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Focused Review
Brain oscillatory correlates of working memory constraints
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ABSTRACT

It has been claimed that the coordination of neuronal oscillations differing in frequency is relevant for cognition. However, the validity of this claim has scarcely been investigated. Recent studies revealed that cross-frequency phase coupling and modulations of alpha-power dissociate between retention of relevant and suppression of irrelevant information in visual working memory (WM). We summarize these important results, and discuss possible implications for understanding the neural mechanisms of WM constraints.

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1. Introduction

Mainly based on behavioral assessments, cognitive theories traditionally assume a fixed upper limit for the available storage space in WM (Luck and Vogel, 1997; Miller, 1956). Estimates for capacity limits thereby range from 4 (± 1) (Cowan, 2001; Luck and Vogel, 1997) to 7 (± 2) items (Lisman and Idiart, 1995; Miller, 1956). Recent neuroscientific investigations point to interacting neuronal processes that jointly limit performance in WM tasks (D'Esposito, 2007; Zimmer, 2008). Accordingly, efficient performance on WM tasks requires at least the maintenance of relevant information over a short time-period and, at the same time, inhibition of distracting, non-task relevant information from entering visual awareness (Gazzaley et al., 2005; Vogel et al., 2005).

From the mid 1990s onwards, the so-called 'change-detection paradigm' (CD-paradigm, e.g. Luck and Vogel, 1997) has become a popular tool for studying properties of WM in neuroscience. In CD tasks, observers are presented with a memory display that contains a variable amount of information (e.g. colored squares). After a brief retention interval (e.g., around 1 s) a probe display asks the participant to judge whether the currently presented information has changed relative to the representation retained in WM. Since the initial report (Luck and Vogel, 1997), this paradigm has been repeatedly applied to investigate neuronal activity related to WM retention (for a recent review see, Drew et al., 2006).

In a recent development, Vogel and Machizawa (2004) included cues prior to the onset of the memory display to direct the observers' attention to information in only one visual

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hemifield while simultaneously presenting to-be-ignored information in the uncued hemifield (e.g., Fig. 1A). This procedure enabled the identification of a negative posterior EEG slow-wave that reflects neuronal activity associated with WM retention (Ikkai et al., 2010) and the ability to filter distracting information (Vogel and Machizawa, 2004), the so-called contra-lateral delay activity (CDA). Nevertheless, due to strong interactions between perceptual and attentional demands in CD tasks (Bays and Husain, 2008; Emrich et al., 2009; Fukuda and Vogel, 2009), it remained difficult to separate mechanisms related to item selection from mechanisms related to retention proper.

Although the working memory system is often conceptualized to comprise mechanisms for maintenance and utilization of information (e.g., Baddeley, 1992; Baddeley, 2000), here, we strongly focus on the retention aspect and its corresponding neural correlates. More precisely, the present review article reports on recent evidence for possible oscillatory neuronal correlates of inhibition and retention mechanisms relevant for successful WM performance as derived from MEG/EEG research (for a recent review on physiological studies please refer to Duzel et al., 2010). In the following, we specifically focus on studies relating the amplitude of alpha

oscillations to inhibition of distracting information and the synchronized co-activation of low-frequency theta and high-frequency beta and gamma oscillations to WM-maintenance. Finally, the two phenomena reported in recent WM-studies are then related to an intermediate model of working memory constraints.

2. Alpha oscillations and inhibition of distracting information

The alpha rhythm is supposed to arise from cortico-thalamic (Nicolelis and Fanselow, 2002; Silberstein et al., 2001; Steriade, 1999) or cortico-cortical network activity (Bollimunta et al., 2008; Nunez et al., 2001). So far, a concise physiological model of potential alpha generators remains to be established (Jensen and Mazaheri, 2010). But, however, according to one interpretation, oscillations like the alpha rhythm are likely induced by inhibitory inter-neurons (Buzsáki and Chrobak, 1995; Crunelli and Leresche, 1991), and represent fluctuations between excitatory and inhibitory phases that are relevant for neural communication (Klimesch et al., 2007a). Accordingly, alpha oscillations seem to support WM performance indirectly

