COGNITIVE MECHANISMS AND NEURONAL DYNAMICS OF MENTAL IMAGES

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Content

1. SUMMARY

This dissertation serves the better understanding of the process of mental imagery and therefore deals with the neuronal dynamics underlying this ability. During imagery, it is possible to integrate distinct visual impressions to one coherent visual representation mentally. This ability of manipulating the content of visual working memory (vWM) is crucial to plan foreseeingly, for example in engineering or architecture and therefore highly important for creation and progress in general. Concretely, this dissertation deals with the process of maintenance of internally generated visual representations in vWM and its relationship with long-term memory (LTM).

For that in two experiments behavioral measurements as well as the long-range synchronization of electroencephalogram (EEG) oscillations of that process were compared with those assessed during the maintenance of completely presented stimuli. In this way it was possible to have a look at the specific neuronal mechanisms underlying the maintenance of a newly created visual representation and at their functional relevance for successful LTM encoding. We hypothesized that images constructed from their elements require more neural coupling than images based on a complete percept and that this effect could be shown to foster LTM encoding.

Increased coupling between fronto-parietal to occipital cortical sources was generally found for the maintenance of constructed in comparison to non-constructed mental images and similarly for later remembered in comparison to non-remembered objects in the theta, alpha, beta, and gamma frequency bands. We conclude from these findings that the maintenance of constructed images in vWM requires additional attentional processes taking

place in the fronto-parietal attention network to keep object elements together as a coherent representation. These processes are also supportive for successful encoding into LTM.

To be able to distinguish between a general effect of increased vWM load and the specific process responsible for the maintenance of a newly created coherent representation we also varied the mental construction demand parametrically in the first experiment. For that we varied the number of features that had to become mentally combined as well as the number of features present in the completely presented object. Similar to the general effect found for the maintenance of constructed objects, fronto-parietal to occipital coupling was found for an increase in the number of features of non-constructed objects. Under increased construction demands, that means more features having to be combined, however, the pattern of electroencephalogram (EEG) synchronization was restricted to fronto-parietal couplings. That suggests that the fronto-parietal attention network is coping with the higher attentional demands involved in maintaining constructed images, albeit without increasing the communication with the occipital visual buffer in which the visual representations are assumed to be stored.

In the second experiment, a separate analysis of the subsequent memory effect for constructed and non-constructed objects showed a similar pattern of synchronization for the theta and gamma frequency bands for both conditions, thus probably reflecting a general process of successful encoding. In contrast, for the alpha and beta frequency bands, specific functions of phase coupling for successful encoding depending on the specific level of processing during vWM maintenance are suggested by the dissociable synchronization patterns.

Overall, these findings can be interpreted as the fronto-parietal attention network increasingly getting involved during the maintenance of a constructed image while communicating with the occipital visual buffer. Additionally, this attention network serves to promote LTM encoding during the maintenance of the image in vWM.

This work offers neuronal support for ideas how mental imagery may be conceptually organized. It also suggests possible neuronal mechanisms during the maintenance of mental images that foster successful LTM encoding. In this way this dissertation helps to explain the cognitive mechanisms underlying the crucial ability of mental imagery.

2. INTRODUCTION

2.1. IMAGERY

Humans have the ability to keep a visual image in front of their inner eye, even if there is no stimulus present in the environment. This ability is commonly referred to as visual imagery (Kosslyn and Pomerantz, 1977; Mechelli, Price, Friston, & Ishai, 2004; Pearson, Naselaris, Holmes, & Kosslyn, 2015; for a review, see Ganis and Schendan, 2011). Imagery can take place in every modality, e.g. hearing, smelling, touch, but the most commonly used modality and therefore the one with the most scientific attention is vision (but see e.g. Zvyagintsev et al., 2013 for an example of research including auditory imagery). Visual imagery is conceptually overlapping with the concept of visual working memory (vWM) (Baddeley and Hitch, 1974; Postle, 2006; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; for a review, see Baddeley, 2000) and may rely on the same neuronal structures (for a review, see Zimmer, 2008). Some authors even claim that there is no functional difference between the two processes imagery and vWM, since both serve the maintenance and manipulation of visual information and only differ in the origin of the visual representation: Imagery is the ability to form "percept-like" sensory states from memory without the corresponding input from the environment, whereas vWM maintenance generally refers to the maintenance of visual representations gained through perception (Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Tong, 2013). Visual imagery is useful in a huge variety of tasks that involve planning and creative processes. Imagining possible future states is fundamental for progress in technology, arts or in general a society. An architect or artist will have a visual image in front of his or her "inner eye" before he or she puts it into a model or picture, for example. This anticipation of possible outcomes of real operations is an evolutionary beneficial way to avoid having to deal with real, sometimes negative, consequences of a trial-and-error approach.

Such an image can have features that were never actually perceived in that very combination. A known object can be imagined to have a different color, for example. By recombining existing visual properties new visual representations can be created and maintained for further mental use. Mental simulation as a special case of mental imagery is a crucial method of planning the future for various purposes, whereupon it does not solely has to rely on visual simulations (Hegarty, 2004; Taylor, Pham, Rivkin, & Armor, 1998). To stick with the architect´s example, a house that is going to be built is first imagined and then sketched as a model. In this process the mental manipulation of the visual representation allows the architect to create new forms of buildings in his mind. This newly created visual image now can or cannot be represented differently than the visual image that the architect´s colleague, who saw the draft, holds in his mind. The second architect saw the complete external stimulus and could maintain it mentally, whereas the first built up the representation out of formerly distinct representations. Do these two mental representations differ conceptually and in their neuronal implementation? The visual content of both representations is the same in both cases, but the origin differs.

To further understand the cognitive processes underlying imagery a look at the neuronal level provides additional insight. Specific patterns of neuronal activation provide indication of the brain structures involved in certain mental processes, leading to a better understanding of the process itself and in relation to other mental functions, which might be associated with the same or other brain structures. In this way the development of new hypothesis is fostered as well. The same mental processes should be reflected by the same neuronal activation, since electrical activity in the brain is the basis for all cognitive functions. By testing for differences in the neuronal responses, different cognitive mechanisms can be told apart. Additionally, by analyzing the neuronal activity, the underlying biological mechanisms responsible for mental processes can be explained more detailed.

If it was possible to reliably distinguish both forms of vWM content objectively, this had immense impact, for example in the assessment and interpretation of witness reports. One possibility of a reliable method could be the analysis of neuronal responses during vWM maintenance, if developed accordingly. A real memory could be told apart from a made up one if there were different cognitive mechanisms during the maintenance of the memory in vWM and methods to assess them. Of course, if such methods are ever developed and applied, the memory would have to be fresh to not having been prone to too many alterations over time (Loftus, 2005).

Increased knowledge about the interplay between working- and long-term memory (LTM) allows the optimization of teaching and learning methods. If the computation and encoding of the representation in vWM differs depending on the form of presentation, it is important to assess which form of presentation is most effective for better learning.

The later described two experiments serve the better understanding of the functional-anatomical structures underlying the maintenance of visual images. It is evaluated how far visual information processing is modulated in dependence of the origin of the image. For that behavioral measurements and EEG are assessed. Furthermore, the relationship between synchrony between brain areas and later memory in dependence of the origin of the image is assessed.

2.2. THEORETICAL FRAMEWORK

Kosslyn, Ganis and Thompson (2001) showed that mental images activate the same visual brain areas that are also activated by real visual input. Their research provided convincing evidence that thoughts can be depictive at a certain processing level and thereby contradicted the view of Pylyshyn (e.g. Pylyshyn, 2002), who claimed that thoughts were purely abstract in nature (see Kosslyn, 2005 for a summary). The topographically correct activation that represents the mental image speaks clearly in favor of a depictive, rather than an abstract representation, at least in early visual areas.

Kosslyn (2005) speaks of a “visual buffer“, consisting of all topographically organized areas of the visual cortex. Here visual perceptions as well as mental images are represented topographically. Probably the information about single object features is represented in higher, non-topographical areas. In this “visual buffer” imagery, or vWM (see again Tong, 2013), takes place. Real life visual impressions as well as created visual images are maintained here.

Baddeley´s model of working memory includes a visuo-spatial sketchpad, a phonological loop and an episodic buffer (Baddeley and Hitch, 1974; Baddeley, 2000). The visuo-spatial sketchpad is supposed to be located in the right hemisphere, the phonological loop in the left hemisphere in Broca´s area. The episodic buffer is most likely located right-frontal and integrates information of different modalities, e.g. auditory and visual impressions. Here not only information from the other two subsystems gets integrated, but also from LTM. That makes the episodic buffer, controlled by the central executive, the most likely candidate for consciousness to take place. It´s capacity is limited and it serves as buffer for information, for example visual images.

In visual working memory even images can be maintained that don´t have a name yet, or whose phonological description would take longer than the production of the visual image. In this way pictoral imaginations are an effective way of mental manipulation of issues, for example in the process of planning. The human ability to anticipate possible outcomes is partially based on the deduction from spatio-visual images. Creativity, e.g. the development of completely new images, is possible through recombination of old impressions in visual working memory.

To answer the question how human processing of pictoral material after mental manipulation is done, the processes involved in the maintenance of purely perceived and mentally manipulated information should be compared.

Baddeley, Allen and Hitch (2011) suggest the binding of visual object properties takes place in the visuo-spatial sketchpad. This is done automatically, without additional cognitive effort. The binding of properties of different modalities, however, is supposed to take place in the episodic buffer, which is provided with attention by the central executive. But Baddeley also raises the question, if the integration of more complex information, for example the combination of different objects, would not need the help of the central executive, even if only visual information is combined. That means, complex mental images are probably also built and maintained within the episodic buffer under control of the central executive.

2.3. UNDERLYING NEURONAL PROCESSES

In creative working, something new is formed by recombining something existing. It is not possible to imagine something that was never experienced, except after combining already experienced single parts. It is e.g. possible to imagine a pink elephant without having seen one, because the shape of an elephant is known and the color pink as well. This imagination can subjectively be as clear as a memory of something that actually was experienced. How is this ability implemented neuronally? Which cognitive subsystems are involved during the maintenance of a newly generated visual image and how are they represented on a neuronal level?

This thesis serves to answer these questions. I analyzed if, and if so, then how, the neural mechanisms during the maintenance of a visual image differ in dependence of the origin of the image. For that the mental processing of whole visual objects was compared with the processing of single features that were deliberately combined to a coherent visual object.

A precise understanding of the neuronal dynamics underlying the mental processes during the maintenance of visual images includes insights about the involved brain areas. In this way existing theoretical concepts of mental imagery can be attributed to distinct brain areas or distributed brain networks and be further tested. Since the process of interest is keeping several formerly distinct representations together coherently, a likely candidate for the underlying neuronal process is oscillatory coupling. Oscillatory coupling is thought to reflect communication between functionally associated neural populations in different brain areas and the exchange of information between neuronal networks on local and global scales (Fell and Axmacher, 2011; Sauseng and Klimesch, 2008). Whereas oscillatory power reflects the local synchronization of neuronal populations, oscillatory coupling over larger distances, e.g. between frontal and occipital areas, is assessed with different measurements. Instead of interpreting the amplitude of the signal, the phase difference of the two signals is observed between the two distant sites. The more stable that phase difference is, the more the two sites are in synchrony.

Synchronization, or phase coupling, is linked to vWM processes like maintenance (Palva, Monto, Kulashekhar, & Palva, 2010; Salazar, Dotson, Bressler, & Gray, 2012) and allows inference about underlying processes or communication between different brain areas (e.g. Handy, 2004; Herrmann, Grigutsch, & Busch, 2004). Frequencies between 4 and 90 Hz are especially interesting, because they have been linked to several mental processes before (see Herrmann, Grigutsch, & Busch (2004) for an overview). A classical partition is the splitting in the theta frequency band, ranging from about 4 to 7 Hz, the alpha frequency band, ranging from about 8 to 12 Hz, the beta frequency band, ranging from about 13 to 30 Hz and the gamma frequency band, summarizing all higher frequencies. These frequency bands are linked to different mental stages after visual inspection of the raw signal, especially in sleep research (e.g. Olbrich and Achermann, 2005), but cannot be clearly divided up by functionality yet.

Early work by Sarnthein, Petsche, Rappelsberger, Shaw and von Stein (1998) already showed a synchronization between frontal and occipital brain areas during a vWM maintenance task in the theta frequency range. Jensen and Tesche (2002) confirmed these findings and additionally found a parametrical increase of coupling with increasing working memory load. Since then a lot of work has been done in the field, broadening the oscillatory spectrum to all psychologically relevant frequencies (Palva and Palva, 2012).

The phase coupling should be stronger within the fronto-parietal attention network already found to be important for imagery and vWM in humans and monkeys (Deiber et al., 2007; Sack and Schuhmann, 2012; Salazar et al., 2012) for constructed in comparison to non-constructed visual images, because more attentional resources should be necessary for the maintenance of the integrated image. Frontal and parietal areas are found to be important for goal directed attention (Corbetta and Shulman, 2002), which is necessary to mentally keep the formerly distinct features together. Axmacher, Schmitz, Wagner, Elger, & Fell (2008) argue that a network of prefrontal, temporal and parietal brain areas applying attentional mechanisms like enhancing relevant and suppressing irrelevant sensory input underlies the maintenance of visual images (for a review, see Ganis and Schendan, 2011). Since the superior parietal cortex seems to be crucial for the manipulation of vWM content (Formisano et al., 2002; Koenigs et al., 2009) it could as well play a role in maintaining manipulated stimuli. According to Sack et al. (2005), the left parietal lobe is likely to serve the building of a mental image and can be compensated by the right parietal lobe, if necessary. Mechelli et al. (2004) suggested an "imagery network" consistent of the parietal cortex generally associated with attentional functions and prefrontal areas mediating stimulus-specific activation in sensory areas. This fronto-parietal network is supposed to serve in maintaining dynamic functional links to object representations in primary and secondary visual cortex in the occipital brain area, where, according to numerous authors, a visual buffer could be located (e.g. Albers et al., 2013; Cichy et al., 2012; Slotnick, Thompson, & Kosslyn, (2012); for reviews, see Kosslyn et al., 2006; Zimmer, 2008). Based on these findings a fronto-parietal attentional control network acting on visual representations located in early visual areas could mediate the maintenance of a coherent visual representation that was mentally constructed.

Because an according oscillatory synchronization could just as well represent general vWM load, the amount of to be integrated features was varied in the two following experiments as well. By comparing both conditions the effects of the process of more active mental construction could be assessed in contrast to mere increased vWM load.

2.4. SUBSEQUENT MEMORY

Besides the assumed function of maintaining a coherent visual image constructed from single parts, I was further interested in additional implications of increased oscillatory synchrony within the fronto-parietal network. Considering the higher elaborateness of an image being mentally constructed, a positive effect of encoding into LTM could be assumed according to Craik and Lockhart (1972). Does an increased synchronization between frontal- and parietal areas during maintenance reflect the more elaborate processing and is therefore predictive of successful later memory?

In general, vWM maintenance is found to be accompanied by distinct electrophysiological activation that is higher for later correctly remembered stimuli (Khader, Ranganath, Seemüller, & Rösler, 2007). Oscillatory coupling as well is found to be stronger during maintenance for later remembered objects (Fellner, Bäuml, & Hanslmayr, 2013; Sarnthein et al., 1998; Summerfield and Mangels, 2005). This is direct evidence for the functional importance of neuronal synchronization, as has been stated by Hummel and Gerloff (2005) for another context, sensory integration performance, as well.

But are the synchronization processes that are associated with better memory performance dependent on the task preceding the maintenance phase? Is, for example, a different pattern of neuronal phase coupling during maintenance correlated with successful later decoding when a more elaborative vWM task has to be fulfilled?

The second experiment deals with the interaction between specific ways of processing during vWM and the according neuronal coupling that is associated with successful LTM performance. It is investigated, whether the neuronal foundations are sensitive to different task demands, or if successful later memory depends on a general process, equal for all preconditions.

In the two experiments that are described in detail below, the way of processing of visual information was manipulated. In one experimental condition, participants had to maintain an object that was presented to them, in the other condition, they had to construct a complete object out of individual features before maintaining the completely constructed image. Additionally, the complexity of the objects was varied to be able to assess the effect of vWM load and construction load. EEG phase coupling was assessed to account for interareal binding and communication between subfunctions of vWM. In the second experiment, a subsequent memory test served to investigate the relevant neuronal coupling for later memory. In this way, the neuronal processes relevant to build a stable memory trace, dependent on the origin of the vWM content, could be identified.

2.5. SUMMARY OF THE INTRODUCTION

To summarize, I expected that a mental construction task would lead to a stronger coupling between fronto-parietal and occipital regions during a phase of maintenance. These regions are known to be relevant for vWM maintenance (e.g. Palva et al., 2010) and I assumed a representation combined out of single features would need more cognitive control to be kept active than a formerly completely perceived representation. This increased cognitive control should be reflected in increased neuronal coupling between these areas to mentally hold the parts together. Through a parametrical design I expected to eliminate a special effect of binding of several features in contrast to a general vWM load effect. Additionally, I was interested in whether stronger synchronization between frontal- and parietal areas could also be identified to foster encoding into LTM and therefore conducted a subsequent memory test in a second experiment. Here I additionally investigated, whether the neuronal foundations associated with successful encoding are sensitive to different levels of elaborateness of the maintained representation.

3. STUDIES

3.1. NEURAL CORRELATES OF MAINTAINING GENERATED IMAGES IN VISUAL WORKING MEMORY

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3.1.1. ABSTRACT

How are images that have been assembled from their constituting elements maintained as a coherent representation in visual working memory (vWM)? Here, we compared two conditions of vWM maintenance that only differed in how vWM contents had been created. Participants maintained images that they either had to assemble from single features or that they had perceived as complete objects. Object complexity varied between two and four features. We analyzed EEG phase coupling as a measure of cortical connectivity in a time interval immediately before a probe stimulus appeared. We assumed that during this time both groups maintained essentially the same images, but that images constructed from their elements require more neural coupling than images based on a complete percept. Increased coupling between frontal and parietal-to-occipital cortical sources was found for the maintenance of constructed in comparison to non-constructed objects in the theta, alpha, beta, and gamma frequency bands. A similar pattern was found for an increase in *vWM load* (2 vs. 4 features) for non-constructed objects. Under increased *construction load* (2 vs. 4 features for constructed images), the pattern was restricted to fronto-parietal couplings, suggesting that the fronto-parietal attention network is coping with the higher attentional demands involved in maintaining constructed images, but without increasing the communication with the occipital visual buffer in which the visual representations are assumed to be stored. We conclude from these findings that the maintenance of constructed images in vWM requires additional attentional processes to keep object elements together as a coherent representation.

