Neural Correlates of Maintaining Generated Images in Visual Working Memory

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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 electroencephalogram 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 would 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 nonconstructed 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 nonconstructed 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. *Hum Brain Mapp* 37:4349–4362, 2016. © 2016 Wiley Periodicals, Inc.

Key words: mental imagery; visual working memory; phase coupling; electroencephalogram; phase-locking value; fronto-parietal network

INTRODUCTION

Visual imagery is the ability to “see with the mind’s eye,” that is, 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

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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, that is, 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 toward 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 interareal synchronization of source-localized MEG data has revealed 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 for the maintenance of items in vWM [Gevins et al., 1997; Jensen and 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, 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 electroencephalogram (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, that is, 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 nonconstructed 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]. Hence, alpha oscillation amplitudes have been suggested to reflect the enhanced executive functions required for coping with the excess of sensory information and suppression of task-irrelevant information, respectively. However, in contrast to its amplitude, the strength of alpha-band interareal *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 generally 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

Figure 1.

A. Design and exemplary stimuli. In the mental construction condition, single features in varying numbers were shown, whereas in the nonconstruction 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.

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 Figs. 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 a beetle. In the control condition, participants had to simply maintain stimuli they saw 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 to be maintained successfully. Those processes should serve a binding function that connects object parts in vWM and keeps the connections active during maintenance.

We hypothesized that interareal 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

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.

nonconstruction conditions, in the construction condition its coupling with the fronto-parietal network should be strengthened.

MATERIALS AND METHODS

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 except 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).

MATERIAL

Participants maintained in vWM schematic drawings of beetles with a varying number of features (two, three, or four; see Fig. 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 and Nosofsky, 2007]. We varied the number of features to assess the effect of stimulus complexity on visual imagery in a *construction* and a *nonconstruction* condition. In the construction condition participants had to mentally combine two, three, or four presented features into one single object and maintain it in vWM, whereas in the nonconstruction 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 Fig. 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 $4 \times 4 \times 3$ 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, for example, a specific color, was not more likely to occur together with a certain other feature, for example, 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 Fig. 2). The features were presented within individual white rectangles (also 6.8×5.6 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.

PROCEDURE

Stimuli were presented on a 17" standard CRT monitor with a refresh rate of 75 Hz. During the experiment, in which the EEG was recorded, participants sat in a dimly lit room at a distance of about 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 (Fig. 1) at the beginning of the instruction.

The main task in the construction condition was to memorize pictures of beetles that first had to be mentally constructed from single beetle features (see Fig. 2). In the nonconstruction condition, these pictures of beetles were presented without the necessity of constructing them. Participants were instructed to visualize the image of the constructed or nonconstructed 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 3–5 s (jittered in steps of 400 ms), until a probe stimulus appeared in the same location, on which they had to give a match/nonmatch 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 1,500 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 1,500 ms. This was in general confirmed by postexperimental reports of the participants.

In addition to the short time limit for the match/nonmatch 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 2,500 ms. Memory for this secondary WM load was tested at the end of the trial. Specifically, after the match/nonmatch 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 intertrial interval, a fixation cross was presented for 1,200 to 3,200 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 1,500 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. nonconstruction) changed (again participants first completed 12 training trials to familiarize

Figure 3.

RT and error rates for all experimental conditions. Error bars are 95% confidence intervals, corrected after Morey [2008].

themselves with the new condition). One half of the participants first did the experimental condition, the other half the control condition. There were $24 \times 12 = 288$ trials in total, with 48 trials for each of the 2×3 conditions (mental construction $\times$ number of features).

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 0.01 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 k Ω . 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 channel comprising electrodes F7 and F8.

Initial data processing was done with BrainVision Analyzer® 2.0.3. EEG segments of the 1,000 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 semiautomatic filtering procedure (maximum allowed amplitude difference between adjacent voltage values = 40 μ V/ms; maximum allowed difference in any interval of 1,000 ms length = 150 μ V; minimum allowed difference in any interval of 200 ms length = 0.5 μ V). The average number of remaining artifact-free segments was comparable across conditions: 36.76 in the “construction (C)/2 features” condition, 33.94 for C/3, 32.18 for C/4, 38.06 for “nonconstruction (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. Fig. 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 including both the left and right hemispheric BAs. 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

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 nonconstruction 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 BA.

choosing a rather coarse graduation, we also substantially reduced the number of statistical comparisons. An even coarser graduation (such as left/right $\times$ 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). 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. This was done to avoid confounding effects of unequal

Figure 5.