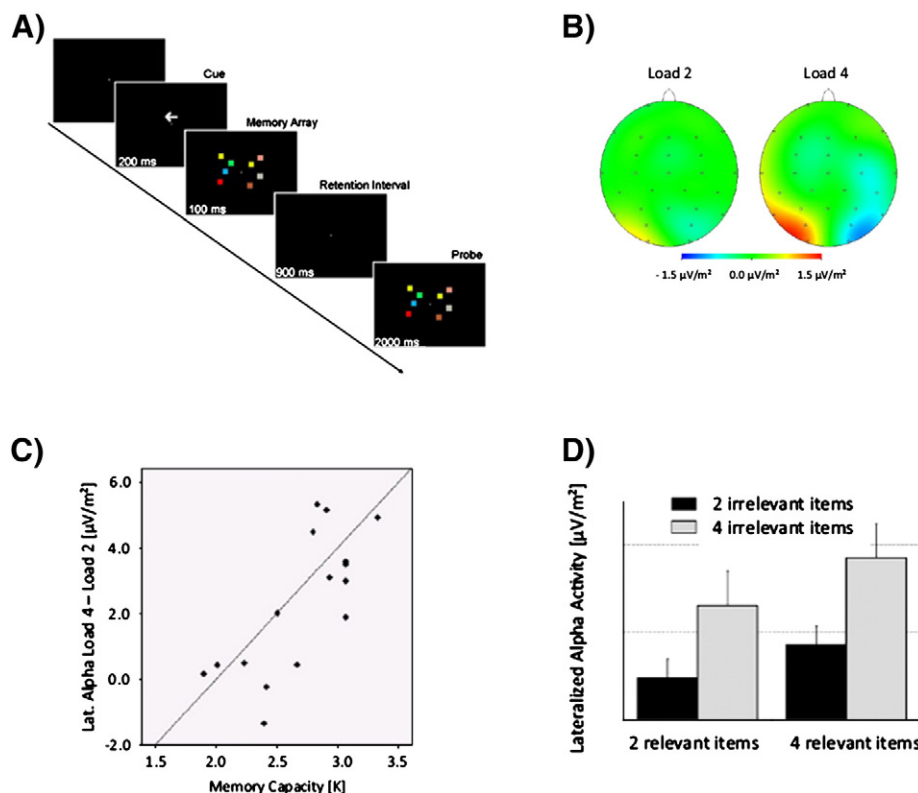


Fig. 1 – Alpha amplitude increase and inhibition of distracting information. A) The classic change-detection paradigm from Vogel and Machizawa (2004) as used in the study by Sauseng et al. (2009). The subject's task is to memorize the cued item array. B) The retention interval was analyzed for oscillatory differences. The topographical maps of alpha amplitude of the differences between 'memorize left' minus 'memorize right' items are shown (=lateralized alpha activity). Items presented on the left lead to an amplitude decrease on the right (contralateral) and to an increase on the left (ipsilateral) side and vice versa. The difference is stronger for load 4 compared to load 2. C) Memory capacity can be predicted by lateralized amplitude modulations. Higher alpha amplitudes ipsilateral to the attended hemifield improve memory performance. D) The lateralized alpha-amplitude effect is influenced by the number of irrelevant items. Data are from Sauseng et al. (2009). *Curr. Biol.*

by filtering out irrelevant information and preventing interference from conflicting stimuli (Klimesch et al., 2007a; Rihs et al., 2007; Tuladhar et al., 2007).

As can be derived from recent electrophysiological investigations, behaviorally relevant alpha effects can either appear prior or after stimulus onset. Both phenomena are likely to interact (Klimesch et al., 2007b) and can be interpreted as a top-down mechanism that gates the processing of stimulus representations (Jensen and Mazaheri, 2010). Here, we raise the claim that during effective retention of representations alpha oscillations suppress distracting environmental input.

With regard to spatial WM, Sauseng et al. (2009) recently demonstrated that the amplitude of alpha oscillations systematically increases with load during the retention interval in a cued CD paradigm. Critically, this increase was more pronounced at sites ipsi-lateral to the attended hemifield than at contra-lateral sites at which stimulus processing/maintenance is expected to occur (cf. Fig. 1). In addition, the lateralized alpha load effect was strongly correlated with individual WM capacity. Importantly, a follow-up experiment revealed that the lateralized alpha power increase was specifically driven by the amount of to-be-ignored information and not by the amount of to-be-maintained items.