3.1.2. INTRODUCTION

Visual imagery is the ability to “see with the mind´s eye”, i.e., to internally create a percept-like mental state without the corresponding external stimulus (Kosslyn, 2005; Kosslyn et al., 2001). These mental images are maintained and manipulated in visual working memory (vWM), for example in daydreaming (Tong, 2013). Mental imagery serves several important cognitive functions such as planning or being creative in an imaginative fashion. An architect, for example, will have an image of the house she is planning to build in her mind before she starts working on a model. A fundamental feature of such a creative process is that image parts become recombined and maintained in vWM. How does the brain manage to maintain a coherent representation of a stimulus that formerly only existed as distinct parts?

It is generally assumed that pictures of formerly seen or even newly combined stimuli are topographically represented in the visual cortex (Kosslyn et al., 2001). According to Kosslyn et al. (2006), mental images can be created by combining perceptual representations (also described as “mental simulation”; Buckner et al., 2008). Current theories of mental imagery converge on the notion that the manipulation of mental images is governed by an attentional control process assumed to be located in the fronto-parietal attentional network (Corbetta and Shulman, 2002; Ganis and Schendan, 2011), which acts in a top-down manner by maintaining dynamic functional links to object representations in a visual buffer assumed to be primarily located in more occipital areas, i.e., in primary and secondary visual cortex (e.g. Albers et al., 2013; Cichy et al., 2012; for reviews, see Kosslyn et al., 2006; Zimmer, 2008). Connections from the prefrontal cortex have been found to mediate stimulus-specific activation during imagery (Mechelli et al., 2004), suggesting that the prefrontal cortex is forming an “imagery network” based on attentional functions together with the parietal cortex, which is involved in the maintenance of an image. Especially, the superior parietal cortex is assumed to be crucial for manipulating the contents of vWM (Formisano et al., 2002; Koenigs et al., 2009) and could therefore as well play a role in maintaining manipulated stimuli. In classical mental-rotation tasks, pronounced activation is found in right parietal and, simultaneously, left frontal areas (for a review, see Zacks, 2008). The left parietal lobe most likely serves to build up mental images and can be compensated by the right parietal lobe, if necessary (Sack et al., 2005).

Based on these findings, we assumed that a fronto-parietal attentional control network acting on visual representations should mediate the maintenance of a coherent representation of a visual object constructed through mental imagery. But how could such a control system accomplish this on a neural level? One possible clue towards such a mechanism of keeping together different parts of a representation could lie in the synchronization of neural oscillations. Phase synchronization has been shown to underlie the integration of anatomically distributed neuronal processing (Singer, 1999) and the coordination of attentional interactions among the visual system (Bosman et al., 2012; Womelsdorf and Fries, 2007) as well as to reflect vWM contents (Salazar et al., 2012) in cat and monkey local field potential (LFP) recordings. Also in humans there is abundant evidence that phase coupling between neural oscillations at distinct cortical regions and in distinct frequency bands is correlated with successful task performance, suggesting that it may reflect communication among distributed neuronal assemblies (for reviews, see Fell and Axmacher, 2011; Klimesch et al., 2010; Lachaux et al., 1999; Palva and Palva, 2012; Sauseng and Klimesch, 2008). Analysis of inter-areal synchronization form source-localized MEG data has shown that synchronization concurrently in the alpha, beta, and gamma frequency bands is load-dependently correlated with vWM performance (Palva et al., 2010).

Several studies have suggested that theta-band oscillations (~4-7 Hz) are especially relevant in the maintenance of items in vWM (Gevins et al., 1997; Jensen & Tesche, 2002; Kahana et al., 2001). Theta-band phase coupling has been found to be correlated with successful vWM task performance, (Sauseng et al., 2004; Sauseng et al., 2010; Summerfield and Mangels, 2005; see Colgin, 2013, for a review). For example, increased neural coupling in the theta band has been observed between frontal and posterior EEG electrodes during successful vWM maintenance (Sarnthein et al., 1998) and for increased central executive demands (Sauseng et al., 2006). Moreover, the integration of features, i.e., word and color information, during encoding in vWM has been found to be accompanied by increased fronto-posterior theta coupling that was associated with successful retrieval of the integrated information from vWM (Summerfield and Mangels, 2005). In a recent review, Sauseng and colleagues (Sauseng et al., 2010) suggest theta coupling to be the key mechanism in coordinating several cognitive processes involved in vWM. Polanía et al. (2012) even provided causal evidence for fronto-parietal theta coupling improving cognitive performance in a transcranial alternating current stimulation study. In line with these theories and findings, we expect increased fronto-parietal theta coupling during the maintenance of constructed in comparison to non-constructed images, because increased control should be necessary to actively maintain the links between the single features.

Also alpha (~8-13 Hz) oscillations have been associated with successful vWM maintenance (Bonnefond and Jensen, 2012; Haegens et al., 2010; Palva and Palva, 2011). In general alpha oscillations are thought to mediate top-down modulation of sensory and memorized information (Klimesch et al., 2010; Palva and Palva, 2007). In vWM, the amplitude of alpha oscillations is negatively correlated with vWM capacity (Palva and Palva, 2011) and is pronounced for to be ignored objects (Bonnefond and Jensen, 2012) and hence alpha oscillation amplitudes have been suggested to reflect the enhanced executive functions for coping with the excess of information and suppression of task irrelevant information, respectively. However, in contrast to amplitudes, the strength of alpha-band inter-areal synchronization is positively correlated with the individual vWM capacity limitation (Palva et al., 2010).

The literature on beta (~14-30 Hz) is more sparse, however, synchronisation between fronto-parietal and occipital areas in the beta band has been found to be important for vWM retention (Fell and Axmacher, 2011; Hanslmayr and Staudigl, 2014; Palva et al., 2010).

Last, but not least, the gamma frequency range (above 30 Hz) has also been found to be load-sensitive in amplitude in vWM tasks in prefrontal and visual cortices (Howard, 2003; Palva et al., 2011; Roux et al., 2012; Tallon-Baudry and Bertrand, 1999). Moreover, gamma-band synchronization has been found to be load-dependently coupled between parietal and visual cortices during vWM maintenance (Palva et al., 2010). Importantly, prior studies have shown that in humans the amplitude of gamma-band oscillations was positively correlated with vWM capacity (Palva et al., 2011) and was sensitive to and correlated with the maintenance of stimulus features specifically when these features form coherent object representations (Honkanen et al., 2015; Tallon-Baudry et al., 1998).

To investigate how the brain manages to maintain a coherent representation of a stimulus that formerly only existed as distinct parts, we developed an experimental paradigm in which participants had to maintain a visual object that they constructed in vWM out of individual features (see Figures 1 and 2). After a few seconds of maintenance (the exact interval varied randomly and was thus unpredictable), the mental image had to be matched to a comparison object. Most importantly, we compared two conditions of vWM maintenance that only differed in how the vWM contents had been *created*: In the construction condition, two, three or four features like the shape or the color of a beetle had to be merged mentally into one coherent representation of the complete beetle. In the control condition, participants had to simply maintain stimuli that they had seen on the screen before, varying in complexity between two and four features. Accordingly, in the control condition everything but the construction process was the same as in the experimental condition. We expected that a mental image that formerly existed only in parts would require additional attentional control processes in order to be maintained successfully. Those processes should serve a binding function that connects object parts in vWM and keeps the connections active during maintenance.

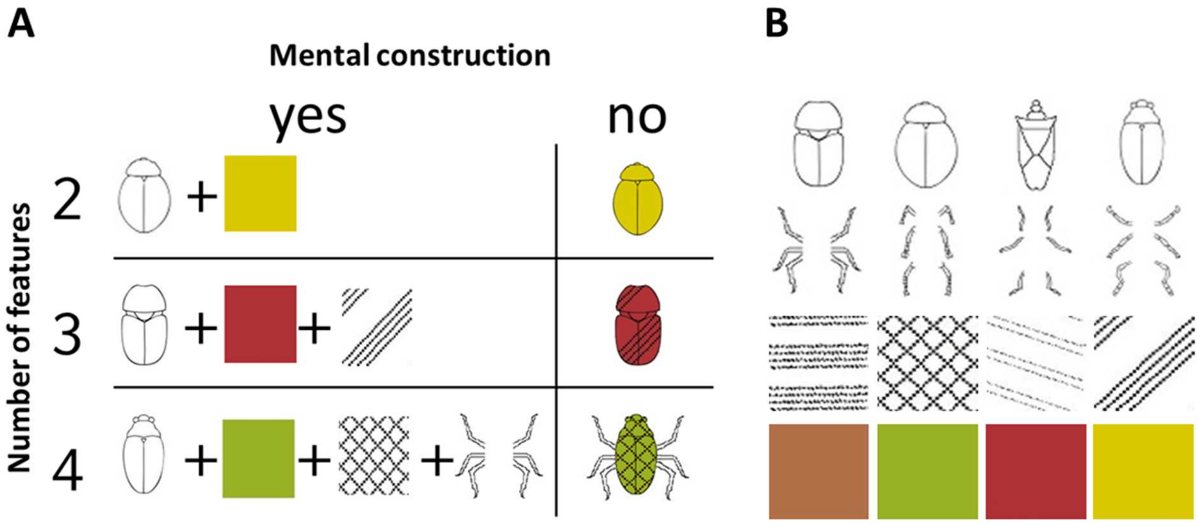

Figure 1. A: Design and exemplary stimuli. In the mental construction condition, single features in varying numbers were shown, whereas in the non-construction condition, objects with varying complexity were shown. Stimuli consisted of two, three or four features. For the exact layout of the presentation see Figure 2. B: All possible features. This table was shown to the participants as part of the instruction.

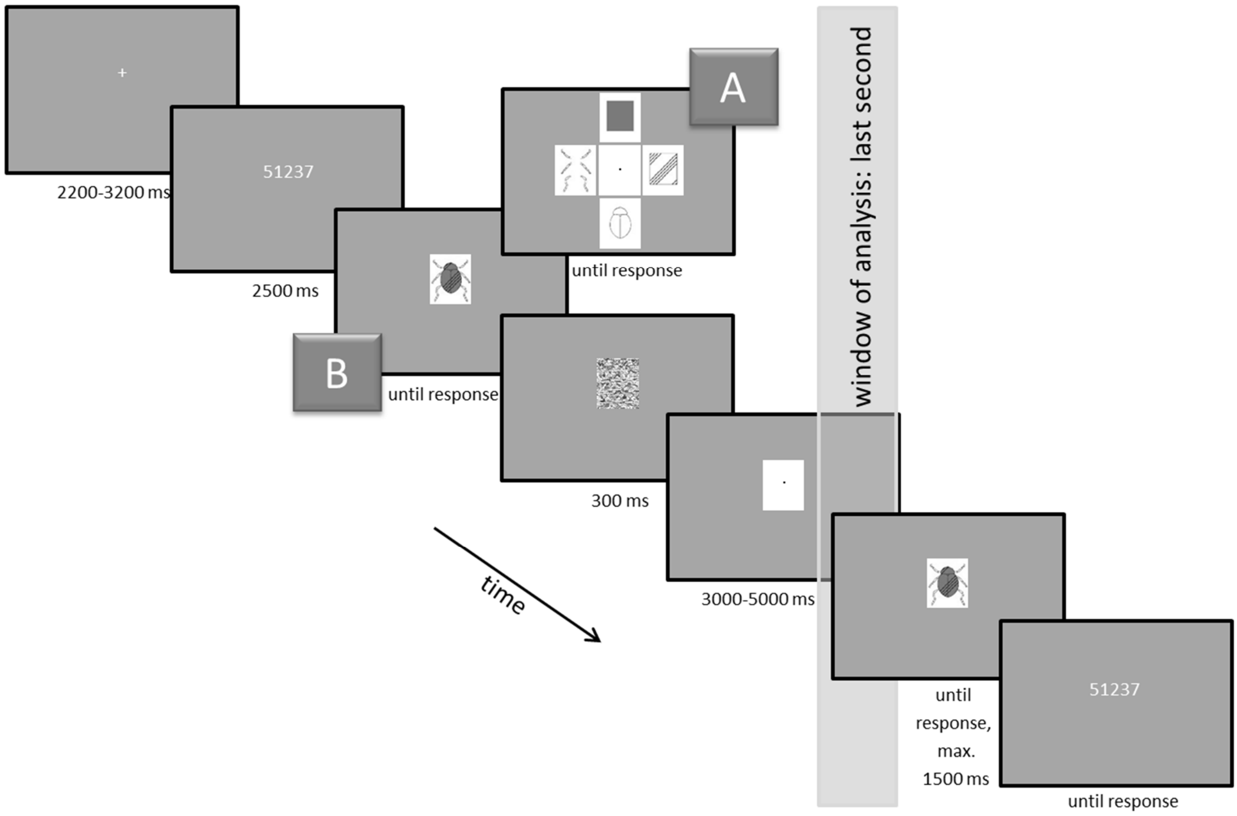

Figure 2. Stimulus timing and layout of the experiment. *A* marks the mental construction condition, *B* the condition without mental construction. The proper mental imagery task was framed by a digit-maintenance task to avoid verbalization of the to-be-imagined objects. There was always a 50 % chance of seeing the same or a different picture or digit.

We hypothesized that inter-areal phase synchronization could underlie the maintenance of coherent objects constructed from object features in vWM and that this phase-synchronization should reflect the stronger attentional control necessary to actively “hold the pieces together” in vWM compared to that of simply maintaining percepts without the necessity to have manipulated it mentally.

Accordingly, we assumed stronger phase synchronization in the construction condition between frontal and parietal regions where attentional control processes like the manipulation of objects in vWM are presumably located (Koenigs et al., 2009; Salazar et al., 2012; Sarnthein et al., 1998) and between frontal and occipital regions where the representation of the image is assumed to be stored (Kosslyn, 2005). Furthermore, we hypothesized that the strength of synchronization should increase parametrically with vWM load, that is, with the number of features maintained in vWM.

To conclude, we expect a neural implementation of a vWM control process that serves to keep distinct object parts together as a unified representation to be found in phase coupling of oscillations between the fronto-parietal network and occipital cortex. The fronto-parietal network might provide the additionally required attentional resources and the control mechanism necessary to keep object parts together while forwarding it to the visual buffer located in occipital areas. While the visual buffer should face very similar demands in both the construction and non-construction conditions, in the construction condition its coupling with the fronto-parietal network should be strengthened.

3.1.3. MATERIALS AND METHODS

3.1.3.1. PARTICIPANTS

Twenty-one students (12 female) of the Ludwig-Maximilians-Universität München, aged 19–31 years (mean age: 23.8) participated in the study. All participants but one were right-handed by self-report, all except one were native speakers of German, and all had normal or corrected-to-normal vision. The study was performed in accordance with the Revised World Medical

Association's Declaration of Helsinki (Nicogossian et al., 2014). The participants gave informed consent to the procedure and were naive with regard to the aims of the study.

Participants took part for either course credit or payment. One participant was excluded due to less than 65% of correct trials in one of the experimental conditions. Three other participants were excluded because the EEG recording was too noisy (criteria for artifact rejection see below). The remaining 17 participants (10 female) were aged 19–31 years (mean age: 24).

3.1.3.2. MATERIAL

Participants maintained in vWM schematic drawings of beetles with a varying number of features (two, three, or four; see Figure 1 for examples). Beetles were chosen as stimuli, because they can be varied in complexity and still be recognized as concrete objects (see also Bergert & Nosofsky, 2007). We varied the number of features to assess the effect of stimulus complexity on visual imagery in a construction and a non-construction condition. In the construction condition, participants had to mentally combine two, three, or four presented features to one single object and maintain it in vWM, whereas in the non-construction condition they had to maintain one object which was presented as a whole, comprising either two, three, or four features.

Each beetle comprised a body shape out of four possible body shapes and, depending on the number of features, at least one additional feature, that is, a color out of four, a pattern out of four, or a leg shape out of four (see Figure 1 for all possible features). A balanced subset of 144 of the possible feature combinations was presented, with 48 stimuli for each number of features. Since there were 4x4x3 possible combinations in the 2-feature condition, all possible feature combinations were presented there. In the 3- and 4-feature conditions, a fixed subset of all possible combinations was created with equally distributed feature combinations. Thus, a certain feature, e.g. a specific color, was not more likely to occur together with a certain other feature, e.g. a specific body shape. The stimuli were randomly chosen out of this predefined subset for each participant.

In the experimental condition, either two, three, or four features were shown randomly arranged at the top, bottom, left, and right sides of a white rectangle (height = 6.8 cm, width = 5.6 cm) in the middle of the screen (see Figure 2). The features were presented within individual white rectangles (also 6.8 x 5.6 cm). In the conditions with fewer than four features, gray (RGB = 150/-150/-150) rectangles with a thin darker gray frame to contrast them with the background were shown in the same place instead. In the control condition, the beetles were presented in the center of the screen within a white rectangle.

3.1.3.3. PROCEDURE

Stimuli were presented on a 17″ standard CRT monitor with a refresh rate of 75 Hz. During the experiment, in which the electroencephalogram (EEG) was recorded, participants sat in a dimly lit room at a distance of ca. 100 cm in front of the screen, and gave their responses by means of a standard computer keyboard. Participants were shown a table of all possible features (Figure 1) at the beginning of the instruction.

The main task in the *experimental* condition was to memorize pictures of beetles that first had to be mentally constructed from single beetle features (see Figure 2). In the *control* condition, these pictures of beetles were presented without the necessity of constructing them. Participants were instructed to visualize the image of the constructed or non-constructed stimulus, respectively, in a white rectangle in the middle of the screen. After the participants confirmed per button press (“space” on the keyboard) that they now have a vivid image of the constructed or perceived stimulus in mind, a visual mask was presented for 300 ms covering the central white rectangle to prevent iconic memory traces. Participants had to maintain the mental image of the stimulus for three to five s (jittered in steps of 400 ms), until a probe stimulus appeared in the same location, upon which they had to give a match/non-match response. Jittering was installed to avoid expectancy effects. The probe was either identical to the memorized stimulus (which was the case in 50 % of the trials) or differed in one randomly determined feature. Importantly, participants had only 1500 ms time to respond “same” or “different” by pressing either the “Alt” or “AltGr” key (counterbalanced across participants) with their left or right index finger to indicate whether the presented stimulus corresponded to their mental image or not. This short interval was chosen to enforce participants to rely on the visual image they were holding active. We assumed that a verbal strategy to match the up to four features would require more time than 1500 ms. This was in general confirmed by post-experimental reports of the participants.

