



Unimodal and crossmodal processing of visual and kinesthetic stimuli in working memory

Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)

dem
Fachbereich Psychologie
der Philipps-Universität Marburg
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Anna Christine Seemüller
aus Darmstadt

Marburg/Lahn 2010

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Table of contents

I.	Cumulus	4
1.	Introduction	4
1.1	Visual working memory	5
1.2	Kinesthetic working memory	7
1.3	Crossmodal working memory	9
2.	Overview	14
2.1	Pilot study	17
2.2	Study I	18
2.3	Study II	19
2.4	General conclusions	20
3.	References	26
II.	Experimental studies	34

Pilot study: **Unimodal and crossmodal comparison of visual and kinesthetic stimuli**

Study I: Seemüller, A., Fiehler, K., & Rösler, F. (2010). **Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories.** *Acta Psychologica* doi: 10.1016/j.actpsy.2010.09.014

Study II: Seemüller, A., & Rösler, F. (submitted). **EEG-power and -coherence changes in a unimodal and a crossmodal working memory task with visual and kinesthetic stimuli.** *International Journal of Psychophysiology*

III. Zusammenfassung

I. Cumulus

1. Introduction

Our everyday life requires us to handle objects so we can interact with our environment. As defined by the Merriam-Webster Online Dictionary, an object is “something material that may be perceived by the senses”, most commonly vision, hearing, touch, and kinesthesia. In order to recognize and compare objects within or across modalities, object representations built by one sensory modality have to be matched with those obtained from the same sense or other senses. It is not yet understood how objects are represented and maintained to allow a unimodal or crossmodal comparison, which working memory processes enable this comparison, and what underlying neural processes play a role.

In this thesis, specific aspects of unimodal and crossmodal object processing were investigated, i.e., the processing of visually or kinesthetically perceived object features in unimodal and crossmodal working memory tasks. The kinesthetic modality together with the tactile modality forms the haptic sense and refers to the sensory processing of perceived movement direction and spatial position, for example, of one’s own hand (for a detailed definition, see section 1.2).

Object features can be classified as geometric (e.g., shape, size) or as material (e.g., texture, hardness, and temperature) (Klatzky & Lederman, 1993; see also Klatzky & Lederman, 2002), also referred to as macrogeometric and as microgeometric (O’Sullivan, Roland, & Kawashima, 1994; Roland, O’Sullivan, & Kawashima, 1998; see Gallace & Spence, 2009, for a review). While geometric features are specific to an object, material features are independent of a particular object. An extended definition comprises a third class of spatial object features (e.g., location) (see Gallace & Spence, 2009, for a review). Moreover, object features may be invariant across modalities, i.e., provide information that can be perceived by more than one sensory modality, like shape, texture, and location, or they may be specific to a single sensory modality such as color or temperature (Lewkowicz, 1994; Lewkowicz, 2000). The two-dimensional simple components of object shapes investigated in the present studies fall into the class of macrogeometric, modality-invariant object features.

In the following, an overview of the previous literature on unimodal visual object processing (section 1.1) and kinesthetic object processing (section 1.2) is given in the first

part. Then, past findings on crossmodal object processing (section 1.3) are presented as well as its implications for the present thesis are introduced. In the second part of the cumulus, the main research questions leading to the outline of the studies and a short overview of the studies will be presented. This is followed by the general conclusions of the present thesis. Finally, a summary of the thesis will be given in German.

1.1 Visual working memory

The processing of visually perceived objects has been intensely studied in the past, providing insights how a visual object shape is represented in working memory and which brain structures are involved in its processing and maintenance. Recognizing an object that has previously been perceived or comparing two objects that have been presented at different time points, relies on working memory which has been defined as “the temporary retention of information that was just experienced but no longer exists in the external environment, or was just retrieved from long-term memory” (D’Esposito, 2007, p. 761). Based on cognitive models, working memory representations, i.e., representations of previously perceived information that are maintained over a certain time period, have a higher activation level than irrelevant representations that are not maintained in working memory. Thus, these different activation levels allow the discrimination of task-relevant and task-irrelevant representations for a successful performance (Anderson, 1983; Cowan, 1988, 1999). This approach has been transferred to neural models by proposing that working memory representations rely on the activation of the same neuroanatomical structures that have been involved in their sensory processing (D’Esposito, 2007; Postle, 2006). Empirical evidence supporting this hypothesis, also known as ‘sensory recruitment hypothesis’, has been found in studies on human visual working memory (see D’Esposito, 2007; Postle, 2006, for an overview) and in studies on sensory working memory of primates (see Pasternak & Greenlee, 2005, for an overview). Moreover, it has been proposed as a general theory for long-term memory storage and retrieval (McClelland, McNaughton, & O’Reilly, 1995).

In particular, specific geometrical shapes, such as angles that are perceived as abrupt orientation changes, might be processed and maintained over several seconds in early visual areas such as V2 and V4 (Connor, Brincat, & Pasupathy, 2007; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009; Tootell, Tsao, & Vanduffel, 2003). More commonly, the encoding and maintenance of objects and geometrical object shape is related to higher-

order visual cortex areas such as the lateral occipital complex (LOC) and inferior temporal cortex in the ventral processing stream (e.g., Banati, Goerres, Tjoa, Aggleton, & Grasby, 2000; Grefkes, Weiss, Zilles, & Fink, 2002; Gazzaley, Rissman, & D'Esposito, 2004; Hadjikhani & Roland, 1998; Malach et al., 1995; Ranganath & D'Esposito, 2005; see Connor et al., 2007; Grill-Spector & Malach, 2004, for overviews). This also seems to be the case for motion-defined object shape, i.e., shapes perceived via patterns of moving dots, which has been associated with LOC activity (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998). Nevertheless, recent studies suggest that motion-defined object stimuli are represented in ventral and dorsal stream areas, i.e., in LOC and the human motion complex in the occipito-temporal cortex (hMT+) which is known to be sensitive to motion and motion direction (Lehky & Sereno, 2007; Sereno, Trinath, Augath, & Logothetis, 2002; Kriegeskorte et al., 2003; see Farivar, 2009, for an overview on dorsal-ventral interactions, and Grill-Spector & Malach, 2004, on visual motion processing). Again, motion direction seems to be maintained in hMT+ (Silvanto & Cattaneo, 2010) and simple shape information in extrastriate visual cortex areas including hMT+ (Tallon-Baudry, Bertrand, & Fischer, 2001).

The visual working memory model for objects proposed by Ranganath (2006) extends the sensory recruitment hypothesis and is based on two principles. The first principle relies on the hierarchical processing of visual information, arguing that the maintenance of this information is probably possible at multiple processing stages. While low-level object features may be maintained in early visual cortex areas, overall object representations may be maintained in higher-order visual cortex areas (Pasternak & Greenlee, 2005; Ranganath, 2006; Ranganath & D'Esposito, 2005). Among others, this has implications for behavioral tasks that investigate working memory maintenance by presenting an additional behavioral task during the retention interval (dual-task paradigm). This additional task might impair the working memory representations differentially, i.e., it may disturb representations at one level, whereas representations at other levels may remain undisturbed. The second principle proposes that working memory maintenance is constructive. This means that representations in visual cortex areas can be changed and stabilized by top-down processes, i.e., they may be recoded in order to allow active maintenance. In particular, this implicates that maintenance can consist of more than one processing stage. During the first seconds of maintenance, top-down cognitive processes are recruited to build a stable representation of the previously perceived visual information, i.e., re-instantiate the corresponding activity pattern. A second stage then involves the relatively effortless maintenance of this information without external

stimulation. Similarly, two components of short-term maintenance, an initial short-term consolidation component and a more automatic component of actual working memory maintenance, were suggested by Jolicœur and Dell'Acqua (1998) on the basis of behavioral findings in a dual-task study. Based on these principles and neuroanatomical findings, the model argues that visual objects and object features are maintained in the previously described visual cortex areas through persistent activity. In addition, top-down mechanisms facilitate this activation, e.g., feedback from medial temporal lobe regions. Top-down input, for example from the prefrontal cortex, can facilitate or inhibit representations and is involved in their manipulation.

1.2 Kinesthetic working memory

Besides visual input, object processing is based on haptic information, if available, which can be structured into tactile or cutaneous sensory input and kinesthetic sensory information, according to the sensory systems involved (Gibson, 1966; Schiffman, 1990). Tactile input is processed by mechanoreceptors in the skin, while kinesthetic sensory information is based on mechanoreceptors in the joints, muscles, tendons, and ligaments (McCloskey, 1978), thus providing information about movement direction and position of the limbs. Because object encoding and recognition can contain either active exploration of an object or passive perception of object information, further distinctions can be made on the basis of active or passive movement involved. Loomis and Lederman (1986) defined five different categories: (i) tactile (cutaneous) perception, (ii) passive kinesthetic perception (kinesthetic afferents respond without voluntary movement), (iii) passive haptic perception (cutaneous and kinesthetic afferents respond without voluntary movement), (iv) active kinesthetic perception, and (v) active haptic perception (see also Klatzky & Lederman, 2002; Gallace & Spence, 2009). The present thesis focuses on the processing of kinesthetic sensory information which corresponds either to category (ii) or (iii), since cutaneous information might have contributed to a small extent.

Like the visual modality, the kinesthetic sense is able to acquire object shape, which can be shared across modalities. This means that it is possible to recognize a previously seen object in the kinesthetic modality at another point in time or vice versa. Thus, a functional equivalence between both modalities seems to exist, although the spatial range of each modality may vary broadly (Newell, 2004). While the encoding of kinesthetic object shape is

based on a serial or sequential acquisition of information in a limited spatial range next to our body, visual object information can be processed in a parallel way and can be acquired in a wider spatial range. Comparing performance in tasks using two- or three-dimensional geometric stimulus features mostly led to a better results in visual versus haptic comparison tasks (see Walk & Pick, 1981, for a review). This might be due to the same duration of stimulus presentation for both modalities in these early studies, yielding an advantage of vision over haptics. If the acquisition of object information is adjusted to the haptic modality, either by providing sequential visual input (Loomis, 1990; Loomis, Klatzky, & Lederman, 1991) or less time for visual encoding (Lacey & Campbell, 2006; Newell, Ernst, Tjan, & Bühlhoff, 2001), behavioral performance is comparable across modalities. This has also been found for stimuli presented sequentially in the visual and kinesthetic modality (Reuschel, Drewing, Henriques, Rösler, & Fiehler, 2010).

The idea that the same cortex areas are recruited for the maintenance and storage of information that were involved in its sensory processing has also been proposed for the haptic/tactile modality (Gallace & Spence, 2009; Pasternak & Greenlee, 2005), although processing of haptic and especially kinesthetic object information is sparse compared to visual object processing. Haptic processing of geometrical shapes is associated with early somatosensory areas and higher-level areas like the supramarginal gyrus and adjacent areas of the intraparietal sulcus (Bodegard et al., 2001; O'Sullivan et al., 1994; Roland et al., 1998). Other studies suggest an involvement of the secondary somatosensory cortex and the insula in haptic object processing (Reed, Shoham, & Halgren, 2004; see also Mishkin, 1979). Specifically, kinesthetic information is processed in similar cortex regions, including the early somatosensory cortex, supplementary motor area and inferior parietal cortex (Druschky et al., 2003; Mima et al., 1999; Radovanovic et al., 2002; Weiller et al., 1996). Working memory maintenance of haptic object information has been associated, among others, with the secondary somatosensory cortex (Bonda, Petrides, & Evans, 1996), the posterior parietal cortex, the frontal cortex and the insula (e.g. Reed, Caselli, & Farah, 1996; Reed et al., 2004), suggesting that besides unisensory cortex areas other brain structures seem to be functionally involved as well (see also Gallace & Spence, 2009).

The temporal stability of these representations during working memory maintenance has been investigated in few behavioral experiments leading to varying conclusions. While some studies observed a decrease in performance with longer maintenance intervals suggesting a decay function of haptic working memory (Kiphart, Hughes, Simmons, & Cross,

1992; Millar, 1974), others did not observe performance changes during longer retention intervals (Bowers, Mollenhauer, & Luxford, 1990). For example, Kiphart et al. (1992) investigated the maintenance of complex objects that were encoded for three seconds and had to be held in working memory for 5, 15, 30, or 45 seconds before comparing them to another object. Performance decreased after 15 seconds for both high and low performance groups. In contrast, maintenance was comparable for 5, 10, and 20 seconds for haptically explored simple geometric shapes in a shared-attention recall task (Bowers et al., 1990). When working memory is compared directly for the tactile and the visual modality, performance decreased faster in the tactile than in the visual modality as measured by the number of correct rejections at 0, 15, and 30 seconds of delay (Woods, O'Modhrain, & Newell, 2004). On the other hand, working memory performance was found to be comparable for intervals ranging from 1 to 30 seconds in visual and tactile matching tasks (Garvill & Molander, 1973) and for intervals up to 20 seconds in movement positioning tasks (Martenuik & Rodney, 1979)

1.3 Crossmodal working memory

Object information that is initially perceived separately in visual and kinesthetic modalities has to be integrated or compared in order to enable object recognition across modalities. Since research on visual and haptic crossmodal processing is only at the beginning, so far no unitary theory has been phrased. Thus, different views arising from behavioral, neuroimaging, and electrophysiological findings will be presented.

Based on the mode of stimulus presentation and the type of processing required, two types of crossmodal tasks can be distinguished (Calvert, 2001). In crossmodal integration tasks, object information is provided simultaneously in more than one modality, leading to the perception of a unitary object. In crossmodal matching tasks, object information is presented sequentially. In that case, a comparison across two distinct objects is necessary. While a simultaneous object presentation relies mainly on integration processes that yield a unitary percept, a sequential object presentation that comprises a comparison of distinct representations depends on working memory processes, especially working memory maintenance. This leads to the question how visual and kinesthetic object information is represented in working memory in order to allow crossmodal comparison. Based on previous research on visual and haptic working memory, two opposing theoretical hypotheses emerged. One suggests that crossmodal object recognition is based on multisensory

representations that integrate information across modalities; the other assumes modality-specific representations which are transformed into each other for crossmodal recognition.

The existence of multisensory representations is supported by crossmodal priming studies showing comparable priming for visually and haptically learned objects (Easton, Greene, & Srinivas, 1997; Reales & Ballesteros, 1999). In particular, Easton et al. (1997) used unfamiliar two-dimensional shapes (three-line patterns) as learning material that were presented either in the visual modality on a computer screen or in the haptic modality as a set of vibrating pins and as a raised line-drawings. After a five minutes distractor task, participants were tested in a priming test that presented the stimulus either visually or haptically before it had to be drawn. In the visual and haptic priming test, facilitation of learned two-dimensional shapes compared to non-studied shapes occurred in both tasks independently of the encoding modality, i.e. whether the shape had been learned visually or haptically. This facilitation irrespective of the encoding modality was also found for three-dimensional objects. In conclusion, these results suggest the existence of shared representations. A potential neuronal basis for multisensory haptic representations is provided by neuroimaging studies observing activity in the visual cortex region LOC during tactile object recognition (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001). Thus, the LOC has been suggested to process geometrical object shape in the visual and tactile modalities (see Grill-Spector, Kourtzi, & Kanwisher, 2001; Lacey, Tal, Amedi, & Sathian, 2009, for reviews).

However, a crossmodal transfer of unimodal information might be enabled by other multisensory regions (Banati et al., 2000; Grefkes et al., 2002). For example, Grefkes et al. (2002) used a delayed matching-to-sample task including an encoding, maintenance, and recognition phase. During encoding, abstract three-dimensional objects were presented visually or haptically for five seconds. After a retention interval of one second, a visual or haptic comparison object was presented for five seconds and the participants decided whether both objects were same or different. Comparing the neural activity during unimodal (visual–visual, haptic–haptic) tasks with crossmodal (visual–haptic, haptic–visual) tasks, increased activity was revealed in the anterior intraparietal sulcus. This strengthens the idea of multisensory representations in working memory for crossmodal recognition. Nevertheless, it is not possible to distinguish underlying representations and processes specific to the particular working memory phases, namely, encoding, maintenance, and recognition. Besides

this study, others have observed multisensory areas interacting with frontal (executive) regions (Banati et al., 2000).

In contrast, other findings rather suggest modality-specific representations. Behavioral experiments using unimodal and crossmodal working memory tasks with either varying maintenance intervals up to 30 seconds or a comparison between simultaneous and sequential presentation of visual and haptic object shape led to the support of modality-specific representations sharing related functional features, such as mediating surface-dependent representations (Woods et al., 2004; Woods & Newell, 2004). Unimodal working memory tasks with maintenance intervals over short time delays of 20 seconds revealed a larger performance decrease for kinesthetic than for visual information, encoded as positioning movements (Posner, 1967). While these studies draw conclusions on the basis of the length of the maintenance phase and the presentation mode, this view is further corroborated by interference effects observed as working memory performance decrease due to additional behavioral tasks during the maintenance phase (Ittyerah & Marks, 2007; Millar, 1972).

To enable successful crossmodal comparison, information transfer might then take place either by always recoding representations into the other modality before recognition (Connolly & Jones, 1970) or by selectively recoding representations into the format best suited to the task (Freides, 1974; Martenuik & Rodney, 1979; Newell, Shapiro, & Carlton, 1979). In the latter case, the representation format is selected according to the criterion that it provides the most relevant and reliable information. In most cases, this should be the visual modality, as revealed by crossmodal tasks (Lacey & Campbell, 2006; Martenuik & Rodney, 1979; Newell et al., 1979), and because vision is the most dominant sense in sighted people (e.g., Rock & Victor, 1964; Posner, Nissen, & Klein, 1976, for a review).

On the other hand, a more efficient way to transfer information during successful crossmodal comparison might be carried out by underlying direct or indirect interactions between unisensory cortex areas. Human neuroimaging and animal studies support the idea of an indirect interaction of unisensory areas via posterior multisensory mediator structures (e.g., Hadjikhani & Roland, 1998; see Ettliger & Wilson, 1990, for a review). The insular cortex/clastrum has been claimed to be such a convergence zone, as this area has been observed to be more active during haptic–visual compared to unimodal visual or unimodal haptic matching of object shape (Hadjikhani & Roland, 1998). Brain lesion and animal studies also support the notion that modality-specific brain areas communicate via the ventral clastrum (see Ettliger & Wilson, 1990, for a review). Thus, it has been suggested that two

distinct routes for crossmodal information processing might exist (Calvert, 2001): one that combines modality-specific information in multisensory areas and another that enables information transfer between unisensory areas via the claustrum. However, a second view can be deduced from EEG studies on crossmodal and visuo-motor integration, that is, that unisensory cortex areas interact directly (Classen, Gerloff, Honda, & Hallett, 1998; Hummel & Gerloff, 2005; Plewnia et al., 2008). In particular, Hummel and Gerloff (2005) used a visuo-tactile integration task with sets of three Braille letters presented simultaneously as a dot pattern on the computer screen to the visual modality and as relief pattern to the tactile modality. In a control condition, a random dot pattern was presented providing no relevant tactile input. Task-related EEG coherence relative to a pre-trial baseline was obtained as a synchronization measure during integration. It could be shown to increase between electrodes of interest over the occipital and the somatosensory cortex for good compared to poor behavioral performance or the control condition (see Figure 1).

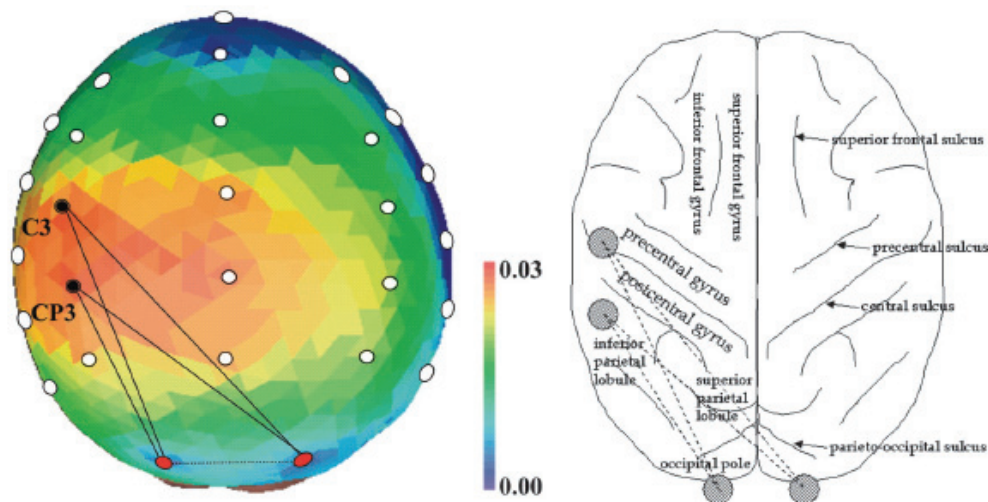


Figure 1. Left: Comparison of the task-related coherence magnitudes between good and poor behavioral performance in a crossmodal integration task. Red color coding represents areas with the largest task-related coherence difference (good > poor) during the crossmodal integration task. The electrode pairs of interest with the largest task-related coherence difference between good and poor performance are drawn in black. *Right:* Schematic of the cerebral cortex regions involved in the visuotactile task and of the electrode positions with maximal difference between good and poor task performance. (Text has been modified. Source: Hummel & Gerloff, 2005)

More importantly, this task-related increase in coherence was topographically specific, since it was found only between electrode sites over the occipital and the left somatosensory cortex (i.e., contralateral to the hand obtaining the sensory information), and not between those over the occipital cortex and the right somatosensory cortex (i.e., ipsilateral to the hand obtaining

the sensory information). Thus, increased task-related coherence between unisensory brain regions reflecting neural synchronization of activity can be linked to successful task performance. This indicates a functional significance of synchronization for successful crossmodal integration. Whether functionally relevant synchronization can be observed during crossmodal comparison in working memory tasks as well is still an open question.

2. Overview

As described in the previous section, it is currently under debate how object information is represented in unimodal and crossmodal working memory tasks and which processes are involved in crossmodal comparisons. This leads to the following questions that were addressed in the present thesis:

- (i) Does performance in unimodal and crossmodal comparison tasks with sequentially presented object features differ depending on whether the stimuli are presented in the visual and kinesthetic modality? How accurate is their representation within and across modalities?
- (ii) Are visually and kinesthetically presented object features stored as multisensory, modality-unspecific representations or as modality-specific representations during maintenance in unimodal and crossmodal working memory?
- (iii) Do EEG power and EEG coherence reveal cortex regions associated with unimodal and crossmodal comparison, thus providing insight into the neural networks related to crossmodal recognition? How do these regions interact and how do these interactions differ during distinct phases of working memory?

These questions were addressed by measuring behavioral and electrophysiological variables. An extensive pilot study addresses the first question by investigating the acuity of unimodal and crossmodal object shape discrimination in the visual and kinesthetic modality and, furthermore, provided the basis of the stimulus construction for the subsequent studies. To this end, unimodal and crossmodal comparison tasks were employed with acute and obtuse movement-defined angles, i.e., angle shape was presented as a moving dot on the screen along an angle contour in the visual modality or as a passively guided hand movement via a device in the kinesthetic modality. Thus, encoding in the visual modality was adapted to the encoding in the kinesthetic modality by sequential stimulus presentation. Using an adaptive staircase procedure, the absolute bias was determined as measure of sensory acuity, i.e., the deviance between a presented angle and the actually perceived angle.

The first study addresses the question whether working memory representations of object shape that are presented in the visual and kinesthetic modalities are stored in a multisensory, modality-unspecific or a modality-specific format. Moreover, the temporal stability of these representations was investigated. In previous studies, the format of

crossmodal working memory representations has been tested indirectly by varying the length of the delay (e.g., Woods & Newell, 2004) or by using a dual-task paradigm (Ittyerah & Marks, 2007). In the latter case, the interference tasks used were suboptimal, because they differed in several aspects from the primary working memory task. However, as the dual-task paradigm has been proven as an effective tool to study dissociations of visual and spatial working memory (see Klauer & Zhao, 2004, for an overview), this paradigm was used in the present study too, but the interference task was presented in the same mode as the working memory task and only the stimulus type was varied. Thus, angles were used as stimuli in the working memory task and ellipses in the interference task. Stimuli were presented in the visual or kinesthetic modality during encoding and recognition in either a unimodal or a crossmodal delayed matching-to-sample task (primary working memory task). During the 6 second-maintenance interval, a visual or a kinesthetic interference task (secondary task) was inserted, either immediately after encoding or with a delay. Modality and interference effects were measured as percentage of correct responses and difference errors with respect to a control working memory task with no interference task present during the maintenance. Thus, this study tested the format of representation in crossmodal working memory and the type of underlying consolidation processes in the visual and kinesthetic modality.

In the second study, the main objective was to investigate the underlying process related to unimodal and crossmodal comparison in working memory. In particular, the questions whether relevant cortex regions and their potential interactions can be revealed by EEG power and EEG coherence were addressed. Based on the previous findings on crossmodal integration and crossmodal matching, these questions can be specified for the neural synchronization measured as coherence (see Figure 2). Thus, it is investigated whether neural synchronization changes occur between unisensory regions, i.e., visual and somatosensory/motor regions, or between these areas and mediating or multisensory structures. Furthermore, the question whether potential synchronization is specific to either encoding, maintenance, or recognition, was addressed. To this end, the EEG signal was analyzed during unimodal (visual–visual, kinesthetic–kinesthetic) and crossmodal (visual–kinesthetic, kinesthetic–visual) delayed matching-to-sample tasks with either visually or kinesthetically presented stimuli. The maintenance interval had a length of one second. The analysis of the EEG signal in the frequency domain provides power and coherence measures that reflect the oscillatory activity and the neural synchronization.

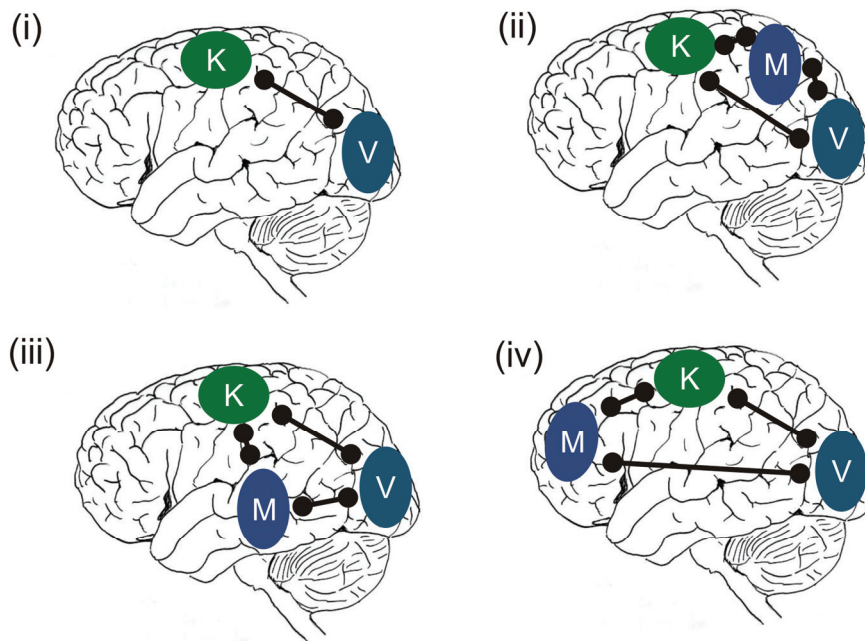


Figure 2: Hypothetical scenarios for crossmodal recognition through neural coherence in the case of visual and kinesthetic input (adapted and modified figure from Senkowski, Schneider, Foxe, & Engel, 2008). (i) Crossmodal recognition might be associated with neural synchronization between unisensory cortex regions, i.e., visual cortex regions and somatosensory/motor cortex regions. (ii), (iii), (iv) Alternatively, crossmodal recognition might be achieved by neural synchronization between unisensory areas and mediating or multisensory structures in frontal, temporal, or parietal cortex. Which specific multisensory areas might be involved seems to be task-dependent and material-dependent.