PLV averaged over all significantly stronger couplings found for $4 > 2$ features in the mental construction and the nonconstruction 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].

numbers of trials on the phase-locking values (PLV) (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 PLV according to Lachaux et al. [1999] was calculated for each pair of ROIs (78), participants (17), frequency layers (25), and experimental conditions (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 and Rösler, 2011; Khader et al., 2010], and also in the present study, that the nonparametric 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 distribution].

Furthermore, instead of a strict correction of alpha-error inflation, we rather 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 increasingly 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). Specifically, the Bonferroni-corrected threshold for the 78 comparisons of all ROI pairs ($13 \times 12/2$) would be at $p = .00064$ for an alpha level of 5%, which we consider too conservative. None of the observed comparisons had a smaller p value. However, given an alpha level of 5% and 78 tests, results with four or less significant comparisons, which is the expected number of false positives ($78 \times .05$), should be interpreted with caution (correspondingly, only one false positive test would be expected with an alpha level of 1%). As can be seen in Figure 4, most of the observed coupling patterns would surpass this threshold. Moreover, if the results would be only due to false positives, one would expect more random patterns that would not necessarily match with our a priori defined predictions of frontal to parieto-occipital synchronization. As can be seen in Figure 4, the majority of significant couplings took place between these expected sites. Last, but not least, we were also able to replicate the patterns of fronto-parietal coupling in a second experiment, which is currently under submission, and we only interpret relatively coarse topographical patterns of couplings and not individual edges.

Three effects were of interest: first, the general effect of *construction*, that is, the comparison between the *construction* and the *nonconstruction* 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 *nonconstruction* conditions ("*vWM load*"). The latter two effects were tested by means of comparing the conditions with two versus 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.

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 nonconstruction condition in the theta and alpha bands. We therefore refrain from interpreting any of those intrafrontal couplings because we cannot exclude that they are influenced by eye-modulated activity.

RESULTS

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).

As can be seen in Figure 3, both RT and error rate were generally higher for matching constructed compared to nonconstructed objects. Both measurements increased with the number of features in both the construction and nonconstruction conditions, with this increase being weaker (RT) or even absent (error rates) in the nonconstruction condition. This pattern was supported by the statistical

analysis. For RTs, significant main effects were found for factors *construction*, $F(1, 16) = 12.66$; $p = .003$, $\epsilon = 1$, and *number of features*, $F(2, 32) = 48.19$; $p < .001$, $\epsilon = 0.956$. In addition, the interaction *construction* $\times$ *number of features* was significant, $F(2, 32) = 13.40$; $p < .001$, $\epsilon = 0.771$. 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, that is, *two versus three features* ($t = 7.33$, $p < .001$) and *three versus four features* ($t = 4.28$, $p = .004$) differed significantly. In the nonconstruction 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 versus nonconstruction* differed significantly with three ($t = 3.23$, $p = .037$) and four features ($t = 4.93$, $p = .001$).

The analysis of the error rates revealed corresponding results, with significant main effects for factors *construction*, $F(1, 16) = 26.95$; $p < .001$, $\epsilon = 1$, and *number of features* $F(2, 32) = 22.85$; $p < .001$, $\epsilon = 0.890$, as well as a significant interaction *construction* $\times$ *number of features*, $F(2, 32) = 7.82$; $p = .002$, $\epsilon = 0.925$. 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 nonconstruction condition, no significant increases were found. Finally, *construction versus nonconstruction* 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.

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 interareal 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 nonconstructed 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 nonconstructed 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.

Alpha

In the alpha band, we observed stronger coupling for constructed in comparison to nonconstructed 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. Fig. 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, intrafrontal 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 nonconstructed 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 nonconstructed 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 nonconstructed 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, that is, 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 nonconstructed objects) was found between frontal, parietal, and occipital ROIs, that is, 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. Fig. 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 nonconstruction condition displayed higher power. The effects of the number of features were, in contrast to the PLVs (see Fig. 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.

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 stronger interareal 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 the 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 are 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 versus 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 nonconstructed 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 et al., 2012], and alpha-band phase locking with the detection of somatosensory stimuli [Hirvonen and Palva, 2016], 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 aforementioned, 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 nonconstructed 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 nonconstructed 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 nonconstructed 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 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, that is, 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.

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]. 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.

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