

VU Research Portal

Oscillatory Control over Representational States in Working Memory

de Vries, Ingmar E J; Slagter, Heleen A; Olivers, Christian N L

published in

Trends in Cognitive Sciences
2020

DOI (link to publisher)

[10.1016/j.tics.2019.11.006](https://doi.org/10.1016/j.tics.2019.11.006)

document version

Publisher's PDF, also known as Version of record

document license

Article 25fa Dutch Copyright Act

[Link to publication in VU Research Portal](#)

citation for published version (APA)

de Vries, I. E. J., Slagter, H. A., & Olivers, C. N. L. (2020). Oscillatory Control over Representational States in Working Memory. *Trends in Cognitive Sciences*, 24(2), 150-162. <https://doi.org/10.1016/j.tics.2019.11.006>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Review

Oscillatory Control over Representational States in Working Memory

Ingmar E.J. de Vries,^{1,*} Heleen A. Slagter,¹ and Christian N.L. Olivers¹

In the visual world, attention is guided by perceptual goals activated in visual working memory (VWM). However, planning multiple-task sequences also requires VWM to store representations for future goals. These future goals need to be prevented from interfering with the current perceptual task. Recent findings have implicated neural oscillations as a control mechanism serving the implementation and switching of different states of prioritization of VWM representations. We review recent evidence that posterior alpha-band oscillations underlie the flexible activation and deactivation of VWM representations and that frontal delta-to-theta-band oscillations play a role in the executive control of this process. That is, frontal delta-to-theta appears to orchestrate posterior alpha through long-range oscillatory networks to flexibly set up and change VWM states during multitask sequences.

Selective Control over Working Memory-Guided Attention

Everyday life overloads us with sensory information, forcing us to ignore distractions and selectively focus on what is relevant to our current goal. Attention is the collection of mechanisms that serves this challenging task. Attention can be regarded as an input filter [1], which, through the preactivation of sensory representations relevant to our behavioral goal, prioritizes the sensory processing of matching information [2]. This preactivated sensory filter is often referred to as the **attentional template** (see [Glossary](#)) and, within the visual domain, models assume that it is part of VWM [3,4]. However, traditionally, research on attentional templates has made use of single task paradigms, in which the observer's perceptual goal remains constant throughout a trial, a block, or even an entire experiment. This ignores the dynamic nature of everyday activities, which are often characterized by complex **multitask sequences** that cause the relevance of specific sensory information to rapidly change depending on the stage of the sequence ([Figures 1A and 2A](#)). For example, when searching for a specific screwdriver in the DIY store, one may first look for the tool aisle, then for the screwdrivers, and then for the specific type that one requires. Such task sequences imply important, yet relatively little-studied functionalities of VWM, as they require the system to flexibly exchange attentional templates. Here, we review recent work showing that neural oscillations play an important role in the control over these attentional templates.

Different Representational States in Working Memory

The recent use of multitask sequences has brought important new insights for our understanding of working memory. Specifically, studies have investigated how, besides serving our current perceptual goals, working memory also allows us to plan ahead and maintain representations for future goals across a series of tasks. To prevent interference, such **prospective representations** should be shielded from interacting with the current sensory input. Indeed, evidence indicates that while stimuli matching a currently relevant representation attract attention, stimuli matching a prospectively relevant representation held in memory do not bias attention to the same extent during the working memory maintenance period prior to task execution ([Figure 1](#); see [5,6]). Im-

Highlights

Neural oscillations serve important regulating functions in the interaction between working memory and sensory input in sequences of visual selection tasks.

During multitask sequences, alpha (~10 Hz) oscillations above visual cortex regulate which sensory working memory representation in early visual cortex is activated and, therefore, interacts with the current sensory input, and which information is (temporarily) deactivated, to prevent such interaction.

Delta-to-theta (~2–8 Hz) oscillations above frontal brain regions orchestrate alpha oscillations above visual cortex during both the initialization and switching of representational states in VWM when executing multitask sequences.

¹Department of Experimental and Applied Psychology and Institute for Brain and Behavior Amsterdam, Faculty of Behavioural and Movement Sciences, Vrije Universiteit Amsterdam, Van der Boerhorststraat 7, 1081BT, Amsterdam, The Netherlands

*Correspondence
i.e.j.de.vries@gmail.com (I.E.J. de Vries).



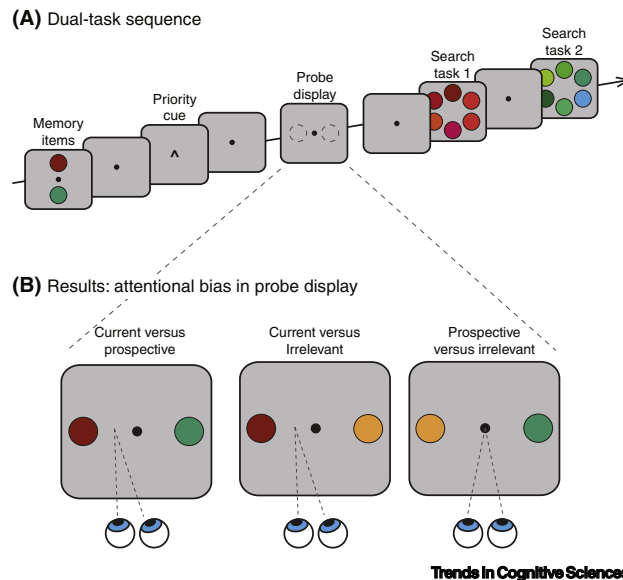


Figure 1. Selective Attentional Guidance by Working Memory Content. This figure does not represent real data, but rather summarizes the results from a recent study [5]. (A) Observers were instructed to memorize two colors as targets for a sequence of two visual search tasks. A priority cue informed them which color was needed for the first search task (with the remaining color being needed for the second task). During the delay period leading up to the first task, two task-irrelevant probe colors appeared in the periphery. (B) Although observers were required to maintain fixation, subtle eye movements revealed a bias towards probes that matched the target for the first upcoming task, but not towards probes that matched the target for the prospective task. These results demonstrate that which of the multiple items in memory is allowed to guide attention is under strategic control.

Importantly then, whether or not memories are allowed to drive attention is at least in part under strategic control [7]. Inspired by these and similar findings, governing theories now distinguish two functionally different representational states in WWM [8–10]: (i) the currently relevant, prioritized, representation that is needed for the imminent, upcoming task and that is able to directly interact with sensory input; and (ii) prospectively relevant representations needed for future tasks, which, while still being accurately retained, are shielded from interaction with the current task to prevent interference. Additionally, if afforded by the available information, the prioritized representation might include an action plan that allows for a direct interaction with response output [11, 12]. The exact neurophysiological nature of these states remains elusive, although neuroscientific evidence indeed supports the existence of dissociable storage mechanisms for (at least) two representational states within WWM (Box 1).

One important aspect that only recently started to receive attention are the mechanisms that enable the dynamic control over this prioritization process in WWM. Specifically, which neural signals initiate the prioritization of representational states and subsequent switches between them when task demands change? Most interest thus far has been in how different representational states differ in terms of storage. Therefore, most studies have utilized pattern classification of fMRI data, which allows for the decoding of specific low-level features from the spatial pattern of activity in visual cortex (Box 1; [13–15]). However, the main disadvantage of fMRI is its low temporal resolution in the order of several hundreds of milliseconds to seconds, caused by the sluggishness of the blood oxygen level-dependent signal. The dynamic control over different representational states during multitask sequences, and switches between those states in between tasks, generally occur at the subsecond time scale and may be served by relatively fast neural

Glossary

Attentional template: an active (also commonly termed prioritized or attended) working memory representation that serves to bias sensory processing towards task-relevant input. It is also commonly referred to as target template, search template, or attentional set. The attentional template in working memory undergoes a flexible functional transformation from abstract goal towards task-specific feature filter that optimizes target detection by enhancing matching sensory input [12,86,87], utilizing all necessary brain structures in its path [63]. In multitask sequences, this state allows a working memory representation to directly guide the current or imminent perceptual task.

