, 564-576.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery & Psychiatry, 20*, 11-21.

Simons, J. S. (2009). Constraints on cognitive theory from neuroimaging studies of source memory. In F. Rösler, C. Ranganath, B. Röder & R. H. Kluwe (Eds.), *Neuroimaging of human memory: Linking cognitive processes to neural systems,* (pp. 405-425). New York: Oxford University Press.

Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience, 4*, 637-648.

Slotnick, S. D. (2004). Visual memory and visual perception recruit common neural substrates. *Behavioral and Cognitive Neuroscience Reviews, 3*, 207-221.

10. REFERENCES

Smith, E. E., & Jonides, J. (1997). Working memory: a view from neuroimaging. *Cognitive Psychology, 33*, 5-42.

Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: applications to dementia and amnesia. *Journal of Experimental Psychology. General, 117*, 34-50.

Spunt, R. P., Satpute, A. B., & Lieberman, M. D. (2011). Identifying the what, why, and how of an observed action: An fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience, 23*, 63-74.

Squire, L. R. (2004). Memory systems of the brain: a brief history and current perspective. *Neurobiology of Learning and Memory, 82*, 171-177.

Suchan, B. (2008). Neuroanatomical correlates of processing in visual and visuospatial working memory. *Cognitive Processing, 9*, 45-51.

Szekely, A., D'Amico, S., Devescovi, A., Federmeier, K., Herron, D., Iyer, G., . . . Bates, E. (2005). Timed action and object naming. *Cortex, 41*, 7-25.

Szekely, A., Jacobsen, T., D'Amico, S., Devescovi, A., Andonova, E., Herron, D., . . . Bates, E. (2004). A new on-line resource for psycholinguistic studies. *Journal of Memory and Language, 51*, 247-250.

Talairach, J., Tournoux, M. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Georg Thieme.

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review, 80*, 352-373.

Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience, 8*, 505-511.

Tunik, E., Lo, O.-Y., & Adamovich, S. V. (2008). Transcranial magnetic stimulation to the frontal operculum and supramarginal gyrus disrupts planning of outcome-based hand-object interactions. *Journal of Neuroscience, 28*, 14422-14427.

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *NeuroImage, 36*, T77-T86.

10. REFERENCES

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing. a neurophysiological study. *Neuron, 31*, 155-165.

Umla-Runge, K., Zimmer, H. D., Krick, C. M., & Reith, W. (2011). fMRI correlates of working memory: Specific posterior representation sites for motion and position information. *Brain Research, 1382*, 206-218.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In M. A. G. R. J. W. M. D.J. Ingle (Ed.), *Analysis of visual behavior* (pp. 549-586). Cambrige: MIT Press.

Vaidya, C. J., Zhao, M., Desmond, J. E., & Gabrieli, J. D. E. (2002). Evidence for cortical encoding specificity in episodic memory: memory-induced re-activation of picture processing areas. *Neuropsychologia, 40*, 2136-2143.

Ventre-Dominey, J., Bailly, A., Lavenne, F., Lebars, D., Mollion, H., Costes, N., & Dominey, P. F. (2005). Double dissociation in neural correlates of visual working memory: a PET study. *Cognitive Brain Research, 25*, 747-759.

Vingerhoets, G. (2008). Knowing about tools: Neural correlates of tool familiarity and experience. *NeuroImage, 40*, 1380-1391.

Vingerhoets, G., Acke, F., Vandemaele, P., & Achten, E. (2009). Tool responsive regions in the posterior parietal cortex: Effect of differences in motor goal and target object during imagined transitive movements. *NeuroImage, 47*, 1832-1843.

Vingerhoets, G., Vandekerckhove, E., Honoré, P., Vandemaele, P., & Achten, E. (2011). Neural correlates of pantomiming familiar and unfamiliar tools: Action semantics versus mechanical problem solving? *Human Brain Mapping, 32*, 905-918.

von Essen, J. D., & Nilsson, L.-G. (2003). Memory effects of motor activation in subject-performed tasks and sign language. *Psychonomic Bulletin & Review, 10*, 445-449.

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: a meta-analysis. *Cognitive, Affective & Behavioral Neuroscience, 3*, 255-274.

10. REFERENCES

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences, 9*, 445-453.

Wang, L., Fu, X., Aschersleben, G., & Zimmer, H. (in press). Familiarity and complexity modulate the way children imitate tool-use actions: A cross-cultural study. *Journal of Cognitive Psychology.*

Watanabe, M., & Munoz, D. P. (2010). Presetting basal ganglia for volitional actions. *Journal of Neuroscience, 30*, 10144-10157.