EEG power indicates the proportion of each frequency component on the signal variance. The measure has proven to be sensitive to the sensory, motor and working memory demands (e.g., Andres & Gerloff, 1999; Gevins, Smith, McEvoy, & Yu, 1997; Pfurtscheller & Klimesch, 1991; see von Stein & Sarnthein, 2000, for a review). EEG coherence, which is derived from the power spectra, indicates the similarity of the signals of two sensors. It varies between 0 (no similarity) and 1 (maximal similarity). As measure of the neural synchronization, increased coherence is assumed to indicate functional coupling during information processing (e.g., Andres & Gerloff, 1999; Classen et al., 1998; Hummel & Gerloff, 2005; Mima, Oluwatimilehin, Hiraoka, & Hallett, 2001; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999). In particular, changes in coherence have been found to be related to sensorimotor and crossmodal integration (Classen et al., 1998; Hummel & Gerloff, 2005; Plewnia et al., 2008) and to working memory maintenance (e.g., Sarnthein et al., 1998). In the present study, power and coherence were calculated relative to a pre-trial baseline yielding dB-power values and task-related coherence values and were averaged for the a priori defined frequency bands theta (3.5–7.5 Hz), alpha (7.5–13.5 Hz), and beta (13.5–32 Hz), which had been related to sensory and motor processing, and working memory processes in previous

studies (e.g., Andres & Gerloff, 1999; Classen et al., 1998; Pfurtscheller & Klimesch, 1991; Sarnthein et al., 1998). Power was compared for unimodal visual and unimodal kinesthetic conditions relative to a baseline to investigate correlates specific to each modality, and for unimodal and crossmodal tasks separately for each stimulus modality to test for processing differences due to a subsequently expected modality switch. Coherence changes were obtained for the combined crossmodal conditions compared to the unimodal conditions to observe processes specific to the crossmodal comparison in working memory. All comparisons were made during encoding, maintenance, and recognition.

2.1 Pilot study

Unimodal and crossmodal comparison of visual and kinesthetic stimuli

The pilot study investigated the acuity of unimodal and crossmodal angle discrimination in the visual and kinesthetic modality. Moreover, it provided the basis for the stimulus material used in the subsequent studies. Angle stimuli were presented as angular movement trajectories either visually as a moving white light spot on the black computer screen or kinesthetically as a passively guided right hand movement via a programmable apparatus. In a between-subject design, unimodal (visual–visual, kinesthetic–kinesthetic) and crossmodal (visual–kinesthetic, kinesthetic–visual) comparison tasks were employed. Participants judged whether the size of a reference angle that was either acute (30° , 60°) or obtuse (120° , 150°) was smaller or larger than the size of a comparison angle. Using an adaptive staircase procedure, the psychometric function was obtained for each reference angle and participant on the basis of 80 trials (Kesten, 1958; Robbins & Monro, 1951; see Treutwein, 1995, for a review). As a measure of the discrimination acuity, the absolute bias was determined at 50 % of the sensitivity function. Thus, it reflects the point of subjective equivalence between comparison angle and reference angle. The results showed that unimodal discrimination acuity for angle-shaped stimuli is good irrespective of the encoding modality, i.e. vision or kinesthesia with absolute biases of 5° and 3° , respectively. However, acuity was higher within modalities than across modalities without differing between visual–kinesthetic and kinesthetic–visual comparison (absolute biases were 8° and 7° , respectively). The angle size did not influence the discrimination acuity. On the other hand, response variability and discrimination threshold variance were high. In order to ensure that participants were able to perform well in the matching tasks of

the subsequent studies, difference thresholds were determined at 10 % and 90 % of the sensitivity function as the basis to select the comparison angles in these studies.

2.2 Study I

Seemüller, A., Fiehler, K., & Rösler, F. (2010). **Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories.** *Acta Psychologica* doi: 10.1016/j.actpsy.2010.09.014

The first study investigated the representation of visually and kinesthetically presented information during unimodal and crossmodal working memory maintenance. To this end, unimodal (visual–visual, kinesthetic–kinesthetic) and crossmodal (visual–kinesthetic, kinesthetic–visual) delayed matching-to-sample tasks with a maintenance interval of six seconds were employed. Stimuli were angle-shaped movement trajectories that were presented visually as a moving white light spot on a black computer screen or kinesthetically as a passively guided right hand movement via a programmable apparatus. Participants had to decide whether the angle of the maintained sample stimuli and of the presented test stimuli matched in size. In order to investigate whether the representation format was modality-specific or multisensory, additional visual and kinesthetic interference tasks were inserted during the maintenance interval. Here, participants had to decide whether presented elliptic movement trajectories were horizontal or vertical relative to their body midline. The difficulty of visual and kinesthetic interference tasks was matched in an additional pilot experiment. Furthermore, the temporal stability of the working memory representations was tested by presenting the interference task either immediately or later during the maintenance interval. Unimodal and crossmodal working memory tasks without interference tasks served as control conditions. The mean percentage of correct responses and the difference errors, i.e. the mean percentage of correct responses in the interference conditions minus the mean percentage of correct responses in the control condition, were calculated as dependent measures. The results showed two main effects. First, working memory after visual encoding was more strongly impaired by a visual interference task, while working memory after kinesthetic encoding was more strongly impaired by a kinesthetic interference task. Second, at the beginning of the maintenance interval modality-unspecific interference effects were larger for visual than for kinesthetically encoded stimuli, while later in the maintenance interval the opposite held, i.e.

interference effects were larger for kinesthetically than for visually encoded stimuli. These findings indicate that visually and kinesthetically encoded movement trajectories are represented in unimodal and crossmodal working memory, at least partially, in a modality-specific format. Thus, an exclusively multisensory, modality-unspecific representation by default can be excluded. Equally important, different consolidation processes are suggested dependent on the encoding modality. In particular, consolidation seems to last longer for kinesthetically than visually presented movement trajectories, thus further supporting a modality-specific representation format.

2.3 Study II

Seemüller, A., & Rösler, F. (submitted). **EEG-power and -coherence changes in a unimodal and a crossmodal working memory task with visual and kinesthetic stimuli.** *International Journal of Psychophysiology*

In the second study, the neural processes related to unimodal and crossmodal working memory were investigated. In particular, this experiment addressed the question whether relevant cortex regions and their potential interactions during the working memory phases of encoding, maintenance, and recognition can be revealed by means of electroencephalography (EEG). To this end, EEG power as a measure of oscillatory activity and EEG coherence as a measure of neural synchronization were analyzed during unimodal (visual–visual, kinesthetic–kinesthetic) and crossmodal (visual–kinesthetic, kinesthetic–visual) delayed matching-to-sample tasks. Stimuli were angle-shaped movement trajectories presented visually as a moving white light spot on a black computer screen or as a passively guided right hand movement via an x-y-plotter-like apparatus. Based on the results of the pilot study the angle size of the target stimuli was varied systematically such that either easy or hard matching tasks resulted dependent on the deviance between sample and test stimulus. Identical angles were presented in 50 % of the trials. Overall, 384 trials with 96 trials per modality condition were presented. The baseline was measured at the beginning of each trial and participants were instructed to fixate the fixation cross over the course of the entire trial. The EEG signal was analyzed in the frequency domain in non-overlapping time epochs of one second each, during encoding, maintenance, and recognition. Power and coherence were calculated relative to a pre-trial baseline yielding dB-power values and task-related coherence

values and were averaged separately for three frequency bands – theta (3.5–7.5 Hz), alpha (7.5–13.5 Hz), and beta (13.5–32 Hz). Besides the analysis of 19 standard electrodes of the 10-20 system, additional electrodes-of-interest were chosen a priori over left central and occipital scalp regions (cf. Classen et al., 1998; Hummel & Gerloff, 2005). The results showed systematic power and coherence changes. In particular, the results emphasize the relevance of modality-specific representations and processes in unimodal and crossmodal working memory. Alpha power was modulated by the encoding modality showing modality-specific topographical patterns over central cortex regions during kinesthetic encoding and maintenance and over occipital cortex regions during visual encoding and maintenance. In crossmodal tasks, alpha power was additionally modulated during encoding and maintenance by the modality of the expected test stimulus. The main finding of this study was an increase of theta coherence between electrodes-of-interest over left central and occipital cortex regions during crossmodal compared to unimodal recognition. Systematic coherence changes were only observed during recognition and not during encoding or maintenance. The results of this study are compatible with the idea that there exist modality-specific representations and anticipation processes, but in addition, that crossmodal recognition is related to a direct interaction of somatosensory/motor and visual cortex regions that occurs when it is relevant.

2.4 General conclusions

Crossmodal object comparison comprises the matching of object representations provided by one sensory modality with those obtained from other modalities. The aim of the present thesis was to investigate the characteristics of working memory representations, the processes related to encoding, maintenance, and recognition in working memory, and their neural correlates in unimodal and crossmodal matching tasks. Differently shaped stimuli were presented either in the visual or in the kinesthetic modality. The present findings suggest that modality-specific representations and modality-specific processes play a relevant role in unimodal and crossmodal working memory. In the following, the main results and conclusions will be highlighted and discussed. A more detailed discussion can be found in the experimental studies in the second part of the present thesis.

The data of the two studies provided new details about the format and temporal stability of working memory representations in unimodal and crossmodal tasks and about their underlying neural processes. Based on the modality-specific effects observed for

unimodal and crossmodal working memory, it can be concluded that visual and kinesthetic information is built and maintained in a modality-specific representation format over short time intervals. In particular, electrophysiological power changes over unisensory cortex regions, i.e. occipital and central cortex, suggest modality-specific representations during encoding and working memory maintenance of one second, while behavioral effects indicate, at least in part, modality-specific representations for maintenance intervals over six seconds. Thus, other representations seem to be established during working memory maintenance over several seconds as well. With regard to the representation of spatial information (e.g. Cattaneo & Vecchi, 2008; Struiksma, Noordzji, & Postma, 2009), one might suggest a coexistence of modality-unspecific, multisensory and modality-specific representations which might then imply that these different types of representations have different impact depending on the task demands. Based on this, it might be speculated that a clear dichotomy between modality-specific and multisensory representations does not exist. Other additional representation formats, such as supramodal verbal, seem to be unlikely considering the stimulus material (see also Woods et al., 2004). Overall, the findings of both studies clearly exclude the possibility of two alternative theoretical positions. First, working memory representations are not formed and maintained exclusively in a multisensory, modality-unspecific format (cf. Easton et al., 1997; Reales & Ballesteros, 1999). In that case, unimodal and crossmodal working memory should have displayed comparable visual and kinesthetic interference effects and EEG power modulations. Second, stimuli are not represented by default in a format that is best suited for the task, i.e. in the present case, a visual representation format (e.g. Freides, 1974; Rock & Victor, 1964; see Posner et al., 1976, for a review). If so, it had to be expected that unimodal and crossmodal working memory were impaired to the same extent by a visual interference and that power decreases were observed at the same electrode sites during visual and kinesthetic maintenance.

The idea that representations in unimodal and crossmodal working memory are first of all built and maintained in a modality-specific format is further strengthened by another aspect of the present findings, namely that representations built from visual and kinesthetic stimuli showed different timing characteristics over short intervals. In the first study, immediate interference effects during maintenance were larger for visually than for kinesthetically presented stimuli. In contrast, interference impaired memory later in the maintenance interval for kinesthetically presented stimuli. The interference effect was modality-unspecific, suggesting the involvement of general attentional processes. This fits the concept that consolidation is a constructive process (see Ranganath, 2006) and that memory

traces can be stabilized during maintenance. In particular, two stages of maintenance were assumed: one phase to build a stable representation that can be maintained without external stimulation, and a second phase involving automatic, relatively effortless maintenance of the representation in working memory (see also Johnson, Reeder, Raye, & Mitchell, 2002; Jolicœur & Dell'Acqua, 1998; Naveh-Benjamin & Jonides, 1984). Thus, the first stage is based on processes to consolidate the encoded information that have been termed as 'short-term consolidation' (Jolicœur & Dell'Acqua, 1998), 'recoding' (Miller, 1956) or 'refreshing' (e.g., Johnson et al., 2002; Raye, Johnson, Mitchell, Reeder, & Greene, 2002). Furthermore, the first stage of maintenance may not always be strictly separable from encoding (Jolicœur & Dell'Acqua, 1998), suggesting that differences between visual and kinesthetic processing might already occur during the encoding phase. This is supported by the observed EEG power modulations in the second study that found preparatory effects with respect to the test stimulus starting during late encoding for visually presented stimuli and during maintenance for kinesthetically presented stimuli indicating longer consolidation processes in the kinesthetic modality. While the described concept of working memory maintenance has been proposed for visual working memory, extending it to kinesthetic working memory with similar stages, but different temporal characteristics, can explain the present results. The first phase of stabilization then takes longer for kinesthetically encoded object features than for visually encoded object features. How visual and especially kinesthetic information is represented over longer time intervals should be addressed in future studies.

Regarding the underlying neuronal processes, the present EEG findings are in line with the sensory recruitment hypothesis, i.e., the idea that the same cortex areas that process sensory information are involved in its maintenance in working memory and in its LTM storage (D'Esposito, 2007; Gallace & Spence, 2009; McClelland et al., 1995). In particular, topographical patterns showed power decreases over the occipital cortex for visual and over the central cortex regions for kinesthetic stimuli during both unimodal encoding and maintenance. Thus, the sensory recruitment hypothesis that was originally formulated for unimodal visual working memory and long-term memory seems to hold for other modalities as well. This was already suggested for the haptic/tactile modality (Gallace & Spence, 2009; Pasternak & Greenlee, 2005), but the present findings add that the same principle also applies to kinesthetic information. Overall, the findings also fit Hebb's idea that memory representations are maintained by sustained firing of neurons in reverberating circuits and, thus, consolidate over time (Hebb, 1949).

Another aspect is the comparable unimodal visual and unimodal kinesthetic acuity in the pilot study indicating that a similar precision of representations can be achieved by adjusting the encoding conditions, i.e., by using a sequential presentation of both unimodal visual and kinesthetic object information (cf. Loomis, 1990; Loomis et al., 1991; Reuschel et al., 2010). This underlines a functional equivalence of the visual and kinesthetic system which means that, despite different spatial bandwidths, information can be encoded in a similar manner in vision and kinesthesia, i.e. both can be described as “image-processing systems” according to Newell (2004). Similarly, the direction of the crossmodal comparison, i.e., whether visual sample stimuli were compared or matched to kinesthetic test stimuli or vice versa, did not influence precision in comparison tasks or working memory performance. However, both were better in unimodal than in crossmodal comparison and matching task conditions. This might be partly confounded with the stimulus presentation mode, i.e. the presentation of visual and kinesthetic stimuli in different planes (vertical vs. horizontal), which could not be controlled without distorting the visual stimulus presentation. In future studies, it might be possible to control for using different stimulus material.

With regard to the crossmodal comparison, EEG power was modulated as a function of the modality of the upcoming test stimulus prior to recognition during encoding and maintenance. Similarly, a series of previous ERP studies showed that a participant’s expectation of the upcoming test stimulus as well as preparatory processes can be observed in the EEG signal during encoding and maintenance of a crossmodal tactile-visual working memory task (Ku et al., 2007; Ohara, Lenz, & Zhou, 2006a; Ohara, Lenz, & Zhou, 2006b). The present findings show that expectation and preparation processes in a crossmodal working memory task with visual and kinesthetic stimuli can also be observed in the frequency domain. In the described ERP studies, participants were instructed to maintain the test stimulus (a LED color) they had learned to be associated with the presented sample stimulus (vibration stimulus) and not the sample stimulus itself. In contrast, no prior associations were learned in the present study and participants were instructed to maintain the sample stimulus during maintenance. Hence, the observed effects in the present study can be attributed to the participants’ expectations rather than to the previously learned association between kinesthetic and visual stimuli as in the ERP study. As mentioned above, anticipation effects in the present EEG study additionally exhibited temporal differences dependent on the encoding modality, i.e. occurred earlier for visually than kinesthetically presented stimuli. In sum, modality-specific anticipation and/or preparatory processes that involve correspondent

brain regions seem to be relevant for the subsequent crossmodal comparison in working memory tasks.

Crossmodal comparison itself is related to a direct interaction of unisensory cortex regions in the early recognition phase when test stimuli have to be processed and compared with previously stored stimuli. This is suggested by an increased EEG coherence in the theta band between electrode sites over the left central cortex and the occipital cortex during crossmodal compared to unimodal working memory tasks. Thus, synchronization measured as EEG coherence seems to be not only functionally relevant for crossmodal or sensorimotor processes in integration or tracking tasks (Classen et al., 1998; Hummel & Gerloff, 2005), but also for crossmodal transfer in working memory tasks. In general, this is in line with evidence for binding and top-down processing through synchronization (e.g. see Engel, Fries, & Singer, 2001; Senkowski et al., 2008, for reviews). Coherence modulations in the theta band are consistent with the idea that low frequency oscillations rather reflect long-range interactions between distant brain regions than local synchronization and that they are involved in cognitive or top-down processing rather than in sensory stimulus processing (Sarnthein et al., 1998; see von Stein & Sarnthein, 2000, review). Systematic coherence changes were observed during recognition and not during encoding or maintenance phases of the working memory tasks supporting the conclusion that interactions take place during crossmodal comparison when needed. With regard to EEG research, the restricted spatial resolution and the difficulty in localizing generators of the EEG signal has to be kept in mind. However, the observed effects are in line with previous literature (Classen et al., 1998; Hummel & Gerloff, 2005; Plewnia et al., 2008). Moreover, although the present results seem to underline the relevance of modality-specific representations in crossmodal working memory tasks, it has to be mentioned that unisensory cortex regions can also be associated with the processing of stimuli in other modalities. Previous findings suggest that visual cortex areas can be related to processing in unimodal tactile discrimination and recognition tasks (Amedi et al., 2002; Amedi et al., 2001; Deibert, Kraut, Kremen, & Hart, 1999; Sathian, Zangaladze, Hoffman, & Grafton, 1997; Zangaladze, Epstein, Grafton, & Sathian, 1999). Various explanations might account for these findings, e.g., spatial processing, imagery, backprojections from other sensory or multisensory areas, or reactivation of learned associations (see Newell, 2004). Based on the present results, two alternative mechanisms underlying crossmodal recognition do not seem to play a crucial role. First, a complex coherence pattern involving unisensory cortex regions and additional multisensory or mediating cortex regions in the same frequency band was not observed. Thus, a crossmodal transfer of modality-specific information into a

multisensory representation cannot be associated with the observed coherence patterns. However, alpha and beta coherence modulations can be described and might hint to the additional involvement of executive and/or multisensory processes. Second, a crossmodal transfer prior to recognition, i.e., during the encoding or the maintenance phase, seems unlikely because no systematic coherence changes were observed during encoding or maintenance for crossmodal compared to unimodal tasks. In addition, interference effects in the behavioral study occurred irrespective of the recognition modality. These findings do not support a transfer into the test modality or the modality best suited for the task before recognition. Whether these mechanisms can be generalized to crossmodal working memory tasks as such should be investigated in future studies.

In summary, the present thesis provides new findings on how visually and kinesthetically presented object features are represented and processed for unimodal and crossmodal working memory. The conducted studies show the relevance of modality-specific representations and modality-specific processes. Besides behavioral and functional imaging approaches, electroencephalography analyzed in the frequency domain seems to offer a useful method to investigate crossmodal working memory.

3. References

- Amedi, A., Jacobson, G., Hendler, T., Malach, R., & Zohary, E. (2002). Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cerebral Cortex, 12*, 1202–1212.
- Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience, 4*(3), 324–330.
- Anderson, J. R. (1983). *The architecture of cognition*. Cambridge, MA: Harvard University Press.
- Andres, F. G., & Gerloff, C. (1999). Coherence of sequential movements and motor learning. *Journal of Clinical Neurophysiology, 16*, 520–527.
- Banati, R. B., Goerres, G. W., Tjoa, C., Aggleton, J. P., & Grasby, P. (2000). The functional anatomy of visual–tactile integration in man: a study using positron emission tomography. *Neuropsychologia, 38*, 115–124.
- Bodegard, A., Geyer, S., Grefkes, C., Zilles, K., & Roland, P. E. (2001). Hierarchical processing of tactile shape in the human brain. *Neuron, 31*, 317–328.
- Bonda, E., Petrides, M., & Evans, A. (1996). Neural systems for tactual memories. *Journal of Neurophysiology, 75*, 1730–1737.
- Bowers, R. L., Mollenhauer, M. S., & Luxford, J. (1990). Short-term memory for tactile and temporal stimuli in a shared-attention recall task. *Perceptual and Motor Skills, 70*, 903–913.
- Calvert, G. A. (2001). Crossmodal processing in the human brain: insights from functional neuroimaging studies. *Cerebral Cortex, 11*, 1110–1123.
- Cattaneo, Z., & Vecchi, T. (2008). Supramodality effects in visual and haptic spatial processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 34*, 631–642.
- Classen, J., Gerloff, C., Honda, M., & Hallett, M. (1998). Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. *Journal of Neurophysiology, 79*, 1567–1573.
- Connolly, K., & Jones, B. (1970). A developmental study of afferent-reefferent integration. *British Journal of Psychology, 61*(2), 259–266.
- Connor, C. E., Brincat, S. L., & Pasupathy, A. (2007). Transformation of shape information in the ventral pathway. *Current Opinion in Neurobiology, 17*, 140–147.

References

- Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information processing system. *Psychological Bulletin*, *104*, 163–171.
- Cowan, N. (1999). An embedded-process model of working memory. In A. Miyake & P. Shah (Eds.), *Models of working memory: mechanisms of active maintenance and executive control* (pp. 62–101). Cambridge: Cambridge University Press.
- Deibert, E., Kraut, M., Kremen, S., & Hart, Jr., J. (1999). Neural pathways in tactile object recognition. *Neurology*, *52*, 1413–1421.
- D’Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society B*, *362*, 761–772.
- Druschky, K., Kaltenhäuser, M., Hummel, C., Druschky, A., Huk, W. J., Neundörfer, B., & Stefan, H. (2003). Somatosensory evoked magnetic fields following passive movement compared with tactile stimulation of the index finger. *Experimental Brain Research*, *148*, 186–195.
- Easton, R. D., Greene, A. J., & Srinivas, K. (1997). Transfer between vision and haptics: Memory for 2-D patterns and 3-D objects. *Psychonomic Bulletin & Review*, *4*(3), 403–410.
- Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top-down processing. *Nature Reviews Neuroscience*, *2*, 704–716.
- Ettlinger, G., & Wilson, W. A. (1990). Cross-modal performance: behavioral processes, phylogenetic considerations and neural mechanisms. *Behavioral and Brain Research*, *40*, 169–192.
- Farivar, R. (2009) Dorsal-ventral integration in object recognition. *Brain Research Reviews*, *61*, 144–153.
- Freides, D. (1974). Human information processing and sensory modality: Cross-modal functions, information complexity, memory, and deficit. *Psychological Bulletin*, *81*(5), 284–310.
- Gallace, A., & Spence, C. (2009). The cognitive and neural correlates of tactile memory. *Psychological Bulletin*, *135*, 380–406.
- Garvill, J., & Molander, B. (1973). Effects of standard modality, comparison modality and retention interval on matching form. *Scandinavian Journal of Psychology*, *14*, 203–206.
- Gazzaley, A., Rissman, J., & D’Esposito, M. (2004). Functional connectivity during working memory maintenance. *Cognitive, Affective, and Behavioral Neuroscience*, *4*, 580–599.

References

- Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*, 374–385.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Grefkes, C., Weiss, P. H., Zilles, K., & Fink, G. R. (2002). Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. *Neuron*, *35*, 173–184.
- Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience*, *27*, 649–677.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.
- Grill-Spector, K., Kushnir, T., Edelman, S., Itzhak, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron*, *21*, 191–202.
- Hadjikhani, N., & Roland, P. E. (1998). Cross-modal transfer of information between the tactile and the visual representations in the human brain: a positron emission tomographic study. *The Journal of Neuroscience*, *18*, 1072–1084.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*, 632–635.
- Hebb, D. O. (1949). *The organization of behavior: a neuropsychological theory*. New York: Wiley.
- Hummel, F., & Gerloff, C. (2005). Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans. *Cerebral Cortex*, *15*, 670–678.
- Ittyerah, M., & Marks, L. E. (2007). Memory for curvature of objects: Haptic touch vs. vision. *British Journal of Psychology*, *98*, 589–610.
- Johnson, M. K., Reeder, J. A., Raye, C. L., & Mitchell, K. J. (2002). Second thoughts versus second looks: An age-related deficit in reflectively refreshing just-activated information. *Psychological Science*, *13*, 64–67.
- Jolicœur, P., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation. *Cognitive Psychology*, *36*, 138–202.
- Kesten, H. (1958). Accelerated stochastic approximation. *Annals of Mathematical Statistics*, *29*, 41–59.
- Klatzky, R. L., & Lederman, S. J. (1993). Toward a computational model of constraint-driven exploration and haptic object identification. *Perception*, *22*, 597–621.

References

- Klatzky, R. L., & Lederman, S. J. (2002). Touch. In B. Weiner (Series Ed.), A. F. Healy, & R. W. Proctor (Vol. Eds.), *Handbook of Psychology: Vol. 4. Experimental Psychology* (pp. 147–176). New York: Wiley.
- Klauer, K. C. & Zhao, Z. (2004). Double dissociations in visual and spatial short-term memory. *Journal of Experimental Psychology*, *133*(3), 355–381.
- Kiphart, M. J., Hughes, J. L., Simmons, J. P., & Cross, H. A. (1992). Short-term haptic memory for complex objects. *Bulletin of the Psychonomic Society*, *30*, 212–214.
- Kriegeskorte, N., Sorger, B., Naumer, M., Schwarzbach, J., van den Boogert, E., Hussy, W., & Goebel, R. (2003). Human cortical object recognition from a visual motion flowfield. *Journal of Neuroscience*, *23*, 1451–1463.
- Ku, Y., Ohara, S., Wang, L., Lenz, F. A., Hsiao, S. S., Bodner, M., Hong, B., & Zhou, Y. D. (2007). Prefrontal cortex and somatosensory cortex in tactile crossmodal association: an independent component analysis of ERP recordings. *PLoS ONE*, *2*(8), e771. doi:10.1371/journal.pone.0000771
- Lacey, S., & Campbell, C. (2006). Mental representation in visual/haptic crossmodal memory: evidence from interference effects. *The Quarterly Journal of Experimental Psychology*, *59*, 361–376.
- Lacey, S., Tal, N., Amedi, A., & Sathian, K. (2009). A putative model of multisensory object representation. *Brain Topography*, *21*, 269–274.
- Lehky, S. R., & Sereno, A. B. (2007). Comparison of shape encoding in primate dorsal and ventral visual pathways. *Journal of Neurophysiology*, *97*, 307–319.
- Lewkowicz, D. J. (1994). Development of intersensory perception in human infants. In D. J. Lewkowicz, & R. Lickliter, *The development of intersensory perception: comparative perspectives* (pp. 165–203). Hillsdale, NJ: Erlbaum.
- Lewkowicz, D. J. (2000). The development of intersensory temporal perception: an epigenetic systems/limitations view. *Psychological Bulletin*, *126*, 281–308.
- Loomis, J., & Lederman, S. J. (1986). Tactual perception. In R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (Vol. 2, pp. 31–44). New York: Wiley.
- Loomis, J. M. (1990). A model of character recognition and legibility. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 106–120.
- Loomis, J. M., Klatzky, R. L., & Lederman, S. J. (1991). Similarity of tactual and visual picture recognition with limited field of view. *Perception*, *20*, 167–177.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. H. (1995). Object-related activity

References

- revealed by functional magnetic resonance imaging in human occipital cortex. *PNAS*, 92, 8135–8139.
- Martenuik, R. G., & Rodney, M. (1979). Modality and retention effects in intra- and cross-modal judgements of kinaesthetic and visual information. *British Journal of Psychology*, 70, 405–412.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102, 419–457.
- McCloskey, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews*, 58(4), 763–820.
- Millar, S. (1972). Effects of interpolated tasks on latency and accuracy of intramodal and cross-modal shape recognition by children. *Journal of Experimental Psychology*, 96, 170–175.
- Millar, S. (1974). Tactile short-term memory by blind and sighted children. *British Journal of Psychology*, 65(2), 253–263.
- Miller, G. A. (1956). The magical number seven plus or minus two: some limits on our capacity for processing information. *Psychological Review*, 63, 81–97.
- Mima, T., Sadato, N., Yazawa, S., Hanakawa, T., Fukuyama, H., Yonekura, Y., & Shibasaki, H. (1999). Brain structures related to active and passive finger movements in man. *Brain*, 122, 1989–1997.
- Mima, T., Oluwatimilehin, T., Hiraoka, T., & Hallett, M. (2001). Transient interhemispheric neuronal synchrony correlates with object recognition. *The Journal of Neuroscience*, 21, 3942–3948.
- Mishkin, M. (1979). Analogous neural models for tactual and visual learning. *Neuropsychologia*, 17, 139–151.
- Naveh-Benjamin, M., & Jonides, J. (1984). Maintenance rehearsal: A two-component analysis. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 10, 369–385.
- Newell, F. N. (2004). Cross-modal object recognition. In G. A. Calvert, C. Spence, & B. E. Stein (Eds.), *The handbook of multisensory processes* (pp. 123–139). Cambridge, MA: MIT Press.
- Newell, K. M., Shapiro, D. C., & Carlton, M. J. (1979). Coordinating visual and kinaesthetic memory codes. *British Journal of Psychology*, 70, 87–96.
- Newell, F. N., Ernst, M. O., Tjan, B. S., & Bühlhoff, H. H. (2001). Viewpoint dependence in visual and haptic object recognition. *Psychological Science*, 12, 37–42.