These findings were further corroborated by application of repetitive transcranial magnetic stimulation (rTMS) in two separate experiments. Specifically, rTMS over cortical sites – processing irrelevant information – increased WM performance. Intriguingly, this effect was specific to 10 Hz as compared to 15 Hz rTMS, supporting the claim that entrainment to alpha frequencies may provide the physiological basis for the reported behavioral improvements. It could also be argued that this effect can be attributed to TMS interfering with item representations leading to reduced competition. This cannot be ruled out so far but seems unlikely because the effect was specific to 10 Hz stimulation when compared to 15 Hz and sham, thus linking to the inhibition-timing hypothesis of alpha oscillations (Klimesch et al., 2007a). Nevertheless, the study by Sauseng et al. (2009) therefore provides evidence for a situation in which alpha entrainment reflects an active rather than a passive (or random) phenomenon that enables suppression of interfering environmental input during retention that is beneficial for WM performance.

In addition to the CD task, many variants of the Sternberg memory scanning paradigm (Sternberg, 1966) have been used to study WM capacity limits. The Sternberg task generally consists in presenting a certain amount of items (either sequentially or simultaneously) that have to be encoded and held in memory over a short retention period. Increased alpha synchronization has been observed over areas not directly related to maintenance of items (Klimesch et al., 1999; Tuladhar et al., 2007), suggesting that alpha serves not as a mechanism primarily involved in retaining relevant information.

Along similar lines, Freunberger et al. (2009) applied a version of the Sternberg paradigm in which participants received cues prior to stimulus-onset at encoding that indicated whether the upcoming item would have to be remembered or not. Analysis of amplitude modulations of ongoing alpha oscillations revealed a stronger increase for *not-remember* items as compared to *remember* items. This effect

was already present within the cue-target interval and persisted during stimulus presentation. Those observations suggest that items that should not be encoded and stored for later retrieval receive more inhibitory supply (Klimesch et al., 2007a) which is reflected in enhanced alpha amplitude.

A possible function for amplitude modulations of alpha rhythms relevant for WM is further suggested by studies measuring visual perception performance (e.g., Babiloni et al., 2006; Ergenoglu et al., 2004; Hamm et al., 2010; Hanslmayr et al., 2007; Mathewson et al., 2009) and spatial attention (e.g., Foxe et al., 1998; Freunberger et al., 2008; Rihs et al., 2007; Sauseng et al., 2005; Thut et al., 2006). For example, Hanslmayr et al. (2007) briefly presented letters that had to be categorized. In this task, detection performance could be predicted by the pre-stimulus alpha amplitude, that is, relatively high alpha amplitude prior to stimulus presentation was associated with detection failures. In an MEG study investigating oscillatory correlates of behavioral errors (Mazaheri et al., 2009), increased pre-stimulus alpha amplitude was shown to be indicative for an upcoming error (Go–NoGo task). In these examples, an increased amplitude of alpha oscillations prior to stimulus appearance had a detrimental effect on performance. In those studies, the strength of alpha amplitudes seemingly varies “by chance” on a random trial-by-trial basis (Mathewson et al., 2009; Mazaheri and Jensen, 2008), or may reflect a trait factor that varies between individuals (e.g., Hanslmayr et al., 2007).

Alternatively, however, alpha oscillations may rather reflect top-down processes in the service of attentional control. This suggestion is in line with findings from spatial attention tasks, in which the amplitude of alpha oscillations in response to the attentional cue is generally higher on sites that are not involved in target processing (Foxe et al., 1998; Freunberger et al., 2008; Rihs et al., 2007; Sauseng et al., 2005; Thut et al., 2006) but also enhances the probability of detecting the upcoming contra-lateral target stimuli. This interpretation could recently been corroborated by studies that combined spatial attention manipulations with the TMS method (Capotosto et al., 2009; Romei et al., 2010). Also here, the results suggest that top-down modulated alpha rhythms are not a mere correlate of visual perception but a mechanism that influences the perceptual fate of an upcoming stimulus.

Taken together, the reviewed studies from the fields of WM, perception, and spatial attention cumulate on the suggestion that alpha oscillations may serve a common control mechanism related to the inhibitory gating of information processing (Jensen and Mazaheri, 2010; Klimesch et al., 2007a).

3. Functional similarity of slow event-related potentials and amplitude modulations of neural oscillations for attentional control of working memory contents

Whether oscillatory activity influences or even generates event-related potentials is still under debate (e.g., Klimesch et al., 2006, 2009; Sauseng et al., 2007), but, functional similarities between early evoked potentials and oscillatory activity suggest the plausibility of a direct link (Freunberger et

al., 2008). Theoretical considerations assume that both, pre and post-stimulus oscillatory activity can modulate or generate evoked potentials (Klimesch et al., 2007b).