In addition to the short time limit for the match/non-match response, we implemented a secondary task to suppress verbalization of the constructed visual images. Before the to-be-memorized beetle stimulus was presented, participants had to read and keep in mind a string of five random digits presented for 2500 ms. Memory for this secondary vWM load was tested at the end of the trial. Specifically, after the match/non-match response to the probe beetle, a string of five digits was presented with one digit differing from the to-be-maintained array in 50 % of the trials. Participants had all the time they needed to compare the digits and give their answer (using the same keys as for the probe beetle). With this second answer the trial ended. In the inter-trial interval, a fixation cross was presented for 1200 to 3200 ms (jittered in steps of 400 ms). The whole trial sequence is shown in Figure 2.

Before EEG recording, the task was practiced for 12 trials, in which feedback (correct, incorrect) was provided for 800 ms after each response. If the response window of 1500 ms passed without a response, the feedback “too late!” was provided. Each block of the following main experiment with EEG recording comprised 24 trials. After each block feedback on the number of correct responses was provided. After six blocks the experimental condition (construction vs. non-construction) changed (again participants first completed 12 training trials to familiarize themselves with the new condition). Half of the participants first did the experimental condition, the other half the control condition. There were 24 x 12 = 288 trials in total, with 48 trials for each of the 2 x 3 conditions (mental construction x number of features).

3.1.3.4. EEG RECORDING AND ANALYSIS

EEG was recorded with two 32-channel amplifiers (Brain Products GmbH, Gilching, Germany) in AC mode with a time constant of 10 s (except the first two subjects whose data were recorded in DC mode, but subsequently filtered with an .01 Hz high-pass filter) from 61 scalp electrodes, an inferior ocular channel, and two electrodes at both earlobes, of which one served as online reference (alternating across participants). The ground electrode was placed on either the left or the right mastoid alternating across participants. We used Ag/AgCl ring electrodes arranged according to the extended 10–20 system (Jasper, 1958). Average impedance was kept below 10 kΩ. Sampling rate was 500 Hz. The vertical electrooculogram was calculated by re-referencing the inferior ocular electrode to Fp1; the horizontal EOG was recorded by a bipolar recording of F7 vs. F8.

The initial processing of the EEG data was done with BrainVision Analyzer® 2.0.3. EEG segments of the 1000 ms immediately preceding the onset of the probe beetle were extracted. During this time, both groups should have maintained essentially the same objects in vWM, and the maintained image had to be as vivid as possible to enable the participant to answer correctly. According to the experimental factors of *mental construction* (yes/no) and *number of features* (2, 3 or 4), six different groups of segments resulted. All segments of trials with errors in one or both of the two matching tasks were excluded from the analysis to make sure that only trials with a vivid image and successful verbal suppression were analyzed. Segments with eye blinks, eye movements, muscle potentials, and other artifacts were excluded by means of a semi-automatic filtering procedure (maximum allowed amplitude difference between adjacent voltage values = 40 µV/ms; maximum allowed difference in any interval of 1000 ms length = 150 µV; minimum allowed difference in any interval of 200 ms length = .5 µV). The average number of remaining artifact-free segments was equivalent in all conditions: 36.76 in the "construction (C)/2 features" condition, 33.94 for C/3, 32.18 for C/4, 38.06 for "non-construction (NC)/2 features", 38 for NC/3, and 36.94 for NC/4. Signals were re-referenced to the common average.

In a next step, LORETA analysis (Pascual-Marqui et al., 1994) was applied to the artifact-free segments to reduce the number of scalp locations and effects of volume conduction. Specifically, source components from the three spatial axes (X, Y, and Z) were extracted and averaged to form a measure of the electrical activity in specific regions of interest (ROIs) defined from anatomical templates as implemented in the BrainVision-Analyzer software. The following ROIs were defined (cf. Figure 4): Anterior cingulate cortex (ACC; Brodmann Areas (BA)

24, 32, 33), visual cortex (BA 17, 18, 19), superior parietal cortex (BA 5, 7), inferior parietal cortex (BA 39, 40), superior frontal gyrus (BA 4, 6, 8), middle frontal gyrus (BA 10, 46, 9), and inferior frontal gyrus (BA 11, 47, 45, 44). All ROIs were defined separately for the two hemispheres, except the ACC, which was defined as one single ROI with both the left and right hemispheric BAs included. We chose 13 ROIs to account for the relatively low spatial resolution of scalp EEG data due to volume conduction on the one hand (see, e.g., Ferree et al., 2001; Srinivasan et al., 1998), while minimizing the loss of information on the other hand. By choosing a rather coarse graduation, we also substantially reduced the number of statistical comparisons. An even coarser graduation (such as left/right x frontal/central/posterior) would have further reduced the number of tests, but would have increased the risk that effects get averaged out due to the large pooling of signals.

The resulting ROI-averaged data were then further analyzed with continuous 5-cycle complex Morlet Transformation and Gabor Normalization. Frequencies between 3 and 90 Hz in 25 logarithmic steps were chosen. The complex values of these 25 frequency layers were extracted.

Further analysis was done with MatLab R2007b (The MathWorks Inc., Natick, MA, USA). 200 ms at the edges of each segment were trimmed to exclude any filter ringing artifacts. To keep the number of trials constant within participants, the smallest number of trials that occurred in one of the six conditions was determined per participant. That was done to avoid confounding effects of unequal numbers of trials on the phase-locking values (see below). Subsequently, all following calculations were iterated 100 times in a bootstrap-like approach with randomly chosen subsets of trials corresponding to the smallest trial number, and with the results averaged across the iterations.

Finally, the Phase-Locking Value (PLV) according to Lachaux et al. (1999) was calculated for each pair of ROIs (78), participant (17), frequency layer (25), and experimental condition (6). Frequency layers were averaged according to the different frequency bands of interest: theta (3.983 - 7.021 Hz), alpha (8.090 - 12.376 Hz), beta (14.261 - 28.965 Hz), and gamma (33.375 - 90.000 Hz). To test for systematic increases of phase locking with construction or with the number of features, one-tailed (parametric) *t* tests between experimental conditions were conducted for each pair of ROIs, separately for each frequency band. We decided to use *t* tests because we experienced in numerous previous frequency-domain EEG studies (e.g., Khader et al., 2010; Khader and Rösler, 2011), and also in the present study, that the non-parametric alternative, the Wilcoxon test, substantially reduces test power, increasing type-2 error (an assumption that has been repeatedly discussed in the statistical literature; see, e.g., Boneau, 1960; Rasch and Guiard, 2004, arguing that the *t* test is reasonably robust against deviations from normal distributions). For the same reason we decided against correcting for alpha error inflation. So instead of making the analysis more conservative, we plotted the couplings at different levels of significance ("significance probability mapping"; see, e.g., Duffy et al., 1981; Hassainia et al., 1994), allowing for an evaluation of how the overall pattern becomes narrowed and more focused with a stricter threshold. Besides this statistical mapping, we also provide the absolute changes in phase coupling in the Supporting Information.

Three effects were of interest: first, the general *effect of construction*, that is, the comparison between the *construction* and the *non-construction* condition, irrespective of the number of features. Second, the effect of *mental load* in the *construction* conditions *("construction load")*, and third, the effect of *mental load* in the *non-construction* conditions *("vWM load")*. The latter two effects were tested by means of comparing the conditions with two vs. four features.

To analyze whether the significant increases in coupling from two to four features were parametric, we averaged the PLVs over all significant pairs of ROIs per frequency band and condition to check whether the three-feature-condition had an average PLV in between that of two and four features. As can be seen in Figure 5, this applied to most cases, except for the construction-load effect for alpha and the vWM-load effect for gamma, which, accordingly, should be interpreted more carefully.

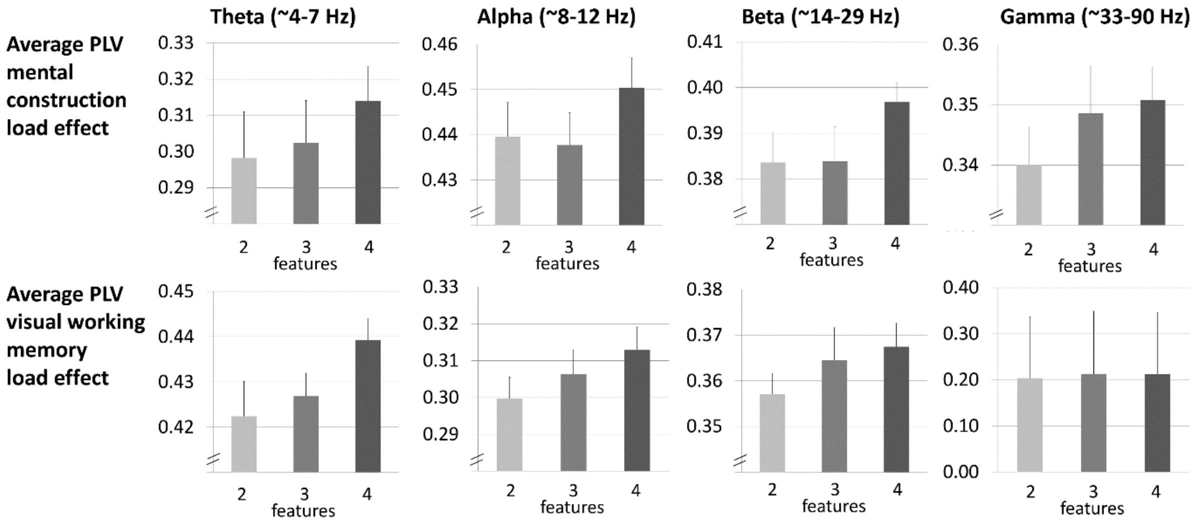

Figure 5. Phase-Locking Values averaged over all significantly stronger couplings found for 4 > 2 features in the mental construction and the non-construction condition, separately for two, three, and four features. It can be seen that in the majority of cases the three-feature-condition has an average PLV between that of two and four features, suggesting parametric increases with the number of features. The mental construction load effect for alpha and the working memory load effect for gamma, however, should be interpreted more carefully (see main text for details), since the PLVs are not increasing parametrically with the number of features. Error bars are 95% confidence intervals, corrected after Morey (2008).

Finally, besides phase locking, we also analyzed spectral power in the different frequency bands of interest by extracting the squared absolute values of the complex wavelet coefficients and the vertical and horizontal eye movements with respect to their power in the different conditions to test for a possible influence on our data (e.g. "microsaccades"; Keren et al., 2010). The results can be found in the Supporting Information. We could exclude any influence of high-frequency eye movements on our results, but revealed a possible confound on the load effect in the non-construction condition in the theta and alpha bands. We therefore refrain from interpreting any of those intra-frontal couplings because we cannot exclude that they are influenced by eye-modulated activity.

3.1.4. RESULTS

3.1.4.1. BEHAVIORAL DATA

Response times (RT) and error rates were analyzed with repeated-measures ANOVAs including factors *mental construction* (yes, no) and *number of features* (2, 3, 4). Corrected *p* values (Greenhouse and Geisser, 1959), epsilon, and non-corrected degrees of freedom are reported. Significant interactions were further analyzed by means of planned *t* tests. Trials with incorrect responses in the number-comparison task were excluded from the analysis of the error rates. For the RT analysis, also trials with incorrect responses in the picture-comparison task were excluded. The behavioral data were analyzed using SPSS (version 21; IBM, Armonk, NY, USA).

As can be seen in Figure 3, both RT and error rate were generally higher for matching constructed compared to non-constructed objects. Both measurements increased with the number of features in both the construction and non-construction conditions, with this increase being weaker (RT) or even absent (error rates) in the non-construction condition. This pattern was supported by the statistical analysis. For RTs, significant main effects were found for factors *construction*, *F*(1, 16) = 12.66; *p* = .003, *ε* = 1, and *number of features, F*(2, 32) = 48.19; *p* < .001, *ε* = .956. In addition, the interaction *construction* x *number of features* was significant, *F*(2, 32) = 13.40; *p* < .001, *ε* = .771. Pairwise one-tailed *t* tests, Bonferroni-corrected for seven tests, revealed that in the *construction* condition the RTs increased significantly with the numbers of features, i.e., *two vs. three features* (*t* = 7.33, *p* < .001) and *three vs. four features* (*t* = 4.28, *p* = .004) differed significantly. In the non-construction condition, the conditions with different number of features did not differ significantly (*p* = .259 for 2 vs. 3 and *p* = .151 for 3 vs. 4 features). *Construction vs. non-construction* differed significantly with three (*t* = 3.23, *p* = .037) and four features (*t* = 4.93, *p* = .001).

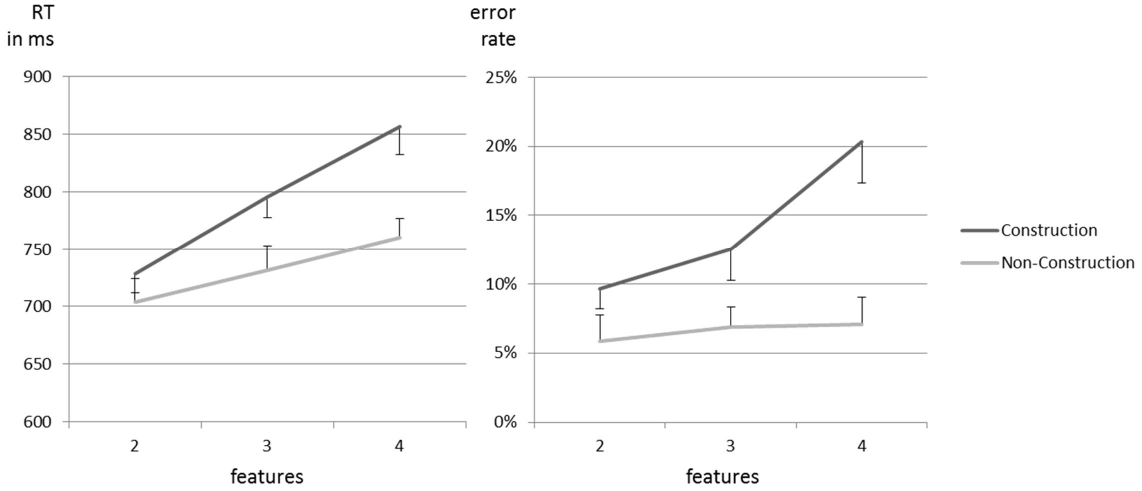

Figure 3. Response times (RT) and error rates for all experimental conditions. Error bars are 95% confidence intervals, corrected after Morey (2008).

The analysis of the error rates revealed corresponding results, with significant main effects for factors *construction*, *F*(1, 16) = 26.95; *p* < .001, *ε* = 1, and *number of features* *F*(2, 32) = 22.85; *p* < .001, *ε* = .890, as well as a significant interaction *construction* x *number of features*, *F*(2, 32) = 7.82; *p* = .002, *ε* = . 925. Planned comparisons showed that the error rates in the construction condition increased significantly from three to four features (*t* = 3.73, *p* = .013). In the non-construction condition, no significant increases were found. Finally, *construction vs. non-construction* differed significantly with three (*t* = 3.12, *p* = .046) and four features (*t* = 5.16, *p* < .001).

Analysis of the secondary task (maintaining numbers) revealed no significant difference between the experimental conditions in error rates.

3.1.4.2. EEG DATA

Figure 4 gives an overview of significant couplings between the ROIs in the different frequency bands. Panel A shows that the main effect of mental construction irrespective of the number of features was associated with increased inter-areal synchrony between frontal and posterior sources. Strengthened synchrony in the theta and gamma bands was observed between frontal and parietal-to-occipital cortical sources, while in the alpha band it was observed between anterior cingulate and parietal as well as parietal and occipital sources. Panel B shows significantly stronger synchronization during the maintenance of four compared to two features, separately for constructed objects (*construction-load* effect; upper map) and non-constructed objects (*vWM-load* effect; lower map). While the phase coupling for increased construction load was restricted to fronto-parietal synchronization, the phase coupling for increased vWM load was associated, like the general mental-construction effect, with fronto-parietal-occipital synchronization. We will describe these effects in more detail separately for each frequency band

Theta. In the theta band, stronger coupling for constructed in comparison to non-constructed images was found between the left occipital and both the left middle and superior frontal ROIs, as well as between the left middle frontal and right superior parietal ROIs. We also found stronger coupling between the left inferior and right superior parietal ROIs, as well as between the left inferior parietal and left occipital ROIs. Within the construction conditions, stronger phase coupling for four compared to two features was found between the left inferior frontal and left superior parietal ROIs, as well as between the right superior frontal and the left superior parietal ROIs. Within the non-construction condition, stronger phase coupling for four compared to two features was found between bilateral frontal and parietal ROIs, as well as between the right superior frontal and the left superior parietal ROIs. Moreover, a vWM-load effect was found between the left occipital and both the medial (ACC) and lateral frontal ROIs, as well as between the left superior frontal and the left occipital ROIs.