References

- Ohara, S., Lenz, F. A., & Zhou, Y. D. (2006a). Modulation of somatosensory event-related potential components in a tactile-visual cross-modal task. *Neuroscience*, *138*, 1387–1395.
- Ohara, S., Lenz, F. A., & Zhou, Y. D. (2006b). Sequential neural processes of tactile-visual crossmodal working memory. *Neuroscience*, *139*, 299–309.
- O’Sullivan, B. T., Roland, P. E., & Kawashima, R. (1994). A PET study of somatosensory discrimination in man. Microgeometry versus macrogeometry. *European Journal of Neuroscience*, *6*, 137–148.
- Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, *6*, 97–107.
- Pfurtscheller, G., & Klimesch, W. (1991). Event-related desynchronization during motor behavior and visual information processing. In C. H. M. Brunia, G. Mulder & M. N. Verbaten (Eds.), *Event-Related Brain Research*, 58–65, Elsevier, Amsterdam.
- Plewnia, C., Rilk, A. J., Soekadar, S. R., Arfeller, C., Huber, H. S., Sauseng, P., Hummel, F., & Gerloff, C. (2008). Enhancement of long-range EEG coherence by synchronous bifocal transcranial magnetic stimulation. *European Journal of Neuroscience*, *27*, 1577–1583.
- Posner, M. I. (1967). Characteristics of visual and kinesthetic memory codes. *Journal of Experimental Psychology*, *75*(1), 103–107.
- Posner, M. I., Nissen, M. J., & Klein, R. M. (1976). Visual dominance: An information-processing account of its origins and significance. *Psychological Review*, *83*(2), 157–171.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- Radovanovic, S., Korotkov, A., Ljubisavljevic, M., Lyskov, E., Thumberg, J., Kataeva, G., Danko, S., Roudas, M., Pakhomov, S., Medvedev, S., & Johansson, H. (2002). Comparison of brain activity during different types of proprioceptive inputs: a positron emission tomography study. *Experimental Brain Research*, *143*, 276–285.
- Ranganath, C. (2006). Working memory for visual objects: complementary roles of inferior temporal cortex, medial temporal, and prefrontal cortex. *Neuroscience*, *139*, 277–289.
- 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.

References

- Raye, C. L., Johnson, M. K., Mitchell, K. J., Reeder, J. A., & Greene, E. J. (2002). Neuroimaging a single thought: Dorsolateral PFC activity associated with refreshing just-activated information. *Neuroimage*, *15*, 447–453.
- Reales, J. M., & Ballesteros, S. (1999). Implicit and explicit memory for visual and haptic objects: Cross-modal priming depends on structural descriptions. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*(3), 644–663.
- Reed, C. L., Shoham, S., & Halgren, E. (2004). Neural substrates of tactile object recognition: an fMRI study. *Human Brain Mapping*, *21*, 236–246.
- Reed, C. L., Caselli, R. J., & Farah, M. J. (1996). Tactile agnosia: underlying impairment and implications for normal tactile object recognition. *Brain*, *119*, 875–888.
- Reuschel, J., Drewing, K., Henriques, D. Y. P., Rösler, F., & Fiehler, K. (2010). Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry. *Experimental Brain Research*, *201*, 853–862.
- Robbins, H., & Monro, S. (1951). A stochastic approximation method. *Annals of Mathematical Statistics*, *22*, 400–407.
- Rock, I., & Victor, J. (1964). Vision and touch: an experimentally created conflict between the two senses. *Science*, *143*, 594–596.
- 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 USA*, *95*, 3295–3300.
- Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during human working memory. *Proceedings of the National Academy of Sciences USA*, *95*, 7092–7096.
- Sathian, K., Zangaladze, A., Hoffman, J. M., & Grafton, S. T. (1997). Feeling with the mind’s eye. *Neuroreport*, *8*, 3877–3881.
- Schiffman, H. R. (1990). Somesthesia I: Kinesthesia and cutaneous sense. In H. R. Schiffman (Ed.), *Sensation and perception: An integrated approach* (pp. 119–138). New York: John Wiley & Sons.
- Senkowski, D., Schneider, T. R., Foxe, J. J., & Engel, A. K. (2008). Crossmodal binding through neural coherence: implications for multisensory processing. *Trends in Neurosciences*, *31*, 401–409.
- Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-specific delay activity in human primary visual cortex. *Psychological Science*, *20*, 207–214.

References

- Sereno, M. E., Trinath, T., Augath, M., Logothetis, N. K. (2002). Three-dimensional shape representation in monkey cortex. *Neuron*, *33*, 635–652.
- Silvanto, J., & Cattaneo, Z. (2010). Transcranial magnetic stimulation reveals the content of visual short-term memory in the visual cortex. *Neuroimage*, *50*, 1683–1689.
- Struiksma, M. E., Noordzij, M. L., & Postma, A. (2009). What is the link between language and spatial images? Behavioral and neural findings in blind and sighted individuals. *Acta Psychologica*, *132*, 145–156.
- Tallon-Baudry, C., Bertrand, O., & Fischer, C. (2001). Oscillatory synchrony between human extrastriate areas during visual short-term memory maintenance. *Journal of Neuroscience*, *21*, RC177 (1–5).
- Tootell, R. B. H., Tsao, D., & Vanduffel, W. (2003). Neuroimaging weighs in: humans meet macaques in “primate” visual cortex. *Journal of Neuroscience*, *23*, 3981–3989.
- Treutwein, B. (1995). Adaptive Psychophysical Procedures. *Vision Research*, *35*, 2503–2522.
- von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: from local gamma to long range alpha theta synchronization. *International Journal of Psychophysiology*, *38*, 301–313.
- von Stein, A., Rappelsberger, P., Sarnthein, J., & Petsche, H. (1999). Synchronization between temporal and parietal cortex during multimodal object processing in man. *Cerebral Cortex*, *9*, 137–150.
- Walk, R. D., & Pick, H. L., Jr. (1981). *Intersensory perception and sensory integration*. New York: Plenum.
- Weiller, C., Jüptner, M., Fellows, S., Rijntjes, M., Leonhardt, G., Kiebel, S., Müller, S., Diener, H. C., & Thilmann, A. F. (1996). Brain representation of active and passive movements. *Neuroimage*, *4*, 105–110.
- Woods, A. T., O’Modhrain, S. & Newell, F. N. (2004). The effect of temporal delay and spatial differences on cross-modal object recognition. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 260–269.
- Woods, A. T., & Newell, F. N. (2004). Visual, haptic and cross-modal recognition of objects and scenes. *Journal of Physiology – Paris*, *98*, 147–159.
- Zangaladze, A., Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, *401*(6753), 587–590.

II. Experimental studies

Pilot study

Unimodal and crossmodal comparison of visual and kinesthetic stimuli.

Study I

Seemüller, A., Fiehler, K., & Rösler, F. (2010). **Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories.** *Acta Psychologica* doi: 10.1016/j.actpsy.2010.09.014

Study II

Seemüller, A., & Rösler, F. (submitted). **EEG-power and -coherence changes in a unimodal and a crossmodal working memory task with visual and kinesthetic stimuli.** *International Journal of Psychophysiology*

Pilot study

Unimodal and crossmodal comparison of visual and kinesthetic stimuli.

Unimodal and crossmodal comparison of visual and kinesthetic stimuli

Introduction

Interacting with an object involves processing of information from different sensory modalities about shared object features, such as size and shape. Among others, visual and kinesthetic sensory information can thus be used to perceive and discriminate objects with commonly encountered elementary geometric features like lines, curvatures, or angles.

Here, we utilized angles due to the following reasons. First, they can be easily presented in the visual and, more importantly, in the kinesthetic modality by moving the hand passively along an angle trajectory with an apparatus. This allows a controlled kinesthetic stimulus presentation in contrast to free haptic exploration of an object. Second, metrically varied angle sizes are hard to verbalize, thus allowing to focus on the visual and kinesthetic processing itself.

In order to select the appropriate stimulus material for the following studies and to investigate the discrimination ability in unimodal and crossmodal tasks, we measured the discrimination acuity for different angles. Hence, we employed a comparison task presenting a reference angle followed by a target angle either in the same (visual–visual, kinesthetic–kinesthetic) or different modality (visual–kinesthetic, kinesthetic–visual).

Previous research on simple geometrical object features investigated unimodal discrimination in the haptic, tactile, and kinesthetic sense (Fiehler, Reuschel, & Rösler, 2009; Henriques & Soechting, 2003; Levy, Bourgeon, & Chapman, 2007; Voisin, Benoit, & Chapman, 2002a; Voisin, Lamarre, & Chapman, 2002b) as well as in the visual modality (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Kennedy, Orbach, & Loffler, 2006; Regan, Gray, & Hamstra, 1996). Moreover, a recent study compared unimodal visual and unimodal kinesthetic discrimination (Reuschel, Drewing, Henriques, Rösler, & Fiehler, 2010). These studies systematically tested the influence of various parameters on the discrimination acuity such as angle size, angle orientation (i.e. rotating an angle of a given size), angle line lengths, and reference frames (egocentric vs. allocentric).

Comparing contributions of tactile and kinesthetic sensory information to the haptic modality, discrimination acuity was better, if haptic rather than solely tactile or solely

kinesthetic sensory information was available, but it was comparable for tactile and kinesthetic discrimination (Voisin et al., 2002b). Thus, the authors concluded that tactile and kinesthetic senses were both equally contributing submodalities of the haptic sense which is in line with the definition of haptics (cf. Gibson, 1966). In contrast, discrimination acuity was found to be comparable for haptic and tactile sensory information, but decreased in kinesthetic sensory conditions (Levy et al., 2007). These findings indicate a higher contribution of tactile input to the discrimination performance using the haptic sense. Besides varying the sensory input, different exploration strategies during the scanning of an angle with the finger were tested (Alary et al., 2008). No difference in discrimination acuity was found whether participants moved their whole arm or whether they moved only their wrist and finger during scanning which refers to an invariant representation of object shape irrespective of the joints involved in the exploration. Furthermore, varying the angle orientation (up to 8°) of the reference angle or target angle in a comparison task had no effect on the discrimination acuity in the haptic modality indicating an independent judgement of each angle (Voisin et al., 2002a). So far, these unimodal haptic tasks used 90° as a reference angle and found difference thresholds from 4° up to 9.6° (Alary et al., 2008; Levy et al., 2007; Voisin et al., 2002a; Voisin et al., 2002b). In sum, the discrimination acuity seems to vary with the type of sensory input provided (tactile, kinesthetic, or haptic).

Comparing kinesthetic discrimination in different reference frames, acuity was similar for angle discrimination in an egocentric reference frame, i.e. representing objects relatively to one's own body, and an allocentric reference frame, i.e. representing objects relatively to each other (Fiehler et al., 2009). On the other hand, estimating the tilt direction compared to horizontal or vertical directions with reference to one's body, participants showed a bias of 2° - 3° (Henriques & Soechting, 2003), which was smaller than biases in tasks with matching the orientation of two bars in horizontal or vertical directions in relation to each other (Kappers & Koenderink, 1999). Thus, participants' performance in egocentric and allocentric reference frames might be task-dependent.

In the visual modality, discrimination acuity was tested in several studies not only for 90° but for a broad range of angle sizes from 20° up to 180° finding an acuity between 0.7° and 5° (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996). Mostly, acuity was higher for acute than obtuse angles with a maximum threshold at 130° - 150° and showed a minimal threshold at 90° (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996). Comparable to haptic angle discrimination, angle orientation had no effect on discrimination

acuity, even though angles were rotated at 45° or 90° (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996). In contrast, angle discrimination seems to be dependent on the length ratio of the lines forming the angle. For a 60° angle, discrimination was better for angles built of identical long lines than for those built of lines with different length (Kennedy et al., 2006). For the so far described studies, visual angle discrimination acuity seems to be better than haptic discrimination acuity, at least for 90° angle sizes.

However, visual and kinesthetic discrimination ability for 90° angles was found to be comparable in a recent study (Reuschel et al., 2010) which might be due to the stimulus presentation. While visual stimulus presentation was sequential showing a moving light dot along an angular trajectory in the latter study, visual stimuli were presented as a static, holistic image in the studies described above. Similarly, the performance in letter identification as well as in picture recognition was only equivalent across vision and haptics, if the encoding of the visually presented stimuli was customised to the sequential encoding of haptics (Loomis, 1990; Loomis, Klatzky, & Lederman, 1991; see also Newell, 2004).

As for the crossmodal discrimination acuity of angles, no previous findings are reported to our knowledge. Nevertheless, unimodal and crossmodal comparison of distances were tested in several studies. Visually and kinesthetically presented distances had to be compared resulting in larger errors in the crossmodal than unimodal conditions for immediate and delayed performance (Martenuik & Rodney, 1979; Newell, Shapiro, & Carlton, 1979).

In the present study, we investigated quantitative differences between unimodal and crossmodal discrimination acuity of visually and kinesthetically presented angles, i.e. how accurately participants could discriminate angles within the visual or kinesthetic modality as well as across modalities. Therefore, we employed unimodal (visual–visual, kinesthetic–kinesthetic) and crossmodal (visual–kinesthetic, kinesthetic–visual) comparison tasks to obtain the bias and difference threshold for four different angle sizes, namely 30°, 60°, 120°, and 150°, respectively.

Based on previous results on visual and haptic discrimination acuity as well as a sequential presentation for visual and kinesthetic stimuli, we expect a comparable acuity in the visual and kinesthetic sense (cf., Reuschel et al., 2010), i.e. a similar deviance of the subjective angle size from the objective angle size in the visual and kinesthetic comparison tasks. Moreover, we expect discrimination acuity to be better in the unimodal than in the crossmodal conditions (cf. Martenuik & Rodney, 1979; Newell et al., 1979).

Methods

Participants

Forty-four right-handed students were recruited at the University of Marburg. Four participants had to be excluded from the analysis due to technical problems in at least one condition or because they did not follow the instructions. The final sample comprised ten participants per experimental group (V–V: 1 male, 9 females, mean age = 23.3 years, range 19–32 years; K–K: 1 male, 9 females, mean age = 21.2 years, range 19–26 years; V–K: 3 males, 7 females, mean age = 20.5 years, range 19–23; K–V: 3 males, 7 females, mean age = 19.1, range 19–29). All participants reported normal or corrected-to-normal vision, gave written informed consent before participating and received either monetary compensation or course credit. The experiment was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Materials and apparatus

Angles were presented visually or kinesthetically. Each angle was presented as a forward movement travelling along a left opened angle. The first segment was rotated 45° counter-clockwise, in order to reduce the use of a body reference. Reference angles were 30°, 60°, 120°, or 150° (see Figure 1C). In order to obtain the bias and difference threshold for each reference angle over the course of 80 trials, they were assigned to target angles determined in each trial by an adaptive staircase procedure (Treutwein, 1995). Here, we used two staircases each containing 40 steps, resulting in 80 randomly intertwined steps per reference angle. In the first trial, the target angle deviated from each reference angle with +25° or -25° resulting in target angles of 5° and 55° for a 30° reference angle, 35° and 85° for a 60° reference angle, 95° and 145° for a 120° reference angle and 125° and 175° for a 150° reference angle (see Figure 1C). In this case, the participants could clearly distinguish the target angle from the reference angle. They decided in each trial whether the target angle was larger or smaller than the reference angle. If the response was given correctly, the target angle in the following trial converged towards the reference angle, whereas, if the response was incorrect, the following target angle diverged from the reference angle. Therefore, a stochastic approximation was

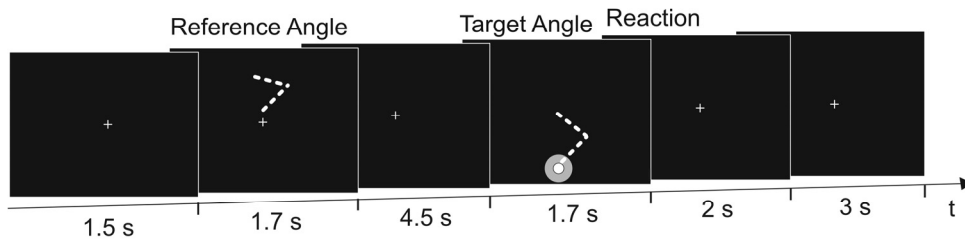
used in the first two trials according to the left formula (Robbins & Monro, 1951), and in the following trials an accelerated approximation according to the right formula (Kesten, 1958):

$$X_{n+1} = X_n - \frac{c}{n}(Z_n - \phi) \quad (1) \quad X_{n+1} = X_n - \frac{c}{2 + m_{shift}}(Z_n - \phi), \quad n > 2 \quad (2)$$

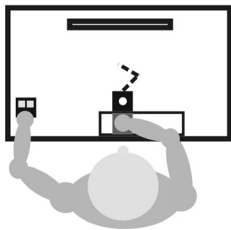
At the beginning, the size of the target angle X in trial $n + 1$ is calculated on the basis of the size of the target angle in trial n minus the product of (i) the constant initial step size ‘ c ’ (here, 10°) relative to the number of trials ‘ n ’ and (ii) the difference between the response Z in trial n (either correct ‘1’ or incorrect ‘0’) and the probability ϕ to respond correctly which is 0.5 for two response options. For this probability, upward or downward steps are equal in trial n with a step size $\delta = c/(2n)$ (Treutwein, 1995). In the following trials, the size of the target angle in trial $n + 1$ was determined taking into consideration the change in response category which refers to a change from a correct to an incorrect response and vice versa. m_{shift} then indicates the number of response category shifts.

Kinesthetic stimuli were realized as passive right hand movements applied via an apparatus located in front of the participant. The apparatus was constructed as an x-y plotter and was controlled by two servomotors operating under LabView (<http://www.ni.com/labview/>). The device allows to present straight and curved movements on a 1.3 m x 1.7 m two-dimensional workspace. Participants were instructed to hold a stylus mounted on the device with the right hand between their thumb, index and middle finger (see Figure 1B). Hand and arm were passively guided along the movement trajectory of the angle or the ellipse (average velocity 0.12 m/s; acceleration 0.3 m/s²) yielding kinesthetic information of movement direction via joints, muscles, tendons, and ligaments (McCloskey, 1978). To prevent visual input during kinesthetic stimulus presentation, the apparatus was covered and the room was completely dark. Kinesthetic stimuli presentations started at the body midline. Additionally, a hand and arm rest was positioned in front of the participant containing a 10 cm x 10 cm pushbutton which could be pushed down by the hand of the participant simply lying on it (see Figure 1B). To hold the stylus mounted on the apparatus, they had to execute a short vertical movement which was practiced prior to the experiment.

A Trial timing



B Experimental set-up



C Angles

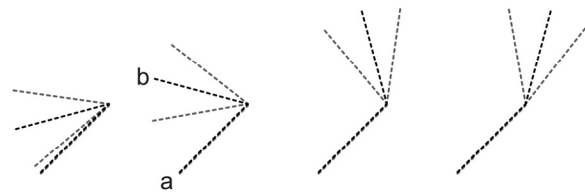


Figure 1. Schematic trial timing of the adaptive staircase procedure, experimental set-up, and stimuli. *A:* The experimental protocol is exemplarily illustrated for the visual–kinesthetic task. *B:* Schematic overview of the experimental setup with the apparatus for kinesthetic stimulus presentation, the arm rest, the computer screen for visual stimulus presentation, and the response box. *C:* Sample angles (black), and initial target angles (gray). The first and second segment of the angular trajectory is marked with *a* and *b*, respectively.

Visual stimuli were presented as a moving light spot on a black computer screen 110 cm in front of the participant. Angles had a size of 1.4° and ellipses a size of 1.0° visual angle. They were presented with an average velocity of $0.03^\circ/\text{s}$ and approximately at eye level 0.7° above a fixation cross (0.2° size). The fixation cross was visible at the center of the screen during the entire experiment. Participants' body midlines were aligned with the center of the computer screen and their position was held constant with an individually adjustable chin rest.

Design and procedure

We used a 4×4 between-subject design with the between-subject factor task modality (visual–visual (V–V), kinesthetic–kinesthetic (K–K), visual–kinesthetic (V–K), kinesthetic–visual (K–V)) and the within-subject factor angle size (30° , 60° , 120° , 150°). Tasks were blocked according to their modality and angle size in order to determine the bias and difference threshold for each experimental condition. Overall, 320 trials with 80 trials per

angle size in each modality condition were presented in 4 blocks that were randomized across participants. The experiment lasted approximately 2 h per participant.

Participants sat on a chair with their head on a chin rest in front of the apparatus facing straight ahead (see Figure 1B). Their left index finger and middle finger were positioned on a response box, while their right hand was positioned on the pushbutton of the arm rest directly in front of them (in the following referred to as starting position). When the participants' hand rested on the starting position, the button was pushed down permanently.

The comparison task was as follows (see Figure 1A). Each trial started with a 1.5 s interval initiated by an auditory tone and a fixation cross remaining visible for the duration of the trial. Then a reference angle was presented for 1.7 s (visual or kinesthetic) followed by an interval of 4.5 s and a target angle (visual or kinesthetic) of 1.7 s. After the angle offset, participants had 2 s to decide as fast and accurately as possible whether the target angle was smaller or larger than the reference angle. The inter-trial interval lasted for 3 s. In conditions with kinesthetic reference angle presentation (kinesthetic–kinesthetic, kinesthetic–visual), participants had to grasp the stylus in the initial trial interval and release it after presentation during the beginning of the delay interval by moving the hand back on the starting position. Similarly, in conditions with kinesthetic target angle presentation (kinesthetic–kinesthetic, visual–kinesthetic), they had to grasp the stylus in the middle of the delay interval and release it *after* they responded to the task by moving it back on the starting position. Each time, the grasping was indicated by a high pitched auditory signal (440 Hz) and the releasing by a low pitched auditory signal (240 Hz). The stylus of the apparatus returned to the initial position, while the participant moved his hand back on the starting position. This procedure was trained before the experiment.

Data analysis

Discrimination acuity

We obtained 80 target angle size values and the corresponding responses for each participant, modality condition and reference angle size (see Fig. 2, exemplarily). Then, we determined an individual standard psychometric function using the `psignifit` toolbox for MATLAB for each modality condition and reference angle size (see Fig. 3, for an example). The bias is defined as the 50 % point of the psychometric function referring to the point where participants rate the target angle smaller/larger than the reference angle in 50% of the trials. At this point, the

target angle is perceived as the reference angle. Moreover, it is a measure for the direction of the deviance from the reference angle, i.e. whether the angle was over- or underestimated. In contrast, the absolute bias refers to the overall extent of the deviance independent of the direction. Thus, bias and absolute bias reflect the sensory accuracy of the visual and kinesthetic sense. Furthermore, the response variability can be obtained by calculating the difference between the upper and lower difference threshold at 75% and at 25% of the sensitivity function (cf. Fiehler et al., 2009).

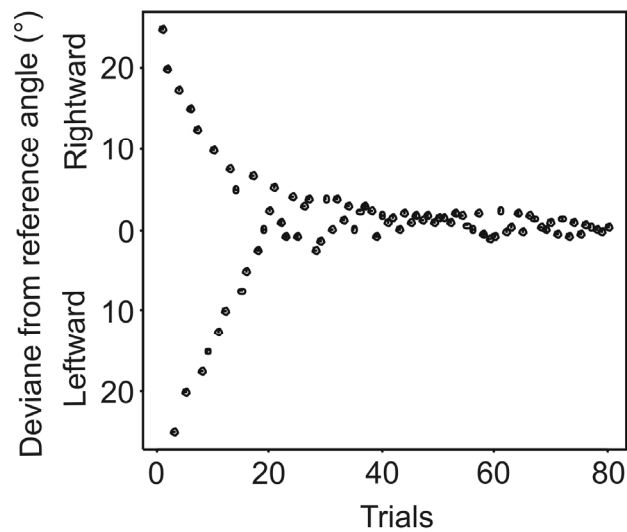


Figure 2. Results of one participant in the visual–visual condition for the 30° reference angle with the deviance from the reference angle across the 80 trials.

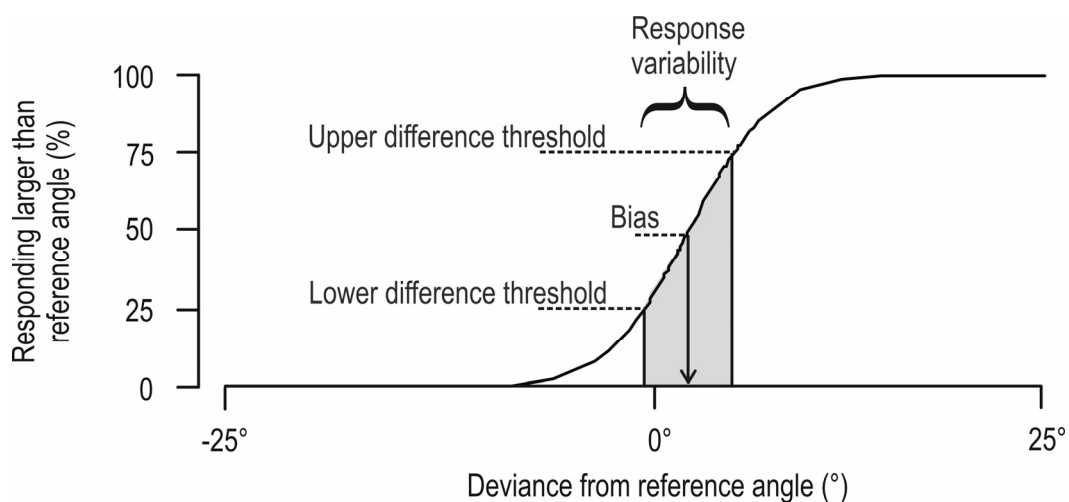


Figure 3. A psychometric function is exemplarily shown per reference angle, modality condition and participant. Obtained measures are depicted at 50% of the sensitivity function (bias) as well as at 25% (lower difference threshold) and at 75% (upper difference threshold) for the response variability (gray-shaded area).