Current findings reveal striking similarities between slow evoked potentials like the CDA and 10 Hz alpha oscillations (Nikulin et al., 2007). Furthermore, asymmetric modulations of alpha oscillations are currently discussed as a potential origin of the CDA (Mazaheri and Jensen, 2006, 2010; van Dijk et al., 2010). According to this view, amplitude modulations of ongoing alpha oscillations occur asymmetrically (non-sinusoidal) around baseline implying that oscillatory peaks are stronger modulated than troughs (or vice versa). As the power of alpha oscillations usually decreases after stimulus presentation averaging over trials would result in a slow drift reflected in the event-related potential (Mazaheri and Jensen, 2008). A different viewpoint holds that the non-zero mean of oscillations and not an asymmetry of peaks and troughs is responsible for the generation of slow potentials (Nikulin et al., 2010). Thus, in how far alpha and CDA are 'causally' related remains an open question. Nevertheless, van Dijk et al. (2010) convincingly demonstrated that the CDA shares functional similarities with lateralized posterior alpha activity (i.e. both, CDA and alpha power, increase with increasing WM load), possibly pointing to the same set of WM-relevant neural processes. Together with recent CDA evidence on attention (Drew and Vogel, 2008; Emrich et al., 2009), these findings strengthen the interpretation that CDA and alpha amplitude modulations during WM performance reflect attentional resource allocation, rather than retention per se.

4. Cross-frequency coupling of theta and beta/gamma mirrors retention of relevant information

Regarding oscillatory brain activity, it has frequently been shown that alpha but also theta (~6 Hz) oscillations increase in amplitude with increasing load during maintenance in WM tasks (e.g., Gevins et al., 1997; Grimault et al., 2009; Jensen et al., 2002; Jensen and Tesche, 2002; Klimesch et al., 1999, 2007a; Raghavachari et al., 2001). Accordingly, different types of theta amplitude modulations were reported to subservise a variety of cognitive processes including sustained attention, working memory maintenance, episodic encoding/retrieval processes (see Buzsáki, 2005; Kahana et al., 2001; Klimesch et al., 1994; Klimesch, 1996; Klimesch et al., 1996; Klimesch, 1999; Klimesch et al., 2001, 2005, 2007a, 2008), and may induce long-term potentiation (LTP), the candidate cellular-molecular mechanism for the formation of enduring memory traces (Greenstein et al., 1988; Huerta and Lisman, 1995). Furthermore, numerous studies provide evidence that theta oscillations are relevant to control WM-contents by providing an organizing principle for the relevant memory representations (for review see Sauseng et al., 2010).

Mounting evidence suggests a hierarchical organization of neuronal oscillations (i.e., oscillations of different frequencies are nested in a sense that the faster rhythm is coupled to the phase of the slower one) as a coding scheme to efficiently structure the information flow in the brain (Basar et al., 2001; Canolty and Knight, 2010; Schroeder and Lakatos, 2009; Whittingstall and Logothetis, 2009). To date, the interplay

between oscillations of different frequencies has mainly been studied in the hippocampal region (Axmacher et al., 2010; Buzsáki and Draguhn, 2004; Jutras and Buffalo, 2010; Lisman, 2005; Mormann et al., 2005) and, such methods have barely been applied to MEG/EEG data from humans.¹ Only recently, hierarchically organized task-relevant oscillatory activity has also been reported for human neocortex during performance of cognitive tasks using subdural (Canolty et al., 2006) and surface electrode recordings (Demiralp et al., 2007; Kaminski et al., in press; Palva et al., 2010; Sauseng et al., 2008; Sauseng et al., 2009; Schack et al., 2005).

The amplitude of oscillations may reflect the number of neurons synchronously firing within a specific network, whereas the phase determines the timing of neural activity (Fries, 2005; Klimesch et al., 2007a; Palva and Palva, 2007). According to this line of reasoning, phase-based measures capture the efficient segregation and integration of information carried by different cell-assemblies in a temporal code. By this, not only the amplitude but also the oscillatory phase is a marker of information encoding during perception and memory (Busch et al., 2009; Freunberger et al., 2009; Klimesch et al., 2010; Rizzuto et al., 2003; Rizzuto et al., 2006; Siegel et al., 2009).

With regard to WM especially the phase of theta oscillations seems well suited to act as coordinator to which higher-frequency oscillations can entrain to (Jensen and Colgin, 2007; Kahana et al., 2001; Mormann et al., 2005). In direct support of this conjecture, Axmacher et al. (2010) conducted a sequential memory task (Sternberg paradigm with faces) and intracranially recorded neuronal activity from the hippocampus in epileptic patients. Specifically, the authors analyzed phase-to-amplitude couplings (for methodological details see also, Canolty et al., 2006) and demonstrated stronger theta-locked gamma amplitude modulations during WM maintenance (Fig. 2A). In addition, higher WM load was related to a significant decline of the modulating theta frequency (Fig. 2B).