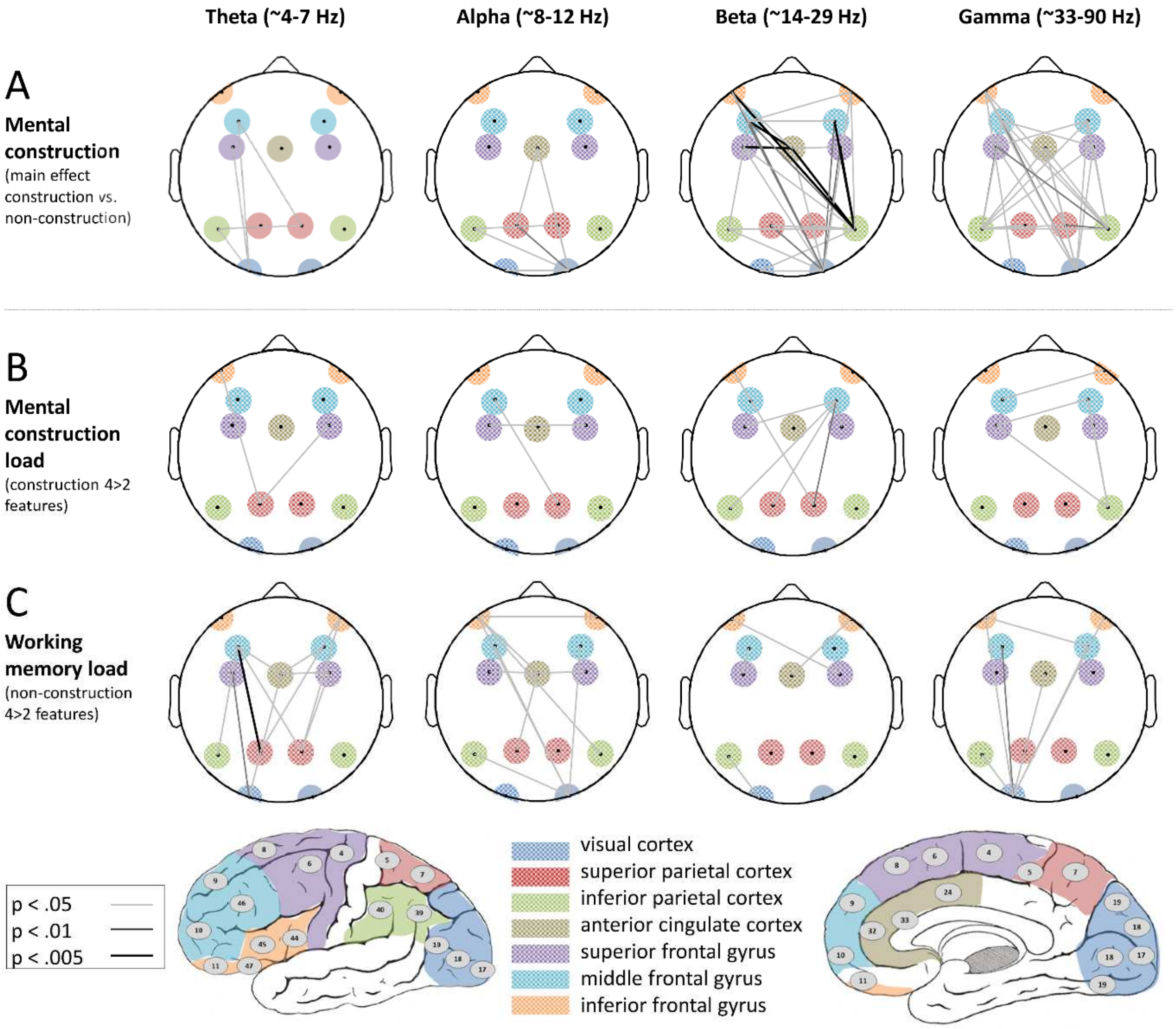

Figure 4. (A) Significantly stronger phase couplings between ROIs (as computed from LORETA source distributions; see Methods) in the mental construction condition in comparison to the non-construction condition, irrespective of the number of features. (B) Significantly stronger couplings under increased construction load (4 > 2 features) for constructed objects and (C) under increased WM load (4 > 2 features) for objects presented as a whole without construction requirements. The thickness of the lines corresponds to the *p* value, see legend. LORETA ROIs are color-coded, numbers indicate Brodmann areas.

Alpha. In the alpha band, we observed stronger coupling for constructed in comparison to non-constructed images between the right occipital ROI and both superior parietal ROIs, as well as the left occipital ROI. Moreover, the left and right superior parietal ROIs were coupled, with both showing additional coupling with the ACC ROI. In addition to the main effect of mental construction, a *construction-load* effect was found between the superior frontal ROIs and between the left middle frontal and right superior parietal ROI, without an involvement of occipital ROIs. The absence of a stronger occipital involvement resembles the corresponding effects found for the theta and gamma bands (see below), and therefore seems to be stable across frequency bands. However, the effect in the alpha band should be interpreted with caution, since the *three-feature* condition turned out to have a lower PLV than expected (cf. Figure 5). A widespread *vWM-load* effect was found, with the right occipital ROI showing couplings with frontal ROIs (i.e., left inferior and right middle frontal), as well as the left inferior parietal ROI. Furthermore, fronto-parietal couplings were found between the left inferior frontal and right inferior parietal ROI, as well as between the ACC and the left superior parietal ROI. Finally, intra-frontal couplings showed up between the left and right inferior frontal ROIs and between the ACC and bilateral superior frontal ROIs (as stated above, we cannot exclude that these intra-frontal couplings were influenced by eye movements, so they should be interpreted with caution). To conclude, the patterns in the alpha band corresponded to those found for theta in a way that both the effects of general mental construction and vWM load comprised frontal, parietal, and occipital ROIs, whereas the effect of construction load did not invoke occipital ROIs. As outlined below, this also held for gamma.

Beta. Consistent with the corresponding findings for the other frequency bands, the maintenance of constructed in comparison to non-constructed objects was accompanied by widespread fronto-parietal coupling, especially with the right inferior parietal ROI, and fronto-occipital coupling with the right occipital ROI. The ACC also coupled stronger with the superior frontal ROIs, the right inferior parietal ROI and the right occipital ROI. In addition, the occipital

ROIs, especially the right one, were also stronger coupled with parietal ROIs. Both occipital ROIs were stronger coupled with each other and we found an increased intra-frontal coupling as well. Also consistent with the findings for the other frequencies, we found a construction-load effect mainly restricted to fronto-parietal couplings, in this case between the right middle frontal and both left as well as the right superior parietal ROIs and between the left inferior frontal ROI and the right superior parietal ROI. The left superior frontal and the right middle frontal ROIs were also stronger coupled in this comparison. Different from the findings for the other frequencies, an effect of vWM load (for non-constructed objects) was only found between the left middle and left superior frontal, the left inferior and the right superior frontal, and the right inferior frontal and the ACC ROIs. More posterior, only the left inferior parietal and the left occipital ROIs were stronger coupled in this comparison.

Gamma. In the gamma band, the maintenance of constructed in contrast to non-constructed objects was accompanied by widespread fronto-parietal coupling. In addition, pronounced fronto-occipital coupling was found between the left occipital and left inferior frontal ROIs and between the right occipital and almost all frontal ROIs. As found for the lower frequencies, we also found a construction-load effect restricted to fronto-parietal couplings here, i.e., between the left superior frontal, right middle frontal, and right inferior parietal ROIs, as well as between the left middle and right inferior frontal ROIs. Also consistent with the findings for the lower frequencies, an effect of vWM load (for non-constructed objects) was found between frontal, parietal, and occipital ROIs, i.e., the left occipital ROIs was coupled with the left inferior parietal, the left and right inferior and middle frontal and the ACC ROIs. There was also intra-frontal coupling between the left inferior and the right middle frontal ROI. Again, this latter effect should be interpreted with caution, since the *three-feature* condition was higher than expected (cf. Figure 5).

For the analysis of spectral power, with the exception of the alpha and beta bands, no significant effects of vWM load or the number of features were found. In the alpha and beta band, the found effects were not topographically specific and went in the opposite direction, that is, the non-construction condition displayed higher power. The effects of the number of features were, in contrast to the PLVs (see Figure 5), not parametrically increasing with 2 < 3 < 4 features. Therefore, we refrained from considering these results any further. The results of the amplitude analysis can be found in the Supporting Information.

3.1.5. DISCUSSION

The aim of the present study was to investigate how visual objects that have been constructed from object features through mental imagery are maintained in vWM and whether a mental representation of a visual object would be maintained differently in dependence of its origin. We hypothesized that the maintenance of an object that was mentally constructed from its features before vWM maintenance, compared to the maintenance of an object that was perceived as a whole, would be accompanied by a stronger inter-areal neuronal synchronization between the task-relevant fronto-parietal and visual regions known to support vWM maintenance.

To this end, we recorded EEG during a task in which the participants maintained visual information in vWM in two different conditions that only differed in how the vWM contents were *created*. Participants maintained objects in vWM that either had to be created out of single features or that were presented to them as complete objects. The complexity of the objects varied parametrically between two and four features. We estimated phase synchrony from source-localized EEG data during the vWM retention period when the participants maintained either completely presented objects in vWM or those that were created from single features.

Our results show that the maintenance of those objects in vWM that were created from single features were correlated with increased theta- and gamma-band synchronization compared to those which were memorized as a whole.

The behavioral results are in line with the expectations and validate the experimental design. They indicate that it took longer for the participants to respond to objects made up of single features in contrast to those made up from whole objects, showing that it is harder to access specific features of a maintained object when the object had been constructed in vWM from single features. This suggests that the construction of objects from single features perhaps requires increased cognitive control. This interpretation is also supported by the error rates, which also show an increase with the number of memorized features when objects had to be constructed from single features but not when objects were memorized as a whole.

In the EEG data, we observed that increased phase synchronization was associated with the maintenance of those objects that were constructed from individual object features. Increased synchronization was observed in the theta, alpha, and gamma frequency bands, with this effect being most extensive in the gamma frequency. Here, phase synchronization was observed between frontal and parietal-to-occipital cortical sources bilaterally while in theta synchronization was observed predominantly in the left hemisphere.

These findings suggest that synchronization in the theta and gamma frequency bands may be a neural mechanism underlying coordination and integration within the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012).

Interestingly, we found that across frequencies phase synchronization was positively correlated with vWM load independent from construction requirements. In the theta band the pattern of synchronization was similar for the vWM load and construction effect. This result suggests that keeping constructed objects in mind is associated with increased vWM load in comparison to keeping complete objects in mind, maybe reflecting general effects of increased attention. However, in the gamma band synchronization correlated with vWM load was not as extensive as it was for the main effect of construction, suggesting more processes being reflected by the latter. These data is supportive of the idea that gamma-band synchronization is specifically associated with the maintenance of constructed objects in vWM.

In addition to an increase in vWM load, maintaining constructed objects seems to require additional synchronization within the fronto-parietal network that is specific for construction, as suggested by the coupling pattern when maintaining four vs. two features in constructed objects (construction load). Interestingly, load-dependent synchronization was observed among fronto-parietal areas and did not include occipital ROIs in any of the three targeted frequency bands. This could be interpreted in a way that the fronto-parietal attention network is coping with the higher attentional demands involved in maintaining constructed images, but without increasing the communication with the occipital visual buffer in which the visual representations are assumed to be stored (Baddeley, 2003; Coull et al., 1996; Kosslyn, 2005).

Increased theta-band synchronization for increased vWM load and for maintaining constructed in comparison to non-constructed objects is in line with the findings of Sauseng et al. (2006) and Summerfield and Mangels (2005), who found increased theta coupling between these areas for increased executive control demands.

In addition, phase synchronization in the alpha band was observed between the ACC and parietal ROIs, which indicates that ACC may have a major role in the feature integration in vWM within the fronto-parietal network, as suggested by prior studies (see Munk et al., 2002; also discussed by Zimmer, 2008). Importantly, alpha-band amplitudes in ACC are positively correlated with activity in the fronto-parietal network as well as with detection of weak auditory stimuli (Sadaghiani, 2012) and alpha-band phase locking with the detection of somatosensory stimuli (Hirvonen and Palva, 2015), indicating a close relationship between control functions and the alpha-band activity in cingulate structures. Increased alpha-band synchronization was correlated positively with both vWM load and increasing construction demands, suggesting that it seems to reflect a general higher control demand for more complex stimuli, irrespective of whether they were constructed or not. As mentioned before, since the load effect in the construction condition was not parametrical, this specific result should be interpreted as preliminary and requires further experimental confirmation.

Synchronisation between fronto-parietal and occipital areas in the beta band has been found to be important for vWM retention (Fell and Axmacher, 2011; Hanslmayr and Staudigl, 2014; Palva et al., 2010). However, our findings suggest that this coupling does not seem to be generally load-dependent, but is restricted to construction load. For pure vWM load, only the stronger coupling with higher vWM load between the left inferior parietal and the left occipital cortex resembles the effects of beta-load-dependency found by Axmacher et al. (2008). In contrast, a strong synchronisation of fronto-parietal and occipital areas was found as an effect of mental construction. All in all, different from the theta and alpha bands, but similar to the gamma band, the fronto-parietal increase in coupling is selective for the effect of construction and does not reflect an effect of general vWM load. This finding suggests that the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012) coupled with occipital areas becomes increasingly activated when object parts have to be kept together in vWM in the beta band.

The widespread and strong fronto-parietal to occipital synchronization in the gamma band is in agreement with prior data showing that specifically gamma-band synchronization in animal LFP recordings is correlated with the integration of object features into perceptual objects (Singer, 1999). It is also consistent with the finding that gamma amplitudes in MEG are correlated with the objects features maintained in vWM and specifically pronounced for those objects that require the integration of object features (Honkanen et al., 2015; Tallon-Baudry et al., 1998).

Importantly, synchronization in the gamma band took place among frontal, parietal, and occipital cortices and hence might underlie the binding and controlling of the visual representation represented in the occipital cortex. The present results of gamma phase coupling being sensitive to construction load and being stronger for maintaining constructed in comparison to non-constructed objects suggest a functional role beyond maintaining perceived stimuli (Palva et al., 2010). Gamma seems to play a major role in maintaining visual representations by keeping object parts together, with this function becoming increasingly important when objects have to be constructed in vWM.

Maintaining constructed in comparison to non-constructed objects was associated with pronounced fronto-parietal-occipital couplings, suggesting a specific role for keeping object features together. However, fronto-parietal-occipital couplings were also found for the vWM–load effect (for non-constructed objects). Thus, they probably reflect generally higher vWM demands required for maintaining constructed objects. Specifically, the vWM-load-sensitive fronto-parietal to occipital connections found in the alpha and theta bands can be interpreted as a load-dependent increase of communication between the fronto-parietal attention network and the visual buffer. Accordingly, these couplings probably reflect a generally higher mental effort required in the construction condition, without being specifically responsible for the process of maintaining constructed objects that have been integrated by means of mental imagery.

Importantly, this interpretation that holds for theta and alpha cannot be readily applied to gamma. Here, a different picture emerged, i.e., a double dissociation between a construction-load effect and general vWM load could be observed. Specifically, fronto-parietal coupling was only sensitive to mental construction load, whereas fronto-occipital couplings were sensitive to vWM load. Thus, with respect to gamma, fronto-parietal couplings were more purely related to the maintenance of mentally constructed objects.

3.1.5.1. CONCLUSION

In general, our results suggest a role of fronto-parietal theta and gamma-band synchronization in the maintenance of constructed objects in vWM. This pattern of fronto-parietal theta and gamma band synchronization could reflect the process of a top-down updating of the constructed mental image during its maintenance, especially transmitted in the gamma frequency. Accordingly, the findings support current theories of mental imagery, assuming that the manipulation of mental images is governed by an attentional control process mediated by the fronto-parietal attentional network (Corbetta and Shulman, 2002; Ganis and Schendan, 2011). The reported pronounced coupling of the fronto-parietal network with the occipital ROIs support the claim that the proposed attentional control process acts in a top-down manner by maintaining dynamic functional links to object representations in a visual buffer primarily located in more occipital areas (e.g. Albers et al., 2013; Cichy et al., 2012; for reviews, see Kosslyn et al., 2006; Zimmer, 2008). However, importantly, such a process seems to be increasingly involved not only when constructed objects have to be maintained in vWM, but also under increased vWM load in general. Under increased construction load we found increased synchrony within the fronto-parietal network without a stronger communication with the visual buffer. We conclude from this finding that the maintenance of constructed objects in vWM requires additional executive processes to keep the object parts together as a coherent representation. The task of maintaining a constructed representation is apparently functionally different from maintaining it in the visual buffer.

3.1.6. ACKNOWLEDGMENTS

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3.1.7. REFERENCES

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3.1.8. SUPPORTING INFORMATION

(for manuscript: “Neural correlates of maintaining generated images in visual working memory” by J. A. Ewerdwalbesloh, S. Palva, F. Rösler, and P. H. Khader)

3.1.8.1. GENERAL POWER AND EOG EFFECTS

3.1.8.1.1. GENERAL POWER EFFECTS

In addition to phase coupling, we also analyzed possible effects of spectral power ($|W|^2$) of the wavelet coefficients W. This was done by averaging the power values of the relevant time interval (i.e., the second of interest) and comparing conditions for each ROI and frequency band separately by means of a 2*3 ANOVA (construction * number of features). These ANOVAs revealed effects in the alpha and beta, but not in the theta and gamma bands.

Starting with alpha, an effect of higher power for non-construction (main effect of the number of features) was found in the ACC, the right superior frontal gyrus and the right middle frontal gyrus (all $p < .01$). However, as these effects are in the opposite direction than expected, they cannot have contributed to the effect of stronger phase locking in the construction condition.

Since the separate analysis of ROIs all revealed (1) a significant main effect of the number of features (all $p < .003$), (2) a significant interaction in all but one cases ($p < .029$), and (3) looked highly similar in the descriptive comparison, we averaged the power values across ROIs (Figure S1, left panel). Irrespective of the particular ROI, a reversed-U-shaped effect of the number of features was found in the alpha band, which was more pronounced in the construction condition. Since the found effect of the number of features on the power is not parametrical or U-shaped, as the effect of phase coupling, it cannot have contributed to the latter.

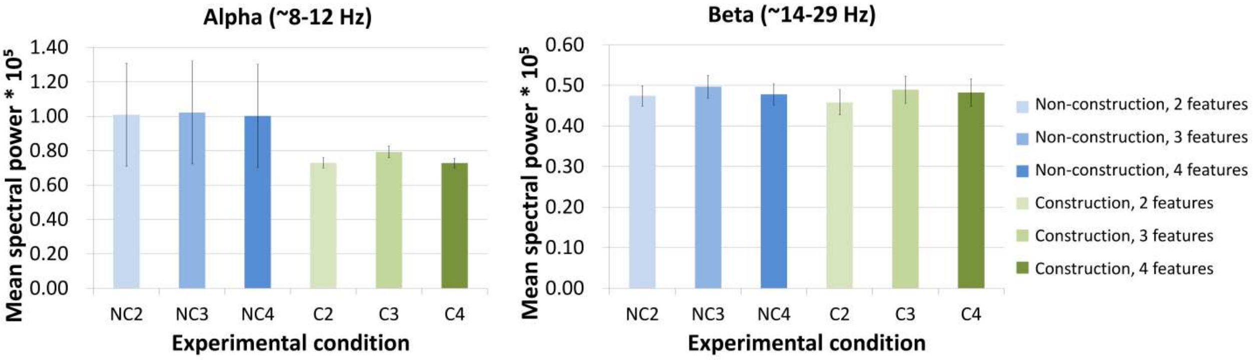

Figure S1. Mean spectral power of the alpha and beta band for the six experimental conditions. Error bars indicate 95% confidence intervals.

For beta, an effect of higher power for non-construction in the left superior frontal gyrus, the left and right superior parietal cortex, and the left inferior parietal cortex was found (all $p < .034$). Again, these power effects were in the direction opposite than expected and therefore cannot have contributed to the effect of stronger phase locking in the construction condition.

The ROI-wise analysis for beta revealed main effects of the number of features (all $p < .001$) and significant interactions with the construction factor (all $p < .045$) in all ROIs except the left and right inferior and left middle frontal gyri. Since all significant ROIs also looked highly similar in the descriptive comparison, we computed the average across all ROIs (Figure S1, right panel). Irrespective of the particular ROI, a reversed-U-shaped effect of the number of features was found in the beta band. Again, since this effect was not parametrical, as is the case for phase coupling, it cannot have contributed to the latter.

3.1.8.1.2. EOG EFFECTS

We also checked the VEOG and HEOG channels with respect to their power in the different conditions to exclude any effects of vertical and horizontal eye movements on our data. For that we conducted ANOVAs with the factors task (2) x load (3) for the power of the VEOG and HEOG channels in the four frequency bands.