Hence, it reflects the response variance and is inversely related to the slope of the sensitivity function that is to say the greater the slope the smaller the response variability. In order to test for accuracy differences between task modality and reference angle size, mean absolute bias and mean response variability were analyzed separately in a 4 x 4 repeated measurements analysis of variance with the between subject factor modality (V-V, K-K, V-K, K-V) and the inner subject factor angle size (30°, 60°, 120°, 150°). Post-hoc analyses were conducted by t tests ($p < .05$, two-sided, Bonferroni-corrected).

Construction of the stimulus material

Besides the above described analysis of the discrimination acuity, we used the difference threshold in order to determine the stimulus material for the subsequent studies. In order to ensure that participants are able to perform most accurate in the subsequent studies, we additionally calculated the lower difference threshold at 10% and the upper difference threshold at 90% of the sensitivity function as basis for the stimulus generation.

Results

Absolute bias

For the discrimination acuity measured as the mean absolute bias, the results are shown in Figure 4 and Table 1. The analysis revealed a main effect of modality ($F(3, 36) = 5.141$, $p < .01$) showing a higher discrimination acuity in the unimodal kinesthetic than in the visual-kinesthetic ($t(18)=-3.116$, $p < .05$) or the kinesthetic-visual task ($t(18)=-4.275$, $p < .01$). Thus, participants' absolute angle estimates differed more from the reference angle in crossmodal than unimodal kinesthetic tasks, i.e. the difference between the subjective angle size and the objective angle size was larger. A similar accuracy was found in the unimodal visual compared to the visual-kinesthetic ($t(18)=-1.746$, $p = .098$) or the kinesthetic-visual task ($t(18)=-1.935$, $p = .069$). Within unimodal tasks and within crossmodal tasks, absolute biases were also comparable ($t(18)=1.895$, $p = .074$; $t(18)=.393$, $p = .699$). Regarding the direct comparison of unimodal and crossmodal conditions, we found better discrimination acuity in the unimodal than crossmodal conditions ($t(18)=-4.260$, $p < .01$). We found no main effect of

angle size ($F(3, 36) = 1.864, p = .140$) and no interaction modality \times angle size ($F(9, 108) = 1.340, p = .225$).

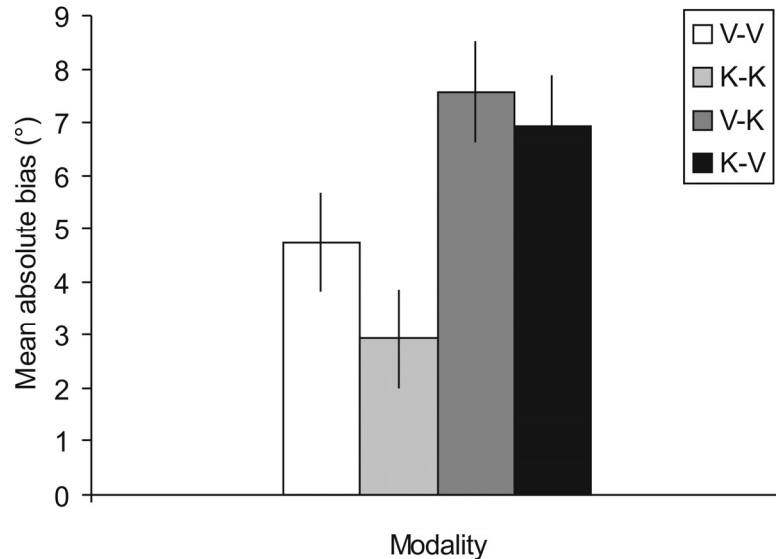


Figure 4. Mean absolute bias with standard errors of the mean in the four modality groups (V-V: visual-visual, K-K: kinesthetic-kinesthetic, V-K: visual-kinesthetic, K-V: kinesthetic-visual). It is calculated as the absolute value of the bias at the 50% point of the sensitivity function.

For unimodal discrimination, mean biases ranged from 0.28° to -1.50° for the unimodal visual condition and from 0.26° to -1.34° for the unimodal kinesthetic condition. Moreover, for crossmodal discrimination, mean biases ranged from 5.33° to -8.38° for the visual-kinesthetic condition and from 4.67° to -3.71° for the kinesthetic-visual condition. Regarding the bias, positive values indicate an overestimation of the reference angle, i.e. a larger angle size is perceived as being the actual reference angle, while negative values refer to an underestimation of the reference angle, i.e. a smaller angle size is perceived as being the actual reference angle (cf. Tab.1). Smaller mean biases compared to the absolute biases that are due to the summation of positive and negative bias values indicate that participants did not constantly over- or underestimate the reference angles.

Table 1
Mean absolute bias and mean bias (and standard deviations, respectively) for the combinations modality (V-V: visual-visual, K-K: kinesthetic-kinesthetic, V-K: visual-kinesthetic, K-V: kinesthetic-visual) and angle size.

Modality	Mean absolute bias in degree (SD)					Mean bias in degree (SD)				
	Angle size					Angle size				
	30°	60°	120°	150°	30°	60°	120°	150°		
V-V	2.99 (3.26)	4.32 (2.88)	7.09 (5.78)	4.55 (4.15)	-1.50 (4.25)	0.28 (5.38)	-0.72 (9.41)	0.10 (6.34)		
K-K	2.41 (2.41)	3.50 (2.57)	2.22 (2.48)	3.59 (3.02)	0.26 (3.15)	-1.17 (4.32)	-1.34 (3.10)	-1.25 (4.66)		
V-K	7.52 (5.39)	5.48 (4.63)	8.38 (5.30)	8.90 (8.61)	-7.52 (5.39)	5.33 (4.81)	-8.38 (5.30)	-6.00 (11.05)		
K-V	6.03 (3.20)	7.52 (5.18)	9.21 (5.50)	4.98 (3.30)	3.47 (6.12)	-3.71 (8.63)	3.37 (10.57)	4.67 (3.76)		

Response variability

For the response variance measured as the response variability, the results are shown in Figure 5. The analysis of the response variability revealed a significant interaction of modality and angle size ($F(9, 108) = 3.216, p < .01$) and a main effect of angle size ($F(3, 36) = 3.089, p < .05$) which were due to the larger response variability for the 120° reference angle compared to 30°, 60° and 150° reference angles in the unimodal visual task (all comparisons, $p < .05$). We found no main effect of modality ($F(3, 36) = 1.203, p = .323$). Thus, unimodal and crossmodal response variability did not differ.

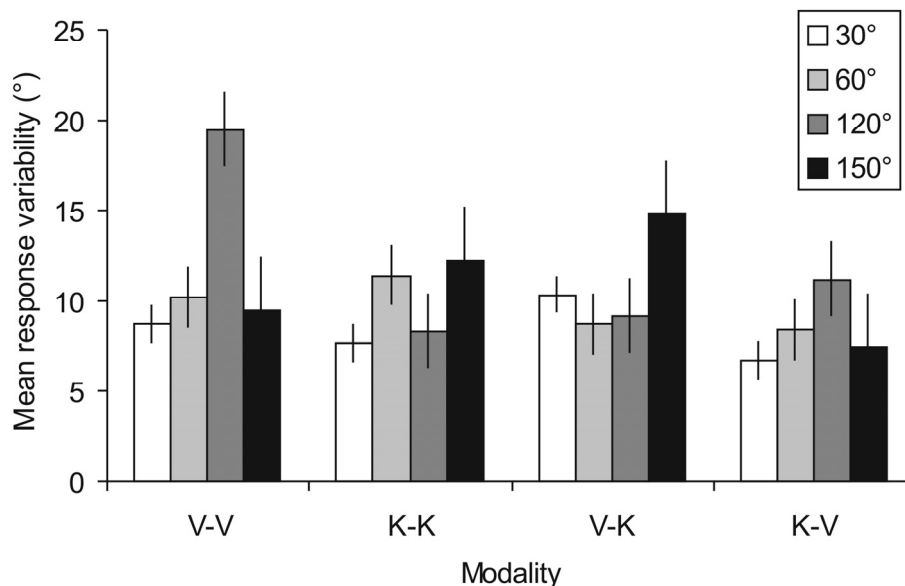


Figure 5. Mean response variability with standard errors of the mean for the four modality groups (V–V: visual–visual, K–K: kinesthetic–kinesthetic, V–K: visual–kinesthetic, K–V: kinesthetic–visual) and for the angle size. It is calculated as the difference between the upper difference threshold (value at 75% of the sensitivity function) and the lower difference threshold (value at 25% of the sensitivity function).

Difference thresholds

For the construction of the subsequently used stimulus material, the mean lower and upper difference thresholds as well as the standard deviations of the mean were obtained. We found a mean lower difference threshold at 10% of the sensitivity function of 10.64° (SD = 10.25°) and a mean upper difference threshold at 90% of the sensitivity function of 8.88° (SD = 8.84°).

Discussion

In the present study, discrimination acuity of two-dimensional angle stimuli was investigated in unimodal and crossmodal tasks presented in the visual or kinesthetic modality. Our results demonstrate a comparable acuity for unimodal visual and unimodal kinesthetic angle discrimination as well as for visual–kinesthetic and kinesthetic–visual discrimination. In contrast, acuity was higher in the unimodal kinesthetic than in the crossmodal conditions and, overall, discrimination acuity was better for unimodal than crossmodal comparison tasks. The latter effect is independent of the response variability which was comparable for unimodal and crossmodal angle discrimination. Differences in the response variability were only found for 120° in the unimodal visual discrimination tasks with a higher response variability for the 120° reference angle compared to other reference angles. Below, implications of the findings are discussed with respect to the previous findings on discrimination ability in the visual and haptic sense.

We observed no difference between the visual and kinesthetic discrimination acuity with absolute biases of 5° and 3°, respectively. This is in line with previous studies of visual angle discrimination (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Kennedy et al., 2006; Regan et al., 1996) and some studies investigating tactile and kinesthetic angle discrimination (Alary et al., 2008; Fiehler et al., 2009) which found discrimination acuity in a similar range. However, our findings seem to be at variance with studies on the contribution of tactile and kinesthetic sensory information to the haptic input in discrimination tasks (Levy et al., 2007; Voisin et al., 2002a; Voisin et al., 2002b; Voisin, Michaud, & Chapman, 2005). They found better discrimination acuity for haptic input or haptic/tactile sensory information compared to kinesthetic sensory information (Levy et al., 2007; Voisin et al., 2002b). Since the kinesthetic discrimination acuity was similar to the visual discrimination acuity in our task, it seems to be more precise than previously suggested. Furthermore, the acuity of the relative angle judgement in our kinesthetic discrimination tasks seems to be comparable to absolute judgments in kinesthetic orientation tasks (Henriques & Soechting, 2003). Regarding the comparable discrimination acuity of visual and kinesthetic discrimination, it can be concluded that the visual and the kinesthetic sense are both similarly sensitive in detecting angular differences. This might have been enhanced by the sequential presentation of the visual angle which was adapted to the sequential perception of the kinesthetic sense and not presented as a static, holistic visual angle as in previous studies (Chen & Levi, 1996; Heeley

& Buchanan-Smith, 1996; Regan et al., 1996). Overall, both senses seem to be precise enough in order to contribute to sensorimotor control processes.

Moreover, discrimination acuity was better in the unimodal than crossmodal tasks, but we found comparable acuity within crossmodal discrimination with absolute biases around 8° and 7° , respectively. Thus, discrimination seems to be independent of the direction of the comparison, i.e. visual–kinesthetic or kinesthetic–visual. Moreover, crossmodal discrimination acuity appears to be similar to haptic discrimination acuity in previous studies (Alary et al., 2008; Fiehler et al., 2009; Levy et al., 2007; Voisin et al., 2002b). On the one hand, the crossmodal cost in discrimination acuity could be due to a recoding of representations across modalities or additional control processes to compare relevant representations (e.g. Newell et al., 1979; Woods, O’Modhrain, & Newell, 2004). During these processes stimulus details might get lost, thus leading to an increase of errors. On the other hand, the effect could result from the fact that specific stimulus characteristics are only available in unimodal but not in crossmodal versions of the task. In unimodal conditions, reliable location and distance information in space as well as velocity information of the moving stimulus is available during encoding of the reference stimulus and the comparison with the target stimulus. These data can be used for comparing reference and target stimulus in addition to the angle-specific movement trajectory. In contrast, in crossmodal conditions only information about the angle-specific movement trajectory can be matched for stimulus comparison. Thus, in unimodal conditions the stimulus comparison might be based on a richer, more detailed representation. Additionally, crossmodal performance might have been impaired because the stimuli were presented in different planes. Visual stimuli appeared on the frontal plane of the computer monitor and kinesthetic stimuli on the horizontal plane of the haptic device. This different presentation mode was inevitable, because a presentation of visual stimuli in the same horizontal plane of the haptic device had led to distortions of the size of the angle that had to be perceived and compared.

Regarding the participants’ response variability, we found larger variance for 120° compared to other reference angles in the unimodal visual discrimination task. This result is surprising given that the response variability did not vary for 120° in other conditions or for 150° as the other obtuse angle. In that case, response variability would have been higher for obtuse compared to acute angles which was found in several studies (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996). Previous studies on visual angle or orientation discrimination found lower discrimination acuity for 135° (Orban, Vandenbussche, & Vogels,

1984; Snippe & Koenderink, 1994) or 120° (Kennedy, Orbach, & Loffler, 2008), but also for other obtuse angles. For further explanations, it seems necessary to test these findings in another study to investigate the stability of the effect. Moreover, possible contributions to the effect, like the angle orientation, overall angle size, and the position in the visual field should be tested to provide a reasonable explanation.

Overall, the visual and the kinesthetic sense seem to be comparable in discrimination acuity, and therefore, an appropriate basis for sensorimotor control mechanisms. A cost in acuity was found for crossmodal compared to unimodal discrimination which might indicate additional crossmodal processing in order to accomplish the discrimination task. On the basis of the observed difference thresholds, the construction of the stimulus material was carried out. In the subsequent studies, matching tasks with a sample angle and a target angle were employed. Thus, we selected the sample angles as 30°, 60°, 120°, and 150°. Due to the large variances of the difference threshold, the target angles were determined either at 1.5 SD of the mean difference threshold providing easy matching tasks or at 1 SD of the mean difference threshold yielding difficult matching tasks.

References

- Alary, F., Goldstein, R., Duquette, M., Chapman, C. E., Voss, P., & Lepore, F. (2008). Tactile acuity in the blind; a psychophysical study using a two-dimensional angle discrimination task. *Experimental Brain Research, 187*, 587–594.
- Chen, S., & Levi, D. M. (1996). Angle Judgement: Is the whole the sum of its parts? *Vision Research, 36*, 1721–1735.
- Fiehler, K., Reuschel, J., & Rösler, F. (2009). Early non-visual experience influences proprioceptive-spatial discrimination acuity in adulthood. *Neuropsychologia, 47*, 897–906.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Heeley, D. W., & Buchanan-Smith, H. M. (1996). Mechanisms specialized for the perception of image geometry. *Vision Research, 36*, 3607–3627.
- Henriques, D. Y. P., & Soechting, J. F. (2003). Bias and sensitivity in the haptic perception of geometry. *Experimental Brain Research, 150*, 95–108.
- Kappers, A. M., & Koenderink, J. J. (1999). Haptic perception of spatial relations. *Perception, 28*, 781–795.
- Kennedy, G. J., Orbach, H. S., & Loffler, G. (2006). Effects of global shape on angle discrimination. *Vision Research, 46*, 1530–1539.
- Kennedy, G. J., Orbach, H. S., & Loffler, G. (2008). Global shape versus local feature: An angle illusion. *Vision Research, 48*, 1281–1289.
- Kesten, H. (1958). Accelerated stochastic approximation. *Annals of Mathematical Statistics, 29*, 41–59.
- Levy, M., Bourgeon, S., & Chapman, C. E. (2007). Haptic discrimination of two-dimensional angles: influence of exploratory strategy. *Experimental Brain Research, 178*, 240–251.
- Loomis, J. M. (1990). A model of character recognition and legibility. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 106–120.
- Loomis, J. M., Klatzky, R. L., & Lederman, S. J. (1991). Similarity of tactual and visual picture recognition with limited field of view. *Perception, 20*, 167–177.
- Martenuik, R. G., & Rodney, M. (1979). Modality and retention effects in intra- and cross-modal judgements of kinaesthetic and visual information. *British Journal of Psychology, 70*, 405–412.

- McCloskey, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews*, *58*(4), 763–820.
- Newell, F. N. (2004). Cross-modal object recognition. In G. A. Calvert, C. Spence, & B. E. Stein (Eds.), *The handbook of multisensory processes* (pp. 123–139). Cambridge, MA: MIT Press.
- Newell, K. M., Shapiro, D. C., & Carlton, M. J. (1979). Coordinating visual and kinaesthetic memory codes. *British Journal of Psychology*, *70*, 87–96.
- Orban, G. A., Vandebussche, E., & Vogels, R. (1984). Human orientation discrimination tested with long stimuli. *Vision Research*, *24*, 121–128.
- Regan, D., Gray, R., & Hamstra, S. J. (1996). Evidence for a neural mechanism that encodes angles. *Vision Research*, *36*, 323–330.
- Reuschel, J., Drewing, K., Henriques, D. Y. P., Rösler, F., & Fiehler, K. (2010). Optimal integration of visual and proprioceptive movement information for the perception of trajectory geometry. *Experimental Brain Research*, *201*, 853–862.
- Robbins, H., & Monro, S. (1951). A stochastic approximation method. *Annals of Mathematical Statistics*, *22*, 400–407.
- Snippe, H. P., & Koenderink, J. J. (1994). Discrimination of geometric angle in the fronto-parallel plane. *Spatial Vision*, *8*, 309–328.
- Treutwein, B. (1995). Adaptive Psychophysical Procedures. *Vision Research*, *35*, 2503–2522.
- Voisin, J., Benoit, G., & Chapman, C. E. (2002a). Haptic discrimination of object shape in humans: two-dimensional angle discrimination. *Experimental Brain Research*, *145*, 239–250.
- Voisin, J., Lamarre, Y., & Chapman, C. E. (2002b). Haptic discrimination of object shape in humans: contribution of cutaneous and proprioceptive input. *Experimental Brain Research*, *145*, 251–260.
- Voisin, J., Michaud, G., & Chapman, C. E. (2005). Haptic shape discrimination in humans: insight into haptic frames of reference. *Experimental Brain Research*, *164*, 347–356.
- Woods, A. T., O'Modhrain, S., & Newell, F. N. (2004). The effect of temporal delay and spatial differences on cross-modal object recognition. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 260–269.

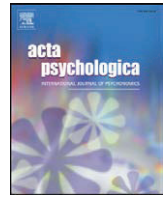
Study I

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Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories

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ABSTRACT

The present study investigated whether visual and kinesthetic stimuli are stored as multisensory or modality-specific representations in unimodal and crossmodal working memory tasks. To this end, angle-shaped movement trajectories were presented to 16 subjects in delayed matching-to-sample tasks either visually or kinesthetically during encoding and recognition. During the retention interval, a secondary visual or kinesthetic interference task was inserted either immediately or with a delay after encoding. The modality of the interference task interacted significantly with the encoding modality. After visual encoding, memory was more impaired by a visual than by a kinesthetic secondary task, while after kinesthetic encoding the pattern was reversed. The time when the secondary task had to be performed interacted with the encoding modality as well. For visual encoding, memory was more impaired, when the secondary task had to be performed at the beginning of the retention interval. In contrast, memory after kinesthetic encoding was more affected, when the secondary task was introduced later in the retention interval. The findings suggest that working memory traces are maintained in a modality-specific format characterized by distinct consolidation processes that take longer after kinesthetic than after visual encoding.

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1. Introduction

Crossmodal working memory refers to the maintenance of sensory information encoded in one modality over short time intervals when the comparison information is given in another modality during recognition. As a consequence, representations built from one sensory modality have to be matched with representations obtained from other senses for crossmodal comparison, i.e. visual information has to be matched with tactile/kinesthetic information and vice versa (Gibson, 1966; Schiffman, 1990). While much is known about visual working memory (see D'Esposito, 2007; Ranganath, 2006), knowledge about tactile/haptic working memory is still sparse (see Gallace & Spence, 2009). Moreover, this holds for the question how information from distinct modalities is represented in crossmodal working memory and integrated to allow successful crossmodal task performance.

Two opposing theoretical accounts emerged from research on visual and haptic working memory: One suggests that representations in crossmodal working memory are multisensory and integrate information from both modalities; the other assumes modality-specific representations which are transformed into each other for crossmodal recognition. The first account is supported by behavioral studies on crossmodal priming which showed comparable unimodal and crossmodal priming effects for visually and tactually studied line patterns and objects (Easton, Greene, & Srinivas, 1997; Reales & Ballesteros, 1999). These findings suggest the existence of shared representations of geometrical object shape and structure. Further evidence comes from neuroimaging studies indicating that tactile object recognition is associated with activity in occipito-temporal cortex areas of the visual pathway (see Grill-Spector, Kourtzi, & Kanwisher, 2001; Lacey, Tal, Amedi, & Sathian, 2009, for reviews). In particular, object-specific tactile activation was reported for the lateral occipital complex (LOC), which is also activated during visual object recognition (Amedi, Malach, Hendler, Peled, & Zohary, 2001). Since the LOC was not activated by object-specific sounds (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002), the authors proposed a region LOTv which is supposed to be exclusively sensitive to both visual and tactile geometric shape information (Amedi et al., 2002). This claim is further supported by a study in which the middle and lateral occipital areas were activated during recognition of visual objects previously presented either in the visual or in the tactile modality (James et al., 2002).

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These findings, however, are at variance with results that support modality-specific representations that only share some related features. A recent study by Woods, O'Modhain, and Newell (2004) investigated unimodal and crossmodal working memory in several experiments by varying the retention interval up to 30 s between sample and test stimulus. They found, for instance, better unimodal visual memory than unimodal tactile memory, but a similar delay effect for both modalities and no difference within crossmodal memory. Thus, the authors argued for separate memory systems which comprise modality-specific representations sharing related functional features (Woods et al., 2004), e.g., mediation by surface-dependent representations (Woods & Newell, 2004). This view is strengthened by findings on visual and tactile storage and retrieval of object features, namely curvatures (Ittyerah & Marks, 2007). Differential interference effects were revealed through spatial, movement, rehearsal, or articulatory secondary tasks dependent on the memory encoding or recognition modality. In contrast to Woods et al. (2004), memory performance was in general better after tactile than after visual encoding. The findings suggest that tactile information is represented, at least in part, in a spatial-motor format, while visual information is possibly represented in a more global format which is supported by verbal rehearsal. Nevertheless, visually and tactually encoded stimuli seem to share some representation characteristics. Further support for modality-specific representations comes from findings on shape recognition in children and crossmodal kinesthetic memory in adults. While unimodal visual shape recognition was impaired by a visual interference task, haptic shape recognition was not affected suggesting differences in the coding of visually and haptically encoded shapes (Millar, 1972). Comparing the retention of visual and kinesthetic information obtained by positioning movements, the performance decrease over 20 s was greater for kinesthetic than visual information (Posner, 1967).

Given the existence of modality-specific representations, crossmodal performance requires a recoding process. One representation must either be recoded into the other modality or it must be transformed into a neutral, modality-unspecific code (Smyth, 1984). Some results from visual and kinesthetic distance reproduction tasks agree with the former hypothesis, i.e. the information is always recoded into the modality relevant for reproduction (Connolly & Jones, 1970). Other studies suggest that visual and kinesthetic information is always represented in the representation format that is best suited for the task, i.e. the modality providing the most relevant and reliable information (Freides, 1974; Martenuik & Rodney, 1979; Newell, Shapiro, & Carlton, 1979). Since vision is dominant in sighted people, this account assumes that coding occurs by default in the visual modality (e.g. Rock & Victor, 1964; Posner, Nissen, & Klein, 1976, for a review). This is supported by findings on crossmodal recognition of unfamiliar objects, where recognition performance decreased when visual and haptic encoding was visually and verbally interfered, but not when it was haptically interfered (Lacey & Campbell, 2006).

Memory performance cannot only be influenced by the stimulus modality but also by the temporal stability of the memory code during maintenance. Results of unimodal working memory showed that memory representations of haptically explored geometrical objects decayed in adults after 15 s (Kiphart, Hughes, Simmons, & Cross, 1992). Haptic working memory maintenance for object shapes decreased after 5 and 30 s compared to 1 s in children (Millar, 1974). In the visual modality, recognition discriminability decreased from 1 s to 5 and 10 s for visual object working memory maintenance and from 5 to 10 s for spatial working memory maintenance (Possin, Filoteo, Song, & Salmon, 2008). Comparison of unimodal visual and unimodal tactile working memory showed a larger decrement in the performance of tactile than visual working memory tasks with a delay of 15 and 30 s compared to no delay (Woods et al., 2004). This held for correct rejections, but not for hits. In contrast, other studies argue for a comparable temporal stability of representations built from input of the visual or tactile/kinesthetic modality. The retention of visual and

kinesthetic information obtained by positioning movements over 20 s led to a similar increase of errors in both modality conditions compared to immediate reproduction (Martenuik & Rodney, 1979). Similar results were demonstrated in unimodal and crossmodal matching tasks of visual and tactile forms for retention intervals of 1, 10 and 30 s (Garvill & Molander, 1973). Thus, the temporal stability of visual and tactile/kinesthetic information in unimodal and crossmodal working memory still remains unclear.

While visual information of objects and object features, such as shape and size, can be processed in a parallel way, haptic or kinesthetic sensory information has to be encoded sequentially. However, visual object information can also be extracted from motion (e.g. Kriegeskorte et al., 2003) or from a sequential stimulus presentation, e.g. giving a limited field of view moving along the lines of an object (e.g. Loomis, Klatzky, & Lederman, 1991), leading to an overall object representation. Thus, a comparable encoding situation for visual and haptic or kinesthetic information can be achieved.

In the present study, we investigated whether visual and kinesthetic angular movement trajectories are represented in a modality-specific or in a modality-unspecific, multisensory code in unimodal and crossmodal working memory. Furthermore, we examined the temporal stability of the working memory code for visual and kinesthetic movement trajectories.

Dual-task paradigms have often been used to examine the format of working memory representations (see Klauer & Zhao, 2004, for an overview on visual and spatial working memory maintenance). In this design, a sample stimulus has to be compared with a later presented target stimulus, while during the retention interval a secondary task is inserted which competes for the same processing resources as the primary task or not. Using this paradigm, several studies provided evidence that the retention of visual shape information is impaired by a secondary visual task (e.g. Logie, 1986), and spatial memory performance by a secondary movement task (Baddeley & Lieberman, 1980; Logie & Marchetti, 1991).

Here, we employed a delayed matching-to-sample task (primary working memory task) with either unimodal or crossmodal comparisons varying both the encoding modality (vision or kinesthesia) and the recognition modality (vision or kinesthesia). The primary task was combined with a secondary interference task presented either in the visual or in the kinesthetic modality. To probe time-related effects, the interference task was presented either immediately after stimulus encoding, or delayed, during the second half of the retention interval.

If stimulus representations in working memory are formed in a modality-specific manner, the interference task should impair memory performance differently depending on the encoding modality. A visual interference task should impair memory performance more strongly after visual than after kinesthetic encoding, while the opposite effect should hold for a kinesthetic interference task, i.e. this should interfere more with maintenance after kinesthetic than visual encoding. If the representation of the sample stimulus is recoded into the modality of the target stimulus, then interference task modality should interact with recognition modality. Under the assumption that memory representations are always formed in the modality best suited for the task, i.e. dominated by the visual system (Freides, 1974; Rock & Victor, 1964), memory representations are expected to be held in the visual modality irrespective of whether stimulus information is encoded visually or kinesthetically. Therefore, a secondary visual task should affect memory for both visually and kinesthetically encoded stimuli, while a secondary kinesthetic task should lead to no impairment. If memory representations are by default multisensory, i.e. modality-unspecific, visual and kinesthetic interference tasks should impair memory in the crossmodal and the unimodal conditions to the same extent. In this case also the temporal stability of the memory code is expected to be similar in different modality conditions. On the other hand, for modality-specific memory representations the temporal stability is expected to differ for the maintenance of visually and kinesthetically encoded information.