A second parameter analyzed by the authors was the modulation width which is the phase range of the modulating theta frequency that has impact on the beta/gamma amplitude. The assumption that a higher memory load would show up in a more extended theta phase range was not supported. But, most interestingly, the variation of modulation phase across trials decreased with increasing memory demands and the modulation width predicted shorter reaction times in load

¹ Currently several approaches to detect oscillatory co-activation of different frequency bands (e.g. theta-to-gamma coupling) have been developed (for an overview, see Canolty and Knight, 2010; Jensen and Colgin, 2007; Penny et al., 2008). A detailed description of the different approaches is unfortunately beyond the scope of the current review. We want to point out that the different cross-frequency coupling measures have to be applied and interpreted with caution as it could be shown that they encompass variable sensitivity to true couplings (e.g., Penny et al., 2008) or could even produce artefactual results under certain conditions (e.g. Kramer et al., 2008). The interested reader may be kindly referred to the original publications. Nevertheless, we are convinced that, beside the difficulties in deciphering the best measure for cross-frequency interactions, studying the interaction between oscillatory patterns provides valuable insights in mechanisms of information processing in the brain.

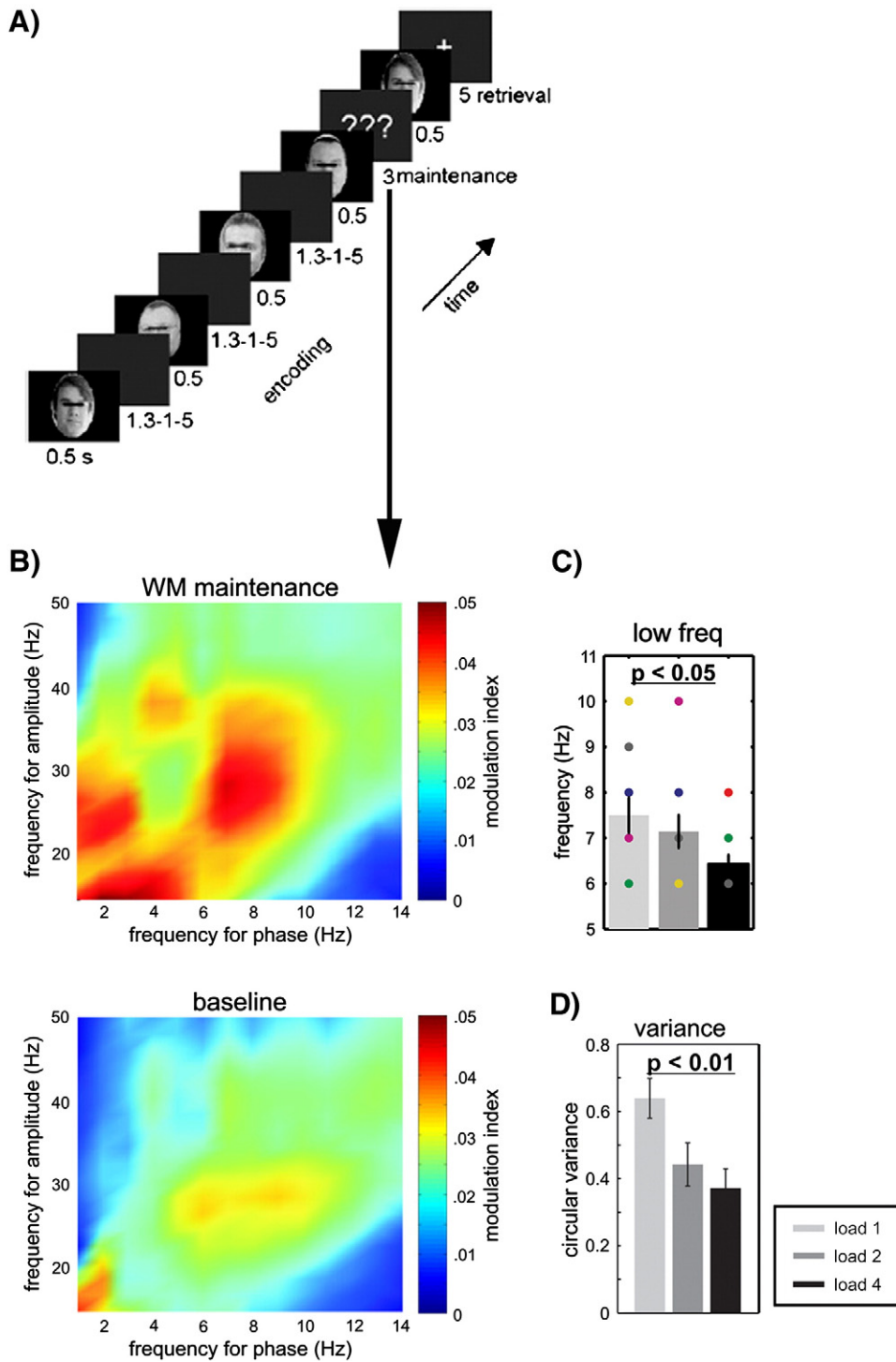