For the high frequency bands, beta and gamma, see figure S3, we found only one task-related effect, i.e., a main effect of construction vs. non-construction for the horizontal EOG channel in the beta band ($p < .05$). However, this effect was opposite to the reported phase coupling effect, with stronger power for the non-construction condition, and therefore cannot have contributed to the construction effect we observed. All other comparisons were not significant, so we conclude that there was no influence of micro saccades on our data. For the low frequency bands, theta and alpha, see figure S4, the analysis revealed significant differences in the theta and alpha bands for task and load, for vertical and horizontal EOG channels (all $p < .001$).

However, as with the effect for beta above, the task effects were stronger for the non-construction condition and therefore cannot have contributed to the construction effect, because they went in the opposite direction. The increasing power for higher load might, on the other hand, have contributed to our observed effect in the non-construction condition in these frequencies.

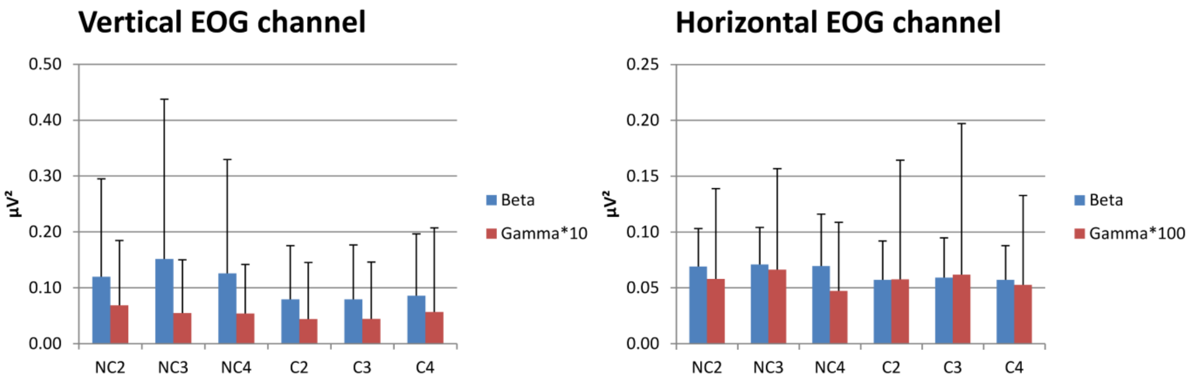

Figure S3: Mean power of vertical and horizontal EOG channels in the beta and gamma band for the six experimental conditions (NC = non-construction condition, C = construction condition, numbers indicating the number of features). Gamma power is adjusted to fit in the graph with beta, see legend. Error bars indicate standard deviation.

The observed working memory load effect has, however, the condition with 3 features arranged linearly between 2 and 4 features, whereas the power of the EOG channels increases markedly from 2 and 3 to 4 features. However, to be on the safe side, we refrain from interpreting couplings between anterior ROIs related to the number of features, because we cannot fully exclude that they are due to eye-modulated activity.

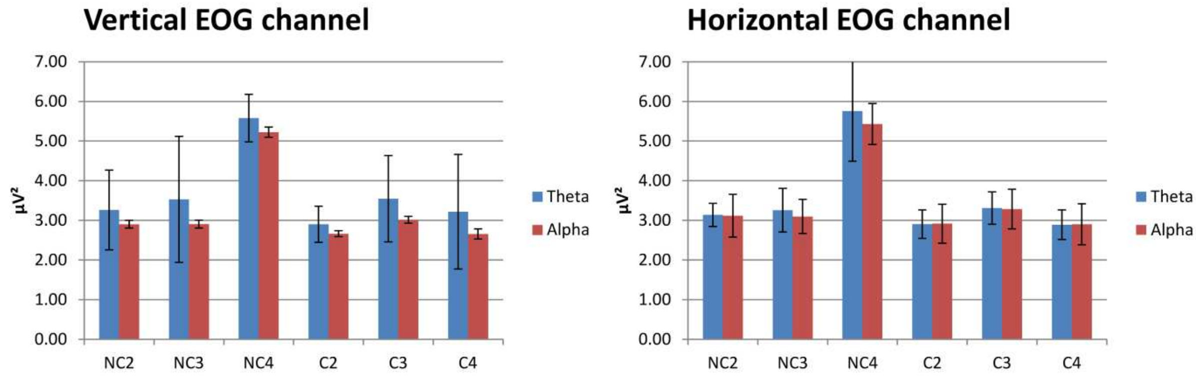

Figure S4: Mean power of vertical and horizontal EOG channels in the theta and alpha band for the six experimental conditions (NC = non-construction condition, C = construction condition, numbers indicating the number of features). Error bars indicate standard deviation.

3.1.8.2. RELATIVE CHANGES IN PHASE LOCKING

In addition to the statistically different phase locking between ROIs depicted in the manuscript, we also had a look at the relative average change in phase coupling in different ranges of percentages (0.001 to 20%, > 20 %, and > 50 %), see figure S2. However, we think that a systematic difference across participants, even if very small, tells us more about its functional significance than its absolute size.

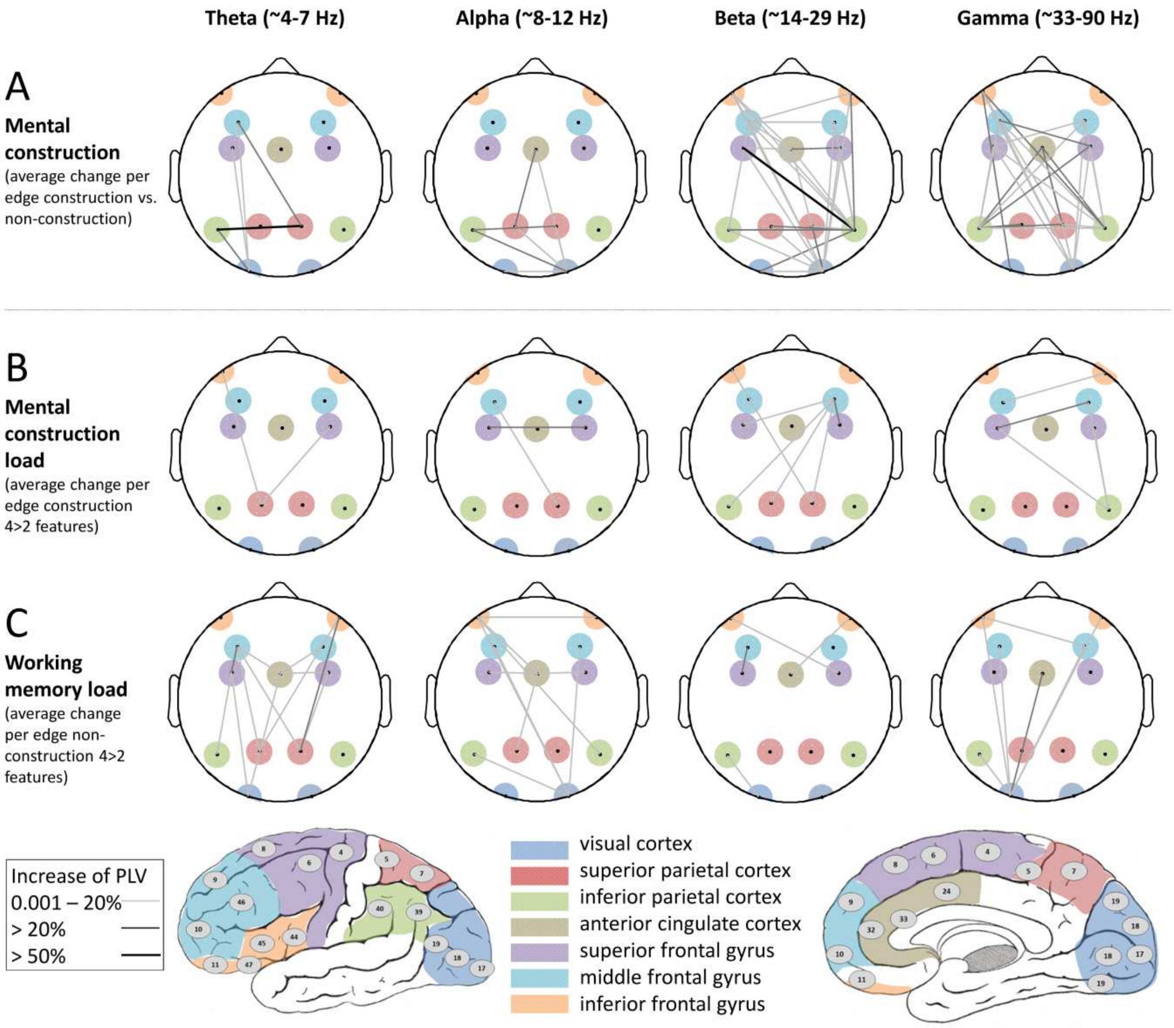

Figure S2: (A) Average change of phase couplings for significantly ($p < .05$) stronger phase couplings between ROIs (as computed from LORETA source distributions; see Methods) in the mental construction condition in comparison to the non-construction condition, irrespective of the number of features. (B) Average change of phase couplings for significantly stronger couplings under increased construction load (4 > 2 features) for constructed objects and (C) under increased WM load (4 > 2 features) for objects presented as a whole without construction requirements. The thickness of the lines corresponds to the percentage of average change, see legend. LORETA ROIs are color-coded, numbers indicate Brodmann areas.

3.2. PHASE COUPLING DURING THE MAINTENANCE OF OBJECTS IN VISUAL WORKING MEMORY CONTRIBUTES TO LONG-TERM MEMORY FORMATION

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Short title: EEG-phase coupling promotes memory encoding

Keywords: Mental imagery, visual working memory, phase coupling, theta, alpha, beta, gamma, EEG, PLV, fronto-parietal network, subsequent memory

3.2.1. ABSTRACT

There is increasing evidence that neural activity during the maintenance of objects in visual working memory (vWM) can promote successful long-term-memory (LTM) encoding. However, the exact neural mechanism mediating this consolidating effect is still unclear. Here, we show that fronto-parietal phase coupling of neural oscillations during vWM maintenance predicts successful remembering. To determine whether this effect would be modulated by the elaborateness of the stimulus during maintenance, we varied the coupling demands such that participants had to maintain images they either had to assemble from single features and keep together in vWM, or that they had perceived as complete objects. Increased coupling between frontal and parietal-to-occipital cortical sources was generally found for the maintenance of later remembered in comparison to non-remembered objects in the theta, alpha, beta, and gamma frequency bands. For theta and gamma, this pattern was found for both constructed and non-constructed objects, thus probably reflecting a general process of successful encoding. In contrast, for alpha, occipital-to-parietal coupling was found for constructed objects, whereas intra-frontal coupling was found for non-constructed objects, suggesting specific functions of alpha phase coupling for successful encoding depending on the specific level of processing during vWM maintenance. For beta, intra-frontal, intra-occipital; and fronto-parietal coupling could be observed for constructed objects, whereas for non-constructed objects, frontal to occipito-parietal coupling as well as intraparietal coupling was observed, suggesting levels-of-elaboration-specific mechanisms in this frequency band as well. Overall, the results suggest that phase coupling of neural oscillations could be a neural implementation of a control process that serves to promote LTM encoding during maintenance in vWM.

3.2.2. INTRODUCTION

A growing number of studies convincingly show that neural activity measured during the maintenance of objects in visual working memory (vWM) can promote successful long-term-memory (LTM) encoding (Blumenfeld and Ranganath, 2006; Davachi, Maril, & Wagner, 2001; Khader, Ranganath, Seemüller, & Rösler, 2007; Ranganath, Cohen, & Brozinsky, 2005; Schon, Hasselmo, LoPresti, Tricarico, & Stern, 2004), an idea that already dates back to Donald Hebb, proposing that “reverberating activity” in material-specific cortical networks serves to strengthen LTM traces in those networks (Hebb, 1949). However, the exact neural mechanism mediating this consolidating effect is still unclear. Here, we propose, based on the important role of neural oscillations for successful LTM encoding and on the results of a previous study (Ewerdwalbesloh et al., under revision), that phase coupling of neural oscillations might mediate the transition from vWM to LTM.

First, there is increasing evidence that subsequent memory is driven by neuronal synchronization (e.g. Axmacher, Mormann, Fernández, Elger, & Fell, 2006; Gruber, Tsivilis, Montaldi, & Müller, 2004; Hsieh and Ranganath, 2014; Summerfield and Mangels, 2005).

Second, these effects can also be seen during WM maintenance (Backus, Schoffelen, Szebényi, Hanslmayr, & Doeller, 2016; Khader et al., 2010; Meeuwissen, Takashima, Fernández, & Jensen, 2011).

Third, there is abundant evidence that the phase coupling of neural oscillations reflect the communication between neural networks to manage successful task performance (Fell and Axmacher, 2011; Klimesch et al., 2010; Lachaux et al., 1999; Palva and Palva, 2012; for a review, see Sauseng and Klimesch, 2008). Phase coupling is most likely the mechanism to coordinate anatomically and functionally distinct neuronal activity, resulting in the binding of distributed cognitive functions to a coherent mental state. It is supposed to be a task-dependent mechanism that links cognitive processes on a larger scale.

Where in the brain should increases in phase coupling that reflect the successful LTM encoding of information maintained in WM be found? We think that one promising candidate could be the fronto-parietal network of attentional control (Corbetta and Shulman, 2002). The fronto-parietal network is known to be correlated with executive functions like attention (Corbetta and Shulman, 2002; Sadaghiani et al., 2012; Salazar et al., 2012). Axmacher, Schmitz, Wagner, Elger, & Fell (2008) argue that a network of prefrontal, temporal and parietal areas serves in maintaining representations in vWM by applying attentional mechanisms like enhancing relevant and suppressing irrelevant sensory input.

In a previous study (Ewerdwalbesloh et al., under revision), we could show that fronto-parietal phase coupling reflects the application of cognitive control on objects held in vWM. The more attentional processes were needed to maintain an object, the stronger the neuronal coupling between frontal and parietal areas was. We concluded, that fronto-parietal phase coupling might serve the purpose of maintaining coherent object representations in vWM under increased attentional demands.

To further qualify the effect of phase coupling for LTM encoding, we manipulated two levels of processing (Craik and Lockhart, 1972) during vWM maintenance, as this factor has been shown to strongly affect LTM encoding (see Craik, 2002, for a review). Accordingly, we varied the level of processing of the information maintained in vWM. To determine whether this effect would be modulated by the level of processing during maintenance, we varied the cognitive demands during maintenance such that participants had to maintain images they either had to assemble from single features and keep together in vWM, or that they had perceived as complete objects. In the *construction condition*, participants did not see the complete objects, but only distinct parts which they had to combine before they had to maintain the objects a couple of seconds, whereas in the *non-construction condition*, they were presented with complete objects. Importantly, participants in both conditions maintained the same objects, but with different attentional requirements. Whereas the maintenance in the *non-construction condition* supposedly was relatively easy, maintenance in the *construction condition* required more cognitive control. We considered the construction task to be the more elaborate one, because here participants not only maintained a perceived object but had to mentally combine a new object out of single parts and maintain it afterwards, thereby holding the different features together. We showed in our previous study (Ewerdwalbesloh et al., under revision), that these two conditions indeed differ on the neuronal level. We found that the maintenance of a mentally constructed in comparison with a non-constructed visual object is associated with increased fronto-parietal EEG coupling in all frequency bands, most extensively in the beta and gamma frequency bands. These increased coupling demands might not only be necessary to keep the object parts together in vWM, but might also lead to a better encoding into LTM.

To conclude: The aim of the present study is to find out whether fronto-parietal phase coupling of neural oscillations during vWM maintenance predicts successful remembering and if such an oscillatory coupling, if found, differs in dependence of the elaborateness of the maintained visual representation.

3.2.3. MATERIALS AND METHODS

3.2.3.1. PARTICIPANTS

21 students (18 female) of the LMU Munich, aged 19-29 years (mean age: 23.19) participated. All participants except one were right-handed by self-report, native speakers of German, and had normal or corrected-to-normal vision. They gave informed consent to the procedure, were naïve with regard to the aims of the study, and took part either for course credit or payment. One participant had to be excluded, because the EEG recording was contaminated with heart artifacts; four participants had to be excluded because after segmentation and artifact correction less than 10 segments were left for analysis in at least one condition. This problem occurred because we were interested in a comparison between later remembered and forgotten stimuli and these participants made too few mistakes in the memory test. The remaining 16 participants (15 female) were aged 19-31 years (mean age: 23.06).

3.2.3.2. MATERIAL

Participants had to maintain in vWM schematic drawings of beetles (see Figure 1 for an example). We varied the maintenance process (*construction* vs. *non-construction*) to assess the effect of different processing demands during vWM maintenance on later retrieval. In the *construction* condition, participants had to mentally combine several presented features and maintain them as one single object, whereas in the *non-construction* condition, participants had to maintain an object that had been presented to them before.

Every beetle had a body shape out of four possible body shapes and either two or three additional features such as a color out of four, a pattern out of four, or a leg shape out of four (see Figure 1 for all possible features). That means, our original design included a parametrical variation of the number of features between three and four features. However, because too few trials survived the artifact correction, we decided to abandon that variation and did not analyze the data separately for the number of features. A fixed subset of 192 out of all possible combinations was created with equally distributed feature combinations. In the three features subset, besides the beetles´ body there were additionally two of the three possible features, the category of the features varying each time. This guaranteed that all feature combinations were equally likely to occur. The beetles were randomly chosen out of that predefined subset for each participant.

For the memory test, 96 additional stimuli with balanced feature combinations were created. During the memory test, already presented stimuli and additional stimuli were presented randomly in the proportion 2:1.

In the *construction* condition the single features were shown randomly arranged within individual white boxes on the top, left, and right sides of another white box in the middle of the screen that always contained a beetle's body (see Figure 2). In the condition with three features, one white box was replaced by a gray box (RGB = 150/-150/-150) with a slightly darker frame. In the *non-construction* condition, each beetle was presented as one single object within a white box in the center of the screen. All boxes had the same size of 6.8 cm (height) x 5.6 cm (width). All stimuli were presented on a gray background (RGB = 150/-150/-150).

3.2.3.3. PROCEDURE

Stimuli were presented on a 17” standard CRT monitor with a refresh rate of 75 Hz. During the experiment, participants sat in a dimly lit room at a distance of ca. 100 cm in front of the screen, and gave their responses by means of a standard computer keyboard. Participants were shown a table of all possible features (upper part of Figure 1) at the beginning of the instruction.