2. Methods

2.1. Participants

Twenty-two students of the University of Marburg were recruited. Six participants had to be excluded from the analysis, because they performed with $\leq 50\%$ mean correct responses in at least one experimental condition. Therefore, the final sample comprised sixteen students (mean age: 21.8 years, range 19–27 years, 15 females). All participants were right-handed, assessed by the German version of the Edinburgh Handedness Inventory (mean, SD: 84.44, 13.76; Oldfield, 1971) and reported normal or corrected-to-normal vision. They received either monetary compensation or course credit. Participants gave their written consent.

2.2. Materials and apparatus

In the primary task, angles were presented either visually or kinesthetically. Sample angles were 30° , 60° , 120° , or 150° . They were assigned to one of two target angles varying with $+23^\circ$ or -25° from each sample angle (see Fig. 1B). Target angles had been determined at

1.5 SD of the mean 90% difference threshold obtained in a pre-experiment. Same target angles were presented in 50% of the trials. Each angle was presented as a forward and backward movement traveling along a left opened angle. The first segment of the movement trajectory was rotated 45° counter-clockwise in order to reduce the influence of a body reference. In the secondary task, a horizontal or vertical ellipse was presented either in the visual or in the kinesthetic modality. Ellipse orientation and width were defined by the eccentricity with 0.6 or -0.6 for visual and 0.8 or -0.8 for kinesthetic ellipses (see Fig. 1C). Eccentricity values were obtained in a second pre-experiment and matched with respect to task difficulty.

Kinesthetic stimuli were realized as passive right hand movements applied via an apparatus located in front of the participant. The apparatus was constructed as an x-y plotter and was controlled by two servomotors operating under LabView (<http://www.ni.com/labview/>). The device allows to present straight and curved movements on a $1.3 \text{ m} \times 1.7 \text{ m}$ two-dimensional workspace. Participants were instructed to hold a stylus mounted on the device with their right hand between thumb, index and middle finger (see Fig. 1D). Hand and arm were passively guided along the movement trajectory of the angle or the ellipse (average velocity 0.12 m/s; acceleration

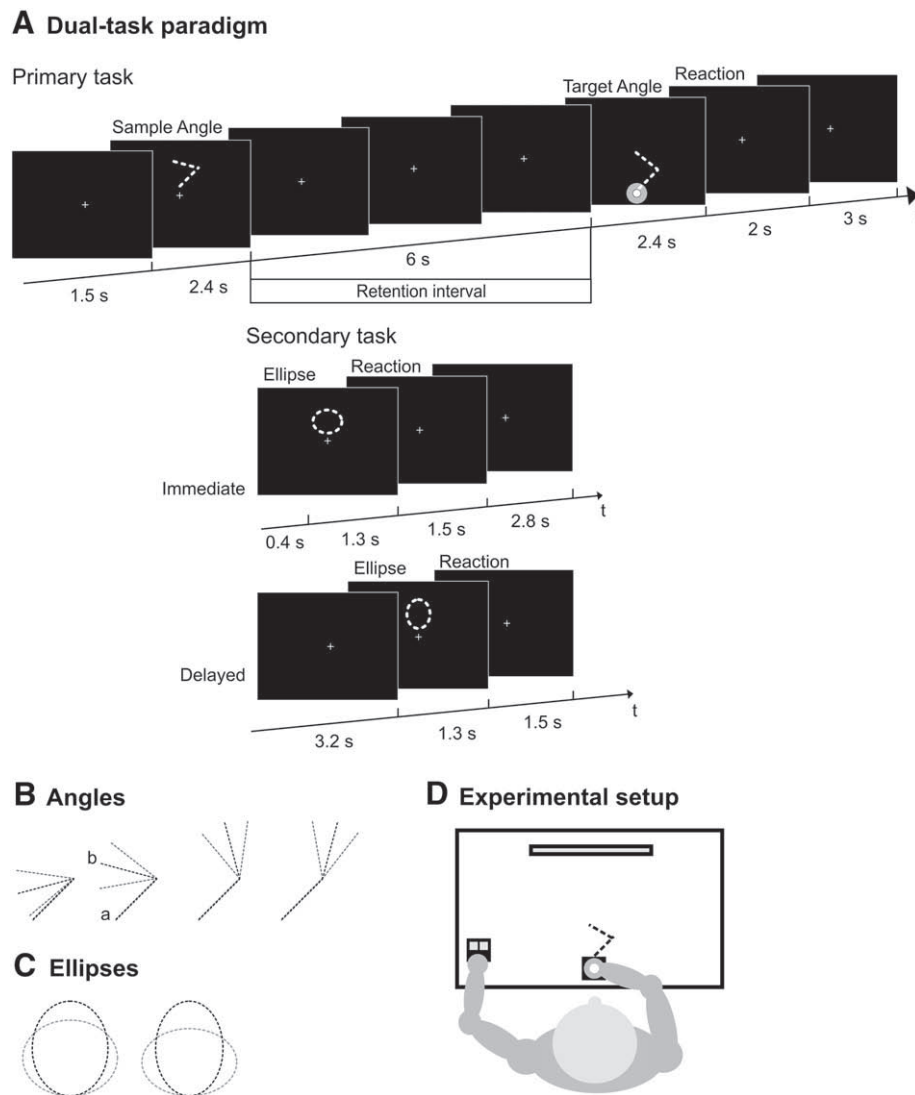


Fig. 1. Schematic trial timing of the dual-task paradigm and stimuli. A: The experimental protocol is exemplarily illustrated for the visual–kinesthetic primary task and the visually presented secondary task. Participants either performed the primary memory task alone or combined with the secondary interference task inserted immediately or delayed in the retention interval (interference time). B: Sample angles (black) and target angles (gray). The first and second segment of the angular trajectory are marked with *a* and *b*, respectively. C: Ellipses presented in the visual modality (left) and kinesthetic modality (right). D: Schematic overview of the experimental setup with the apparatus for kinesthetic stimulus presentation, the computer screen for visual stimulus presentation and the response box.

0.3 m/s²; one way length of the angle path 14 cm) yielding kinesthetic information of movement direction via joints, muscles, tendons, and ligaments (McCloseky, 1978). To prevent visual input during kinesthetic stimulus presentation, the apparatus was covered and the room was completely dark. Participants wore earplugs and headphones emitting white noise during the experiment to mask the noise of the apparatus' servomotors. Visual stimuli were presented as a moving white light spot (0.14° size) on a black computer screen 110 cm in front of the participant. Angles had a max. overall height/width of 1.4° and ellipses a size of 1.0° visual angle along the major axis. They were presented with an average velocity of 0.03°/s and approximately at an eye level 0.7° above a fixation cross (0.2° size). The fixation cross was visible at the center of the screen during the entire experiment. Participants' body midlines were aligned with the center of the computer screen and their position was held constant with an individually adjustable chin rest. Kinesthetic stimuli presentations started at the body midline.

2.3. Design and procedure

We used a 2×2×3×2 repeated measures design with the factors memory task encoding modality (visual, V; kinesthetic, K), memory task recognition modality (visual, V; kinesthetic, K), secondary interference task (visual, kinesthetic, and none), and interference time (immediate and delayed). The interference time was randomized across conditions. The modality conditions of the memory task (V–V, K–K, V–K, and K–V, respectively) and interference task were blocked in order to avoid too many switches of attention across modalities. Control trials with no interference task were also blocked for the memory task modality and presented in 4 blocks with 32 trials. Overall, 640 trials with 32 trials per condition were presented in 20 blocks. The experiment lasted approximately 4 h and was partitioned into two equally long sessions on consecutive days. Blocks were randomized across participants and across sessions.

Participants sat on a chair with their head on a chin rest in front of the apparatus facing straight ahead. In their right hand, they were holding the stylus, and their left index finger and middle finger were positioned on a response box. As primary task, they performed a delayed matching-to-sample task (see Fig. 1A, upper row) and, as secondary task, a 2-alternative-forced-choice task (see Fig. 1A, middle and lower row). Each trial started with an auditory warning signal (440 Hz) for 300 ms and a fixation cross remaining visible for the duration of the trial. Participants were instructed to fixate the fixation cross during the entire trial. After 1 s, a sample angle was presented for 2.4 s (visual or kinesthetic) followed by a retention interval of 6 s. Then a target angle (visual or kinesthetic) was shown for 2.4 s. After the angle offset, participants had 2 s to decide as fast and as accurately as possible whether both angles were the same or different. The inter-trial interval lasted for 3 s. In control trials, the retention interval was unfilled (see Fig. 1A, upper row). During all other trials, a secondary task was inserted in the 6 s retention interval. In the immediate condition, an ellipse (visual or kinesthetic) was presented for 1.3 s, starting 400 ms after the sample angle offset (see Fig. 1A, middle row). Participants had 1.5 s to decide whether the ellipse was horizontal or vertical relative to their body midline. In the delayed condition, an ellipse was presented in the middle of the retention interval 3.2 s after the sample angle offset (see Fig. 1A, lower row). The target angle was shown directly after the 1.5 s ellipse response period. The first three blocks comprised practice trials for the primary task only (16 trials), the secondary task only (8 trials) and the dual-task paradigm (16 trials).

2.4. Data analysis

Mean correct responses were analyzed separately for both tasks. The memory task analysis included only trials with reaction times ≥200 ms

and ≤mean + 2 SD ($M = 709.3$ ms, $SD = 314.4$). Additionally, the interference conditions comprised only trials with correct responses to the secondary task. In order to test for differences between unimodal and crossmodal memory and overall interference effects, mean correct responses were analyzed in a 2×2×3 repeated measurements analysis of variance with the factors encoding modality (visual and kinesthetic), recognition modality (visual and kinesthetic) and interference task (visual, kinesthetic, and none). Furthermore, in order to test for specific interference and interference time effects, a 2×2×2 repeated measurements analysis of variance with the factors encoding modality (visual and kinesthetic), recognition modality (visual and kinesthetic), interference task modality (visual and kinesthetic), and interference time (immediate and delayed) was calculated for difference errors (mean % correct responses in the interference conditions minus mean % correct responses in the control condition, calculated per subject). Post-hoc analyses and secondary task analyses were conducted by *t* tests ($p < .05$). Mean reaction times of the memory task were not further analyzed because of a task-dependent time delay of the response interval that did not start before the offset of the second stimulus.

3. Results

3.1. Primary memory task

3.1.1. Correct responses

Overall task performance was 80.25% ($SD = 5.07$) after the exclusion of the six participants that performed with ≤50% mean correct responses in at least one experimental condition (see Section 2.1). Analysis of correct responses revealed a significant interaction of encoding modality and recognition modality ($F(1, 15) = 75.425$, $p < .001$, $\eta_p^2 = .834$; depicted in Fig. 2) showing that memory was better in the unimodal than in the crossmodal conditions (all comparisons, $p < .05$, Bonf. corr.; kinesthetic–kinesthetic compared to kinesthetic–visual condition, $p < .009$, uncorr.). Within the unimodal conditions, memory was better in the visual than the kinesthetic modality ($t(15) = 3.156$, $p < .05$, Bonf. corr.). The two crossmodal conditions, on the other hand, did not differ significantly ($t(15) = -.427$, $p = .675$). Furthermore, the ANOVA showed a significant main effect of the interference task ($F(2, 15) = 8.535$, $p < .01$, $\eta_p^2 = .363$; depicted in Fig. 2) with better memory in the control than in the visual interference ($t(15) = -3.356$, $p < .05$, Bonf. corr.) or kinesthetic interference condition ($t(15) = -3.234$, $p < .05$, Bonf. corr.). Memory performance did not differ between the visual and the kinesthetic interference task condition ($t(15) = .501$, $p = .624$). We also found a main effect of encoding modality ($F(1, 15) = 6.142$, $p < .05$, $\eta_p^2 = .291$) and recognition modality ($F(1, 15) = 6.980$, $p < .05$, $\eta_p^2 = .318$), but no further interactions. Mean correct responses for all conditions are shown in Table 1.

3.1.2. Difference errors

Analysis of difference errors – measured as difference between memory performance in interference task conditions and the control condition – revealed two significant interactions with encoding modality. First, an interaction of encoding modality and interference task modality proved significant ($F(1, 15) = 9.493$, $p < .01$, $\eta_p^2 = .388$; depicted in Fig. 3). This indicates increased errors for visual interference (4.10%) than kinesthetic interference (2.27%) when encoding was visual and the opposite effect when the encoding was kinesthetic, namely increased errors for kinesthetic interference (5.27%) than for visual interference (2.66%). Second, an interaction of encoding modality and interference time ($F(1, 15) = 4.611$, $p < .05$, $\eta_p^2 = .235$; depicted in Fig. 3) was found indicating an error decrease from immediate (4.13%) to delayed interference (2.20%) in the visual encoding condition and an error increase from immediate (2.80%) to delayed (5.14%) in the kinesthetic encoding condition. There were no

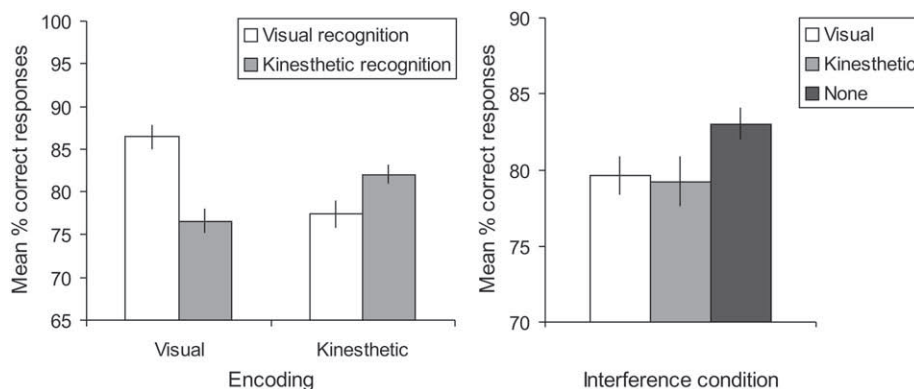


Fig. 2. Left: Mean percentage of correct responses with standard errors of the mean for the interaction encoding modality \times recognition modality of the memory task. Right: Mean percentage of correct responses with standard errors for the interference conditions (visual, kinesthetic, and none).

other significant interactions or main effects. Mean errors for all conditions are shown in Table 2.

3.2. Secondary interference task

Task difficulty of the visual and kinesthetic secondary task was matched according to the results of a pilot experiment. Consequently, no significant difference was found between mean correct responses of the visual and the kinesthetic secondary task ($t(15) = -545$, $p = .594$). Performance was almost perfect in both tasks ($M_{\text{visual}} = 95.36\%$, $SD = 4.25$; $M_{\text{kinesthetic}} = 96.39\%$, $SD = 6.86$). Furthermore, mean reaction times of the two interference tasks did also not differ ($M_{\text{visual}} = 500.8$ ms, $SD = 121.7$; $M_{\text{kinesthetic}} = 499.1$ ms, $SD = 124.4$; $t(15) = .041$, $p = .968$).

4. Discussion

In the present study, participants performed a primary working memory task in which they encoded and retrieved an angular movement trajectory either visually or kinesthetically, and in which an additional secondary interference task was early or late presented in the maintenance interval. As expected, the interference task impaired primary memory task performance compared to a control condition without interference. Our results demonstrated two interactions with the encoding modality of the memory task. First, the encoding modality was clearly modulated by the modality of the interference task. After visual encoding, memory was more impaired by a visual than by a kinesthetic secondary task, while after kinesthetic encoding the pattern was reversed, i.e. a secondary kinesthetic task interfered more than a secondary visual task. This effect was independent of the recognition modality. Second, encoding modality also varied as a function of the time when the secondary task had to be performed. For visual encoding, memory performance was reduced when the secondary task was immediately performed in the maintenance interval. In contrast, memory performance after kinesthetic encoding was impaired when the secondary task was later

executed in the retention interval. Both findings suggest different storage characteristics of visual and kinesthetic movement information in working memory. Overall, working memory was better in the unimodal (visual–visual and kinesthetic–kinesthetic) than in the crossmodal conditions (visual–kinesthetic and kinesthetic–visual). Within the unimodal conditions, performance was better for visual than kinesthetic memory, while within the crossmodal conditions, memory did not differ.

In the following, we discuss the implications of these findings with respect to the theoretical accounts on modality-specific and modality-unspecific multisensory memory representations outlined in the introduction.

4.1. Interference

The modulation of the encoding modality by the interference task modality suggests that memory traces are formed and maintained in a modality-specific format. This is in line with previous behavioral studies reporting distinct representations for visually and haptically encoded stimuli (Woods et al., 2004; Ittyerah & Marks, 2007). The angle stimuli used in the present study were presented as movement trajectories that were either viewed or passively felt by the moved hand. Likewise, the interfering stimuli of the secondary task were also presented as visual or kinesthetic movement trajectories. We observed a performance decrement due to the interference task which varied with sensory modality. Stimulus encoding was impaired more strongly when the modality of the encoding stimulus matched the modality of the interference task. This implies that the memory trace established during stimulus encoding is, at least partially, overwritten by the secondary task competing for the same processing resources. Although reliable, these effects are small in size. Therefore, and because overall recognition memory was fairly good, it has to be concluded that besides modality-specific representations other representations are additionally established which are less prone to interference. In particular, results on unimodal and crossmodal spatial

Table 1

Mean percentage of correct responses (and standard deviations) for the combinations of encoding and recognition modality of the memory task and the interference task conditions (CO: control condition, VIT: visual interference task, KIT: kinesthetic interference task).

Recognition	Mean % correct responses (SD)					
	Encoding			Kinesthetic		
	Visual			CO	VIT	KIT
	CO	VIT	KIT	CO	VIT	KIT
Visual	89.96 (8.47)	84.45 (6.71)	84.93 (6.45)	80.10 (7.71)	76.12 (8.22)	76.00 (9.32)
Kinesthetic	77.36 (5.25)	74.67 (7.57)	77.77 (8.62)	84.65 (4.85)	83.18 (4.80)	78.26 (7.28)

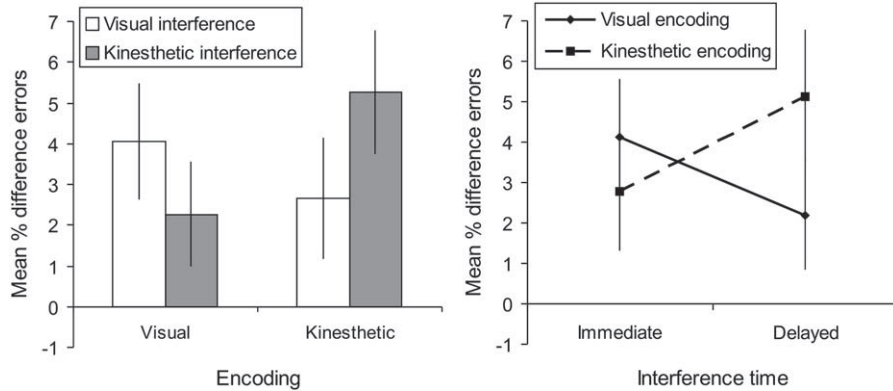


Fig. 3. Left: Mean and standard error of difference error scores for the interaction encoding modality × interference condition. Right: Mean and standard error of difference error scores for the interaction encoding modality × interference time.

working memory for visually and haptically presented matrix positions suggest that modality-specific and additional supramodal representations exist simultaneously (Cattaneo & Vecchi, 2008). In a general cognitive framework, spatial images seem to be represented in a combined format (Struiksmá, Noordzij, & Postma, 2009). However, based on the present findings visual and kinesthetic information is not solely represented in a modality-unspecific multisensory code in working memory. This is consistent with EEG studies measuring power and coherence during crossmodal integration of visual and tactile/kinesthetic information. Hummel and Gerloff (2005) found higher alpha-coherence between electrodes of interest over modality-specific areas, in particular occipital cortex and somatosensory cortex, for good matching performance of seen and felt Braille letters than for bad matching performance or a control condition with no matching. Moreover, Classen, Gerloff, Honda, and Hallett (1998) revealed higher beta-coherence in a visual-motor tracking task between electrodes over occipital as well as somatosensory and motor cortex compared to presentation of visual information or motor performance without tracking.

Moreover, it seems unlikely that the representations are formed in a supramodal verbal format. Our sample and target stimuli differed metrically rather than categorically and the differences between sample and target angles were generally very small due to their proximity to the just noticeable difference revealed in the pilot study. Hence, the stimuli and stimulus differences were hard to verbalize. Debriefing of subjects also revealed that they had either used strategies like an auxiliary coordinate system or that they had intuitively responded without using an explicit verbal strategy.

Due to the observed pattern of results, two alternative hypotheses about a modality-specific representational code can be clearly rejected. First, there was no interaction of the secondary task with the recognition modality arguing against the assumption that the memory trace is always transformed into the modality that is best suited for the test situation (cf. Connolly & Jones, 1970). Second, the

pattern of results is inconsistent with the idea that information is always transformed into the dominant visual modality for working memory maintenance (cf. Freides, 1974; Rock & Victor, 1964). As pointed out above, the significant interaction of encoding modality and interference task modality rules out a solely multisensory representation of geometrical shape information in working memory (cf. Easton et al., 1997; see Grill-Spector et al., 2001; Lacey et al., 2009, for reviews on the support of multisensory representations by neuroimaging results). Furthermore, the observed effects cannot be attributed to differences in interference task difficulty, because the visual and the kinesthetic interference tasks were matched on the basis of a pilot experiment and showed comparable accuracy and reaction times. Thus, our results support the conclusion that visually and kinesthetically encoded stimuli are, at least in part, represented and maintained in a modality-specific format.

4.2. Temporal stability

Here, we showed that a secondary task occurring immediately after visual stimulus encoding impaired memory performance more strongly than a secondary task presented later in the retention interval. The opposite effect was observed for kinesthetically encoded stimuli. These temporal differences were independent from the modality of the secondary task, thus, revealing a more general influence of the dual-task situation.

Based on a dual-task study on visually presented letters and symbols, Jolicoeur and Dell'Acqua (1998) suggest that short-term maintenance of visual information can be divided into a short-term consolidation component (which can be seen as part of the encoding process) and a more automatic component of actual working memory maintenance. This means that short-term consolidation may continue until 1 s after stimulus offset and that this consolidation process requires attentional resources whose availability can be easily impaired by a distracting task. Accordingly, in our study visual short-term consolidation seems to be

Table 2 Mean percentage of difference errors (standard deviations) for the combinations of encoding and recognition modality of the memory task, interference task modality (VIT: visual interference task, KIT: kinesthetic interference task) and interference time (IM: immediate, DE: delayed).

Mean % difference errors (SD)								
Encoding								
Recognition	Visual				Kinesthetic			
	VIT		KIT		VIT		KIT	
	IM	DE	IM	DE	IM	DE	IM	DE
Visual	6.41 (8.38)	4.35 (10.31)	6.72 (7.37)	3.34 (8.54)	1.33 (11.31)	6.45 (10.07)	2.91 (11.78)	5.45 (11.02)
Kinesthetic	3.06 (8.49)	2.39 (9.26)	0.33 (10.01)	-1.31 (7.81)	0.88 (5.51)	1.98 (9.17)	6.05 (9.74)	6.66 (7.67)

completed early in the retention interval as the memory trace is only impaired by the secondary task presented immediately after stimulus presentation (400 ms after sample angle offset). The presentation of the secondary task 3.2 s after sample offset hardly had any effect on memory of visually encoded stimuli. Thus, the memory trace seems to be more established and less prone to impairment during late maintenance after visual encoding. In contrast, the increasing impairment of memory for kinesthetically encoded stimuli with increasing delay of the interference task suggests – according to Jolicoeur and Dell'Acqua (1998) – that consolidation processes requiring attentional resources last longer for kinesthetic stimuli.

On the other hand, it was found that proprioceptive information in a hand positioning task was stable over an interval of 20 s (Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000), whereas visual position information decayed over intervals from 3 up to 30 s (Chieffi & Allport, 1997; Chieffi, Allport, & Woodin, 1999). Thus, visual information might have to be transformed more quickly into a stable code than kinesthetic information which could explain our results that an immediate interference task impaired visually encoded stimuli more than a delayed interference task and vice versa for kinesthetically encoded stimuli.

4.3. Unimodal and crossmodal memory

Better performance in unimodal than crossmodal conditions as found here agrees well with the results of previous studies on object recognition (Ernst, Lange, & Newell, 2007; Woods et al., 2004). There are two explanations for these differences. On the one hand, the crossmodal disadvantage could be due to an additional process of recoding one of the representations. As we found evidence for, at least partially, modality-specific memory traces, it can be assumed that either the stored representation or the representation of the perceived test stimulus has to be transformed for the recognition process. Some stimulus details might get lost with such a transformation leading to an increase of errors. On the other hand, the effect could result from the fact that specific stimulus characteristics were only available in unimodal but not in crossmodal versions of the task. In unimodal conditions, reliable location and distance information in space as well as velocity information of the moving stimulus was available during both encoding and recognition. These data can be used for comparing sample and test stimulus in addition to the angle-specific movement trajectory. In contrast, in crossmodal conditions only information about the angle-specific movement trajectory can be matched for stimulus comparison. Thus, in unimodal conditions stimulus comparison might be based on a richer, more detailed representation. In addition, crossmodal performance might have been impaired because the stimuli were presented in different planes. Visual stimuli appeared on the frontal plane of the computer monitor, kinesthetic stimuli on the horizontal plane of the haptic device. This different presentation mode was inevitable, because a presentation of visual stimuli in the same horizontal plane of the haptic device would have led to distortions of the size of the angle that had to be stored and recognized.

Finally, we observed better memory in the visual than in the kinesthetic unimodal tasks. This is consistent with the findings for visual and tactile working memory maintenance of simple L-shaped figures (Woods et al., 2004) and spatial configurations (Cattaneo & Vecchi, 2008) revealing an advantage of the dominant visual modality for working memory tasks.

4.4. Conclusion

The present results demonstrate that memory representations of movement trajectories are coded, at least in part, in a modality-specific representation. Thus, our findings do not support the idea that information which has to be matched between different sensory modalities is automatically transformed into either a solely

modality-unspecific multisensory code or a solely visual code. This is consistent with our findings of distinct consolidation processes for visually and kinesthetically encoded information indicating a longer consolidation for kinesthetically than visually encoded movement trajectories. To further define the representational code, neurophysiological measurements as electroencephalography or functional magnetic resonance tomography can give a clue about the neural networks underlying unimodal and crossmodal working memory tasks.