Fig. 2 – Gamma amplitude is coupled to theta phase during working memory maintenance. A) Memory scanning paradigm (Sternberg task) with faces. **B)** During WM-maintenance (top) stronger cross-frequency coupling (expressed as a modulation index, for details see [Canolty et al., 2006](#)) can be observed compared to a baseline (bottom). **C)** The frequency of the modulating lower frequency oscillation decreases as a function of load. **D)** Phase-variance (circular variance refers to variability for circular data like phase angles) declines with increasing memory load. A higher precision (less variance) of the modulating phase is thus required for increasing memory demands. Adapted from [Axmacher et al. \(2010\)](#). PNAS.

1 conditions (Fig. 2C). This finding indicates that a nesting of multiple beta/gamma cycles into one theta period requires high precision and, thus, low variation.

Along similar lines, [Sauseng et al. \(2009\)](#) reported theta-phase locked modulations of gamma power in a CD task by means of scalp-recorded EEG. However, in their study load

variations did not influence the phase-to-amplitude coupling. Rather, increasing retention demands were reflected in a tight phase-to-phase coupling of theta and gamma oscillations (for an overview about different types of cross-frequency interactions and their relative advantages/disadvantages, see Jensen and Colgin, 2007; Penny et al., 2008; Tort et al., 2010). Moreover, theta:gamma phase-locking (a) was more pronounced contra-

lateral to the cued hemifield; (b) was enhanced with increasing load; and (c) predicted individual WM performance. Thus, the cross-frequency coupling observed in these studies appears as a direct marker for WM maintenance (see Fig. 3).

The precise physiological foundation of these and other coupling mechanisms remain to be discovered (Buzsáki, 2006). For example, not only cross-frequency but also cross-regional