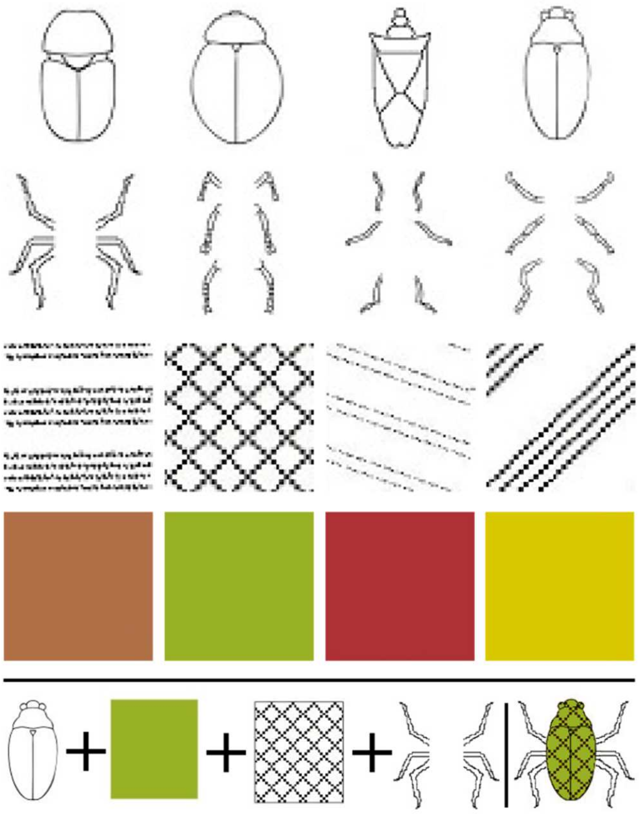

Figure 1. Possible features and an example of how they were combined. In the *construction* condition, single features were shown, whereas in the *non-construction* condition, complete objects were shown.

The main task in the *construction* condition was to memorize pictures of beetles that first had to be mentally constructed from single beetle features. In the *non-construction* condition, these pictures of beetles were presented without the necessity of constructing them. Participants were instructed to visualize the image of the beetle in the *construction* condition in the white box containing the beetle’s body shape in the middle of the screen. After 7000 ms a visual mask was presented for 300 ms, covering all relevant screen positions at which stimuli could have been presented to prevent iconic memory traces. Participants now had to maintain their mental image for 3000-5000 ms (jittered in steps of 400 ms), until a comparison beetle appeared, upon which participants had to give a match/non-match response. Jittering was installed to avoid expectancy effects. The comparison beetle was either identical to the memorized one (which was the case in 50 % of the trials) or differed in one randomly selected feature. Participants had only 1500 ms time to respond “same” or “different” by pressing either “Alt” or “AltGr” (counterbalanced across participants) with their left or right index finger to indicate whether the presented beetle corresponded to their mental image or not. This short response window was chosen to urge participants to rely on the visual image they had hold active, and not on verbal strategies. The use of a visual comparison strategy was in general confirmed by post-experimental reports of the participants.

In addition to the short time limit for the comparison, we implemented a secondary task surrounding the primary task of constructing, maintaining, and comparing beetles to further suppress verbalization of the constructed visual images. Before the to-be-memorized beetle was presented, participants had to read and keep in mind four words consisting of four or five letters that were presented for 2500 ms, which were also tested for at the end of the trial. Specifically, after the match/non-match response to the comparison beetle, single letters with space-holders according to the to-be-maintained words were presented (see Figure 2). In 50 % of the trials one of the four letters differed from the correct letters in the to-be-maintained words, and participants had 5000 ms time to respond same/different (again by pressing “Alt” or

“AltGr”, counterbalanced across participants). With this second answer the trial ended. In the inter-trial interval, a fixation cross was presented for 2200 to 4200 ms (jittered in steps of 400 ms).

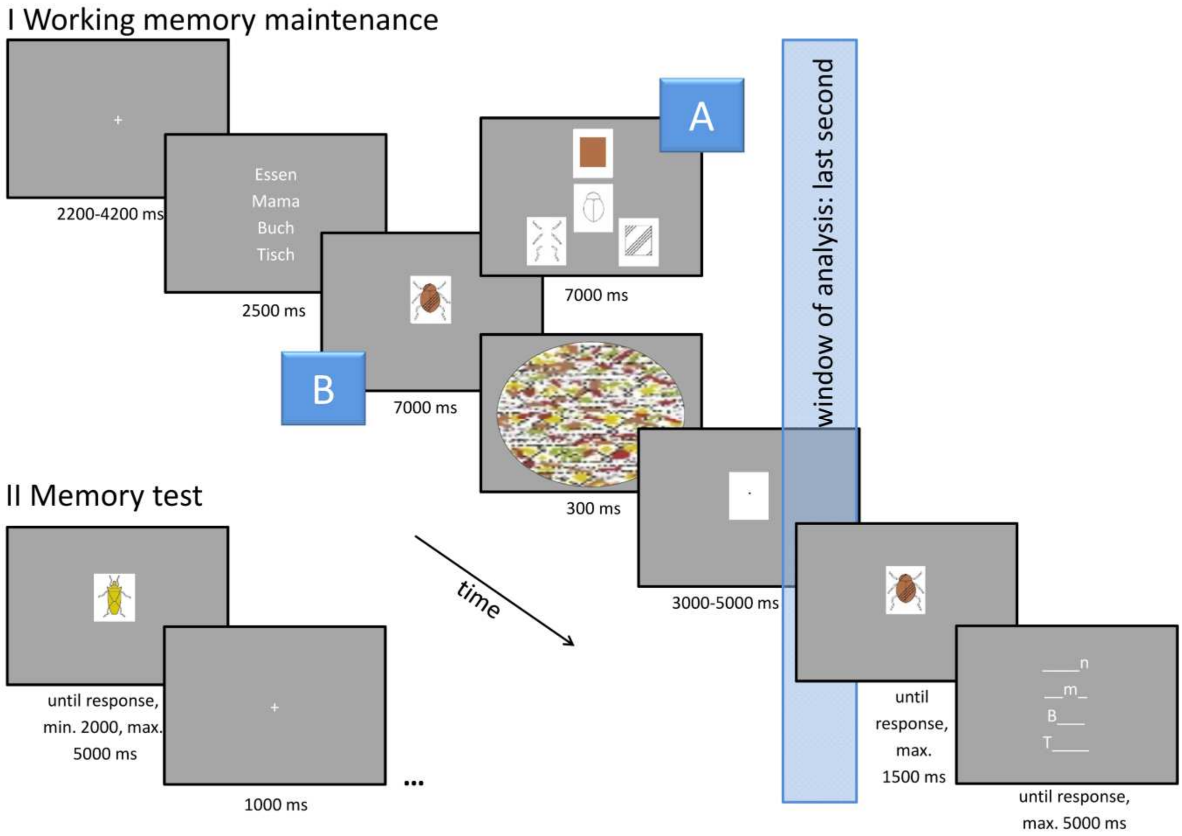

Figure 2. Stimulus timing and layout of the experiment. *I* marks one trial of the maintenance phase. *A* marks the mental *construction* condition, *B* the condition *without mental construction*. The proper mental imagery task was framed by a word-maintenance task to avoid verbalization of the to-be-imagined objects (English translation of shown word examples: “meal”, “mother”, “book”, “table”). There was always a 50 % chance of seeing the same or a different picture or word. *II* marks an example trial of the subsequent retrieval phase.

After each block of six trials a memory test was administered. Participants had to indicate whether they had seen the beetles before by answering “sure old”, “rather old”, “rather new” or “sure new” by pressing “left Ctrl”, “Alt”, “AltGr” or “right Ctrl” (again counterbalanced across participants) within 2000 and 5000 ms after stimulus onset.

Before the EEG recording started, participants completed a training phase where each of both maintenance tasks (*construction* and *non-construction*) was practiced for ten trials. Feedback (correct, incorrect) was provided for 800 ms after each response. If the response window of 1500 ms passed without a button press, the feedback “too late!” was provided. After each of the two tasks a feedback was given about how many of the answers for both the comparison of the beetles and the words had been correct.

Each block of the main experiment with EEG recorded, during which no feedback was given any more, comprised 6 trials, followed by the subsequent memory task. The whole experiment comprised 32 blocks. After each block a feedback similar to the general feedback in the training phase was given. Every second block the experimental condition changed between construction and non-construction, which was signaled to the participants through an instruction on the screen.

3.2.3.4. EEG RECORDING AND ANALYSIS

All programs, EEG caps, and amplifiers were provided by Brain Products GmbH, Gilching, Germany. BrainVision Recorder® was used for EEG recording. EEG was recorded with two 32-channel amplifiers in DC mode from 61 scalp electrodes, an inferior ocular channel, and two electrodes at both earlobes, of which one served as online reference (alternating across participants). The ground electrode was placed alternating on either the left or the right mastoid. We used Ag/AgCl ring electrodes arranged according to the extended 10–20-system (Jasper, 1958). Average impedance was kept below 10 kΩ. Sampling rate was 500 Hz. EEG was re-referenced offline to the average of all scalp electrodes. The vertical electrooculogram was calculated by re-referencing the inferior ocular electrode to Fp1.

The initial processing of the EEG data was done with BrainVision Analyzer® 2.0.3. First, we did a DC correction and calculated the vertical and horizontal EOG for later artifact rejection. EEG segments with a length of 1000 ms, beginning 1000 ms before the onset of the comparison beetle, were extracted to have a measure of the electrical activity just before the comparison. During this time both groups should maintain essentially the same objects in vWM, but with the different conditions putatively requiring different amounts and patterns of neural coupling. The maintained mental image had to be as detailed as possible to enable the participant to answer correctly. According to the experimental factors of *mental construction* (yes/no) and *later memory* (yes/no) four different groups of segments resulted. Segments with artifacts like eye blinks, other eye movements, muscle potentials, and other artifacts were excluded by means of a semi-automatic filtering procedure (maximum allowed amplitude difference between adjacent voltage values = 40 µV/ms; maximum allowed difference in any interval of 1000 ms length = 150 µV; minimum allowed difference in any interval of 200 ms length = .5 µV). The average number of remaining artifact-free segments was 26.38 in the "*construction* (*C*)/*remembered* (*r*)" condition, 23.31 for “*C/not remembered* (*nr*)”, 38.88 for “*non-construction* (*NC*)/*r*” and 19.69 for "*NC*/*nr*". “Sure” and “Rather” responses had to be merged due to otherwise insufficient numbers of trials for further analysis. All segments of trials with errors in one or both of the two matching tasks were excluded from the analysis.

In a next step, LORETA analysis (Pascual-Marqui et al., 1994) was applied to the artifact-free segments to reduce the effects of volume conduction on the EEG data and the number of later statistical comparisons. Specifically, source components from the three spatial axes were extracted and averaged to form a measure of the electrical activity in specific regions of interest (ROIs) defined from anatomical templates as implemented in the BrainVisionAnalyzer software. The following ROIs were defined (cf. Figure 3): Anterior cingulate cortex (ACC; Brodmann Areas (BA) 24, 32, 33), visual cortex (BA 17, 18, 19), superior parietal cortex (BA 5, 7), inferior parietal cortex (BA 39, 40), superior frontal gyrus (BA 4, 6, 8), middle frontal gyrus (BA 10, 46, 9), inferior frontal gyrus (BA 11, 47, 45, 44). All ROIs were defined separately for the two hemispheres, except the ACC, which was defined as one single ROI with the left and right hemispheric BA included. We chose 13 ROIs to account for the relatively low spatial resolution of scalp EEG data due to volume conduction on the one hand (see, e.g., Ferree et al., 2001; Srinivasan et al., 1998), while minimizing the loss of spatial information on the other hand.

The resulting ROI-averaged data were then further analyzed with continuous 5-cycle complex Morlet Transformation and Gabor Normalization. Frequencies between 3 and 90 Hz in 25 logarithmic steps were chosen. The complex values of these 25 frequency layers were extracted.

Further analysis was done with MatLab R2007b (The MathWorks Inc., Natick, MA). The data points over 200 ms on each side of every segment were removed to reduce border artifacts from the wavelet analysis. To keep the number of trials constant within participants, the smallest number of trials that occurred in one of the four conditions was determined per participant. That was done to avoid confounding effects of unequal sample sizes on the statistics (Luck, 2010). Subsequently, all following calculations were iterated 100 times in a bootstrap-like approach with randomly chosen subsets of trials corresponding to the smallest size, and with the results averaged across the iterations.

Finally, the Phase-Locking Value according to Lachaux, Rodriguez, Martinerie & Varela (1999) was calculated for each pair of ROIs (78), participant (16), frequency layer (25), and experimental condition (4). Frequency layers were averaged according to the different frequency bands: theta (3.98 - 7.02 Hz), alpha (8.09 - 12.38 Hz), beta (14.26 - 28.97 Hz) and gamma (33.38 - 90.00 Hz). To compare the conditions, one-tailed *t* tests were conducted for every pair of ROIs, separately for each frequency band. We decided to plot the coupling at different levels of significance ("significance probability mapping"; see, e.g., Duffy et al., 1981; Hassainia et al., 1994), allowing for an evaluation of how the overall pattern becomes narrowed and more focused with a stricter threshold (line thickness in Figure 3 indicates the significance level; see figure legend). Please also note that important restrictions were made in the analysis to suppress spurious results: First, except for the condition with the smallest number of trials per participant, only phase coupling will be reported that is still visible in an average of 100 permutations (as stated previously). Second, only phase coupling will be reported that differentiated between the experimental conditions in a pre-specified direction, i.e., more coupling for later remembered stimuli. Third, we interpreted only relatively coarse topographical patterns of coupling, such as "coupling between frontal and parietal ROIs" but never individual connections between ROIs.

3.2.4. RESULTS

3.2.4.1. BEHAVIORAL DATA

To compare the *construction* with the *non-construction* condition in the retrieval task, error rates for the LTM retrieval were analyzed with paired sample *t*-tests. Trials with incorrect responses in the word-comparison task or the beetle maintenance task were excluded from the analysis of the error rates. The index *d’* was calculated as well to indicate differences in sensitivity of recognizing beetles between the conditions *construction* and *non-construction*. For the retrieval task, means, *t* values, and *p* values are reported (see Table 1). Participants remembered more non-constructed images ($t = 7.85$, $p < .001$). However, a corresponding analysis of *d’* revealed only a marginally significant difference between constructed and non-constructed objects ($t = 1{,}86$, $p = .083$).[1]

To compare the *construction* with the *non-construction* condition in the maintenance task, response times (RT) and error rates were analyzed with paired sample *t*-tests. Means, *t* values, and *p* values are reported (see Table 1). Trials with incorrect responses in the word-comparison task were excluded from the analysis of the error rates of the beetle maintenance

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[1] With respect to the behavioral data, we expected a better later recognition of the constructed objects in a subsequent memory task. Contrary to our expectations the data show that participants remembered non-constructed images better. In this visual task a complete presentation is beneficial for later recognition. This result can be better interpreted in the framework of transfer appropriate processing (Lockhart, 2002; Morris et al., 1977) than in Craik and Lockharts theory of levels of processing (1972). The memory test was transfer appropriate to the non-construction condition, because in both cases a whole object was presented. In the construction condition however, the encoding and decoding mismatched. The contextual overlap of encoding and retrieval plays a crucial role for successful memory function (Hanslmayr and Staudigl, 2014).

task and vice versa for the word-maintenance task. For the RT analyses of the maintenance tasks, trials with incorrect responses in either the one or the other comparison task were excluded. All responses faster than 300 ms and slower than 2.5 standard deviation above the mean were excluded. The behavioral data were analyzed using SPSS (version 21; IBM, Armonk, NY, USA).

As can be seen in Table 1, participants took longer (t = 8.49, p < .001) and committed more errors (t = 5.11, p < .001) when matching constructed compared to non-constructed objects in the maintenance task. Finally, an analysis of the secondary task (maintaining words) revealed no significant differences between the experimental conditions for both RTs and error rates.

Table 1: Error rates, response times and statistical comparison between the construction and non-construction conditions of the maintenance and the retrieval task.

	I Maintenance					
	Error rates			Response times		
	Mean	*t* value	*p* value	Mean	*t* value	*p* value
construction	19.84			946.30		
non-construction	9.45			850.94		
construction vs. non-construction		5.11	< .001		8.49	< .001

	II Retrieval					
	Error rates			d'		
	Mean	*t* value	*p* value	Mean	*t* value	*p* value
construction	50.27			0.66		
non-construction	33.34			0.92		
construction vs. non-construction		-7.85	< .001		-1.86	.083

3.2.4.2. EEG DATA

Figure 3 gives an overview of the subsequent-memory effects of phase coupling. Panel A shows the general effect of correct later retrieval irrespective of whether the objects had been constructed or not prior to their maintenance. As can be seen, increased inter-areal synchrony for successfully remembered compared to later forgotten objects was found between frontal and parietal-to-occipital sources for all frequency bands, but especially for theta and gamma. In the theta frequency, this was accompanied by strong coupling between left and right prefrontal sources. Panels B and C show the subsequent-memory effect separately for constructed (B) and non-constructed (C) objects. For theta, a lateralization occurred with predominately left frontal to bilateral posterior coupling for constructed and predominately right frontal to bilateral posterior coupling for non-constructed objects. In the alpha band, another topographical dissociation was found with fronto-central to parietal and parieto-occipital coupling for the maintenance of constructed objects and intra-frontal coupling for the maintenance of non-constructed objects. For gamma, most of the neural synchrony that we see in the general subsequent-memory effect seems to be due to the *construction* condition, i.e., stronger (predominately right) prefrontal to parieto-occipital coupling was found for later remembered objects that had been constructed from their constituting elements. We will describe the found effects in more detail separately for each frequency band in the following sections.