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References

- Amedi, A., Jacobson, G., Hendler, T., Malach, R., & Zohary, E. (2002). Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cerebral Cortex*, *12*, 1202–1212.
- Amedi, A., Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience*, *4*(3), 324–330.
- Baddeley, A. D., & Lieberman, K. (1980). Spatial working memory. In R. S. Nickerson (Ed.), *Attention and performance, Vol. VIII*. (pp. 521–539) Hillsdale, NJ: Erlbaum.
- Cattaneo, Z., & Vecchi, T. (2008). Supramodality effects in visual and haptic spatial processes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*, 631–642.
- Chieffi, S., & Allport, D. A. (1997). Independent coding of target distance and direction in visuo-spatial working memory. *Psychological Research*, *60*, 244–250.
- Chieffi, S., Allport, D. A., & Woodin, M. (1999). Hand-centered coding of target location in visuo-spatial working memory. *Neuropsychologia*, *37*, 495–502.
- Classen, J., Gerloff, C., Honda, M., & Hallett, M. (1998). Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. *Journal of Neurophysiology*, *79*, 1567–1573.
- Connolly, K., & Jones, B. (1970). A developmental study of afferent–reafferent integration. *British Journal of Psychology*, *61*(2), 259–266.
- D'Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society, B Biological Sciences*, *362*, 761–772.
- Desmurget, M., Vindras, P., Gréa, H., Viviani, P., & Grafton, S. T. (2000). Proprioception does not quickly drift during visual occlusion. *Experimental Brain Research*, *134*, 363–377.
- Easton, R. D., Greene, A. J., & Srinivas, K. (1997). Transfer between vision and haptics: Memory for 2-D patterns and 3-D objects. *Psychonomic Bulletin & Review*, *4*(3), 403–410.
- Ernst, M. O., Lange, C., & Newell, F. N. (2007). Multisensory recognition of actively explored objects. *Canadian Journal of Experimental Psychology*, *61*(3), 242–253.
- Freides, D. (1974). Human information processing and sensory modality: Cross-modal functions, information complexity, memory, and deficit. *Psychological Bulletin*, *81*(5), 284–310.
- Gallace, A., & Spence, C. (2009). The cognitive and neural correlates of tactile memory. *Psychological Bulletin*, *135*, 380–406.
- Garvill, J., & Molander, B. (1973). Effects of standard modality, comparison modality and retention interval on matching form. *Scandinavian Journal of Psychology*, *14*, 203–206.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.
- Hummel, F., & Gerloff, C. (2005). Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans. *Cerebral Cortex*, *15*, 670–678.
- Ittyerah, M., & Marks, L. E. (2007). Memory for curvature of objects: Haptic touch vs. vision. *British Journal of Psychology*, *98*, 589–610.
- James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S., & Goodale, M. A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia*, *40*, 1706–1714.
- Jolicoeur, P., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation. *Cognitive Psychology*, *36*, 138–202.
- Kiphart, M. J., Hughes, J. L., Simmons, J. P., & Cross, H. A. (1992). Short-term haptic memory for complex objects. *Bulletin of the Psychonomic Society*, *30*, 212–214.
- Klauer, K. C., & Zhao, Z. (2004). Double dissociations in visual and spatial short-term memory. *Journal of Experimental Psychology*, *133*(3), 355–381.
- Kriegeskorte, N., Sorger, B., Naumer, M., Schwarzbach, J., van den Boogert, E., Hussy, W., et al. (2003). Human cortical object recognition from a visual motion flowfield. *Journal of Neuroscience*, *23*, 1451–1463.

- Lacey, S., & Campbell, C. (2006). Mental representation in visual/haptic crossmodal memory: Evidence from interference effects. *The Quarterly Journal of Experimental Psychology*, 59, 361–376.
- Lacey, S., Tal, N., Amedi, A., & Sathian, K. (2009). A putative model of multisensory object representation. *Brain Topography*, 21, 269–274.
- Logie, R. H. (1986). Visuo-spatial processing in working memory. *The Quarterly Journal of Experimental Psychology*, 38A(2), 229–247.
- Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive? In R. H. Logie, & M. Denis (Eds.), *Mental images in human cognition* (pp. 105–115). New York: Elsevier.
- Loomis, J. M., Klatzky, R. L., & Lederman, S. J. (1991). Similarity of tactual and visual picture recognition with limited field of view. *Perception*, 20, 167–177.
- Martenuik, R. G., & Rodney, M. (1979). Modality and retention effects in intra- and cross-modal judgements of kinaesthetic and visual information. *British Journal of Psychology*, 70, 405–412.
- McCloseky, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews*, 58(4), 763–820.
- Millar, S. (1972). Effects of interpolated tasks on latency and accuracy of intramodal and cross-modal shape recognition by children. *Journal of Experimental Psychology*, 96, 170–175.
- Millar, S. (1974). Tactile short-term memory by blind and sighted children. *British Journal of Psychology*, 65(2), 253–263.
- Newell, K. M., Shapiro, D. C., & Carlton, M. J. (1979). Coordinating visual and kinaesthetic memory codes. *British Journal of Psychology*, 70, 87–96.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Posner, M. I. (1967). Characteristics of visual and kinesthetic memory codes. *Journal of Experimental Psychology*, 75(1), 103–107.
- Posner, M. I., Nissen, M. J., & Klein, R. M. (1976). Visual dominance: An information-processing account of its origins and significance. *Psychological Review*, 83(2), 157–171.
- Possin, K. L., Filoteo, J. V., Song, D. D., & Salmon, D. P. (2008). Spatial and object working memory deficits in Parkinson's disease are due to impairment in different underlying processes. *Neuropsychology*, 22(5), 585–595.
- Ranganath, C. (2006). Working memory for visual objects: Complementary roles of inferior temporal, medial temporal, and prefrontal cortex. *Neuroscience*, 139, 277–289.
- Reales, J. M., & Ballesteros, S. (1999). Implicit and explicit memory for visual and haptic objects: Cross-modal priming depends on structural descriptions. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 25(3), 644–663.
- Rock, I., & Victor, J. (1964). Vision and touch: An experimentally created conflict between the two senses. *Science*, 143, 594–596.
- Schiffman, H. R. (1990). Somesthesia I: Kinesthesia and cutaneous sense. In H. R. Schiffman (Ed.), *Sensation and perception: An integrated approach* (pp. 119–138). New York: John Wiley & Sons.
- Smyth, M. M. (1984). Memory for movements. In M. M. Smyth, & A. M. Wing (Eds.), *The psychology of movement* (pp. 83–117). London: Academic Press.
- Struiksma, M. E., Noordzij, M. L., & Postma, A. (2009). What is the link between language and spatial images? Behavioral and neural findings in blind and sighted individuals. *Acta Psychologica*, 132, 145–156.
- Woods, A. T., & Newell, F. N. (2004). Visual, haptic and cross-modal recognition of objects and scenes. *Journal of Physiology – Paris*, 98, 147–159.
- Woods, A. T., O'Modhrain, S., & Newell, F. N. (2004). The effect of temporal delay and spatial differences on cross-modal object recognition. *Cognitive, Affective, & Behavioral Neuroscience*, 4(2), 260–269.

Study II

Seemüller, A., & Rösler, F. (submitted). **EEG-power and -coherence changes in a unimodal and a crossmodal working memory task with visual and kinesthetic stimuli.** *International Journal of Psychophysiology*

EEG-power and -coherence changes in a unimodal and crossmodal working memory task with visual and kinesthetic stimuli

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Running head: EEG changes in unimodal and crossmodal working memory

Abstract

We investigated EEG-power and EEG-coherence changes in a unimodal and a crossmodal matching-to-sample working memory task with either visual or kinesthetic stimuli. Angle-shaped trajectories were used as stimuli presented either as a moving dot on a screen or as a passive movement of a haptic device. Effects were evaluated during the different phases of encoding, maintenance, and recognition. Alpha power was modulated during encoding by the stimulus modality, and in crossmodal conditions during encoding and maintenance by the expected modality of the upcoming test stimulus. These power modulations were observed over modality-specific cortex regions. Systematic changes of coherence for crossmodal compared to unimodal tasks were not observed during encoding and maintenance but only during recognition. There, coherence in the theta-band increased between electrode sites over left central and occipital cortex areas in the crossmodal compared to the unimodal conditions. The results underline the importance of modality-specific representations and processes in unimodal and crossmodal working memory tasks. Crossmodal recognition of visually and kinesthetically presented object features seems to be related to a direct interaction of somatosensory/motor and visual cortex regions by means of long-range synchronization in the theta-band and such interactions seem to take place at the beginning of the recognition phase, i.e. when a crossmodal transfer is actually necessary.

Keywords: visual representations; kinesthetic representations; synchronization; crossmodal matching; haptics

Introduction

Crossmodal object recognition involves the comparison of shape, size, texture, and other features across modalities. Most common are situations where representations built from visual input have to be matched with representations built from tactile and kinesthetic (haptic) input or vice versa (Calvert, 2001; Gibson, 1966; Schiffman, 1990). Such crossmodal tasks require different processes. Matching objects presented simultaneously in different modalities needs immediate crossmodal integration processes, while matching objects that are presented sequentially involves crossmodal recognition, comparison and *working memory* maintenance.

Research on the neuronal basis of crossmodal processing afforded different explanations and delineated different neuroanatomical regions relevant for representation and information transfer. Among others, crossmodal comparison has been related to (i) multisensory areas, (ii) multisensory areas interacting with frontal (executive) regions, (iii) unisensory areas interacting via posterior multisensory mediator structures, or (iv) direct interactions of unisensory areas (see Amedi et al., 2005; Calvert, 2001, for reviews).

Direct communication of unisensory areas is supported by EEG-studies in which increased coherence was observed during crossmodal processing between activity over unisensory cortex areas. Hummel and Gerloff (2005) found higher coherence between electrodes of interest located over the occipital and the somatosensory cortex when participants showed good performance in a visuo-tactile matching task compared to either the situation with poor performance or a control condition with no matching. The authors concluded that synchronization between specific brain regions, as measured with EEG-coherence, is functionally significant for successful crossmodal integration. The idea of long-range synchronization during crossmodal processing is further supported by tasks requiring visuo-motor coordination. Comparing a visuo-motor tracking-task with either a motor-task combined with a visual distractor, a sole visual task, or a sole motor-task without visual input revealed increased EEG-coherence between visual and somatosensory/motor cortex areas during the visuo-motor tracking task compared to the other three conditions (Classen et al., 1998). Moreover, EEG-power decreased over central and occipital cortex areas in the visuo-motor condition compared to the visual or the motor condition alone. In the latter conditions, power decreased relative to a baseline over the occipital cortex in the visual, and over the sensorimotor cortex in the motor condition. Further evidence for long-range interactions between visual and motor areas comes from a transcranial magnetic stimulation (TMS) study

in which both sites were simultaneously stimulated for a short time. Compared to a prestimulation baseline EEG-power and EEG-coherence increased between unisensory visual and motor areas after TMS application for several minutes (Plewnia et al., 2008). This suggests that transcortical coupling is a transient phenomenon which can be induced by a co-stimulation of cortical areas.

While EEG-power is sensitive to sensory and motor processing as well as to working memory demands (e.g., Andres and Gerloff, 1999; Gevins et al., 1997; Pfurtscheller and Klimesch, 1991; see von Stein and Sarnthein, 2000, for a review), synchronization of neuronal activity as reflected by an increase of EEG-coherence between brain areas is assumed to be an indicator of functional coupling during attention, information processing, and binding (e.g. Engel et al., 2001; Mima et al., 2001; Siegel et al., 2008; Singer, 1994; Singer and Gray, 1995; von Stein et al., 1999). Particularly, task-related coherence changes were observed in sensorimotor and crossmodal matching tasks (Andres and Gerloff, 1999; Classen et al., 1998; Hummel and Gerloff, 2005; for a review on crossmodal binding see Senkowski et al., 2008). Coherence modulations were also functionally related to modality-unspecific control processes as maintenance in working memory (Sarnthein et al., 1998; von Stein and Sarnthein, 2000, review).

In the present study, we investigated neuronal correlates of crossmodal object processing in a delayed matching-to-sample task. In particular, we tested whether unimodal (visual–visual, kinesthetic–kinesthetic) vs. crossmodal (visual–kinesthetic, kinesthetic–visual) memory based comparisons are associated with distinct EEG-power and EEG-coherence changes during encoding, delay, and recognition epochs. Stimuli that had to be stored and matched to a comparison stimulus were two lines forming an angle. Angular degrees were varied to create distinct stimuli that were either presented as a moving dot along the angle trajectory on a screen in front of the participant or via a haptic manipulandum which was held by the participant with the right hand, passively moving the hand along the angle trajectory.

Considering the neuroanatomical regions that have been identified previously for crossmodal information processing, and considering the spatial resolution of EEG-coherence changes, we can expect at least two distinct patterns. (i) If sensorimotor and visual areas are interacting directly via long-range connections, coherence between these modality-specific areas should be larger in crossmodal than in unimodal tasks. (ii) If information transfer involves additional mediating or multisensory structures, coherence should increase between

the modality-specific areas and additionally between these areas and convergence zones located in the frontal, temporal, or parietal cortex (cf. Senkowski et al., 2008).

According to previous findings (e.g. Classen et al., 1998), we also expect topographically distinct power changes for visual and kinesthetic encoding, i.e. over occipital and central cortex. Moreover, power and coherence patterns are expected to vary across distinct phases of the task. Larger coherence in crossmodal compared to unimodal conditions during the encoding phase would indicate an immediate transfer of a visual into a kinesthetic code and vice versa. Coherence changes occurring during the delay/maintenance phase would indicate that information transfer is not bound to immediate perceptual input but takes place on the basis of stored representations before the actual recognition phase. Finally, a restriction of the observed coherence changes to the recognition/matching phase would indicate that information transfer takes place at the time, when the task actually requires a crossmodal comparison.

Materials and Methods

Participants

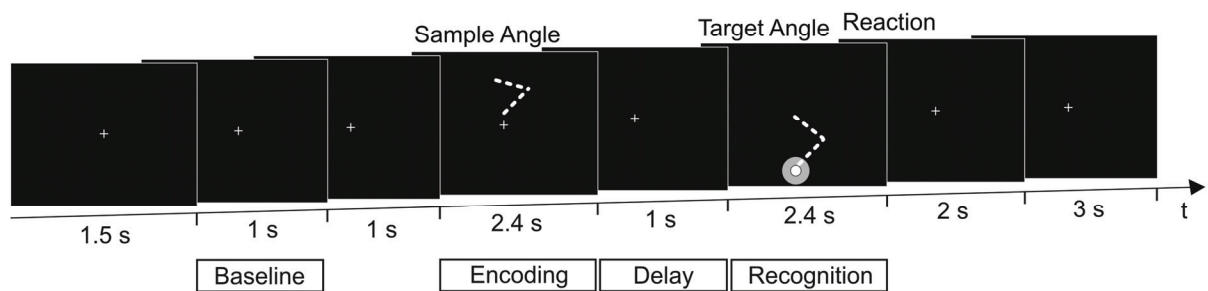
Twenty-one students of the University of Marburg were recruited. Data of three participants had to be excluded due to too many EEG artifacts and of one, because he did not adhere to the instructions. The final sample comprised 9 males and 8 females (mean age, standard deviation: 23.6, \pm 4.0 years). All participants were right-handed as assessed by the German version of the Edinburgh Handedness Inventory (mean, standard deviation: 89.53, \pm 12.50; Oldfield, 1971), and they had normal or corrected-to-normal vision. They gave written informed consent and received either monetary compensation or course credit. The experiment was performed in accordance with the ethical standard laid down in the Declaration of Helsinki (2000).

Materials and apparatus

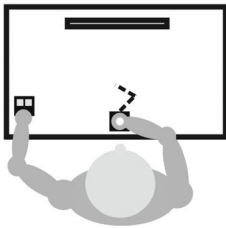
Angles were presented visually or kinesthetically. Sample angles were 30°, 60°, 120°, or 150°. They were combined with one of four target angles deviating from the sample stimulus with either -25° or $+23^\circ$ (large deviation = easy matching) and -20° or $+18^\circ$ (small deviation

= difficult matching) (see Fig. 1C). Targets were selected on the basis of a pilot study in which mean 90 % upper and lower difference thresholds were determined. Easy target angles were defined as 1.5 standard deviation and difficult target angles as 1 standard deviation from the mean difference threshold. Identical target angles were presented in 50 % of the trials. Each angle was presented as a back and forth movement of either a dot on the screen or the manipulandum along the contour of a left-opened angle. The first line segment was rotated 45° counter-clockwise in order to reduce the possibility of using the body axis as a reference.

A Delayed matching-to-sample task



B Experimental set-up



C Angles

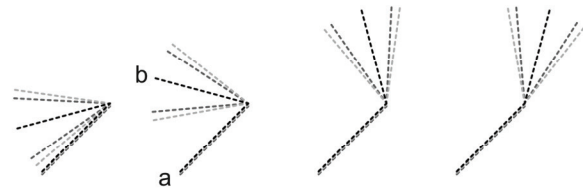


FIG. 1. Schematic trial timing of the delayed matching-to-sample task, experimental setup, and stimuli. *A*: The experimental protocol is exemplarily illustrated for the visual–kinesthetic delayed matching-to-sample task. *B*: Schematic overview of the experimental setup with the apparatus for kinesthetic stimulus presentation, the computer screen for visual stimulus presentation and the response box. *C*: Sample angles (black), target angles with large deviations (light gray), and target angles with small deviations (dark gray). The first and second segment of the angular trajectory is marked with *a* and *b*, respectively.

Kinesthetic stimuli were right hand movements realized via a manipulandum which was constructed as an x-y plotter. The device was controlled by two servomotors operating under LabView (<http://www.ni.com/labview>) allowing the presentation of straight and curved movements on a 1.3 m x 1.7 m two-dimensional horizontal workspace. Participants' body

midline was aligned with the center of the workspace. They were instructed to hold a stylus mounted on the sliding carriage with their right hand between thumb, index, and middle finger (see Fig. 1B). Hand and arm were passively guided along the movement trajectory (average velocity 0.12 m/s; acceleration 0.3 m/s²) providing kinesthetic information of movement direction via joints, muscles, tendons, and ligaments (McCloskey, 1978). Kinesthetic stimuli presentations started at the body midline. To prevent visual input during kinesthetic stimulus presentation, the apparatus was covered and the room was completely dark. Participants wore earplugs and headphones emitting white noise during the experiment to mask the noise of the apparatus' servomotors. The apparatus was grounded to prevent artifacts in the EEG signal.

Visual stimuli were presented as a moving light spot on a black computer screen 110 cm in front of the participant within an area of 1.4° visual angle. The visual dot moved with an average velocity of 0.03°/s and approximately at eye level 0.7° above a fixation cross (0.2° size). The fixation cross was visible at the center of the screen during the entire experiment. Participants' body midlines were aligned with the center of the computer screen and their position was held constant with an individually adjustable chin rest.

The index and the middle finger of the left hand were positioned on a response box to indicate the same-different judgment.

Design and Procedure

We used a repeated measurement design with four levels of factor task-modality: visual–visual (V–V), kinesthetic–kinesthetic (K–K), visual–kinesthetic (V–K), kinesthetic–visual (K–V). Modality conditions were blocked in order to avoid attention switches. Sample and target angle combinations (large deviation, small deviation, identical) were randomized across conditions. Overall, 384 trials with 96 trials per modality condition were presented in 12 blocks that were randomized across participants. In each modality condition of these 96 trials, 24 were difficult, 24 easy, and 48 identical. The experiment lasted approximately 4.5 h including EEG electrode mounting.

Each trial started with a 3.5 s interval initiated by an auditory warning signal (440 Hz) for 300 ms and a fixation cross remaining visible for the duration of the trial (see Fig. 1A). The baseline was measured in this interval. Then, a sample angle was presented for 2.4 s (visual or kinesthetic) followed by a retention interval of 1 s and a target angle (visual or

kinesthetic) of 2.4 s. After stimulus-offset, participants had 2 s to decide as fast and accurately as possible whether both angles were same or different. The inter-trial interval lasted for 3 s. For each modality condition, practice blocks with 16 trials each were run before the experiment until 10 of the 16 trials were answered correctly.

EEG recording

The EEG was recorded from 27 AgAgCl scalp electrodes mounted in a cap (Easycap System, Falk Minow, Munich, Germany) and positioned according to the international 10-20 system. All electrodes were referenced to one earlobe during recording and re-referenced offline to averaged earlobes which is most suitable for EEG-coherence measurements (Essl and Rappelsberger, 1998; Fein et al., 1988; Rappelsberger, 1998). The vertical and horizontal electrooculogram (EOG) were registered with two additional electrode pairs. As ground served the left or right mastoid counterbalanced across participants. Impedances were kept below 5 k Ω . Continuous EEG was recorded by 32 channel amplifiers (Toennies Medical Electronics, Freiburg, Germany) and digitized by means of a LabView program (<http://www.ni.com/labview/>) with a sampling rate of 500 Hz. Frequencies from DC to 50 Hz, with a Notch filter at 50 Hz, were recorded.

EEG analysis

EEG signals were corrected for DC drifts (Hennighausen et al., 1993) using the BrainVisionAnalyzer software (www.brainproducts.com), re-referenced, and digitally band-pass filtered (1–40 Hz, slope 24dB/octave). Five non-overlapping epochs of 1024 ms were analyzed, thus allowing a maximal frequency resolution of approximately 1 Hz. Encoding and recognition epochs were analyzed each with two consecutive epochs starting at stimulus onset and maintenance was analyzed with one epoch. A baseline time window of 1024 ms was chosen one second before onset of the sample stimulus (see Fig. 1A). Single epochs were visually inspected and trials with blinks or other artifacts were rejected. On average, 80 artifact-free trials were included per participant and condition.

Power spectra were calculated using a Fast Fourier Transform (FFT) for each epoch, Hanning-windowed to reduce spectral leakage, and averaged over trials for each participant, electrode, task modality (V–V, K–K, V–K, K–V) and time window. Power was clustered in three frequency bands: theta (3.5–7.5 Hz), alpha (7.5–13.5 Hz), beta (13.5–32 Hz) and

transformed into dB-values relative to the baseline. Frequencies ≥ 32 Hz were not included in the analysis due to possible micro saccade artifacts (Yuval-Greenberg et al., 2008).

EEG-coherence values were computed by normalizing the squared, averaged cross-spectra of two signals by the product of their averaged auto-spectra ($K_{xy}^2(f) = |C_{xy}(f)|^2 / (C_{xx}(f) \times C_{yy}(f))$; for details see Rappelsberger, 1998). After Fisher-z-transformation, they were averaged across the two unimodal (V-V, K-K) and the two crossmodal conditions (V-K, K-V) and for the above described frequency bands. They were further transformed into task-related (TR) coherence values ($TRCoh = Coh_{exp} - Coh_{base}$) to reduce the effect of inter-subject and inter-electrode-pair variability (cf. Classen et al., 1998; Hummel and Gerloff, 2005).

An analysis of power and coherence changes for matching difficulty was not conducted due an insufficient number of trials after artefact exclusion. As only between 20 and 35 trials were available dependent on the condition, analyses do not have enough statistical power (a minimum of 40 trials is needed according to Nunez and Srinivasan, 2006).

Dependent variables and statistical analysis

Behavioral data

Mean percentage of correct responses obtained from trials with $RT \geq 200$ ms were analyzed in a 4×3 repeated measurements analysis of variance with factors task modality (V-V, K-K, V-K, K-V) and matching difficulty (easy, difficult, identical). Post-hoc analyses were conducted by t-tests ($p < .05$, Bonferroni-corrected). Mean reaction times of the memory task were not analyzed because of the delayed response not starting before offset of the second stimulus.

EEG data

In order to test differences between unimodal and crossmodal tasks during encoding and maintenance, dB-power changes were analyzed separately for visual and kinesthetic encoding and maintenance for each time window in a repeated measurements analysis of variance with factors recognition modality (2), frequency band (3), and electrode (19). When the three-fold interaction was significant, an ANOVA with factors recognition modality (2) and electrode (19) was conducted for each frequency band ($p < .05$, Huyhn-Feldt-corrected). Post-hoc analyses were carried out by t-tests ($p < .05$, Bonferroni-corrected). In the same way,

differences between unimodal and crossmodal tasks during visual and kinesthetic recognition were tested using factors encoding modality (2), frequency band (3), and electrode (19).

Electrodes of interest were defined a priori for scalp regions assumed to reflect the processing of visual and kinesthetic information. Primary and secondary somatosensory cortex areas and sensorimotor cortex are known to be associated with the processing of kinesthetic movement information (Druschky et al., 2003; Mima et al., 1999; Weiller et al., 1996) and the occipital cortex and area MT are known to process visual (movement) information (Rizzolatti and Matelli, 2003; Ungerleider and Haxby, 1994). Therefore, left central electrodes (FC3, C3, CP3) and occipital electrodes (O1, O2) were chosen (Classen et al., 1998; Homan et al., 1987). Topographic power differences were further tested by an ANOVA with the factors encoding or recognition modality (V, K) and region (left central, occipital).

Based on the above mentioned anatomical knowledge and previous findings (Classen et al., 1998; Hummel and Gerloff, 2005), task-related coherence differences were tested for the electrode pairs FC3–O1/O2, C3–O1/O2, CP3–O1/O2 and as control FC4–O1/O2, C4–O1/O2, CP4–O1/O2 using t-tests ($p < .05$). An overall coherence description was given by testing task-related coherence differences for the 171 electrode pairs (resulting from 19 electrode sites) between unimodal (V–V, K–K) and crossmodal (V–K, K–V) conditions with non-parametric Wilcoxon tests ($p < .05$) separately for each frequency band and time window of the recognition epoch¹.

Results

Behavioral data

Analysis of correct responses revealed a significant main effect of modality [$F(3, 48) = 27.731, P < .001$] with better performance in the unimodal (V–V, K–K) than crossmodal (V–K, K–V) conditions [all comparisons, $P < .01$] and no difference within unimodal or crossmodal conditions [$t(16) = 1.661, P = .116$; $t(16) = -1.024, P = .321$; see Fig. 2]. Furthermore, the ANOVA showed a significant main effect of matching difficulty [$F(2, 32) = 64.201, P < .001$]. A parametric decrease of correct responses from identical matching to easy

matching to difficult matching was confirmed by t-tests [all comparisons, $P < .01$]. We found no interaction task modality \times matching difficulty [$F(6, 96) = 1.322, P = .255$].

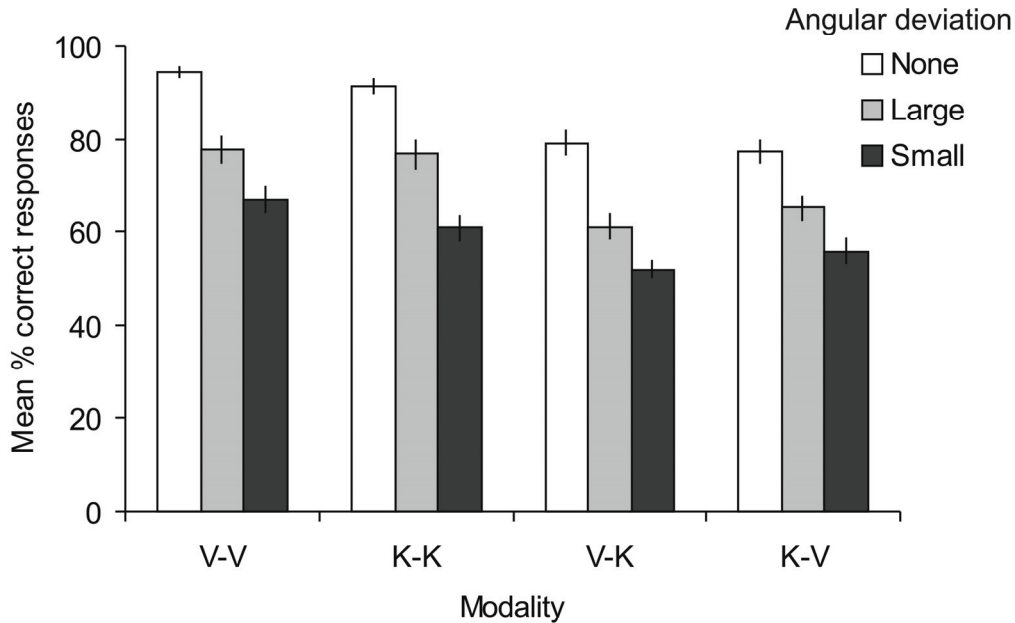


FIG. 2. Behavioral results for the delayed matching-to-sample task showing the mean percentage of correct responses with standard errors of the mean for task modality (V-V: visual-visual, K-K: kinesthetic-kinesthetic, V-K: visual-kinesthetic, K-V: kinesthetic-visual) and matching difficulty (deviance of the sample angle from the target angle: identical, large (easy task), small (difficult task)).