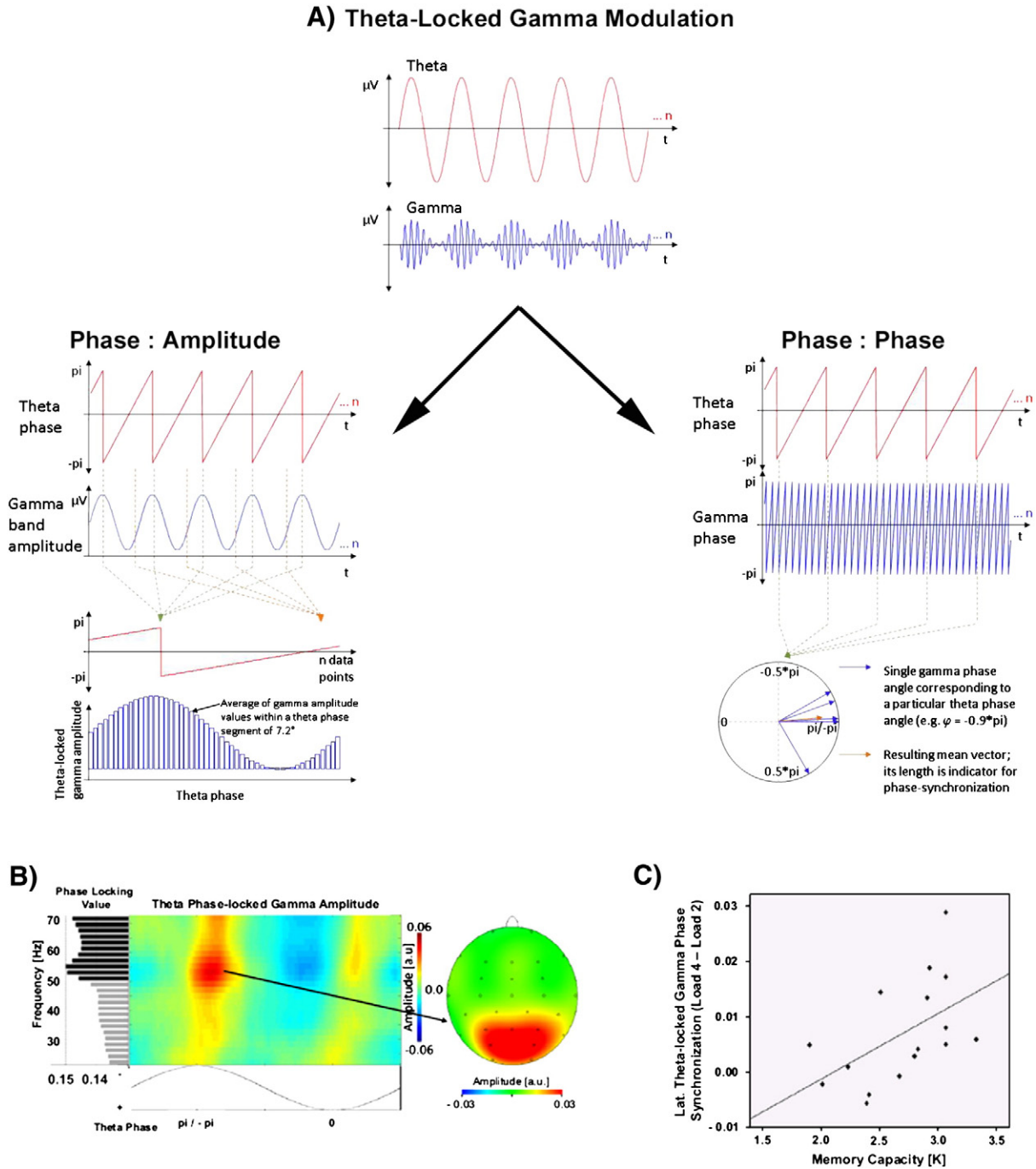


Fig. 3 – Phase and amplitude of gamma are locked to theta. A) Schematic illustration of theta:gamma coupling. The coupling can be analyzed as a phase:amplitude modulation or as a phase:phase modulation. B) High-frequency amplitudes were sorted to theta phases and the amount of phase-locking was calculated. C) Hemispheric differences in theta:gamma phase-locking predict memory capacity.

Figures adapted from Sauseng et al. (2009). *Curr. Biol.*

couplings reflecting the integration of distributed functional networks (Varela et al., 2001) were shown to be markers of WM capacity (e.g., Palva et al., 2010). Moreover, a study by Griesmayr et al. (2010) provided evidence that WM sub-processes are integrated by interregional theta:gamma phase coupling. In this study frontal midline theta was coupled to distributed gamma networks at frontal and left parietal electrode sites within the retention interval of a verbal delayed match to sample task.

5. Implications for models of capacity limits in WM

We summarized recent findings on neural correlates of successful WM maintenance primarily focusing on processes of inhibition and retention. The reported findings have implications for understanding capacity limits in WM.

Currently, two viewpoints dominate the discussions about the nature of WM capacity limits: the discrete slot model suggests an upper capacity limit for a fixed number of items, independent of their complexity (Awh et al., 2007; Luck and Vogel, 1997; Rouder et al., 2008; Vogel et al., 2001). In contrast, the flexible resource model suggests capacity limits to arise from overtaxing a shared resource. This view posits that an increasing number of items can be stored at the cost of decreasing resolution for each single item (Bays and Husain, 2008; Bays et al., 2009; Wilken and Ma, 2004).

Classical CDA findings can be interpreted in support of the fixed-slots model, but not of the resource model (Fukuda et al., 2010). This is based on the observation that behavioral capacity estimates, as well as CDA amplitudes show an increase with increasing WM load, until an asymptotic limit of about four items is reached (e.g., Vogel and Machizawa, 2004; Vogel et al., 2005). Very similar interpretations can be derived from neuroimaging studies showing an association between the number of item representations to be maintained in WM and activity in the intra-parietal sulcus (Todd and Marois, 2004; Todd and Marois, 2005; Xu and Chun, 2006).