Multitask sequences: for the purpose of this review we define multitask sequences as predictable sequences of multiple instances of the same type of working memory-driven tasks, such as searching for a color amongst distractors (Figures 1A and 2A). Importantly, here only the target, and thus the sensory working memory representation, changes from task to task, while the overall task itself remains the same (i.e., find the memorized color). Moreover, such task sequences allow for prospectively planning the next perceptual goal. Note that this is different from typical procedures in the task-switching literature, in which the tasks themselves differ within a sequence, while the perceptual input serving those tasks is unpredictable [61].

Multivariate pattern analysis

(MVPA): utilizes machine-learning algorithms to extract information from a distributed (e.g., spatial or temporal) pattern of neural activity that characterizes the difference in the brain's response between experimental conditions, such as the presentation of two different stimuli, or the inducing of two different attentional states. It usually does so in a data-driven manner, not relying on prior knowledge of the exact nature of these multivariate patterns. Contrary to traditional univariate techniques, it is sensitive to complex and widespread patterns of relevant neural activity, even if these patterns change over time and differ per individual. This procedure is also sometimes termed pattern classification or decoding.

dynamics. These temporal dynamics are therefore better captured by magneto- and electroencephalography (M/EEG), or by invasive electrophysiological recordings in animals or patients, as these methods have superior temporal resolution. Recent findings from human M/EEG studies specifically converge on the importance of neural oscillations (Box 2) for selectively controlling the interaction between VWM and sensory input. One recurring theme that seems especially important in this regard is how frontal executive control areas mediate the selective top-down control over sensory processing in posterior areas of the brain. In this discussion, we will therefore distinguish between sensory control in posterior areas and executive control implemented in frontal areas. Moreover, we focus the discussion on M/EEG findings, as to our knowledge there are no studies using invasive techniques that have investigated task-driven priority in VWM.

Control over Perception through Posterior Alpha (~8–14 Hz) Oscillations

A large body of work points to a crucial role for alpha-band oscillations in modulating visual processing in the posterior brain. Perhaps counterintuitive, a reduction in the amplitude of alpha oscillations, also termed alpha suppression or event-related desynchronization, goes hand in hand with an increase in neural activity in that region [16,17], suggesting that alpha-band oscillations functionally reflect inhibition. Thus, alpha suppression reflects an increase in the excitability (or release of inhibition) of underlying neuronal populations, while alpha enhancement (i.e., increased amplitude, or event-related synchronization) conversely is thought to reflect a decreased excitability or increased inhibition [18,19]. Yet, it should be noted that while alpha oscillations clearly modulate cortical excitability, it is currently debated whether alpha oscillations implement active top-down inhibition of sensory processing (Box 3). Notably, it has been proposed that alpha oscillations may enhance signal-to-noise ratio by allowing only a (comparatively) small number of neurons to process information selectively and silencing the majority of other neurons [20]. That is, alpha oscillations may optimize tuning to task-relevant features in visual regions by selectively suppressing activity of neurons tuned to other features. As such, it provides a prime mechanism for prioritization.

Indeed, attention studies have shown that when the location of an upcoming target is cued, attentional allocation results in alpha suppression above contralateral visual cortex and/or alpha enhancement above ipsilateral visual cortex (i.e., the retinotopic regions responsible for processing information from the task-relevant and -irrelevant visual fields, respectively) [21]. There is ample evidence that these modulations are functionally involved in sensory processing, rather than reflecting a mere epiphenomenon [22–26]. Moreover, recent studies show that the current focus of attention can be decoded and reconstructed from the pattern of alpha-band EEG activity prior to stimulus presentation [27,28]. There is also evidence that alpha-band oscillations play a critical role in the top-down control of preparatory inhibition prior to stimulus encounter [19,29]; however, as detailed in Box 3, the empirical evidence for this notion is ambiguous [30].

Control over Mnemonic Representations through Posterior Alpha Oscillations

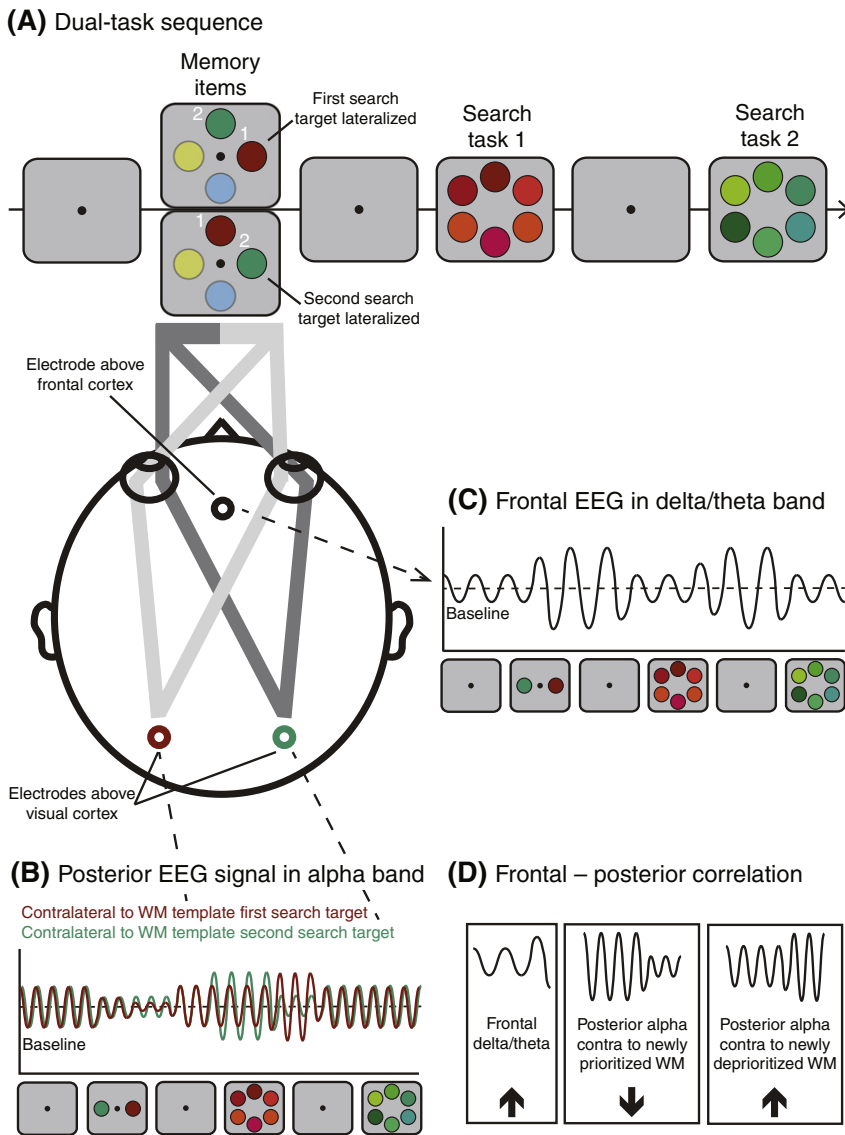
Importantly, modulations of alpha-band activity not only support the prioritization of incoming sensory information, but also of mnemonic representations [31]. In a number of studies, observers were instructed to memorize items presented on each side of fixation and only during maintenance were informed, by means of a *post hoc* cue, which of the items would be eligible for report. This resulted in alpha being more suppressed contralateral to the cued items [32–35], more enhanced contralateral to the uncued items [36], or both [37,38]. Furthermore, alpha enhancement induced by contralateral repetitive transcranial magnetic stimulation (rTMS) at 10 Hz, decreased VWM performance when applied during maintenance, while rTMS applied over ipsilateral sites increased performance [39]. Moreover, contralateral alpha suppression