EEG data

Encoding: Power

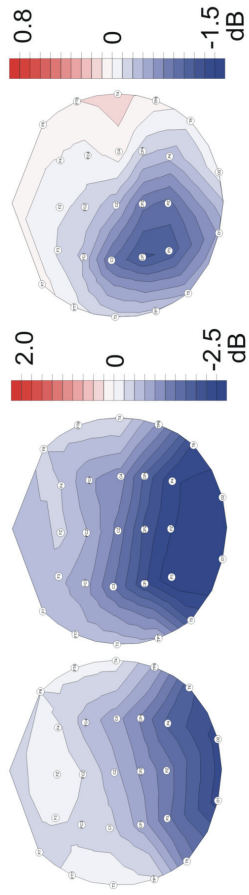
During visual encoding, alpha-power decreased relative to the baseline over occipital regions (see Fig. 3A). Comparing unimodal and crossmodal tasks, power modulations were found in the second encoding phase, revealed by an interaction of recognition modality, frequency band, and electrode [first window $F(36, 576) = 1.429, P = .161$; second window $F(36, 576) = 2.483, P = .002$]. In the crossmodal conditions, alpha-power decrease was additionally influenced by the subsequent recognition modality [recognition modality $F(1, 16) = 8.655, P < .05$; recognition modality \times electrode $F(18,288) = 5.163, P < .001$; see Fig. 3A] and decreased more at left central electrodes (C3, CP3) in crossmodal than unimodal tasks, i.e. when a subsequent kinesthetic compared to a visual recognition was expected. Topographic

differences were further confirmed by a larger power decrease in the left central but not in the occipital electrode cluster for an expected kinesthetic compared to visual recognition [recognition modality \times region $F(1, 16) = 4.608, P < .05$; see Fig. 3A]. Smaller power changes in the same direction were found in the beta-band [$F(18, 288) = 3.035, P < .01$]. We found no differences in the theta-band [$F(1, 16) = .282, P = .603$; $F(18, 288) = .837, P = .536$]. For kinesthetic encoding, alpha-power decreased relative to baseline over left and right central areas (see Fig. 3B). Comparing unimodal and crossmodal conditions, dB-power modulations were neither found in the first nor second encoding phase [recognition modality, frequency band \times electrode: first window $F(36, 576) = 1.114, P = .344$; second window $F(36, 576) = 1.353, P = .178$]. However, a larger power decrease was observed in the alpha-band for kinesthetic encoding followed by visual rather than kinesthetic recognition [recognition modality \times frequency band $F(2, 32) = 3.318, P < .05$; see Fig. 3B] and a larger overall power decrease at centro-parietal electrode sites (Cz, CPz, Pz) for crossmodal than unimodal tasks [recognition modality \times electrode: $F(18, 288) = 3.322, P = .002$] in the second encoding interval.

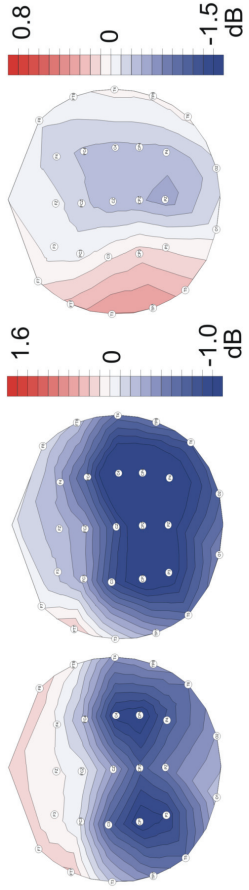
Delay: Power

As during encoding, topographically distinct alpha-power decreases were also present during maintenance for visually and kinesthetically presented sample stimuli (see Fig. 3C, 3D). Additionally, power was modulated by the modality of the upcoming test stimulus in the crossmodal conditions during maintenance for visually [recognition modality, frequency band \times electrode $F(36, 576) = 2.005, P = .018$; see Fig. 3C] and kinesthetically encoded stimuli [$F(36, 576) = 2.188, P = .015$; see Fig. 3D]. For the maintenance of visually encoded stimuli, alpha-power decreased over occipital cortex areas more, when a subsequent test stimulus was expected to be visual rather than kinesthetic [recognition modality \times electrode $F(18, 288) = 3.961, P = .001$; see Fig. 3C]. Analysis of topographic regions further strengthened a larger power decrease at occipital electrodes for expected visual than kinesthetic recognition [recognition modality \times region $F(1, 16) = 35.193, P < .001$; see Fig. 3C]. Similarly, overall power decreases were found in the beta-band [$F(18, 288) = 3.778, P = .003$]. We found no significant theta-power differences [$F(18, 288) = 1.192, P = .323$]. For the maintenance of kinesthetically presented stimuli, alpha-power decreased more over centro-parietal (FCz, Cz, CPz, CP4, Pz) cortex areas when a visual rather than a kinesthetic test stimulus was to be

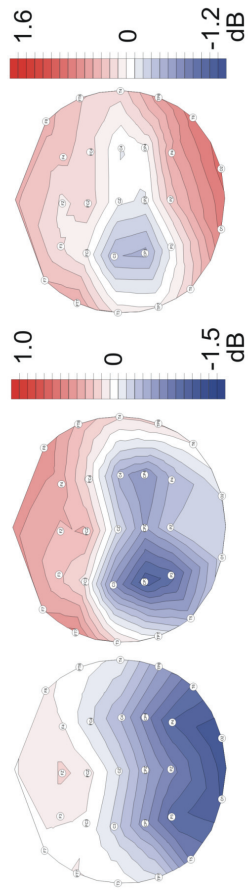
A Visual encoding: 1000-2000 ms



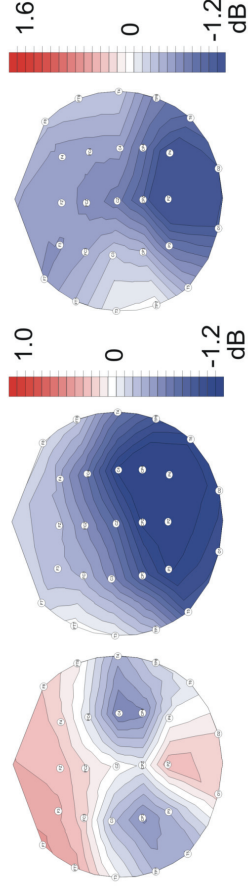
B Kinesthetic encoding: 1000-2000 ms



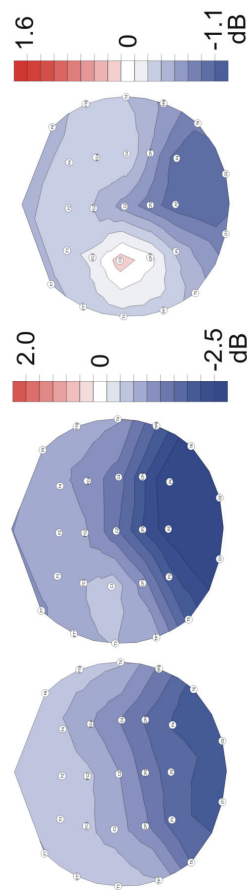
C Delay after visual encoding: 0-1000 ms



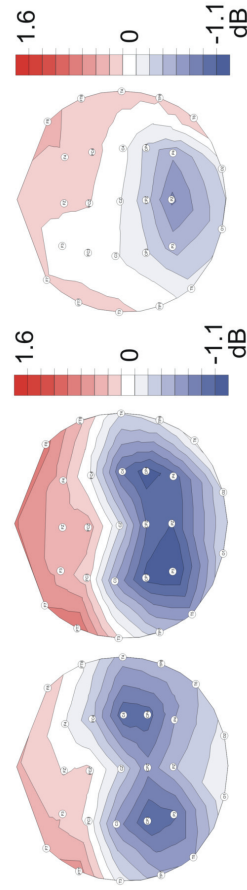
D Delay after kinesthetic encoding: 0-1000 ms



E Visual recognition: 0-1000 ms



F Kinesthetic recognition: 0-1000 ms



Unimodal	Crossmodal	Crossmodal - Unimodal
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FIG. 3. Topographic maps of alpha-dB-power values (7.5–13.5 Hz) for unimodal and crossmodal conditions are shown separately as well as the difference maps crossmodal minus unimodal condition. All maps were interpolated from the 27 recording electrodes. *A*: Maps for the second visual encoding interval in the visual–visual and visual–kinesthetic task. *B*: Maps for the second kinesthetic encoding interval in the kinesthetic–kinesthetic and kinesthetic–visual task. *C*: Maps for the delay after visual encoding in the visual–visual and visual–kinesthetic task. *D*: Maps for the delay after kinesthetic encoding in the kinesthetic–kinesthetic and kinesthetic–visual task. *E*: Maps for the first visual recognition interval in the visual–visual and kinesthetic–visual task. *F*: Maps for the first kinesthetic recognition interval in the kinesthetic–kinesthetic and visual–kinesthetic task.

expected [recognition modality $F(1, 16) = 18.132, P = .001$; recognition modality \times electrode $F(18, 288) = 4.196, P = .002$; see Fig. 3*D*]. Analyzing topographic differences showed a larger power decrease for crossmodal than unimodal tasks at central and occipital electrodes [recognition modality \times region $F(1, 16) = 5.694, P < .05$; see Fig. 3*D*]. Similar results were observed in the beta-band with differences over right temporal-occipital regions [$F(18, 288) = 6.066, P < .001$]. We found no significant differences in the theta-band power [$F(18, 288) = 1.052, P = .397$]. Furthermore, power did not differ between crossmodal and unimodal conditions as a group during maintenance [$F(36, 576) = 1.274, P = .236$].

Recognition: Power

Comparing unimodal visual and kinesthetic recognition, alpha power decreased over occipital regions during visual recognition (see Fig. 3*E*) and over left and right central areas during kinesthetic recognition (see Fig. 3*F*) compared to the baseline. In the crossmodal conditions, power was additionally modulated by the encoding modality confirmed by interactions of encoding modality, frequency band, and electrode for visual recognition [first window: $F(36, 576) = 2.100, P < .05$; second window: $F(36, 576) = 1.211, P = .276$] and for kinesthetic recognition [first window: $F(36, 576) = 1.780, P < .05$; second window: $F(36, 576) = .854, P = .624$] in the first recognition phase. During visual recognition, alpha-power decreased more for kinesthetically encoded than visually encoded stimuli [encoding modality \times electrode $F(18, 288) = 4.042, P = .001$; see Fig. 3*E*]. In the beta-band, the reversed effect was observed at frontal and central electrode sites [encoding modality $F(1, 16) = 23.499, P < .001$; encoding modality \times electrode $F(18, 288) = 5.467, P < .001$]. We found no main effect or interaction in the theta-band [$F(1, 16) = 1.103, P = .309$; $F(18, 288) = .323, P = .896$]. During kinesthetic

recognition, alpha-power decreased more for crossmodal than unimodal matching [encoding modality \times electrode $F(18, 288) = 3.097, P = .015$; see Fig. 3F]. We did not find any effects in the theta-band [$F(1, 16) = 1.133, P = .303$; $F(18, 288) = .449, P = .818$] or in the beta-band [$F(1, 16) = 1.935, P = .183$; $F(18, 288) = .658, P = .691$]. Moreover, alpha-power decreased and beta-power increased in the crossmodal compared to the unimodal conditions as a group during early recognition [encoding modality, frequency band \times electrode $F(36, 576) = 2.414, P < .01$; encoding modality \times electrode: alpha $F(18, 288) = 5.054, P < .001$; beta $F(18, 288) = 2.729, P < .01$]. No effects were observed in the theta-band [$F(18, 288) = .346, P = .882$].

Recognition: Coherence

Coherence was tested separately for the theta-, alpha- and beta-band, and for the different phases of the trial. Significant changes of task-related coherence during unimodal compared to crossmodal recognition were found to be restricted to the first interval of the recognition phase, i.e. there were no reliable coherence changes observed during the encoding or the maintenance phase².

Coherence changes in the theta-band were found at a priori chosen electrode pairs between left centro–occipital pairs and confirmed by comparing the difference between task-related coherence in the crossmodal compared to unimodal recognition for electrode pairs of interest (FC3-O1/O2, C3-O1/O2, CP3-O1/O2) and control electrode pairs (FC4-O1/O2, C4-O1/O2, CP4-O1/O2). The largest difference between electrodes of interest and control electrodes was found between FC3-O1/O2, C3-O1/O2 and FC4-O1/O2, C4-O1/O2 (see Fig. 4A). Task-related coherence differences between crossmodal and unimodal recognition in the theta-band were significantly larger between these electrode pairs of interest than between the electrode pairs of control [$t(16) = -2.391, P = .015$, one-sided t test; see Fig. 4B].

Similar results were also found by describing changes for all 171 electrode pairs in the theta band with higher task-related coherence in the crossmodal than unimodal conditions between FC3/C3/CP3-O2. Furthermore, task-related coherence decreased between frontal and central electrode pairs in the alpha-band (see Fig. 5A) and increased between right parieto–occipital electrodes in the beta-band (see Fig. 5B) during crossmodal compared to unimodal recognition.

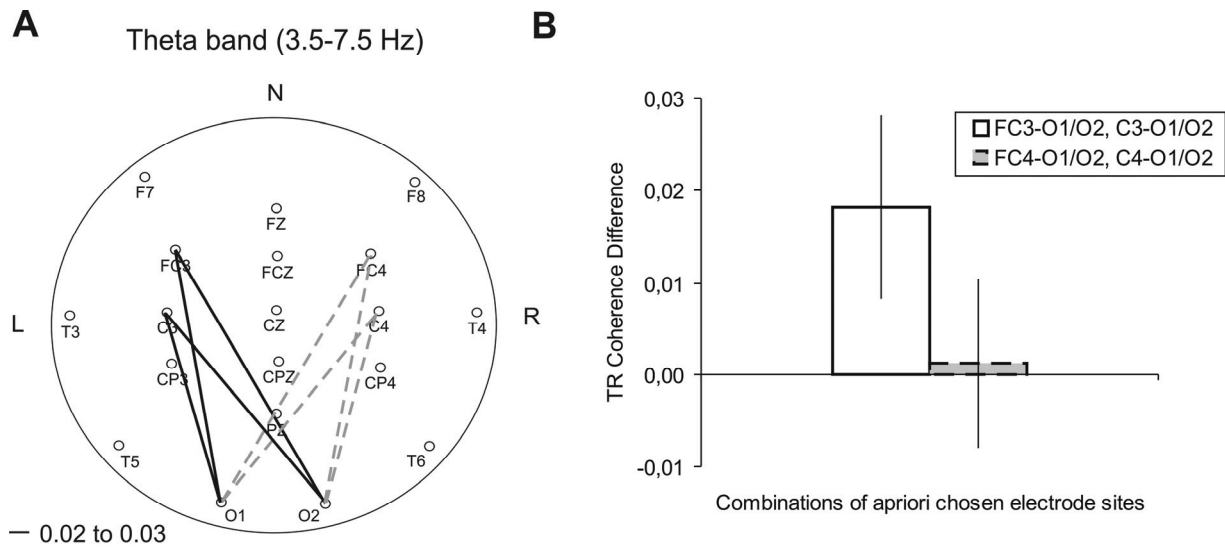


FIG. 4. Contrast of task-related coherence between a priori chosen electrode pairs of interest (FC3-O1/O2, C3-O1/O2; contralateral to the participants' right hand that was stimulated kinesthetically) and a priori chosen control electrode pairs (FC4-O1/O2, C4-O1/O2; ipsilateral to the participants' right hand that was stimulated kinesthetically) in the theta-band. **A**: selected electrode pairs of interest (continuous lines) and control pairs (dashed lines). **B**: Mean task-related coherence differences (crossmodal–unimodal) with standard errors of the mean for left centro-occipital electrode pairs of interest and for right centro-occipital control electrode pairs.

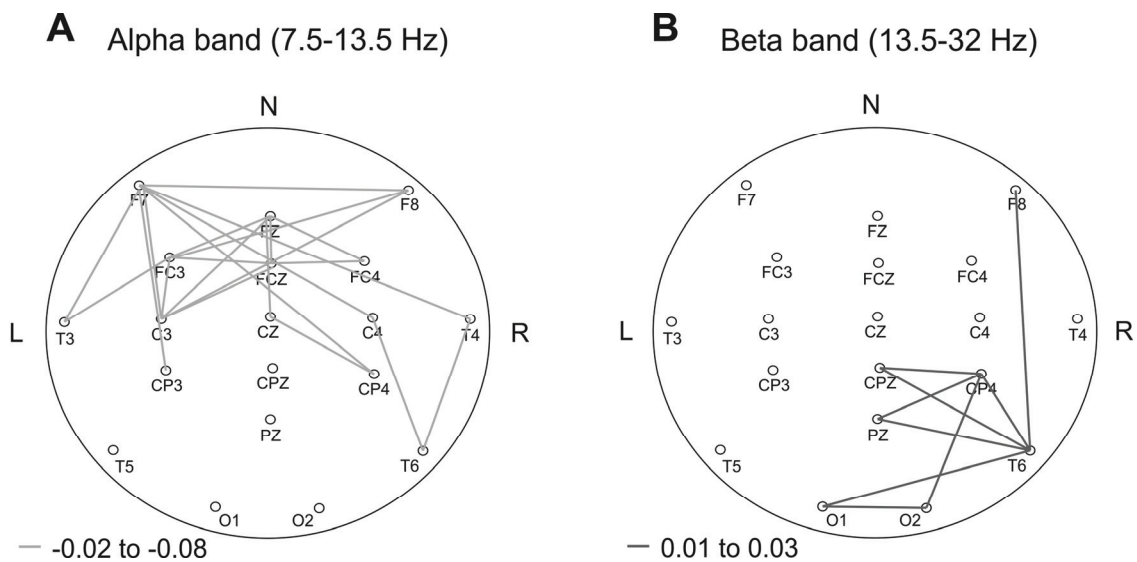


FIG. 5. Probability maps describing a *decrease* of task-related coherence (Wilcoxon tests, $p < .05$) in the crossmodal (visual–kinesthetic, kinesthetic–visual) compared to the unimodal (visual–visual, kinesthetic–kinesthetic) conditions in the alpha-band (7.5-13.5 Hz) (**A**) and an *increase* of task-related coherence in the crossmodal compared to the unimodal conditions in the beta-band (13.5-32 Hz) (**B**). The range of difference values is given for each frequency band.

Discussion

In the present study, the question was addressed whether power and coherence patterns reveal brain regions involved in crossmodal information processing. In more detail, we wanted to learn how brain regions interact during unimodal and crossmodal conditions and how these interactions may depend on distinct phases of encoding, maintenance, and recognition. To this end, we analyzed EEG-power and EEG-coherence in unimodal and crossmodal delayed matching-to-sample tasks with either visually or kinesthetically presented stimuli.

Power differences between unimodal visual and kinesthetic processing

In the unimodal tasks, we observed the expected alpha-power decrease during encoding and recognition over the occipital cortex for visually presented stimuli and over the centro-parietal cortex for kinesthetically presented stimuli (cf. Fig. 3A,E; Fig. 3B,F). This is consistent with former findings in unimodal visual and motor tasks (e.g. Classen et al., 1998, Pfurtscheller et al., 1994). Similarly, we also observed these topographically distinct alpha-power decreases during maintenance of visually or kinesthetically encoded stimuli, i.e. when no sensory stimuli were present (cf. Fig. 3C; Fig. 3D).

Our findings support the idea that cortex regions involved in the sensory processing of stimuli are also engaged in maintenance and long-term storage of their representations. This functional link between “online”-processing and storage has been proposed for the visual modality (D’Esposito, 2007; Postle, 2006) as well as for tactile/haptic information (Gallace and Spence, 2009) and it has been proposed as a more general theory for long-term memory storage and retrieval among others by McClelland et al. (1995).

Moreover, the activations of modality-specific cortex regions during encoding and maintenance of visually or kinesthetically presented stimuli is in accordance with the hypothesis that working memory representations of objects are modality-specific rather than modality-unspecific (e.g. Woods et al., 2004).

Power changes during encoding and maintenance prior to crossmodal recognition

EEG-power differed for encoding and maintenance of visually and kinesthetically presented stimuli as a function of the encoding modality and of the subsequent recognition modality.

Similar to the unimodal conditions, alpha-power decreases relative to the baseline were observed in the crossmodal conditions during late encoding and maintenance over the occipital cortex for visually presented stimuli (cf. Fig. 3A,C) and over the central cortex for kinesthetically presented stimuli (see Fig. 3B,D). Thus, the idea of modality-specific representations in working memory is further strengthened. This finding is at variance with the idea that modality-unspecific representations are formed immediately after encoding. In that case, similar power decreases should have appeared for both visually and kinesthetically encoded stimuli in the maintenance phase.

More interestingly, power modulations were larger in the crossmodal than in the unimodal conditions during encoding and maintenance. Alpha-power decreased more over left centro-parietal cortex during late visual encoding and increased more over occipital cortex during maintenance in crossmodal compared to unimodal conditions, i.e. when the subsequent recognition modality was expected to be kinesthetic rather than visual (cf. Fig. 3A,C). In contrast, alpha-power decreased more over left centro-parietal and occipital cortex during the maintenance of kinesthetically encoded stimuli, when a visual rather than a kinesthetic test stimulus was expected (cf. Fig. 3D). Therefore, specific anticipation or preparation effects seem to occur when recognition is based on a different modality than encoding. Since alpha-power did not differ for crossmodal compared to unimodal conditions as a group, the effects seem to be specific to and preparatory with respect to the expected recognition modality, i.e. cannot be attributed to a general attention effect (cf. Worden et al., 2000).

In addition, distinct temporal characteristics of the power changes were found as a function of encoding modality, i.e. systematic power modulations were observed during late encoding and maintenance for visually presented stimuli, while for kinesthetically presented stimuli these effects were only present during maintenance. This suggests a different time course of the encoding and expectation processes. Expectations seem to build up earlier after visual than after kinesthetic stimuli. One reason could be that encoding of kinesthetic stimuli takes longer. These findings are consistent with a previous behavioral experiment, where we also found a longer consolidation phase for kinesthetically compared to visually presented stimuli in a working memory task (Seemüller et al., 2010).

Regarding the type of frequency bands involved, we observed functional relevant power modulations in the alpha-band only, while beta-power changes proved as inconsistent over task phases and stimulus modalities. The systematic power changes in the alpha-band agree with previous studies on the functional significance of different frequency bands. Alpha

power decreases were most often found with visual sensory and visuo-motor processing (e.g. Classen et al., 1998; Pfurtscheller and Klimesch, 1991; Pfurtscheller et al., 1994; Salmelin and Hari, 1994), while alpha power increases and decreases were found with increasing working memory load (e.g. Gevins et al., 1997; Jensen et al., 2002). According to the alpha inhibition hypothesis, alpha activity reflects functional inhibition in cognitive and motor tasks (see Klimesch et al., 2007 for an overview). In contrast, beta-power changes were associated more often with motor tasks (e.g. Andres and Gerloff, 1999; Classen et al., 1998). The non-systematic beta-power changes in the present study can hardly be due to different motor demands, because they were present during visual encoding and recognition and during visual/kinesthetic maintenance. These epochs did not differ from other epochs and conditions in motor load.

Taken together, the results indicate that modality-specific representations are held in working memory. The modality-specific anticipation effects can have two reasons. Either processing areas expected to be relevant for the recognition process are unspecifically prepared or the encoded stimulus representation is transformed into the other modality. These effects develop earlier for visually than kinesthetically presented stimuli.

Coherence and power effects during crossmodal recognition

During early recognition, alpha-power decreased and beta-power increased in crossmodal compared to unimodal tasks where the behavioral performance was better. This is in line with previous findings that power modulations are associated with increasing task demands (e.g. Gevins et al., 1997; Klimesch et al., 2007 for a review). Interestingly, power changes were found during the early but not the late recognition phase. Thus, it might be concluded that the comparison is accomplished directly at the beginning of the recognition phase which also concurs with the following coherence results. In the theta-band, larger coherence was observed between left central and occipital regions for crossmodal compared to unimodal recognition. In the alpha- and beta-band, coherence modulations can be described during crossmodal compared to unimodal recognition. These changes were only observed during recognition, but not during encoding and maintenance.

Theta coherence

An increase of EEG-coherence between modality-specific cortex regions during crossmodal recognition was previously observed in the alpha- and the beta-band in a visuo-

tactile matching task (Hummel and Gerloff, 2005) and a visuo-motor tracking-task (Classen et al., 1998). In these studies, sensory stimulation occurred simultaneously in more than one modality and an immediate integration of visuo-tactile or visuo-motor information was necessary. In contrast, in the present study, a crossmodal delayed matching-to-sample task was used, in which stimuli were presented sequentially. Therefore, a working memory representation built from an input in one modality had to be compared with a stimulus representation in the same or a different modality during a later recognition phase. These specific working memory demands might be the reason why we found coherence modulations between electrode sites over unisensory cortex areas in the theta-band rather than in the alpha- and beta-band.

In the past, theta-band coherence changes were primarily found to be functionally related to (working) memory processes (Sarnthein et al., 1998; see von Stein and Sarnthein, 2000, for a review), while alpha- and beta-coherence modulations were found to reflect visual and motor processing as well as visuo-haptic or visuo-motor integration (e.g. Classen et al., 1998; Hummel and Gerloff, 2005; Mima et al., 2001; Pfurtscheller and Klimesch, 1991; Plewnia et al., 2008). Generally, long-range coherence has previously been found to be related to cognitive processes (e.g. Engel et al., 2001; Siegel et al., 2008; von Stein et al., 1999). However, the measurement of coherence at sensor level can be influenced by the employed reference (Andrew and Pfurtscheller, 1996) and volume conduction effects (Nunez et al., 1997) which might lead to an artificial increase of coherence. These effects can be invalidated for our present findings based on the following arguments. First, volume conduction effects decay rapidly with increasing distance between electrode sites and cannot be influenced by experimental conditions. As mentioned above, theta coherence increased between electrodes far apart from each other over central and occipital cortex regions in crossmodal compared to unimodal conditions. Second, referencing the data offline to averaged earlobes (with an original reference at one earlobe) minimizes artifacts, especially over longer distances (Essl and Rappelsberger, 1998; Nunez et al., 1997). Third, coherence changes were obtained relative to either the baseline or other conditions which were all based on the same reference and not as absolute values. Another possible caveat might be that coherence effects can be influenced by power and phase coupling changes, and thus coherence might be confounded by power changes. However, for the observed theta-coherence modulations this can be excluded, because regional theta-power differences were not present during encoding, maintenance, or recognition.

Thus, a larger coherence between modality-specific cortex areas during crossmodal compared to unimodal tasks supports the notion of a direct interaction of sensorimotor and visual cortex regions via long-range connections. This is further strengthened by the topographic specificity, i.e. the fact that increased coherence was present between a priori chosen electrode pairs of interest but not between a priori chosen control electrode pairs (cf. Hummel and Gerloff, 2005). Although the topographic maximum of an EEG effect can give only a tentative clue about the localization of its generator, the observed pattern of effects is in line with a priori anatomical knowledge and also agrees well with previous findings (Classen et al., 1998; Homan et al., 1987; Hummel and Gerloff, 2005).