Waugh, N. C., & Norman, D. A. (1965). Primary memory. *Psychological Review, 72*, 89-104.

Wheeler, M. E., Petersen, S. E., & Buckner, R. L. (2000). Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proceedings of the National Academy of Sciences of the United States of America, 97*, 11125-11129.

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion In Neurobiology, 8*, 227-233.

Woloszyn, L., & Sheinberg, D. L. (2009). Neural dynamics in inferior temporal cortex during a visual working memory task. *Journal of Neuroscience, 29*, 5494-5507.

Zalla, T., Labruyère, N., Clément, A., & Georgieff, N. (2010). Predicting ensuing actions in children and adolescents with autism spectrum disorders. *Experimental Brain Research, 201*, 809-819.

Zimmer, H. D. (2008). Visual and spatial working memory: From boxes to networks. *Neuroscience and Biobehavioral Reviews, 32*, 1373-1395.

Zimmer, H. D., Helstrup, T., & Nilsson, L.-G. (2007). Action events in everyday life and their remembering. In S. Magnussen & T. Helstrup (Eds.), *Everyday memory,* (pp. 57-91). New York: Psychology Press.

Zimmer, H. D., Mecklinger, A., Lindenberger, U. (2004). Levels of binding: Types, mechanisms and functions of binding in remembering. In A. Mecklinger, Zimmer, H., Lindenberger, U. (Ed.), *Bound in Memory.* Aachen:Shaker.

10. REFERENCES

ABBREVIATIONS

3D = three-dimensional

AC = anterior commissure

AG = angular gyrus

aIPS = anterior intraparietal sulcus

ANOVA = analysis of variance

BA = Brodmann area

EPI = echo-planar imaging

EPT = experimenter performed task

ERP = event-related potential

FFA = fusiform face area

fMRI = functional magnetic resonance imaging

FOV = field of view

FWHM = full width at half maximum

HSD = honestly significant difference

Hz = Hertz

IFG = inferior frontal gyrus

IPC = inferior parietal cortex

IPL = inferior parietal lobe

LG = lingual gyrus

LH = left hemisphere

MEG = magnetoencephalography

mm = millimeter

MNS = mirror neuron system

MR = magnetic resonance

ms = millisecond

MTG = middle temporal gyrus

MTL = medial temporal lobe

MVPA = multi voxel pattern analysis

PC = a) personal computer, b) posterior cingulate, c) posterior commissure

PET = positron emission tomography

PMC = premotor cortex

PPA = parahippocampal place area

Prec = precuneus

pre-SMA = pre-supplementary motor area

pSTS = posterior superior temporal sulcus

RH = right hemisphere

SD = standard deviation

SMA = supplementary motor area

SPC = superior parietal cortex

SPT = subject performed task

STS = superior temporal sulcus

T = Tesla

TE = echo time

TMS = transcranial magnetic stimulation

ABBREVIATIONS

TR = repetition time

vPMC = ventral premotor cortex

VT = verbal task

ABBREVIATIONS

ACKNOWLEDGEMENTS

Dekan: Prof. Dr. Jochen Kubiniok

Berichterstatter: Prof. Dr. Hubert Zimmer

                        Prof. Dr. Gisa Aschersleben

Tag der Disputation: 21.12.2011

CURRICULUM VITAE

Name	Katja Umla-Runge
Birth	December 8, 1978, Saarbrücken, Germany
Marital status	married, two children

Education

2011	PhD in psychology, Saarland University, Saarbrücken
2006 -2011	PhD student in psychology, Saarland University, Saarbrücken
2005	Diploma in psychology, Saarland University, Saarbrücken
1999-2005	Studies in psychology, Saarland University, Saarbrücken and Macquarie University, Sydney, Australia
1998	Abitur, Christian v. Mannlich Gymnasium, Homburg/Saar

Professional experience

from 2012	Postdoctoral research associate, School of Psychology, Cardiff University, UK
2008 – 2011	Doctoral scholarship within the International Research Training Group "Adaptive Minds - Neural and Environmental Constraints on Learning and Memory". Saarland University, Saarbrücken, Germany and Chinese Academy of Sciences, Beijing, China
2006 - 2008	Post-graduate research assistant, Brain & Cognition Unit, Saarland University, Saarbrücken
2003-2005	Student research assistant, Unit of Experimental Cogni-

	tive Psychology, Saarland University, Saarbrücken
2003-2005	Student research assistant, Unit of Social Psychology, Saarland University, Saarbrücken
2003	Internship in the neuropsychological rehabilitation team of Waldklinik Jesteburg
2000-2002	Tutor in Quantitative Methods of Psychology, Saarland University, Saarbrücken