Prospective representation:

functionally, a working memory representation that should not yet affect current stimulus-response mapping. In a multitask sequence, this state allows a prospectively relevant working memory representation to be temporarily shielded from the current perceptual task, such that it can be safely maintained until it might become relevant for a later perceptual task in the sequence. Current neurophysiological evidence suggests it may be in a deactivated (also commonly termed deprioritized, activity-silent, latent, dormant, hidden, unattended, passive, or accessory) working memory state [10,88].

Key Figure

Frontal–Posterior Oscillatory Control over Representational States



Trends In Cognitive Sciences

Figure 2. This figure does not represent real data, but rather summarizes the results from a selection of studies [43–47,49]. (A) Observers were instructed to memorize two colors for two subsequent visual search tasks. A priority cue informed them on task order, here indicated by white numbers. On each trial, only one of the two memory items was presented lateralized, while the other was presented on the midline. Any lateralized electroencephalography (EEG) patterns could thus be attributed to a specific representation. (B) After presentation of the memory items, the amplitude of alpha oscillations above visual cortex typically decreases (alpha suppression). While initially similar, this decrease becomes transiently stronger contralateral to the prioritized representation in working memory (WM) (red line). After this initial decrease, alpha goes back to baseline. In contrast, the amplitude then increases (alpha enhancement) contralateral to the deprioritized representation (green line). After the first search task has completed, priority switches from the first to the second representation, which is mirrored by

(Figure legend continued at the bottom of the next page.)

scales with the difficulty of the visual task for which the item is memorized, even if the memory item itself did not differ [40]. Last, one study found stronger alpha lateralization for mnemonic representations compared with external attention to empty space [41]. These studies collectively confirm that alpha has a specific role to play in VWM, rather than purely reflecting attention to the outside world.

Crucially, recent work shows that alpha activity does not simply reflect maintenance of items in VWM, but rather their current relevance (see Figure 2A,B, Key Figure, for a graphical overview). That is, alpha activity selectively tracks the item that is currently relevant or prioritized [42]. Moreover, when multiple items are stored for multitask sequences, alpha is suppressed more for the currently prioritized representation, compared with prospective representations [43,44]. Furthermore, as priority switches from one representation to the next in between two search tasks, so does alpha suppression. Specifically, after completing the first search task, alpha suppression selectively re-emerges contralateral to the representation needed for the second search task [43,45,46]. Similarly, contralateral alpha suppression also reappears when a hitherto irrelevant representation is expected to become task relevant in the near future [47]. Together, this suggests that attentional selection and prioritization within multi-item working memory is brought about by a selective and endogenously generated increase in the excitability of the neural populations coding for the sensory memory representation that is currently or imminently task relevant.

Conversely, in anticipation of a first perceptual task in a multitask sequence, alpha is temporarily enhanced contralateral to a prospective memory representation that should not interact with the first task [43], suggesting that the representation itself is being suppressed. One interpretation is that this reflects a mechanism to protect the sensory memory representation from interference of the current perceptual task, by stopping new visual information from being processed at that sensory location [48]. This is supported by reduced perceptual performance at that retinotopic location [43]. However, contralateral alpha enhancement is also observed for a representation that can be dropped from memory completely, because it proves no longer relevant [43,49]. Such to-be-dropped memories would not need protection from perceptual interference. Therefore, an alternative interpretation is that alpha enhancement in working memory serves to prevent irrelevant (temporarily or not) memories from interfering with the current perceptual task (possibly by rendering their representation less precise [42]), rather than the other way around. Interestingly, such a representation-specific mechanism for interference prevention is not utilized if the working memory representation is actually cued to be a salient distractor, rather than a target, on an upcoming task (Box 3). Taken together, the discussed effects in retinotopically selective alpha modulations indicate that alpha suppression and enhancement serve to prioritize and deprioritize working memory representations and may reflect changes in the fidelity of sensory representations so as to gate their interaction with the sensory input. These alpha dynamics occur rapidly, supporting the neural deactivation and reactivation of working memory representations as changing task requirements may also rapidly unfold.

Spatiotemporal Specificity of Alpha Oscillations in Working Memory

One important outstanding question is whether there is any functional significance to the spatial source of alpha-band activity and whether alpha can also be used to track the representational

alpha. That is, alpha now suppresses contralateral to the newly prioritized representation (green line), while alpha enhances contralateral to the newly deprioritized representation (red line). (C) Both after presentation of the priority cue, as well as after completing the first search task, the amplitude of low-frequency (delta-to-theta) oscillations above frontal cortex transiently increases. (D) Importantly, these frontal low-frequency oscillations correlate with modulations in alpha oscillations above visual cortex later in time and the task changes they accompany. Thus, frontal cortex seems to drive the (de)activation of sensory representations in visual cortex.

Box 1. Two Dissociable Mechanisms of VWM Storage

Neuroscientific evidence suggests distinct mechanisms of storage for prioritized and prospective working memory representations. For attention to be optimally guided towards task-relevant information, the prioritized VWM representation should entail as detailed as possible visual feature information. It would therefore benefit from engaging the brain system specialized in representing such detailed visual information: the visual cortex. Indeed, using MVPA, feature-specific visual information can be decoded from the human visual cortex when the actual visual input is absent, both during working memory [13–15] and mental imagery [89,90] tasks. Such findings have provided the foundation for the sensory recruitment theory, which postulates that VWM activates feature-specific sensory processing areas to keep high-fidelity information online, even when the actual sensory input is no longer present [64,91–93]. Moreover, sensory recruitment provides an elegant mechanism for top-down attentional enhancement, as the sensory (pre)activation automatically leads to prioritized processing of matching sensory input, thus providing a mechanism for automatically guiding attention towards task-relevant information [8,12,86,87].