Other previous research nourished an alternative hypothesis viz. that crossmodal comparison/recognition is not achieved via direct interaction of unisensory areas alone, but rather by means of additional mediating or multisensory structures (e.g. Banati et al., 2000; Grefkes et al., 2002; Hadjikhani and Roland, 1998; see Amedi et al., 2005; Calvert, 2001, for a review). In that case, coherence should not only increase between modality-specific regions but also between these regions and multisensory areas possibly located in frontal, temporal, or parietal cortex. A more wide-spread coherence pattern including central and occipital electrode sites and additionally other electrode sites was not found in the present study for any of the frequency bands. Therefore, the observed theta-coherence increase suggests a direct interaction of unisensory areas through synchronization during crossmodal recognition of visually and kinesthetically presented object features.

It is important to notice that functional relevant coherence modulations were observed solely during the recognition phase and not during the encoding or the maintenance phase. Theoretically, the absence of coherence cannot be equalized with the non-occurrence of coherence, because coherence might have been cancelled out by other coherent oscillations originated in adjacent cortex regions. However, this is based on the presumption of an additional generator only present in crossmodal conditions with synchronous activity exactly 180° out of phase which seems implausible and unlikely. Thus, the findings seem to suggest that information transfer between visual and kinesthetic representations takes place at the time of recognition, i.e. when the task actually requires a crossmodal comparison. This fits the idea that just-in-time information is used in tasks involving working memory (Droll and Hayhoe, 2007; Triesch et al., 2003). Visual and haptic information seems not to be integrated by default into a modality-unspecific, multisensory representation during encoding. Also the idea

of an interaction of modality-specific representations during a working memory maintenance phase is not supported by this pattern of results.

Overall, these findings indicate that an information transfer between visual and kinesthetic representations takes place at the beginning of the recognition phase. Moreover, this information transfer seems to be modality-specific with a direct interaction of unisensory areas, i.e. visual and somatosensory/motor cortex regions.

Alpha coherence

Coherence in the alpha-band decreased during crossmodal compared to unimodal recognition in an extended cluster of electrodes over the fronto-central cortex. A similar decrease of frontal alpha-coherence in combination with an increase of fronto-posterior theta-coherence was observed in a visuo-spatial working memory task (Sauseng et al., 2005). The authors interpreted the decrease of alpha-coherence as a manifestation of reduced cortical inhibition due to the task demands. Moreover, they claim the existence of a fronto-posterior network and relate the activity over the frontal cortex with executive functions. However, as mentioned, coherence is influenced by power changes. In the present study, regional alpha-power changes were present during recognition. Hence, alpha-coherence modulations can be confounded with alpha-power changes and the results of a decreased alpha-coherence during crossmodal compared to unimodal tasks might be partly due to regional power differences. Nevertheless, a reduction of alpha-coherence over the frontal cortex can indicate that relevant brain regions are less coupled in the more demanding crossmodal conditions.

Beta coherence

We also found a right occipito-temporal increase of coherence in the beta-band during crossmodal compared to unimodal recognition. This could indicate that a right temporal network is involved in crossmodal information transfer. Previously, increased beta-coherence has been found in multimodal object processing and has been interpreted as correlate of multimodal binding (von Stein et al., 1999). From the present data, it cannot be derived whether this network provides additional attentional control or whether it houses multisensory representations.

Conclusion

The present results underline the importance of modality-specific representations and processes in unimodal and crossmodal working memory tasks. Crossmodal recognition of visually and kinesthetically presented object features seems to be related to a direct interaction of somatosensory/motor and visual cortex regions by means of long-range synchronization in the theta-band and such interactions seem to take place at the beginning of the recognition phase, i.e. when a crossmodal transfer is actually necessary. In addition, modality-specific power changes during encoding and maintenance in the alpha-band suggest some kind of preparation of those brain areas expected to be relevant for an upcoming task. These preparatory effects started earlier after visual than after kinesthetic stimuli suggesting that encoding of kinesthetic stimuli took somewhat longer than encoding of visual stimuli.

Footnotes

¹ Due to the pair-wise comparisons, third-structure mediated influences cannot be removed (cf. Kuś et al. 2004).

² Since stimuli were presented for 2.4 s during encoding, coherence changes were not only analyzed in two non-overlapping epochs of 1024 ms following stimulus onset (see methods section) but additionally in two consecutive epochs during encoding adjoining stimulus offset. Reliable coherence changes were neither found during early nor late encoding epochs.

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References

- Amedi, A., von Kriegstein, K., van Atteveldt, N.M., Beauchamp, M.S., Naumer, M.J., 2005. Functional imaging of human crossmodal identification and object recognition. *Exp Brain Res* 166, 559–571.
- Andres, F.G., Gerloff, C., 1999. Coherence of sequential movements and motor learning. *J Clin Neurophysiol* 16, 520–527.
- Andrew, C., Pfurtscheller, G., 1996. Dependence of coherence measurements on EEG derivation type. *Med Biol Eng Comput* 34, 232–238.
- Banati, R.B., Goerres, G.W., Tjoa, C., Aggleton, J.P., Grasby, P., 2000. The functional anatomy of visual–tactile integration in man: a study using positron emission tomography. *Neuropsychologia* 38, 115–124.
- Calvert, G.A., 2001. Crossmodal processing in the human brain: insights from functional neuroimaging studies. *Cereb Cortex* 11, 1110–1123.
- Classen, J., Gerloff, C., Honda, M., Hallett, M., 1998. Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. *J Neurophysiol* 79, 1567–1573.
- D’Esposito, M., 2007. From cognitive to neural models of working memory. *Philos Trans R Soc Lond B Biol Sci* 362, 761–772.
- Droll, J.A., Hayhoe, M.M., 2007. Trade-offs between gaze and working memory use. *J Exp Psychol: Hum Percept Perf* 33, 1352–1365.
- Druschky, K., Kaltenhäuser, M., Hummel, C., Druschky, A., Huk, W.J., Neundörfer, B., Stefan, H., 2003. Somatosensory evoked magnetic fields following passive movement compared with tactile stimulation of the index finger. *Exp Brain Res* 148, 186–195.
- Engel, A.K., Fries, P., Singer, W., 2001. Dynamic predictions: oscillations and synchrony in top-down processing. *Nat Rev Neurosci* 2, 704–716.
- Essl, M., Rappelsberger, P., 1998. EEG coherence and reference signals: experimental results and mathematical explanations. *Med Biol Eng Comput* 36, 399–406.
- Fein, G., Raz, J., Brown, F.F., Merrin, E.L., 1988. Common reference coherence data are confounded by power and phase effects. *Electroencephalogr Clin Neurophysiol* 69, 581–584.
- Gallace, A., Spence, C., 2009. The cognitive and neural correlates of tactile memory. *Psychol Bull* 135, 380–406.

- Gevins, A., Smith, M.E., McEvoy, L., Yu, D., 1997. High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cereb Cortex* 7, 374–385.
- Gibson, J.J., 1966. *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Grefkes, C., Weiss, P.H., Zilles, K., Fink, G.R., 2002. Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. *Neuron* 35, 173–184.
- Hadjikhani, N., Roland, P.E., 1998. Cross-modal transfer of information between the tactile and the visual representations in the human brain: a positron emission tomographic study. *J Neurosci* 18, 1072–1084.
- Hennighausen, E., Heil, M., Rösler, F., 1993. A correction method for DC drift artifacts. *Electroencephalogr Clin Neurophysiol* 86, 199–204.
- Homan, R.W., Herman, J., Purdy, P., 1987. Cerebral location of international 10-20 system electrode placement. *Electroencephalogr Clin Neurophysiol* 66, 376–382.
- Hummel, F., Gerloff, C., 2005. Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans. *Cereb Cortex* 15, 670–678.
- Jensen, O., Gelfand, J., Kounios, J., Lisman, J.E., 2002. Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb Cortex* 12, 877–882.
- Klimesch, W., Sauseng, P., Hanslmayr, S., 2007. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53, 63–88.
- Kuś, R., Kamiński, M., Blinowska, K.J., 2004. Determination of EEG activity propagation: pair-wise versus multichannel estimate. *IEEE Trans Biomed Eng* 51, 1501–1510.
- McClelland, J.L., McNaughton, B.L., O'Reilly, R.C., 1995. Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychol Rev* 102, 419–457.
- McCloskey, D.I., 1978. Kinesthetic sensibility. *Physiol Rev* 58, 763–820.
- Mima, T., Oluwatimilehin, T., Hiraoka, T., Hallett, M., 2001. Transient interhemispheric neuronal synchrony correlates with object recognition. *J Neurosci* 21, 3942–3948.
- Mima, T., Sadato, N., Yazawa, S., Hanakawa, T., Fukuyama, H., Yonekura, Y., Shibasaki, H., 1999. Brain structures related to active and passive finger movements in man. *Brain* 122, 1989–1997.

- Nunez, P.L., Srinivasan, R., 2006. *Electric fields of the brain. The neurophysics of EEG*. New York: Oxford UP.
- Nunez, P.L., Srinivasan, R., Westdorp, A.F., Wijesinghe, R.S., Tucker, D.M., Silberstein, R.B., Cadusch, P.J., 1997. EEG coherency I: statistics, reference electrode, volume conduction, Laplacians, cortical imaging, and interpretation at multiple scales. *Electroencephalography and Clin Neurophysiol* 103, 499–515.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Pfurtscheller, G., Klimesch, W., 1991. Event-related desynchronization during motor behavior and visual information processing. In: Brunia, C.H.M., Mulder, G., Verbaten, M.N. (Eds.), *Event-Related Brain Research*, Amsterdam, Elsevier, p. 58–65.
- Pfurtscheller, G., Neuper, C., Mohl, W., 1994. Event-related desynchronization (ERD) during visual processing. *Int J Psychophysiol* 16, 147–153.
- Plewnia, C., Rilk, A.J., Soekadar, S.R., Arfeller, C., Huber, H.S., Sauseng, P., Hummel, F., Gerloff, C., 2008. Enhancement of long-range EEG coherence by synchronous bifocal transcranial magnetic stimulation. *Eur J Neurosci* 27, 1577–1583.
- Postle, B.R., 2006. Working memory as an emergent property of the mind and brain. *Neurosci* 139, 23–38.
- Rappelsberger, P., 1998. Probability mapping of power and coherence: technical aspects. In: Petsche, H., Etlinger, S.C. (Eds.), *EEG and thinking*, Wien, Österr. Akad. der Wiss.
- Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153, 146–157.
- Salmelin, R., Hari, R., 1994. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neurosci* 60, 537–550.
- Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G.L., von Stein, A., 1998. Synchronization between prefrontal and posterior association cortex during human working memory. *Proc Natl Acad Sci USA* 95, 7092–7096.
- Sauseng, P., Klimesch, W., Schabus, M., Doppelmayr, M., 2005. Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *Int J Psychophysiol* 57, 97–103.
- Schiffman, H.R., 1990. Somesthesia I: Kinesthesia and cutaneous sense. In: Schiffman, H.R. (ed.), *Sensation and perception: An integrated approach*, John Wiley & Sons, NY, p. 119–138.

- Seemüller, A., Fiehler, F., Rösler, F., 2010. Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories. *Acta Psychologica* doi:10.1016/j.actpsy.2010.09.014
- Senkowski, D., Schneider, T.R., Foxe, J.J., Engel, A.K., 2008. Crossmodal binding through neural coherence: implications for multisensory processing. *Trends Neurosci* 31, 401–409.
- Siegel, M., Donner, T.H., Oostenveld, R., Fries, P., Engel, A.K., 2008. Neuronal synchronization along the dorsal visual pathway reflects the focus of spatial attention. *Neuron* 60, 709–719.
- Singer, W., 1994. Coherence as an organizing principle of cortical functions. *Int Rev Neurobiol* 37, 153–183.
- Singer, W., Gray, C.M., 1995. Visual feature integration and the temporal correlation hypothesis. *Annu Rev Neurosci* 18, 555–586.
- Triesch, J., Ballard, D.H., Hayhoe, M.M., Sullivan, B.T., 2003. What you see is what you need. *J Vis* 3, 86–94.
- Ungerleider, L.G., Haxby, J.V., 1994. ‘What’ and ‘where’ in the human brain. *Curr Opin Neurobiol* 4, 157–165.
- von Stein, A., Sarnthein, J., 2000. Different frequencies for different scales of cortical integration: from local gamma to long range alpha theta synchronization. *Int J Psychophysiol* 38, 301–313.
- von Stein, A., Rappelsberger, P., Sarnthein, J., Petsche, H., 1999. Synchronization between temporal and parietal cortex during multimodal object processing in man. *Cereb Cortex* 9, 137–150.
- Weiller, C., Jüptner, M., Fellows, S., Rijntjes, M., Leonhardt, G., Kiebel, S., Müller, S., Diener, H.C., Thilmann, A.F., 1996. Brain representation of active and passive movements. *Neuroimage* 4, 105–110.
- Woods, A.T., O’Modhain, S., Newell, F.N., 2004. The effect of temporal delay and spatial differences on cross-modal object recognition. *Cogn Affect Behav Neurosci* 4, 260–269.
- Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V., 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific α -band electroencephalography increases over occipital cortex. *J Neurosci* 20, 1–6.

Yuval-Greenberg, S., Tomer, O., Keren, A.S., Nelken, I., Deouell, L.Y., 2008. Transient induced gamma-band responses in EEG as manifestation of miniature saccades. *Neuron* 58, 429–441.

III. Zusammenfassung

Die Verarbeitung von (Objekt-)Informationen im Arbeitsgedächtnis beinhaltet Phasen der Enkodierung, Aufrechterhaltung und Wiedererkennung und wurde in der visuellen Modalität bereits vielfach untersucht (siehe u. a. D'Esposito, 2007; Ranganath, 2006). Im Vergleich hierzu ist wenig über die Verarbeitung kinästhetischer/haptischer oder kreuzmodaler Informationen im Arbeitsgedächtnis bekannt. Bei der Objektverarbeitung spielen insbesondere die Wiedererkennung und der Vergleich von Informationen über die Modalitäten hinweg eine entscheidende Rolle. Dabei müssen Repräsentationen einer sensorischen Modalität mit Repräsentationen anderer Sinnesmodalitäten abgeglichen werden. Wie Objektinformationen bei unimodalen und kreuzmodalen Arbeitsgedächtnisaufgaben repräsentiert werden, welche Prozesse einen unimodalen und kreuzmodalen Vergleich ermöglichen und welche neuronalen Prozesse dabei bedeutsam sind, ist weitgehend ungeklärt. In der vorliegenden Arbeit wurde die Verarbeitung visueller und kinästhetisch wahrgenommener Objekteigenschaften in unimodalen und kreuzmodalen Arbeitsgedächtnisaufgaben systematisch untersucht. Die kinästhetische Modalität bezieht sich auf die sensorische Wahrnehmung von Bewegungsrichtung und räumlicher Position, z. B. der eigenen Hand, (McCloskey, 1978) und bildet gemeinsam mit der taktilen Modalität den haptischen Sinn. Als Hauptbestandteil geometrischer Objektformen wurden in den Studien lineare Bewegungstrajektorien mit unterschiedlichem Öffnungswinkel untersucht.

Eine umfangreiche Vorstudie untersuchte zunächst die Unterscheidungsgenauigkeit visuell und kinästhetisch dargebotener Winkeltrajektorien im unimodalen und kreuzmodalen Vergleich. Diese Studie bildete die Grundlage für die Auswahl des Stimulusmaterials in den nachfolgenden Studien. Verwendet wurde ein Design mit unabhängigen Gruppen ($N = 40$). Probanden mussten entweder unimodale (visuell–visuell, kinästhetisch–kinästhetisch) oder kreuzmodale (visuell–kinästhetisch, kinästhetisch–visuell) Vergleichsaufgaben lösen und entscheiden, ob ein Vergleichswinkel größer oder kleiner als ein zuvor präsentierter Referenzwinkel war. Die Winkeltrajektorien wurden visuell als sich bewegendes Lichtpunkt entlang eines Winkelpfades am Computerbildschirm oder kinästhetisch als passiv geführte rechte Handbewegung mittels eines computergesteuerten Apparates dargeboten. Für jeden der vier Referenzwinkel (30° , 60° , 120° , 150°) wurde mit Hilfe eines adaptiven Schwellenbestimmungsverfahrens (siehe Treutwein, 1995, als Überblicksartikel) auf der Basis von 80 Durch-

gängen innerhalb jeder Modalitätsbedingung die psychometrische Funktion bestimmt. Daraus wurde als Maß sensorischer Genauigkeit die absolute Schwelle bei 50 % der psychometrischen Funktion berechnet, d.h. der Punkt subjektiver Gleichheit des Referenz- und Vergleichswinkels. Die Ergebnisse zeigten eine vergleichbare unimodale sensorische Genauigkeit für die visuelle und kinästhetische Modalität (5° bzw. 3°). Dagegen ergab sich eine höhere Genauigkeit für den Vergleich innerhalb einer Modalität als zwischen den Modalitäten. Keine Unterschiede wurden für die Richtung des kreuzmodalen (visuell–kinästhetisch, kinästhetisch–visuell) Vergleichs gefunden (8° bzw. 7°). Die Winkelgröße beeinflusste die sensorische Genauigkeit nicht. Die Antwortvariabilität sowie die Unterschiedsschwellenvarianz waren hoch. Somit wurde für die Auswahl des Stimulusmaterials für die nachfolgenden Studien die Unterschiedsschwelle bei 10 % und 90 % der psychometrischen Funktion als Basis für die Bestimmung der Vergleichswinkel gewählt, um eine gute Leistung der Probanden in den Arbeitsgedächtnisaufgaben zu ermöglichen.

In der ersten Studie wurden die Repräsentationen visuell und kinästhetisch dargebotener Stimuli während der Aufrechterhaltung im unimodalen und kreuzmodalen Arbeitsgedächtnis untersucht. Dazu wurden unimodale (visuell–visuell, kinästhetisch–kinästhetisch) und kreuzmodale (visuell–kinästhetisch, kinästhetisch–visuell) Wiedererkennungsaufgaben (Delayed matching-to-sample tasks) mit einem Behaltensintervall von sechs Sekunden verwendet. Stimuli waren winkelförmige Bewegungstrajektorien, die entweder visuell als sich bewegender Lichtpunkt am Computerbildschirm oder kinästhetisch als passiv geführte rechte Handbewegung mittels eines computergesteuerten Apparates präsentiert wurden. Die 16 Probanden hatten zu entscheiden, ob die Größe zweier sequentiell präsentierter Winkel übereinstimmte. Um zu untersuchen, ob Arbeitsgedächtnisrepräsentationen modalitätsspezifisch oder modalitätsunspezifisch sind, wurde während des Aufrechterhaltungsintervalls eine zusätzliche visuelle oder kinästhetische Interferenzaufgabe eingefügt (Dual-task paradigm). In dieser Aufgabe sollten die Probanden beurteilen, ob eine dargebotene elliptische Bewegungstrajektorie relativ zur Körpermitte eher horizontal oder vertikal verlief. Der vergleichbare Schwierigkeitsgrad visueller und kinästhetischer Interferenzaufgaben wurde in einem weiteren Pilotexperiment getestet. Um außerdem die zeitliche Stabilität von Arbeitsgedächtnisrepräsentationen zu überprüfen, wurde die Interferenzaufgabe entweder direkt zu Beginn des Behaltensintervalls oder erst später im Intervall dargeboten. Als Kontrollbedingung dienten unimodale und kreuzmodale Arbeitsgedächtnisaufgaben ohne zusätzliche Interferenzaufgabe. Der mittlere Prozentsatz korrekter Antworten und die Leistungsgüte, d.h. die Differenz des mittleren Prozentsatzes korrekter Antworten in den Interferenzbedingungen und des mittleren Prozent-

satzes korrekter Antworten in der Kontrollbedingung, wurden als abhängige Variablen genutzt. Die Ergebnisse zeigten, dass visuell und kinästhetisch präsentierte Bewegungstrajektorien im unimodalen und kreuzmodalen Arbeitsgedächtnis, zumindest teilweise, modalitätsspezifisch repräsentiert werden. Demnach kann eine ausschließlich multisensorische, modalitätsunspezifische Repräsentation ebenso ausgeschlossen werden wie eine alleinig visuelle Repräsentation unabhängig von der Enkodierungsmodalität. Darüber hinaus sprechen die Ergebnisse für Unterschiede im zeitlichen Ablauf der Konsolidierung als Funktion der Enkodierungsmodalität. Die Konsolidierung für kinästhetisch präsentierte Stimuli scheint länger anzudauern als für visuell präsentierte Stimuli, was ebenfalls die Annahme eines modalitätsspezifischen Repräsentationsformats unterstützt.

In der zweiten Studie wurden die neuronalen Korrelate des unimodalen und kreuzmodalen Arbeitsgedächtnisses untersucht. Der Schwerpunkt lag auf der Untersuchung der Frage, ob relevante Kortexregionen und deren Interaktionen während der einzelnen Phasen des Arbeitsgedächtnisses – Enkodierung, Aufrechterhaltung und Wiedererkennung – mit Hilfe der Elektroenzephalographie (EEG) aufgezeigt werden können. Hierzu wurden während unimodaler (visuell–visuell, kinästhetisch–kinästhetisch) und kreuzmodaler (visuell–kinästhetisch, kinästhetisch–visuell) Arbeitsgedächtnisaufgaben zum einen die EEG Power in verschiedenen Frequenzbändern als Maß der oszillatorischen Aktivität, und zum anderen die EEG Kohärenz als Maß der neuronalen Synchronisation bestimmt. Als Stimuli dienten ebenfalls winkelförmige Bewegungstrajektorien, die entweder visuell als sich bewegender Lichtpunkt am Computerbildschirm oder kinästhetisch als passiv geführte rechte Handbewegung mit Hilfe eines computergesteuerten Apparates dargeboten wurden. Durch die Variation der Größe der Vergleichswinkel entstanden, basierend auf der Vorstudie, sowohl einfache als auch schwierige Vergleiche. Identische Ausgangs- und Vergleichsstimuli wurden in 50 % der Fälle präsentiert. Insgesamt wurden 17 Probanden jeweils 384 Trials mit 96 Durchgängen pro Modalitätsbedingung gezeigt. Zu Beginn jedes Durchgangs wurde die Baseline gemessen und die Probanden wurden instruiert während des gesamten Durchgangs die Mitte des Bildschirms zu fixieren. Das EEG-Signal wurde im Frequenzbereich in nicht überlappenden Zeitepochen von jeweils einer Sekunde während der Enkodierung, Aufrechterhaltung und Wiedererkennung ausgewertet. Power und Kohärenz wurden relativ zur Baseline als Dezibel (dB)-Powerwerte und aufgabenbezogene Kohärenzwerte berechnet und für die Frequenzbänder Theta (3,5–7,5 Hz), Alpha (7,5–13,5 Hz) und Beta (13,5–32 Hz) gemittelt. Neben der Auswertung der 19 Standardelektroden des 10-20 Systems wurden für die Kohärenzauswertung a priori Elektroden (Electrodes-of-interest) über dem linken, zentralen Kortex und über dem okzipitalen Kortex

ausgewählt (vgl. Classen et al., 1998; Hummel & Gerloff, 2005). Die Ergebnisse sprechen für die Relevanz modalitätsspezifischer Repräsentationen und modalitäts-spezifischer Prozesse im unimodalen und kreuzmodalen Arbeitsgedächtnis. Die Alphanpower wurde während der Enkodierung und Aufrechterhaltung durch die Enkodierungsmodalität moduliert, was sich in einer modalitäts-spezifischen Topographie über dem zentralen Kortex für kinästhetisch präsentierte Stimuli und über dem okzipitalen Kortex für visuell präsentierte Stimuli zeigte. In den kreuzmodalen Aufgaben wurde die Alphanpower zudem während der Enkodierung und Aufrechterhaltung durch die Modalität des erwarteten Vergleichsstimulus beeinflusst. Als Hauptergebnis konnte eine Kohärenzzunahme zwischen zuvor ausgewählten Elektroden während der kreuzmodalen im Vergleich zur unimodalen Wiedererkennung beobachtet werden. Systematische Kohärenzänderungen wurden nur während der Wiedererkennung, nicht aber während der Enkodierung oder Aufrechterhaltung gefunden. Demnach zeigen sich zum einen Verarbeitungs- und Erwartungsprozesse, zum anderen scheint die kreuzmodale Wiedererkennung mit einer direkten Interaktion zwischen somatosensorischen/motorischen Kortexregionen und okzipitalen Kortexregionen verbunden zu sein, die erst auftritt, wenn sie relevant ist.

Insgesamt zeigt die vorliegende Arbeit, dass modalitätsspezifische Repräsentationen und modalitätsspezifische Prozesse eine Rolle bei der unimodalen und kreuzmodalen Verarbeitung von Objekteigenschaften im Arbeitsgedächtnis spielen.

Literatur

Classen, J., Gerloff, C., Honda, M., & Hallett, M. (1998). Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. *Journal of Neurophysiology*, *79*, 1567–1573.

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

Hummel, F., & Gerloff, C. (2005). Larger interregional synchrony is associated with greater behavioral success in a complex sensory integration task in humans. *Cerebral Cortex*, *15*, 670–678.

McCloskey, D. I. (1978). Kinesthetic sensibility. *Physiological Reviews*, *58*(4), 763–820.

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

Treutwein, B. (1995). Psychophysical Procedures. *Vision Research*, *35*, 2503–2522.

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Erklärung

Ich versichere, dass ich meine Dissertation

Unimodal and crossmodal processing of visual and kinesthetic stimuli in working memory

selbstständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

(Ort/Datum)

(Unterschrift mit Vor- und Zuname)

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Publikationen

- 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, and Behavioral Neuroscience*, 7(3), 212–224.
- Seemüller**, A., Fiehler, K., & Rösler, F. (2010). Unimodal and crossmodal working memory representations of visual and kinesthetic movement trajectories. *Acta Psychologica* doi: 10.1016/j.actpsy.2010.09.014
- Seemüller**, A., & Rösler, F. (submitted). EEG-power and -coherence changes in a crossmodal working memory task with visual and kinesthetic stimuli. *International Journal of Psychophysiology*

Peer-reviewed Abstracts/Vorträge

- Seemüller**, A., Khader, P., Ranganath, C., & Rösler, F. (2006). Aufrechterhaltung im Arbeitsgedächtnis trägt zur Speicherung im Langzeitgedächtnis bei: Eine EEG-Studie. In H. Hecht et al. (Eds.), *Experimentelle Psychologie. Beiträge zur 48. Tagung experimentell arbeitender Psychologen*, Lengerich: Pabst, p.167. (Vortrag)
- Seemüller**, A., Khader, P., Ranganath, C. & Rösler, F. (2007). Working memory maintenance contributes to long-term memory formation: an EEG study. 10th Tübinger Perception Conference, Tübingen, Germany. (Poster)
- Seemüller**, A. (2008). „Kreuzmodale Verarbeitung visueller und kinästhetischer Informationen“. AG-Kolloquium „Medizinische Informatik“ Ruprecht-Karls-Universität Heidelberg, Germany. (Vortrag)
- Seemüller**, A., Fiehler, K., & Rösler, F. (2008). Kreuzmodale Diskriminierung bei der Formerkennung. In P. Khader et al. (Eds.), *Beiträge zur 50. Tagung experimentell arbeitender Psychologen*, Lengerich: Pabst, p.68. (Vortrag)

Fiehler, K., & **Seemüller**, A. (2008). Multisensorische Integration. In P. Khader et al. (Eds.), *Beiträge zur 50. Tagung experimentell arbeitender Psychologen*, Lengerich: Pabst, p.67. (Symposium)

Seemüller, A., Fiehler, K., & Rösler, F. (2008). Crossmodal discrimination of object shape. 9th International Multisensory Research Forum, Hamburg, Germany. (Poster)

Seemüller, A., Fiehler, K., Rösler, F. (2009). Crossmodal short-term memory representation of visual and kinesthetic information. 10th International Multisensory Research Forum (IMRF), New York, USA. (Poster)

Seemüller, A., & Rösler, F. (2009). EEG correlates of crossmodal matching of visual and kinesthetic object features. Symposium and Summerschool, Beijing, China. (Poster)