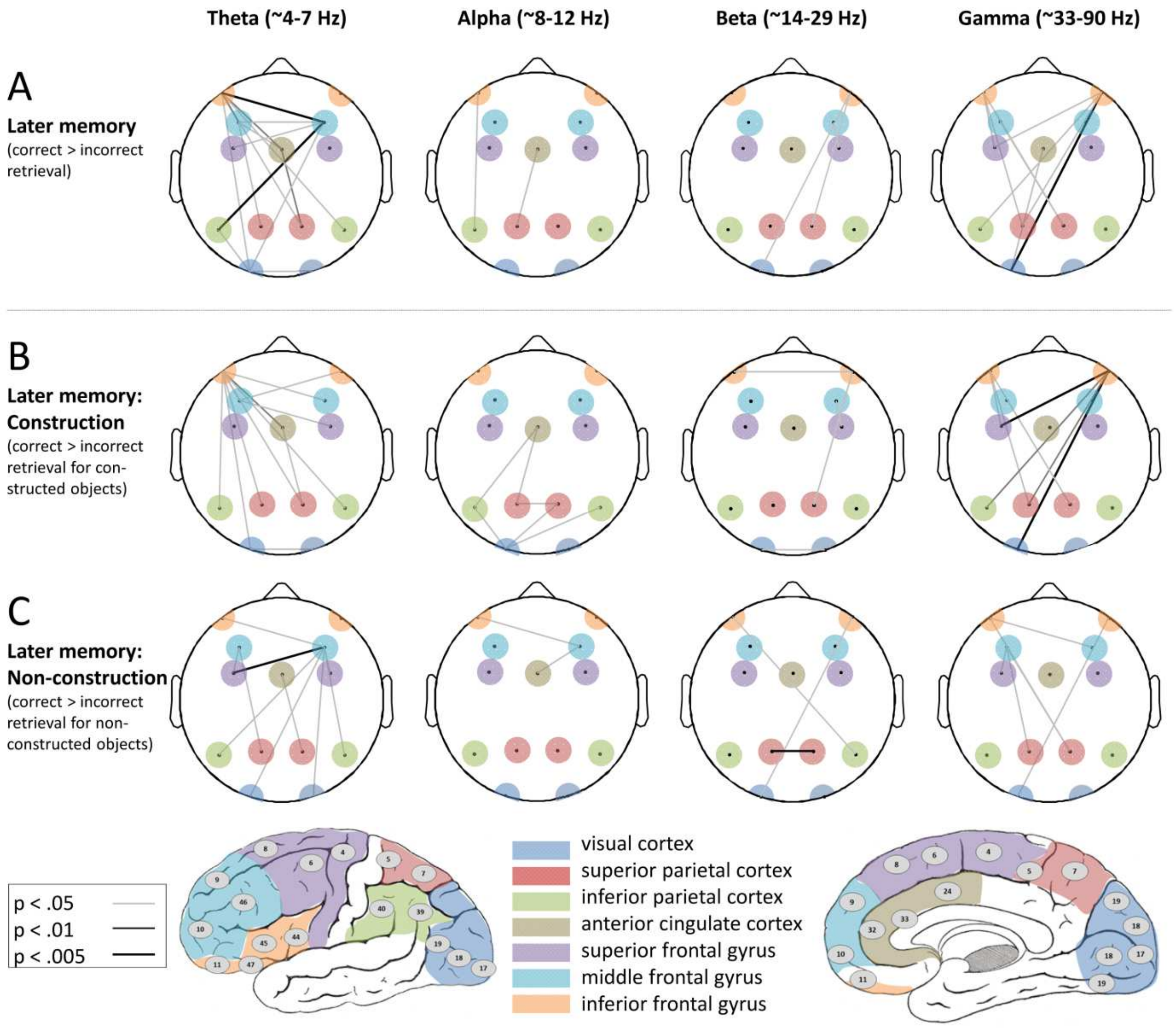

Figure 3. (A) Significantly stronger phase coupling between ROIs (as computed from LORETA source distributions; see Methods) for correct in comparison to incorrect retrieval, irrespective of the WM condition. (B) Significantly stronger coupling for correct in comparison to incorrect retrieval in the *construction* condition and (C) in the *non-construction* condition. Line thickness indicates the significance level (*p* value), see legend. LORETA ROIs are color-coded, numbers indicate Brodmann areas.

Theta. In the theta band, generally stronger coupling for later remembered in comparison to forgotten objects (Figure 3A) mainly comprised fronto-posterior pairs of ROIs, including the left inferior, middle, and superior frontal ROIs, the right middle frontal ROI, and the anterior cingulate cortex (ACC) being coupled with the superior and inferior parietal ROIs and the right occipital ROI. In addition, coupling was found between the left and right occipital ROIs.

Within the *construction* condition (Figure 3B), stronger phase coupling for later remembered compared to forgotten objects was mainly found between the left inferior frontal ROI and the left middle frontal, all parietal, the left occipital, the ACC and the right middle frontal ROIs. The left middle frontal ROI was also stronger synchronized with the right inferior and superior frontal ROIs. We also found stronger coupling between the ACC and the right superior parietal ROIs and between both occipital ROIs.

Within the *non-construction* condition (Figure 3C), stronger phase coupling for later remembered compared to forgotten objects was mainly found between the right middle frontal ROI and the left inferior and superior frontal, both inferior parietal and both occipital ROIs. The left middle frontal ROI was stronger coupled with the left superior frontal and the left superior parietal ROIs. In addition, the ACC ROI was stronger coupled with the right superior parietal ROI.

Alpha. In the alpha band, we observed stronger coupling for later remembered objects between the left inferior frontal and left inferior parietal ROIs, as well as between the ACC and the left superior parietal ROI. The corresponding effect for constructed objects was found between the ACC ROI and both left parietal ROIs as well as between the left occipital ROI and the left inferior parietal and both right parietal ROIs, as well as between both superior parietal

ROIs. The findings including the left inferior parietal ROI should be treated with care, however, because here an increase in spectral power was found as well (the interested reader will find details in the supporting information). With respect to non-constructed objects, significant coupling was found between the right middle frontal ROI and the left inferior frontal and ACC ROIs.

Beta. In the beta band, we found the right inferior frontal ROI to be stronger coupled with the left occipital and right superior parietal ROIs for later remembered objects. The right middle and superior frontal ROIs were stronger coupled as well. When considering constructed objects, the pattern of stronger coupling looked similar, with fronto-occipital coupling being replaced by fronto-frontal coupling between the left and right inferior frontal ROIs. When considering non-constructed objects, however, no intra-frontal coupling could be observed any more. Instead, the right inferior frontal ROI was stronger coupled with the left occipital ROI, the left inferior frontal ROI with the right inferior parietal ROI, and the left with the right superior parietal ROI.

Gamma. In the gamma band, the maintenance of later remembered in comparison to forgotten objects was accompanied by widespread fronto-parietal coupling. Stronger synchronization was found between the left inferior and superior frontal ROIs and both superior parietal ROIs. The right inferior frontal ROI was stronger coupled with the left middle frontal and both left parietal ROIs. In addition, fronto-occipital coupling was found between the left occipital ROI and right inferior frontal and ACC ROIs. As found for theta, we also found the corresponding effect restricted to constructed objects between frontal and parietal-to occipital ROIs here, i.e., the same ROIs were synchronized as for the main effect except for the ACC-left occipital coupling. Also consistent with the findings for theta, a corresponding effect restricted to non-constructed objects was found between frontal, parietal, and occipital ROIs, i.e., the left occipital ROI was coupled with the right inferior frontal ROI, the left inferior frontal ROI with the right middle frontal and right superior parietal ROIs. There was also stronger coupling between the left middle frontal ROI and the left superior frontal and both superior parietal ROIs.

3.2.5. DISCUSSION

With the present study, we wanted to find out whether specific patterns of neural coupling during the maintenance of objects in vWM promote the successful encoding of enduring memory traces. By employing a paradigm in which either constructed or non-constructed objects had to be maintained in vWM, followed by a later memory test for these objects, we could show that fronto-parietal phase coupling of neural oscillations predicts successful remembering. Specifically, frontal and parietal ROIs were stronger synchronized for later remembered objects in all frequency bands, especially in the theta and gamma bands. In the theta, beta, and gamma bands, an additional involvement of the occipital cortex was found. This finding suggests that synchronization in the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012) is relevant for successful encoding, which would be consistent with a stronger involvement of attentional processes that lead to better encoding. The additional coupling with occipital areas in the beta, theta, and gamma bands could reflect an interaction of attentional processes with visual areas, where the visual sketchpad (or visual buffer) is assumed to be located (Baddeley, 2003; Baddeley et al., 2011; Kosslyn, 2005), which would be important for correct later memory.

The results of the separate analysis of the maintenance of constructed and non-constructed objects show a dependency of phase coupling on the level of elaboration, indicating that the neural mechanisms mediating the consolidation of information in vWM are dependent on the history of the maintained representation. Consistent with Craik and Lockhart (1972), who argued that a multitude of factors influence successful memory encoding with level of elaboration and the mode of the memory test being two of them, different processes could be identified on the neuronal level depending on the elaborateness of the material. Although the behavioral data suggest that non-constructed objects were more easily retrieved, which is explainable within the framework of transfer appropriate processing (Lockhart, 2002; Morris, Bransford, & Franks, 1977) (which was not defied by Craik either (Craik, 2002)), it becomes clear that the very process of neuronal long range synchronization leading to successful encoding differs between the conditions.

Although the pattern of increased fronto-parietal coupling was generally found for both constructed and non-constructed objects, thus probably reflecting a general process of successful encoding, we saw a lateralization depending on the type of maintenance in the theta band. Here, the effect of correct later memory was more driven by the left frontal areas for constructed objects and by right frontal areas for non-constructed objects (cf. Figure 3B and C). Previous studies revealed that the retrieval of imagined pictures activated a left fronto-parietal network consisting of the left precuneus and the left prefrontal cortex (Lundstrom, 2003) and that the retrieval of perceptual details also activated the left prefrontal cortex (Ranganath et al., 2000; Ranganath and Paller, 1999). In our study, a stronger involvement of imagination processes and activation of perceptual details might have occurred in the *construction* condition, which would explain the found effect of a left lateralization of the subsequent memory effect in this condition. However, this result has to be seen as preliminary and needs further validation.

In contrast to the theta band, in the gamma band we saw a generally stronger subsequent-memory effect for constructed compared to non-constructed objects. This could be generally interpreted as a stronger consumption of attentional resources during the maintenance of constructed objects, which has been associated with gamma oscillations. Specifically, synchronization in the gamma band is associated with the integration of object features into perceptual objects (e.g., Singer, 1999) in animal local-field-potential recordings. Gamma amplitudes in MEG are also correlated with the objects features maintained in vWM and specifically pronounced for those objects that require the integration of object features (Honkanen et al., 2015; Tallon-Baudry et al., 1998).

The present results of gamma phase coupling being sensitive to a subsequent memory effect suggest a functional role beyond maintaining perceived and especially integrated objects (Palva et al., 2010). Gamma seems to additionally play a major role in encoding visual representations by not only keeping object parts together, but also serving later memory. A similar right-lateralized subsequent memory effect, however of gamma power, was found by Sederberg et al. (2003) in an intracranial EEG study. The stronger coupling in the gamma for constructed objects is in line with the behavioral data, indicating that the construction task was more difficult to execute and therefore consuming more attentional resources.

In the alpha band, the patterns of synchronization differed markedly for constructed in comparison to non-constructed objects. Palva and Palva (2011) suggested synchronization in the alpha band to be important for attentional and executive task-relevant processes. The alpha band synchronization for remembered constructed objects includes fronto-parietal and occipital areas. This could be interpreted as the fronto-parietal attention network communicating with the visual buffer (consistent with the general explanation above). For non-constructed objects, on the other hand, alpha band synchronization is restricted to intra frontal areas, showing that additional communication in the alpha band with visual areas is not predictive for later memory in this simple working memory task without any manipulation requirements. In the beta band, however, the synchronization of frontal with occipital areas for later remembered objects is found in the *non-construction* condition and not in the *construction* condition. That gives rise to the conclusion that both frequency bands serve different mental processes that come into play in tasks with different mental demands.

Overall, the present results suggest that phase coupling of neural oscillations within the fronto-parietal attention and working-memory network could be a neural implementation of a control process that serves to promote LTM encoding during the maintenance of objects in vWM. We provided further evidence of the close link between vWM processes and later memory and offered possible neuronal mechanisms contributing to successful encoding. Interestingly, these neuronal mechanisms differ in dependence of the working memory task, indicating that the successful encoding during a more elaborate visual task is associated with different or even stronger synchronization between cortical areas than successful encoding during a less elaborate task.

3.2.6. ACKNOWLEDGMENTS

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3.2.7 SUPPORTING INFORMATION

(For manuscript: “Phase coupling during the maintenance of objects in visual working memory contributes to long-term memory formation” by J. A. Ewerdwalbesloh, J. Fischer, F. Rösler, and P. H. Khader)

3.2.7.1. POWER EFFECTS

In addition to phase coupling, we also analyzed possible effects spectral power ($|Wi|^2$) of the wavelet coefficients W. This was done by averaging the power values of the relevant time interval (i.e., the second of interest) and compared conditions for each ROI and frequency band separately by means of a 2*2 ANOVA (correctly remembered yes / no * construction yes / no). These ANOVAs revealed two effects in the alpha and beta (see figure S1), but not in the theta and gamma bands.

Starting with alpha, an effect of higher power for correctly remembered objects was found in the left inferior parietal ROI (p = .012). This finding is affecting the interpretability of the couplings between the left inferior parietal and other ROIs in the general subsequent memory effect and the according effect for constructed objects. These couplings should therefore only be interpreted carefully. For beta, an effect of higher power for correctly remembered objects in the ACC ROI was found (p = .033). This is not affecting the interpretability of our results, since we did not find any long range phase synchrony including the ACC in beta.

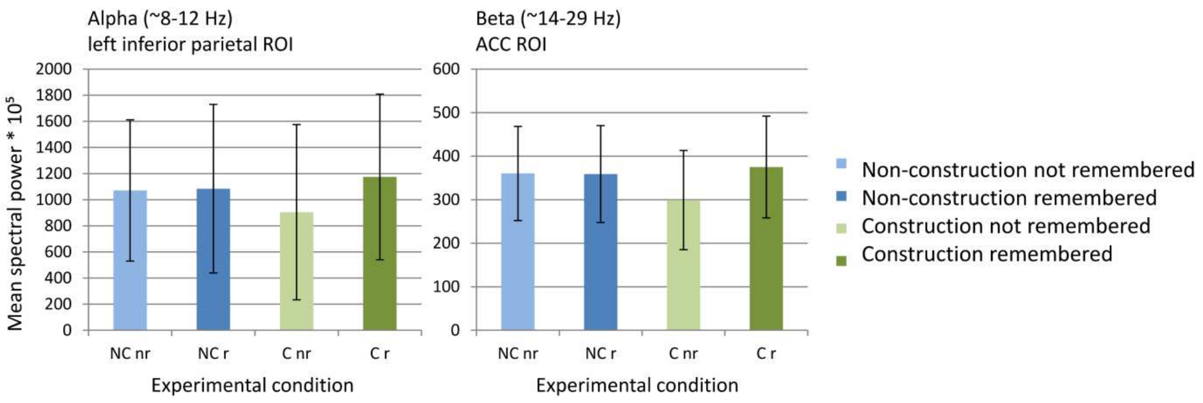

Figure S1. Mean spectral power of the alpha band at the left inferior parietal ROI and the beta band at the ACC ROI for the four experimental conditions. Error bars indicate 95% confidence intervals.

4. OVERALL DISCUSSION

4.1. AIM OF THE STUDIES AND HYPOTHESIS

The described two experiments have been conducted to better understand the functional-anatomical structures involved in mental imagery of newly created visual objects and their role for successful encoding into LTM during the maintenance of the representation. In two studies, we evaluated in how far visual information processing is modulated in dependence of the origin of the image to further understand the cognitive processes underlying and the anatomical structures involved in imagery. We therefore varied whether the image was perceived like it should be maintained or if it was mentally constructed out of single features and maintained afterwards. For that purpose behavioral measurements and EEG were assessed. Furthermore, the relationship between the synchronization of different brain areas during vWM maintenance, reflecting attentional processes that are likely to be stronger involved during more elaborate processing, and later memory in dependence of the origin of the image was assessed.

We expected that mental construction would lead to a stronger coupling between fronto-parietal and occipital regions during maintenance. These regions are known to be relevant for imagery and vWM maintenance (Cichy et al., 2012; Mechelli et al., 2004; Palva et al., 2010; for a review, see Ganis and Schendan, 2011) and we assumed a representation combined out of single features would need more neuronal coupling between these areas to hold the parts together mentally. Besides a possible general effect of more vWM load we also expected to eliminate a special effect of binding of several features through our parametrical design. We were further interested in whether any found pattern of stronger synchronization could also be identified to foster the encoding into LTM in a subsequent memory task as a few other studies suggested for different frequency bands (Fellner, Bäuml, & Hanslmayr, 2013; Summerfield & Mangels, 2005). A specific pattern of synchronization, promoting the successful encoding of enduring memory traces, could also depend on the history of origin of a maintained object, thereby indicating different neuronal processes being responsible for successful encoding depending on the task. We expected a stronger fronto-parietal synchronization for a task including mental construction and assumed this would also be accompanied by a better behavioral performance. Such a finding would have been consistent with the theory of levels of processing (Craik & Lockhart, 1972), where a more elaborate encoding would lead to a better later memory.

To this end, we recorded EEG during a vWM maintenance task that differed in two conditions in how the vWM representations were created. Participants either maintained objects in vWM that they had to create out of single features beforehand or objects that were presented to them completely. In the first experiment, the complexity of the objects varied parametrically between two and four features. In the second experiment, each block of maintenance trials was followed by a memory test for these objects. In both experiments, we analyzed EEG phase coupling from source-localized scalp data that was recorded during the vWM retention period.

4.2. DISCUSSION OF THE ELECTROPHYSIOLOGICAL RESULTS

The electrophysiological results indicate in general that the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012) serves in interaction with the visual buffer (Baddeley, 2003; Baddeley et al., 2011; Kosslyn, 2005) the maintenance and successful encoding of generated images. Phase coupling was assessed through calculating the phase locking value between predefined regions of interest that were calculated with a LORETA (Pascual-Marqui et al., 1994).

The EEG results indicate that the maintenance of mentally constructed objects in comparison to completely perceived objects is accompanied by increased phase synchrony in the theta, alpha, beta and gamma frequency bands between frontal and parietal- to occipital brain areas. This finding suggests that the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012) becomes increasingly activated and connected with the occipital cortex when object parts have to be kept together in vWM. Especially in the beta and gamma frequency bands this effect is most extensive. Since the synchronization in all frequency bands took place among frontal, parietal, and occipital cortices it might underlie the binding and controlling of the visual representation represented in the visual sketchpad (or visual buffer) (Baddeley, 2003; Baddeley et al., 2011; Kosslyn, 2005) located in the occipital cortex.

Interestingly, a similar pattern of couplings emerged after comparing trials with later remembered to trials with later not remembered objects. Those, where later remembered objects were maintained, showed stronger coupling in the theta, alpha, beta and gamma frequency bands between frontal and parietal brain areas, this effect being strongest for theta and gamma. Additionally, in the theta, beta and gamma frequency bands, the occipital cortex was synchronized with fronto-parietal areas as well. This leads to the conclusion, that the above described fronto-parietal attention network (see also Sack & Schuhmann, 2012; Salazar et al., 2012) seems to be important for successful encoding as well. Since its synchronization predicts later memory it is likely that a stronger involvement of attentional processes during vWM maintenance fosters better encoding into LTM. The additional synchronization with the occipital cortex in the beta, theta, and gamma bands could be interpreted in a way that an interaction of attentional processes with the visual sketchpad (Albers et al., 2013; Cichy et al., 2012; Zimmer, 2008) serves successful encoding into LTM as well.