Prospective memory representations, however, should not guide attention and thus must be precluded from direct interaction with the ongoing perceptual task. Here sensory recruitment might actually be detrimental. Indeed, activity-based maintenance in early visual areas has been found to be reserved for items serving the currently prioritized task, as decoding accuracy of prospective memory items temporarily drops to baseline, only to return to reliable levels once they become task relevant and thus reactivated [94]. One proposal is that deprioritized representations are stored in an activity-silent manner, for example, through synaptic weight changes [10] or short-term potentiation [95]. Alternatively, sustained activity for the prospective memory might still be present, yet in more anterior regions (i.e., intraparietal sulcus and frontal eye fields) [96] or in a manner that is not decodable using noninvasive methods (e.g., in firing rates of sparsely distributed neurons) [97]. Yet another possibility is that interference is prevented by inverting or otherwise transforming the pattern of either neural activity or responsibility for the prospective representation [98,99]. No matter the exact storage mechanism, prospective memories can be readily reactivated or exposed in visual cortex with stimulation not specific to the memory [88,100–102], or endogenously, by the observer. Ergo, they are waiting just below the surface to be released from their apparent silent captivity.

state of nonspatial information in working memory. Most research on posterior alpha oscillations in working memory has so far presented items at distinct locations, such that each modulation in alpha power at a specific location can be assigned to a specific item, usually by separating items by hemifield (resulting in alpha lateralization). Indeed, working memory items are initially coded for by spatially specific neuronal populations, which thus represent their locations [50,51]. However, although a handy experimental tool, this spatial specificity does not typically occur for everyday task sequences, where different perceptual goals for current and prospective tasks are not necessarily linked to any specific location, but rather are of a global, nonspatial nature, acting as spatially independent feature filters across the visual field. In these typical paradigms used in the lab, one may therefore expect a transformation from a spatially lateralized to a global representation, mirrored by a change in the spatial pattern of posterior alpha oscillations. Consistent with this, in working memory tasks in which to-be-memorized features are presented left or right from fixation, but in which this spatial location is not relevant for the memory test, the lateralized alpha effect is usually transient and mainly observed early in the working memory delay period [34,40,43,44], likely reflecting a transient selection cue for the recently encoded sensory information that needs to be prioritized [32,37]. In fact, one study showed that shorter alpha lateralization predicted better behavioral performance, suggesting more efficient selection [52]. In contrast, global (i.e., bilateral) alpha suppression has been shown to be more sustained and load-sensitive throughout the delay period [53,54], consistent with a more global representation. Furthermore, we recently showed that the priority status of working memory representations can be decoded from a complex and distributed pattern of alpha activity, which only stabilizes later during the delay period [45]. Note that these possibilities are not mutually exclusive, as spatially local and global representation likely exist in parallel [33,54]. Note also that under certain circumstances it may actually pay off to keep the spatial code, even when nominally task-irrelevant. First, the untransformed, spatially specific memory may provide the highest quality of representation [50]. Second, if available to the observer, spatially separated memory items might provide an additional context cue for separating and selectively retrieving current and prospective

Box 2. Neural Oscillations

Neurons communicate through electrochemical signals, thereby creating electromagnetic fields. If a sufficient number of aligned postsynaptic neurons activate synchronously, they can produce an aggregated electromagnetic field, large enough to be picked up outside the brain. Cortical pyramidal neurons fulfill these requirements and the M/EEG signal is therefore thought to mainly reflect the large-scale synchronous activity of these cells [103].

While the fluctuations observed in the M/EEG signal might seem random at first glance, a closer inspection reveals a highly structured rhythmicity, referred to as neural oscillations. Various forms of neural activity at different scales (including individual neurons) can give rise to such oscillations, but the most common sources of oscillatory activity in M/EEG are assumed to be local networks (i.e., microcircuits) consisting of populations of excitatory pyramidal cells and inhibitory interneurons [104–106]. Neural oscillations as observed in the M/EEG signal are commonly believed to regulate the level of excitability of masses of underlying neurons [16]. While ongoing neural oscillations are an inherent property of spontaneous brain activity [106], experimental events elicit modulations of the signal. Indeed, a plethora of research has now linked specific modulations of oscillations to various cognitive processes, and many neurological and neuropsychiatric conditions exhibit anomalies in oscillatory activity [107].

Neural oscillations are generally grouped into a few characteristic frequency ranges (or bands) that have each been related to specific cognitive processes. Commonly studied properties of neural oscillations that are modulated by cognitive processes include (but are not limited to) the amplitude (also termed power, which is the squared amplitude [108]), the phase [109], and phase coupling (also referred to as phase-synchronization or coherence) [110,111]. Phase coupling reflects a consistent temporal relationship between the phases of multiple oscillatory cycles, between local or distant brain regions, and it allows for the temporal coupling of neural activity, providing an index of their functional connectivity. Most neurocognitive processes require combined effort from multiple specialized brain regions and phase coupling is believed to play a crucial role in information transfer between those regions. While it is perhaps the most commonly studied mode of interareal coupling, amplitude–amplitude coupling and phase–amplitude coupling are also observed in large-scale networks during various cognitive processes [112]. Furthermore, communication through synchronized neural activity does not only occur within, but also across, frequency bands (i.e., cross-frequency coupling [113]), another testament to the versatility of the oscillatory signal.

representations. Indeed, we have observed a transient return of alpha lateralization in the second delay period in some cases [43,45,46]. Interestingly, performance on the second task is higher in those situations in which the alpha lateralization corresponding to the item's original location indeed returns, even though that location was task-irrelevant. Modern techniques such as forward encoding models of the spatial pattern of alpha oscillations might provide a deeper understanding of the role of the spatial code, by allowing for the tracking of a more fine-grained spatial profile of alpha oscillations for different representational states [55–58].

Executive Control through Frontal Low-Frequency (~2–8 Hz) Oscillations

While the above sections illustrate the importance of alpha oscillations in sensory regions for the prioritization of task-relevant memories during multitask sequences, it is unlikely that they carry the task goals themselves, and the planning thereof (i.e., 'I should find a red circle first and a blue circle second'). These types of higher-order cognitive processes are typically associated with the frontal cortex. Indeed, the frontal cortex plays a crucial role in the planning of goal-directed behavior [59], in managing multiple goals [60], and during task switching [61]. Specifically, during working memory tasks, the frontal cortex processes and maintains abstract goal-related representations, as well as item-specific information (i.e., frontal neurons show mixed selectivity; [62]), based on which it coordinates activity in sensory regions [63,64]. For example, fMRI studies show increased connectivity between frontal cortex and posterior task-relevant sensory regions specific to the working memory representation that is currently prioritized by means of a cue presented during the maintenance period (i.e., a retro-cue; [65,66]). This increased connectivity furthermore predicts better performance for the cued memory representation [67]. As such, during multitask sequences, frontal cortex could serve to selectively orchestrate the activation, deactivation, and reactivation of more fine-grained working memory representations in sensory

Box 3. Oscillatory Mechanisms of Preparing for Visual Distraction

In the main text, we discussed how prospective memories are shielded from interaction with perception by alpha enhancement. But what if one actually has advance knowledge about a distractor in an upcoming perceptual task? Is it possible to form a template for rejection in VWM? If so, is such a 'negative' attentional template deprioritized the same way as prospective memories that are irrelevant for the current task, but that do not appear as distractors? Or, alternatively, does it involve a third representational state that actively suppresses activity in visual regions that represent the distracting information in advance, such that attention is not drawn to the distracting input?

Specifically, if an advance inhibitory template would exist, one would predict that the feature-specific sensory memory representation would be inhibited prior to search. If that memory retains a spatial specific code, this should result in posterior alpha enhancement contralateral to the anticipated distractor in memory. However, we recently demonstrated that lateralized posterior alpha suppression does not dissociate between anticipated distractors and anticipated targets [46]. This is in line with other recent experiments that failed to provide strong evidence for such advance distractor inhibition in working memory [114,115]. These and other recent findings call into question the commonly held notion that alpha activity (whether pre- or poststimulus) reflects active top-down inhibition ([19,27,29,30,116,117]; but see [118]). Thus, while alpha-band activity clearly reflects cortical excitability and can be used to track the prioritized item in working memory, currently, there is little evidence that they also play a role in setting up negative attentional templates, or in active inhibition of distractor processing more generally. Distractor inhibition may, in contrast, rely on mechanisms that render the target template maximally distinct from the distractor [119], or may bypass working memory altogether [114].

regions. A recent model of VWM proposes a flexible interaction between general-purpose 'conjunction' neurons in prefrontal cortex which can selectively activate combinations of feature-specific neurons in sensory cortex [68]. The frontal conjunction neurons then regulate their respective priority (i.e., activation and deactivation) through recurrent feedback.