The assumptions of discrete models are consistent with computational models of WM suggesting that theta-phase-locked gamma oscillations may provide a temporal coding scheme for memory maintenance (Jensen and Lisman, 1998; Lisman and Idiart, 1995). In these models, several memory items are bound together within different high frequency gamma cycles (Raffone and Wolters, 2001; Siegel et al., 2009) and the whole sequence of a memory set is repeated in theta cycles. It was suggested that such a coding scheme would enable the generation of LTP in hippocampal areas during sequence learning (Jensen and Lisman, 2005). A major consequence of such a cortical multi-item WM buffer would be that short-term memory capacity is constrained by the number of gamma cycles fitting within one theta cycle. The memory capacity would be predicted by the low:high frequency ratio, which would determine an upper storage limit. It thus could be argued that an increasing memory load would result in a slowing of theta frequency allowing for the encoding of more items, which are represented by gamma cycles that are nested in theta cycles (Jensen and Lisman, 1998).

In support of this theoretical framework Axmacher et al. (2010) showed a slowing of the modulating theta frequency with increasing memory demands.

Furthermore, the tight phase-to-phase coupling observed by Sauseng et al. (2009) and the tensor phase width and lower phase variance with increasing memory load (Axmacher et al., 2010) are consistent with the hypothesis that phase information is crucial for keeping multiple items in WM distinct and separable. Another finding by Axmacher et al. (2010) was that the frequency ratio between the high and the low frequency was constant at ~ 4 . This finding seemingly contradicts the proposed Jensen and Lisman model but, most interestingly, predicts the suggested visual memory span of 4 (± 1) (Cowan, 2001). In a recent approach by Kaminski et al. (in press) theta/gamma ratios were determined individually and also predicted memory capacity. Thus, it seems that with respect to different task demands (memory for faces, letters or spatial locations), subject pools (patients versus healthy subjects) or recording methods (intracranial vs. surface recordings) no completely homogenous findings regarding cross-frequency couplings are derived so far. A future topic for research in this field refers to the questions what physiological mechanism exactly drives the ratio of low:high frequencies, possibly on a trial-by-trial basis. This would promote the question of whether low:high couplings reflect a mechanistic synchronization between oscillations functionally serving WM-retention or a mere statistical dependence between filtered signals (see Canolty and Knight, 2010 for a discussion).

However, some of the evidence summarized here challenge the assumption of discrete slots, and support the multi-component framework, which posits that multiple processes jointly limit performance on WM tasks (e.g., Barton et al., 2009; Fukuda et al., 2010). Specifically the results by Sauseng et al. (2009) demonstrate a clear distinction between oscillatory neuronal mechanisms related to suppression of irrelevant and retention of relevant information that interactively influence WM performance. An intermediate model may therefore assume that a limited number of slots determine the maximum number of representations held in memory, while the resolution of the representation is determined by available attentional resources (Awh et al., 2007; Barton et al., 2009; for a recent review, see Fukuda et al., 2010; Zhang and Luck, 2008). Thus, a two-factor model may be needed to explain WM performance. This view is consistent with recent neuroimaging studies reporting dissociable neural mechanisms that contribute to WM performance (Song and Jiang, 2006; Xu and Chun, 2006; Xu, 2007; Xu, 2009; Xu and Chun, 2009).

6. Conclusions

The reviewed findings suggest an intermediate model of WM capacity limits. According to this view, attentional resources may be implemented in the brain by alpha amplitude fluctuations (Grimault et al., 2009; Klimesch et al., 2007a; Sauseng et al., 2005; Thut and Miniussi, 2009). Alpha activity may serve as an attentional 'gatekeeper' that allocates priority to certain stimuli for WM storage by enabling an optimal signal-to-noise ratio, thus reducing possible interference with conflicting sensory input (Bays and Husain, 2008; Bays et al., 2009; Jokisch and

Jensen, 2007; Payne and Kounios, 2009), a function of utmost importance for successful WM performance.

Both, theta and alpha oscillations seem to reflect control processes serving the memory system but may not be unique to WM. As stated recently (Klimesch et al., 2008), more complex measures that capture low:high frequency coupling might provide the proper tool to study phenomena related to WM maintenance in a strict sense. Especially in situations with increasing memory demands, the high frequency rhythm is enforced to tightly couple to certain phases of low-frequency oscillations to enable and enhance segregation between different memory items. Specifically, phase:phase coupling measures are well suited to reveal tightly synchronized interactions and by this represent an alternative tool that adds knowledge to previous findings on phase:amplitude measures. Along these lines, theta-to-beta/gamma couplings emerge as a neural code for successful retention of relevant information in WM.

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