However, in the alpha frequency band there was no increased coupling with occipital areas for subsequently remembered objects, indicating that in this frequency band, a stronger communication with the visual buffer does not foster later memory. This function seems to be restricted to the other frequency bands. Since this result differs to the general effect of increased attentional demands for constructed objects, where an increase in occipital involvement is found, the latter effect seems to be important for ongoing vWM processes, but not for successful encoding.

4.3. DISCUSSION OF THE BEHAVIORAL RESULTS

The behavioral results of the matching task following vWM maintenance in both experiments are in line with the expectations, showing that it took longer for participants to compare their maintained image to the probe objects when it was made up out of single features in contrast to when it was presented completely from the beginning. Moreover, the response time increased with increasing features in the first experiment, and that more strongly in the construction condition. This indicates that the access to the single features is impaired when the object had been constructed in vWM. This could be due to a weaker representation, as indicated by the subjective reports of the participants, rating the clearness of the constructed visual image constantly lower than the clearness of the complete object. While the subjective impression is very alike in terms of the content (although less clear), the underlying cognitive process seems to differ. This suggests that the construction of objects from single features does not end in a neuronal representation identical to that of a presented object. Since an effortful task of mentally combining several features had to be fulfilled in the construction condition, an additionally required process could be increased cognitive control. This interpretation is supported by the error rates as well. Here, the comparison of constructed image is more prone to errors than that of complete images. Furthermore, an increase of error rate with the number of maintained features was found in the first experiment when objects had to be constructed, but not when objects were presented as a whole. That might signify the increasing cognitive control demands with more and more features that have to be actively held together mentally.

The behavioral results in the subsequent memory task showed a worse performance for constructed in comparison to completely presented objects for later recognition. This is most likely the case, because participants encountered the complete object more often in the non-construction condition and could therefore better strengthen the particular memory trace. One should as well consider the framework of transfer appropriate processing (Morris et al., 1977). A match of encoding and retrieval conditions is given in the conditions where complete objects were presented, thereby improving conditions for successful retrieval.

Overall, the behavioral data support our hypotheses. However, the design was not suited to replicate a behavioral effect of better retrieval for more elaborately encoded objects. Here, the focus lied on the test for the correct mental image and the secondary task to prevent verbalization. To control for different numbers of encounters one would have to add an additional stimulus in a next experiment, making sure that every object is seen the same number of times.

4.4. DISCUSSION OF THE LOAD EFFECTS IN THE FIRST EXPERIMENT

A closer look at the load dependencies of the EEG phase coupling in each experimental condition reveals that the effect described above is likely to be a general vWM load effect in the theta and alpha frequency bands, maybe reflecting general effects of increased attention. This fronto-parietal to occipital coupling that is found to be sensitive to vWM load could be interpreted as a load-dependent increase of communication between the fronto-parietal attention network and the visual buffer. These couplings that are found in the test for vWM load as well as in the test for the effect of construction itself, probably reflect generally higher control demands in the construction condition. A specific role of alpha long-range synchronization for cognitive control processes was also discussed by Sadaghiani et al. (2012). Since the effect of construction load was not completely dissociable from the effect of general vWM load, the found synchronization in the theta and alpha frequency bands is probably not specifically responsible for the process of maintaining visual objects that have been integrated by means of mental imagery. On the other hand, a dissociation is most visible in the beta and gamma frequency bands. Here, the fronto-parietal increase in coupling is selective for the effect of construction and does not reflect a general effect of vWM load.

However, an isolated fronto-parietal coupling is specific for the maintenance of increasingly complex constructed visual objects in all frequency bands. But additionally, in the beta and gamma frequency bands the vWM load effect is dissociable from the construction load effect. Whereas a fronto-parietal coupling occurs with increasing construction load, the synchronization associated with increasing vWM load is independent of fronto-parietal coupling in these two frequency bands. It is also smaller and differently located than the general construction effect. That means a dissociation between two different processes depending on the task can be identified in these two frequency bands. The beta and gamma phase coupling between frontal and parietal sites being sensitive to construction load and being stronger for maintaining constructed in comparison to non-constructed objects suggest a functional role on top of maintaining perceived stimuli, as was suggested for the network of fronto-parietal and occipital areas (Palva et al., 2010).

Synchronisation between fronto-parietal and occipital areas in the beta band has been found to be important for vWM retention before (Fell & Axmacher, 2011; Hanslmayr & Staudigl, 2014; Palva et al., 2010). However, this recent finding suggests that the effect is not load-dependent for mere vWM maintenance. That could indicate that the general construction effect found for beta includes additional processes that are not isolated by a test for either increasing vWM or construction load. This has to be validated by further experiments, however.

Interestingly, load-dependent synchronization in the construction condition did not include occipital ROIs in any of the four frequency bands. This could be interpreted in a way that the fronto-parietal attention network is coping with the higher attentional demands of maintaining constructed images, without increasing the communication with the visual buffer in occipital areas where visual representations are assumed to be stored (Baddeley, 2003; Coull et al., 1996; Kosslyn, 2005).

Increased theta and alpha-band synchronization was correlated positively with both vWM load and increasing construction demands, seemingly reflecting general higher control demands for more complex stimuli, irrespective of their origin. The alpha construction-load effect should be considered preliminary, however, because it was not increasing parametrically with more features. In the theta frequency range increased synchronization was observed predominantly in the left hemisphere for the maintenance of constructed in comparison to non-constructed objects. The general stronger synchronization is in line with the findings of Sauseng et al. (2006) and Summerfield and Mangels (2005), who found increased theta coupling between frontal and occipital areas for increased executive control demands.

These results together with the results in the gamma frequency range add evidence for the theory that synchronization in the theta and gamma frequency bands may be a neural mechanism serving coordination and integration within the fronto-parietal attention network (Corbetta and Shulman, 2002; Coull et al., 1996; Linden et al., 2003; Sadaghiani et al., 2012).

Alpha band phase locking in ACC is found to be correlated with the detection of somatosensory stimuli (Hirvonen and Palva, 2015), indicating a close relationship between control functions and the alpha-band activity in cingulate structures. In our experiments phase synchronization occurred in the alpha band among other sites between the ACC and parietal ROIs, which adds evidence to the theory that ACC may have a role in control functions as well as feature integration in vWM within the fronto-parietal network (Munk et al., 2002; Zimmer, 2008). Additionally, a role for successful LTM encoding of constructed visual images can be suggested based on our data.

The found synchronization in the gamma band is in agreement with prior data indicating that especially phase coupling in the gamma frequency band of animal LFP recordings is associated with feature integration of objects (Singer, 1999). In combination with our data, gamma phase coupling seems to play a major role in the maintenance of visual representations by keeping object parts together, while this function becomes more and more crucial when objects had to be mentally constructed in vWM.

4.5. SUMMARY OF THE DISCUSSION OF THE FIRST EXPERIMENT

The maintenance of constructed in comparison to non-constructed objects was accompanied by increased fronto-parietal-occipital couplings, suggesting a specific role for keeping object features together. However, in the theta and alpha frequency bands, more fronto-parietal-occipital couplings were also found for increasingly complex non-constructed objects, therefore reflecting a general vWM load effect. That means here the stronger synchronization for constructed objects probably reflects generally higher vWM demands required for maintaining constructed objects. Importantly, the synchronization in the beta and gamma frequency bands has to be interpreted differently. Here, a double dissociation between a construction-load effect and the general vWM load effect was observed. Fronto-parietal coupling was only sensitive to mental construction load in these two frequency bands, whereas intra-frontal and parieto-occipital synchronization in the beta frequency band and fronto-occipital synchronization in the gamma frequency band was sensitive to vWM load. Therefore in these two frequency bands, fronto-parietal couplings were distinctively related to the maintenance of mentally constructed visual images. In general, most of the results are in line with the existing literature, suggesting the fronto-parietal network to be an important factor for maintaining mentally created objects in vWM. Oscillatory synchronization within that network and between it and occipital areas are likely to play a crucial role in the process of localizing attentional resources.

4.6. DISCUSSION OF THE TASK EFFECTS IN THE SECOND EXPERIMENT

After having discussed that similar synchronization between fronto-parietal and occipital areas was found for increased attentional demands as well as later correctly retrieved objects earlier, the dependency of that particular effect on the exact vWM task conducted before maintenance is discussed now. Increased fronto-parietal coupling for later correctly retrieved objects was generally found for both constructed and non-constructed objects (except in the alpha frequency band) thus probably reflecting a process of successful encoding independent of the particular vWM requirements.

In the theta band, however, we saw a lateralization depending on the type of visual representation maintained. Here, correct later memory was more associated with synchrony between parietal and occipital areas and the left frontal areas for constructed objects, whereas parietal and occipital areas were more strongly synchronized with right frontal areas for non-constructed objects.

Previous studies found the retrieval of imagined pictures being associated with an activation of a left fronto-parietal network including the left precuneus and the left prefrontal cortex (Lundstrom, 2003). The retrieval of perceptual details activated the left prefrontal cortex as well (Ranganath et al., 2000; Ranganath and Paller, 1999). In the present study, a stronger activation of perceptual details and an increased involvement of imagination processes might have taken place in the *construction* condition, which could explain the left lateralization of the subsequent memory effect in this condition. This result has to be seen as preliminary and needs further validation, however.

In the gamma band a similar, but in total stronger subsequent-memory effect for constructed compared to non-constructed objects was found. This could be interpreted as reflecting an increased demand of cognitive control during the maintenance of constructed objects. Synchronization in the gamma band has been found to be associated with the integration of object features into perceptual objects (Singer, 1999) in animal local field potential recordings before. Although reflecting a different scale of synchronization, gamma amplitudes in MEG were found as well to correlate with vWM maintenance and to be especially pronounced for objects that required the integration of object features (Honkanen et al., 2015; Tallon-Baudry et al., 1998). Whereas local and long-range synchronization are not always reflecting the same mental process, only because they share a certain frequency, in this case it might be the case.

The present subsequent memory effect in the gamma frequency band suggest a functional role beyond maintaining perceived and even especially integrated objects (Palva et al., 2010). Additionally, phase coupling in the gamma frequency band seems to play a major role in encoding visual representations during vWM maintenance. Another right-lateralized subsequent memory effect, again of gamma power, was found by Sederberg et al. (2003) in an intracranial EEG study. Here again the assumption of functionally similar local and long-range synchrony processes in the gamma frequency band holds.

The patterns of synchronization differed completely for constructed in comparison to non-constructed objects in the alpha frequency band. Palva and Palva (2011) suggested that synchronization in the alpha frequency band might be important for attentional and executive task-relevant processes. For constructed objects, the stronger synchronization for remembered objects took place between fronto-parietal and occipital areas. This could reflect the fronto-parietal attention network communicating with the visual buffer (consistent with the discussion of the general effect above). However, for non-constructed objects stronger synchronization for remembered objects was restricted to intra frontal areas. That means, in this simple vWM task without manipulation requirements, additional communication in the alpha frequency band with visual areas is not predictive for later memory.

In the beta frequency band, however, a synchronization between frontal and occipital areas is only found in the *non-construction* condition and not in the *construction* condition for later remembered objects. That suggests that both, the alpha and the beta frequency band, serve several different mental processes that come into play in tasks with different cognitive demands.

4.7. GENERAL CONCLUSION

The two experiments I conducted served the better understanding of the functional-anatomical structures underlying the maintenance of visual images. I evaluated how far visual information processing is modulated on a neuronal level in dependence of the origin of the image and which neuronal synchronization processes serve successful LTM encoding during vWM maintenance. The results support the notion that the maintenance of constructed mental images is an attention demanding process depending on the synchronization between fronto-parietal and occipital areas. I also eliminated a distinct effect of the mental generation of new visual objects on vWM maintenance in the synchronization between frontal and parietal brain areas. I found successful LTM encoding to be correlated with similar synchronization between fronto-parietal and occipital brain areas, the concrete pattern of synchronization varying in dependence of the objects´ origin.

The results of the first experiment suggest a role of fronto-parietal within-frequency coupling across all interesting frequency bands for the maintenance of constructed objects in vWM. This could reflect the process of top-down updating of the actively constructed mental image while maintaining it, especially transmitted in the beta and gamma frequency bands. In this way the findings complement current theories of mental imagery, that assume that the manipulation of mental images is governed by an attentional control process mediated by the fronto-parietal attention network (Corbetta and Shulman, 2002; Ganis and Schendan, 2011). According to the recent findings, the increased attentional control is still needed during sustained maintenance of the manipulated mental image.

The results of the second experiment suggest that phase coupling of neural oscillations within the fronto-parietal attention network could be a neural implementation of a control process active during the maintenance of objects in vWM that serves to promote LTM encoding.

The found pronounced coupling of the fronto-parietal network with occipital brain areas in the first experiment support the claim that the proposed attentional control process acts in a top-down manner by maintaining dynamic functional links to object representations in a visual buffer (e.g. Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Cichy, Heinzle, & Haynes, 2012; for reviews, see Kosslyn, Thompson, & Ganis, 2006; Zimmer, 2008). On one hand, such a process seems to be increasingly involved when constructed objects have to be maintained in vWM as well as under increased vWM load in general. On the other hand, increased construction load did not lead to stronger coupling of the fronto-parietal network with the visual buffer. Instead, the found increased synchrony was restricted to the fronto-parietal network. That indicates that the maintenance of constructed objects in vWM requires additional executive processes to keep the object parts together as a coherent representation. The task of maintaining a mentally constructed visual image is apparently functionally different from maintaining the subjectively identical image that was presented completely in the visual buffer.

Concluding from the results of the second experiment, the neuronal mechanisms responsible for correct later retrieval differ in dependence of the working memory task as well, indicating that the successful encoding during a more elaborate vWM task is associated with different or in case of the gamma frequency band stronger synchronization between cortical areas than successful encoding during a less elaborate task. That adds evidence to the supposed close link between vWM processes and later memory (Ranganath & Blumenfeld, 2005) and suggests a functional role for neuronal synchronization in a broad range of frequency bands beyond vWM maintenance.

This work examined the process of visual imagery, which is useful in a huge variety of tasks that involve planning and creative processes in detail. The ability to imagine possible future states as a fundamental skill needed for progress in technology, arts or in general a society was further investigated. I offered neuronal support for ideas how imagery may be conceptually organized and gave a first outlook on what might be possible in terms of the distinguishing of real and made up visual representations in the future. I further suggested neuronal mechanisms during mental imagery that could contribute to successful LTM encoding. In this way I helped to understand a little further the crucial ability of mental imagery that makes it possible to create things that did not exist before and in this way enables mankind to evolve.

5. REFERENCES (INTRODUCTION AND DISCUSSION)

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7. Curriculum Vitae

Julia Ewerdwalbesloh

Education	
April 2013 to date	**Ludwig-Maximilians-Universität München** Doctoral studies in Psychology Topic: Cognitive Mechanisms and neuronal Dynamics of Mental Images
October 2007 - January 2013	**Philipps-Universität Marburg** **Diploma** in Psychology (1,9) Majors: Cognitive neuroscience, work- and organizational psychology Thesis: *Interaction between Working Memory and Attention base on CDA and N2pc* (1,7)
October 2009 - July 2011	**TransMIT Gesellschaft für Technologietransfer, Gießen** Training as mediator
August 1998 - June 2007	**Taunusgymnasium Königstein** **Abitur** (1,3) Advanced courses: Mathematics and German
Professional experience	
June 2013 to January 2016	**Research assistant at Ludwig-Maximilians-Universität, Münche** Planning, conducting and evaluation of experiments, teaching students about scientific work and statistics, supervising student
August - September 2014	**Lab Visit at Neuroscience Center of University of Helsinki, Helsinki** Collaboration in an international scientific project, development of new analysis routines with MatLab.
October 2012 - January 2013	**Intern at Kienbaum Management Consultants GmbH, Düsseldo** Monitoring of the recruiting process, conception and organizatio of the university marketing, assistance of the alumni program.

May 2012 November 2011 May 2010	**Student assistant for Dr. Reinhardt, Marburg** Conception, execution and evaluation of a training for students with the focus on presentation, learning, stress- and time management.
December 2011 - February 2012 November 2010 - January 2011 October 2009 - December 2009	**Tutor for Prof. Peper and Dr. Chavanon, Marburg** Mentoring of students in planning, execution and data analysis o three experiments, correction of reports.
July 2011 - October 2011	**Student trainee at Kreditanstalt für Wiederaufbau (KfW), Frankfurt** Collaboration in the human resources department, coordination and preparation of job interviews.

Voluntary service

December 2014 - November 2015	Chairwoman of the liberal students groups of Bavaria
March 2013 to July 2015	Voluntary work at the regional group of the German mediation association (Bundesverband Mediation e.V.)
November 2010 - May 2012	Member of the 46th and 47th students’ parliament at Philipps-Universität Marburg, member of the statute committee
October 2008 - November 2010	Member of the interdisciplinary students’ conference
January 2008 - June 2010	Member of the editorial office at „Tellerrand, Zeitschrift der Fachschaftenkonferenz“

Additional skills and information

Scholarship	Stipendiary of Friedrich-Naumann-Stiftung für die Freiheit
Languages	German (native speaker), English (fluent), Latin (Latinum)
DP	Programming in Presentation, MatLab and ePrime, MS Office, SPSS
Graduate School	Member of elite Graduate School of Systemic Neurosciences

Personal interests

reading
cooking
politics

8. LIST OF PUBLICATIONS

-

9. STATUTORY DECLARATION AND STATEMENT

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation „Cognitive Mechanisms and Neuronal Dynamics of Mental Images“ selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation „Cognitive Mechanisms and Neuronal Dynamics of Mental Images“ is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München, den Julia Ewerdwalbesloh

10. DECLARATION OF CONTRIBUTION AS CO-AUTHOR

Für die erste Studie habe ich die Datenerhebung mit Hilfe zweier Studentinnen durchgeführt, für die zweite Studie habe ich bei der Datenerhebung geholfen, wenn nötig. Ich habe bei beiden Experimenten die Datenanalyse in Rücksprache mit meinem Doktorvater Patrick Khader durchgeführt. Bei den beiden vorliegenden Manuskripten habe ich als Erstautor die Erstellung des ersten Entwurfes und die Einarbeitung der Beiträge und Anmerkungen der Co-Autoren des Manuskriptes zu verantworten.

For the first study I collected the data together with two students, for the second I helped, when necessary. For both studies I conducted the data analysis after consultation with my supervisor Patrick Khader. I was responsible for the first draft of the manuscripts for publication and the merging of the inputs of the co-authors.

Signature

Signature Supervisor