But by which signal could such neurons in frontal cortex differentially orchestrate local sensory processing for different representational states in working memory? During visual attention tasks, frontal cortical areas exhibit control over sensory areas through synchronized oscillatory activity [69,70]. Evidence points specifically to frontal oscillatory activity in the lower frequency range (delta-to-theta; 2–8 Hz) as a key mechanism for top-down control over visual selection [71,72] and when preventing distraction [73]. Interestingly, this cross-frequency coupling during selective attention has been shown to be absent in children with attention deficit hyperactivity disorder (ADHD) [74], which supports the notion that it reflects an important neural control mechanism for effective prioritization of information. Importantly, recent findings suggest that frontal low-frequency oscillations [75] and frontal-parietal network interactions are involved in executive control during working memory tasks [40,76–78]. These findings collectively lead to the hypothesis that frontal cortex controls the initiation of, and switching between, different representational states within sensory working memory during multitask sequences and that it might do so through low-frequency oscillations. Indeed, we recently demonstrated that transiently coupled functional networks between frontal and posterior regions underlie the top-down control of goal-driven switches in representational states in VWM, as reflected in both amplitude–amplitude and phase–amplitude coupling between frontal delta (2–4 Hz) and lateralized posterior alpha oscillations ([43]; see Figure 2C,D for a graphical overview). Specifically, when in between tasks priority switched to a hitherto deprioritized (prospective) sensory memory representation, higher frontal delta power predicted stronger contralateral posterior alpha suppression, while the phase of frontal delta coupled more strongly to the amplitude of contralateral compared with ipsilateral posterior alpha. Conversely, for hitherto prioritized representations that became irrelevant and needed deprioritization, higher frontal delta power predicted stronger contralateral posterior alpha enhancement, while the phase of frontal delta coupled more strongly to the amplitude of ipsilateral compared with contralateral posterior alpha. Furthermore, when participants memorized only a single working memory representation that was relevant for either the first or

Box 4. Gamma Oscillations

Gamma oscillations (>32 Hz) are not extensively discussed here, as they are not much studied in terms of representational states in working memory and since they emerge more locally and are therefore arguably less directly related to top-down control. In fact, gamma might more directly reflect dynamics of cortical microcircuits and single neuron firing [120] and are particularly suggested to encode sensory information [121–123], as working memory content can be decoded from EEG gamma [124]. Working memory-related gamma is observed both in frontal and posterior regions, and distinct aspects of working memory are thought to involve distinct cross-frequency coupling ‘codes’ between gamma and either theta or alpha in distinct neural regions [122].

Alpha-gamma coupling is mostly observed in posterior regions (e.g., visual cortex) during sensory working memory [122,125]. Within visual cortex, gamma proceeds in a feed-forward direction, while alpha proceeds in opposite, feedback direction [126]. A very similar beta-gamma coupling is observed during visual attention [127]. While these gamma oscillations presumably reflect the sensory representation itself (be it perceptual or working memory), alpha oscillations modulate these sensory representations through feedback loops. In fact, it has been proposed that different gamma cycles reflect separate visual memories that are temporally organized according to the phase of alpha cycles [128]. Specifically, gamma oscillations appear mainly in the trough of the alpha cycle, mirroring the locking of neuronal firing to the trough of alpha cycles in visual cortex [17]. One prediction of this proposition is that if alpha amplitude increases, troughs become temporally ‘sharper’, leaving room for fewer gamma oscillations and thus fewer working memory representations. However, it is still unclear how this temporal segmentation of multiple representations relates to different representational states during multitask sequences (see [Outstanding Questions](#)). One possibility could be that deprioritized memories become activity-silent when alpha enhances because their respective gamma cycle does not fit in the sharpened alpha trough anymore.

In contrast, theta-gamma coupling during working memory is mostly observed in frontal regions ([122,129]; though see [39]) and mainly during nonvisual or sequential working memory involving multiple representations [79,130]. This segmentation function seems similar to the function of delta-alpha coupling discussed here. Furthermore, comparable to alpha-gamma coupling in posterior regions [126], top-down beta couples to bottom-up gamma in frontal regions during working memory [83]. But it remains unclear how these different codes, delta-alpha, theta-gamma, alpha-gamma, and beta-gamma relate to each other, specifically regarding different representational states (see [Outstanding Questions](#)).

the second of two sequential visual selection tasks, we were able to decode [using **multivariate pattern analysis (MVPA)**] its priority state (i.e., current versus prospective) from delta-band-specific activity [45]. The delta band signal was only transiently involved when initializing the priority status at the start of the first delay, or when switching priority during the second delay, and thus likely reflected the momentary top-down control over sensory activity required to trigger a change in state, rather than the maintenance of that state. While the above-mentioned cross-frequency metrics do not allow for inferences of directionality, posterior alpha oscillations correlated with frontal low frequency oscillations earlier in the trial [43,73], suggesting a causal role. Furthermore, frontal delta power predicted later visual selection performance [43,45]. These findings thus provide initial evidence that frontal low-frequency oscillations drive alpha oscillations through long-range cross-frequency interactions in order to control representational states within VWM. While speculative, it may be that the temporal structure of the task is actually coded in these slow frontal oscillations, by temporally ordering the working memory representations according to the phase of the slow oscillations (e.g., through the theta-gamma code [79]; [Box 4](#)), as to prepare for anticipated representation activation at prespecified points in time. Although the observed transient nature of the delta/theta control signal does not seem to favor such a phase coding model, this remains to be investigated in the future. Interestingly, task-switching research has also found proactive switch-related changes in frontal low frequency (theta) oscillations [80,81], suggesting that the switch in representational state in working memory at the sensory end (i.e., which stimulus should guide action) might be controlled by very similar oscillatory mechanisms as task switching (i.e., which action a stimulus requires).

Involvement of Other Frequency Bands

The theta/delta-alpha interactions are probably not the only oscillatory basis of cognitive control over representational states. One study has shown how beta power in prefrontal cortex is

modulated by delta phase when observers need to remember multiple items in working memory [82]. More recent work in monkeys implicates alpha and beta (10–30 Hz) oscillations in executive control over prefrontal working memory representations, which are in turn encoded in gamma-band activity ([83]; Box 4). That is, alpha and beta activity in (top-down) deep layers of prefrontal regions have been shown to regulate the expression of gamma activity in superficial (bottom-up) layers, resulting in alternating bursts of alpha/beta and gamma activity. It is proposed that this way alpha/beta activity controls which sensory information can gain access to working memory and, additionally, which information is maintained, as gamma activity is necessary to refresh the synaptic weight changes that help maintain the memory. At present, it is unclear how these interactions between alpha/beta and gamma oscillations in prefrontal cortex influence downstream sensory representations and whether they may also play a role in prioritization in working memory, as such high-resolution invasive recordings have not been applied within memory prioritization paradigms yet.

As mentioned in the introduction, the prioritized representation might include an action plan that allows for a direct interaction with response output [11,12]. Recent findings suggest that this prioritized action plan is controlled by oscillations in the mu and beta band above sensorimotor cortex [84]. For example, when the specific response hand could be coupled to a specific visual stimulus during working memory encoding, a retro-cue prioritizing a single working memory representation resulted in a suppression of beta power in motor cortex contralateral to the anticipated response hand [85]. Importantly, the response side was manipulated independently of the location of the VWM item. This result indicates that an action plan can be flexibly included in the prioritized working memory representation, and it emphasizes the action-oriented nature [11,12], as well as the distributed nature, of working memory [63]. While the role of mu/beta suppression above contralateral motor cortex in prioritizing a motor action seems to mirror the effect in contralateral alpha suppression above visual cortex described throughout this review, it remains to be studied how prospective (deprioritized) motor plans for a future action in a task sequence are stored and controlled; both in terms of mu/beta oscillations above motor cortex and low-frequency oscillations in frontal cortex.

Concluding Remarks

In this article we have reviewed the evidence on how neural oscillations may control the representational state of items maintained in working memory depending on their moment-by-moment task-relevance. Based on the reviewed literature, we postulate that modulations in alpha activity above sensory cortices are the direct result of the top-down control mechanism by which internal attention selects which working memory representation should currently be prioritized (i.e., activated in sensory cortex) and thereby allowed to interact with the sensory input, versus which working memory representation should be deprioritized to an activity-silent state. This process is reversible, as alpha modulations flexibly track changes in working memory representational state. We furthermore posit that this top-down control itself over the current state of working memory representations is implemented by frontal delta-to-theta oscillations that orchestrate posterior alpha oscillations through long-range cross-frequency interactions. We focused on the state of memories. Memory content itself is presumably coded in gamma oscillations, which in turn are shaped by lower frequency oscillations. While we focused on prioritization of working memory for visual selection, we briefly touched upon recent findings that suggest similar control mechanisms might underlie prioritization of working memory for action selection. We hope that this review will stimulate additional research that will lead to a more complete understanding of the roles of oscillations and their interactions across frontal, sensory, and motor regions in the control of representational states in working memory (see [Outstanding Questions](#)).

Outstanding Questions

How domain-general is control over representational states in working memory? Do frontal delta oscillations also control the state of auditory or tactile information in auditory/somatosensory cortex?

To what extent do posterior alpha oscillations as measured with M/EEG also reflect the representational state of visual information in working memory that is not tied to a specific spatial location?

What is the role of gamma oscillations in working memory in general and for different representational states specifically? In particular, what is the role of the coupling between the gamma rhythm and the other slower rhythms, within and between different areas of the brain and different cortical layers?

How do different cross-frequency coupling codes relate to each other? Specifically, how does the frontal delta-posterior alpha code observed during representational state switches relate to other cross-frequency codes observed during working memory?

How is information outside of the focus of attention, that is prospectively relevant, maintained at the level of single neurons and populations of neurons?

What happens to the firstly prioritized working memory representation within a sequence when observers prioritize the next item in working memory and it is thus no longer relevant to the task at hand? Is it actively suppressed, or merely left to decay?

What is the exact source of the frontal top-down signal that orchestrates the momentary state of working memory representations during multitask sequences? The EEG evidence presented here only offers a coarse estimation. The combination of M/EEG with (f)MRI or source modeling might give more detailed insights. This may also shed light on possible contributions by subcortical regions, specifically the thalamus and basal ganglia.

Does the switch in representational state in working memory (which

Acknowledgments

This work was supported by the European Research Council (ERC) Consolidator grant (ERC-2013-CoG-615423) to C.N.L.O. Furthermore, we would like to thank Joram van Driel for useful discussions.

References

- Itti, L. and Koch, C. (2001) Computational modelling of visual attention. *Nat. Rev. Neurosci.* 2, 194–203
- Olivers, C.N.L. et al. (2006) Feature-based memory-driven attentional capture: visual working memory content affects visual attention. *J. Exp. Psychol. Hum. Percept. Perform.* 32, 1243–1265
- Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222
- Wolfe, J.M. (1994) Guided search 2.0 a revised model of visual search. *Psychon. Bull. Rev.* 1, 202–238
- van Loon, A.M. et al. (2017) Subtle eye movement metrics reveal task-relevant representations prior to visual search. *J. Vis.* 17, 13
- Olmos-Solis, K. et al. (2017) Oculomotor measures reveal the temporal dynamics of preparing for search. *Prog. Brain Res.* 236, 1–23
- Carlisle, N.B. and Woodman, G.F. (2011) Automatic and strategic effects in the guidance of attention by working memory representations. *Acta Psychol. (Amst)* 137, 217–225
- Olivers, C.N.L. et al. (2011) Different states in visual working memory: when it guides attention and when it does not. *Trends Cogn. Sci.* 15, 327–334
- LaRocque, J.J. et al. (2014) Multiple neural states of representation in short-term memory? It's a matter of attention. *Front. Hum. Neurosci.* 8, 5
- Stokes, M.G. (2015) 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends Cogn. Sci.* 19, 394–405
- Nobre, A.C. and Stokes, M.G. (2019) Premembering experience: a hierarchy of time-scales for proactive attention. *Neuron* 104, 132–146
- Myers, N.E. et al. (2017) Prioritizing information during working memory: beyond sustained internal attention. *Trends Cogn. Sci.* 21, 449–461
- Serences, J.T. et al. (2009) Stimulus-specific delay activity in human primary visual cortex. *Psychol. Sci.* 20, 207–214
- Harrison, S.A. and Tong, F. (2009) Decoding reveals the contents of visual working memory in early visual areas. *Nature* 458, 632–635
- Christophel, T.B. et al. (2012) Decoding the contents of visual short-term memory from human visual and parietal cortex. *J. Neurosci.* 32, 12983–12989
- Laufs, H. et al. (2003) EEG-correlated fMRI of human alpha activity. *Neuroimage* 19, 1463–1476
- Haegens, S. et al. (2011) α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmic inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. U. S. A.* 108, 19377–19382
- Klimesch, W. et al. (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.* 53, 63–88
- Jensen, O. and Mazaheri, A. (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.* 4, 186
- Klimesch, W. (2012) Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.* 16, 606–617
- Widegger, T. et al. (2017) Preparatory alpha-band oscillations reflect spatial gating independently of predictions regarding target identity. *J. Neurophysiol.* 117, 1385–1394
- Spaak, E. et al. (2015) The neural mechanisms of prediction in visual search. *Cereb. Cortex* 26, 4327–4336
- Romei, V. et al. (2010) On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: correlation or causation? *J. Neurosci.* 30, 8692–8697
- Cabral-Calderin, Y. and Wilke, M. (2019) Probing the link between perception and oscillations: lessons from transcranial alternating current stimulation. *Neuroscientist* <https://doi.org/10.1177/1073858419828646> Published online February 7, 2019
- Clayton, M.S. et al. (2019) Electrical stimulation of alpha oscillations stabilizes performance on visual attention tasks. *J. Exp. Psychol. Gen.* 148, 203–220
- Thut, G. et al. (2006) Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502
- van Moorselaar, D. and Slagter, H.A. (2019) Learning what is irrelevant or relevant: expectations facilitate distractor inhibition and target facilitation through distinct neural mechanisms. *J. Neurosci.* 39, 6953–6967
- Foster, J.J. et al. (2017) Alpha-band oscillations enable spatially and temporally resolved tracking of covert spatial attention. *Psychol. Sci.* 28, 929–941
- Foxe, J.J. and Snyder, A.C. (2011) The role of alpha-band brain oscillations as a sensory suppression mechanism during selective attention. *Front. Psychol.* 2, 1–13
- Foster, J.J. and Awh, E. (2019) The role of alpha oscillations in spatial attention: limited evidence for a suppression account. *Curr. Opin. Psychol.* 29, 34–40
- van Ede, F. (2018) Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: a review. *Eur. J. Neurosci.* 48, 2509–2515
- Myers, N.E. et al. (2015) Temporal dynamics of attention during encoding versus maintenance of working memory: complementary views from event-related potentials and alpha-band oscillations. *J. Cogn. Neurosci.* 27, 492–508
- Schneider, D. et al. (2016) The time course of visuo-spatial working memory updating revealed by a retro-cuing paradigm. *Sci. Rep.* 6, 21442
- Schneider, D. et al. (2015) On the fate of non-cued mental representations in visuo-spatial working memory: evidence by a retro-cuing paradigm. *Behav. Brain Res.* 293, 114–124
- Poch, C. et al. (2017) Selection within working memory based on a color retro-cue modulates alpha oscillations. *Neuropsychologia* 106, 133–137
- Poch, C. et al. (2014) Modulation of alpha and gamma oscillations related to retrospectively orienting attention within working memory. *Eur. J. Neurosci.* 40, 2399–2405
- Poch, C. et al. (2017) A dual mechanism underlying alpha lateralization in attentional orienting to mental representation. *Biol. Psychol.* 128, 63–70
- Wallis, G. et al. (2015) Frontoparietal and cingulo-opercular networks play dissociable roles in control of working memory. *J. Cogn. Neurosci.* 27, 2019–2034
- Sauseng, P. et al. (2009) Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* 19, 1846–1852
- van Driel, J. et al. (2017) Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition. *Neuroimage* 149, 114–128
- Hakim, N. et al. (2019) Dissecting the neural focus of attention reveals distinct processes for spatial attention and object-based storage in visual working memory. *Psychol. Sci.* 30, 526–540
- Ester, E.F. et al. (2018) Retrospective cues mitigate information loss in human cortex during working memory storage. *J. Neurosci.* 38, 8538–8548
- de Vries, I.E.J. et al. (2018) Priority switches in visual working memory are supported by frontal delta and posterior alpha interactions. *Cereb. Cortex* 28, 4090–4104
- de Vries, I.E.J. et al. (2017) Posterior alpha EEG dynamics dissociate current from future goals in working memory guided visual search. *J. Neurosci.* 37, 2945–2916
- de Vries, I.E.J. et al. (2019) Decoding the status of working memory representations in preparation of visual selection. *Neuroimage* 191, 549–559
- de Vries, I.E.J. et al. (2019) Oscillatory mechanisms of preparatory for visual distraction. *J. Cogn. Neurosci.* 31, 1873–1894

stimulus guides action) rely on similar oscillatory top-down control mechanisms as task switching (which action a stimulus requires)?

47. van Ede, F. *et al.* (2017) Temporal expectations guide dynamic prioritization in visual working memory through attenuated α oscillations. *J. Neurosci.* 37, 437–445
48. Payne, L. and Sekuler, R. (2014) The importance of ignoring: alpha oscillations protect selectivity. *Curr. Dir. Psychol. Sci.* 23, 171–177
49. Schneider, D. *et al.* (2019) Hemispheric asymmetries in EEG alpha oscillations indicate active inhibition during attentional orienting within working memory. *Behav. Brain Res.* 359, 38–46
50. Pratte, M. and Tong, F. (2014) Spatial specificity of working memory representations in the early visual cortex. *J. Vis.* 14, 1–12
51. van Kerkoerle, T. *et al.* (2017) Layer-specificity in the effects of attention and working memory on activity in primary visual cortex. *Nat. Commun.* 8, 13804
52. Mok, R.M. *et al.* (2016) Behavioral and neural markers of flexible attention over working memory in aging. *Cereb. Cortex* 26, 1831–1842
53. Fukuda, K. *et al.* (2015) α Power modulation and event-related slow wave provide dissociable correlates of visual working memory. *J. Neurosci.* 35, 14009–14016
54. Fukuda, K. *et al.* (2016) Distinct neural mechanisms for spatially lateralized and spatially global visual working memory representations. *J. Neurophysiol.* 116, 1715–1727
55. van Moorselaar, D. *et al.* (2018) Spatially selective alpha oscillations reveal moment-by-moment trade-offs between working memory and attention. *J. Cogn. Neurosci.* 30, 256–266
56. Sutterer, D.W. *et al.* (2019) Item-specific delay activity demonstrates concurrent storage of multiple active neural representations in working memory. *PLoS Biol* 17, e3000239
57. Foster, J.J. *et al.* (2015) The topography of alpha-band activity tracks the content of spatial working memory. *J. Neurophysiol.* 115, 168–177
58. Popov, T. *et al.* (2019) Spatial specificity of alpha oscillations in the human visual system. *Hum. Brain Mapp.* 40, 4432–4440
59. Miller, E.K. and Cohen, J.D. (2001) An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* 24, 167–202
60. Mansouri, F.A. *et al.* (2017) Managing competing goals — a key role for the frontopolar cortex. *Nat. Rev. Neurosci.* 18, 645–657
61. Monsell, S. (2003) Task switching. *Trends Cogn. Sci.* 7, 134–140
62. Fusi, S. *et al.* (2016) Why neurons mix: high dimensionality for higher cognition. *Curr. Opin. Neurobiol.* 37, 66–74
63. Christophel, T.B. *et al.* (2017) The distributed nature of working memory. *Trends Cogn. Sci.* 21, 111–124
64. Sreenivasan, K.K. *et al.* (2014) Revisiting the role of persistent neural activity during working memory. *Trends Cogn. Sci.* 18, 82–89
65. Nelissen, N. *et al.* (2013) Frontal and parietal cortical interactions with distributed visual representations during selective attention and action selection. *J. Neurosci.* 33, 16443–16458
66. Higo, T. *et al.* (2011) Distributed and causal influence of frontal operculum in task control. *Proc. Natl. Acad. Sci. U. S. A.* 108, 4230–4235
67. Kuo, B.C. *et al.* (2011) Functional connectivity during top-down modulation of visual short-term memory representations. *Neuropsychologia* 49, 1589–1596
68. Manohar, S.G. *et al.* (2019) Neural mechanisms of attending to items in working memory. *Neurosci. Biobehav. Rev.* 101, 1–12
69. Paneri, S. and Gregoriou, G.G. (2017) Top-down control of visual attention by the prefrontal cortex: functional specialization and long-range interactions. *Front. Neurosci.* 11, 1–16
70. Baldauf, D. and Desimone, R. (2014) Neural mechanisms of object-based attention. *Science* 344, 424–427
71. Helfrich, R.F. *et al.* (2017) Prefrontal cortex modulates posterior alpha oscillations during top-down guided visual perception. *Proc. Natl. Acad. Sci. U. S. A.* 114, 9457–9462
72. Helfrich, R.F. and Knight, R.T. (2016) Oscillatory dynamics of prefrontal cognitive control. *Trends Cogn. Sci.* 20, 916–930
73. Janssens, C. *et al.* (2018) Occipital alpha power reveals fast attentional inhibition of incongruent distractors. *Psychophysiology* 55, e13011
74. Mazaheri, A. *et al.* (2010) Functional disconnection of frontal cortex and visual cortex in attention-deficit/hyperactivity disorder. *Biol. Psychiatry* 67, 617–623
75. Alagapan, S. *et al.* (2019) Low-frequency direct cortical stimulation of left superior frontal gyrus enhances working memory performance. *Neuroimage* 184, 697–706
76. Johnson, E.L. *et al.* (2017) Bidirectional frontoparietal oscillatory systems support working memory. *Curr. Biol.* 27, 1829–1835
77. Violante, I.R. *et al.* (2017) Externally induced frontoparietal synchronization modulates network dynamics and enhances working memory performance. *eLife* 6, 1–22
78. Berger, B. *et al.* (2019) Dynamic regulation of interregional cortical communication by slow brain oscillations during working memory. *Nat. Commun.* 10, 1–11
79. Lisman, J.E. and Jensen, O. (2013) The theta-gamma neural code. *Neuron* 77, 1002–1016
80. Cooper, P.S. *et al.* (2017) Frontoparietal theta oscillations during proactive control are associated with goal-updating and reduced behavioral variability. *Biol. Psychol.* 129, 253–264
81. Cooper, P.S. *et al.* (2019) Frontal theta predicts specific cognitive control-induced behavioural changes beyond general reaction time slowing. *Neuroimage* 189, 130–140
82. Siegel, M. *et al.* (2009) Phase-dependent neuronal coding of objects in short-term memory. *Proc. Natl. Acad. Sci. U. S. A.* 106, 21341–21346
83. Miller, E.K. *et al.* (2018) Working memory 2.0. *Neuron* 100, 463–475
84. Schneider, D. *et al.* (2017) On the contribution of motor planning to the retroactive cuing benefit in working memory: evidence by mu and beta oscillatory activity in the EEG. *Neuroimage* 162, 73–85
85. van Ede, F. *et al.* (2019) Concurrent visual and motor selection during visual working memory guided action. *Nat. Neurosci.* 22, 477–483
86. Myers, N.E. *et al.* (2015) Testing sensory evidence against mnemonic templates. *eLife* 4, e09000
87. Gayet, S. *et al.* (2017) Visual working memory enhances the neural response to matching visual input. *J. Neurosci.* 37, 6638–6647
88. Wolff, M.J. *et al.* (2017) Dynamic hidden states underlying working memory guided behaviour. *Nat. Neurosci.* 20, 864–871
89. Stokes, M.G. *et al.* (2009) Top-down activation of shape-specific population codes in visual cortex during mental imagery. *J. Neurosci.* 29, 1565–1572
90. Albers, A.M. *et al.* (2013) Shared representations for working memory and mental imagery in early visual cortex. *Curr. Biol.* 23, 1427–1431
91. Chun, M.M. (2011) Visual working memory as visual attention sustained internally over time. *Neuropsychologia* 49, 1407–1409
92. Gayet, S. *et al.* (2018) Visual working memory storage recruits sensory processing areas. *Trends Cogn. Sci.* 22, 189–190
93. Postle, B.R. (2006) Working memory as an emergent property of the mind and brain. *Neuroscience* 139, 23–38
94. LaRocque, J.J. *et al.* (2016) Within-category decoding of information in different attentional states in short-term memory. *Cereb. Cortex* 27, 4881–4890
95. Erickson, M.A. *et al.* (2009) A single brief burst induces GluR1-dependent associative short-term potentiation: a potential mechanism for short-term memory. *J. Cogn. Neurosci.* 22, 2530–2540
96. Christophel, T.B. *et al.* (2018) Cortical specialization for attended versus unattended working memory. *Nat. Neurosci.* 21, 494–496
97. Kornblith, S. *et al.* (2017) Persistent single-neuron activity during working memory in the human medial temporal lobe. *Curr. Biol.* 27, 1026–1032
98. van Loon, A.M. *et al.* (2018) Current and future goals are represented in opposite patterns in object-selective cortex. *eLife* 7, e38677
99. Yu, Q. and Postle, B.R. (2018) Different states of priority recruit different neural codes in visual working memory. *bioRxiv* <https://doi.org/10.1101/334920> Published online October 12, 2018

100. Wolff, M.J. *et al.* (2015) Revealing hidden states in visual working memory using electroencephalography. *Front. Syst. Neurosci.* 9, 123
101. Rose, N.S. *et al.* (2016) Reactivation of latent working memories with transcranial magnetic stimulation. *Science* 354, 1136–1139
102. Sprague, T.C. *et al.* (2016) Restoring latent visual working memory representations in human cortex. *Neuron* 91, 694–707
103. Nunez, P.L. and Srinivasan, R. (2006) *Electrical Fields of the Brain: The Neurophysics of EEG*, Oxford University Press
104. Wang, X.-J. (2010) Neurophysiological and computational principles of cortical rhythms in cognition. *Physiol. Rev.* 90, 1195–1268
105. Cohen, M.X. (2017) Where does EEG come from and what does it mean? *Trends Neurosci* 40, 208–218
106. Buzsáki, G. *et al.* (2004) Neuronal oscillations in cortical networks. *Science* 304, 1926–1929
107. Mazaheri, A. *et al.* (2018) Orchestration of brain oscillations: principles and functions. *Eur. J. Neurosci.* 48, 2385–2388
108. Pfurtscheller, G. and Lopes Da Silva, F.H. (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin. Neurophysiol.* 110, 1842–1857
109. Busch, N.A. *et al.* (2009) The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci.* 29, 7869–7876
110. Fries, P. *et al.* (2001) Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291, 1560–1563
111. Engel, A. *et al.* (2001) Dynamic predictions: oscillations and synchrony in top-down processing. *Nat. Rev. Neurosci.* 2, 704–716
112. Siegel, M. *et al.* (2012) Spectral fingerprints of large-scale neuronal interactions. *Nat. Rev. Neurosci.* 13, 20–25
113. Canolty, R.T. and Knight, R.T. (2010) The functional role of cross-frequency coupling. *Trends Cogn. Sci.* 14, 506–515
114. Noonan, M.A.P. *et al.* (2018) Selective inhibition of distracting input. *Behav. Brain Res.* 355, 36–47
115. Gaspelin, N. and Luck, S.J. (2018) The role of inhibition in avoiding distraction by salient stimuli. *Trends Cogn. Sci.* 22, 79–92
116. Noonan, M.A.P. *et al.* (2016) Distinct mechanisms for distractor suppression and target facilitation. *J. Neurosci.* 36, 1797–1807
117. Vissers, M.E. *et al.* (2016) Proactive, but not reactive, distractor filtering relies on local modulation of alpha oscillatory activity. *J. Cogn. Neurosci.* 28, 1964–1979
118. Wang, B. *et al.* (2019) Anticipatory distractor suppression elicited by statistical regularities in visual search. *J. Cogn. Neurosci.* 26, 1–14
119. Geng, J.J. and Witkowski, P. (2019) Template-to-distractor distinctiveness regulates visual search efficiency. *Curr. Opin. Psychol.* 29, 119–125
120. Buzsáki, G. and Wang, X.-J. (2012) Mechanisms of gamma oscillations. *Annu. Rev. Neurosci.* 35, 203–225
121. Donner, T.H. and Siegel, M. (2011) A framework for local cortical oscillation patterns. *Trends Cogn. Sci.* 15, 191–199
122. Roux, F. and Uhlhaas, P.J. (2014) Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information? *Trends Cogn. Sci.* 18, 16–25
123. Lundqvist, M. *et al.* (2018) Gamma and beta bursts during working memory readout suggest roles in its volitional control. *Nat. Commun.* 9, 1–12
124. Polania, R. *et al.* (2012) Noninvasively decoding the contents of visual working memory in the human prefrontal cortex within high-gamma oscillatory patterns. *J. Cogn. Neurosci.* 24, 304–314
125. Spaak, E. *et al.* (2012) Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. *Curr. Biol.* 22, 2313–2318
126. van Kerkoerle, T. *et al.* (2014) Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 111, 14332–14341
127. Richter, C.G. *et al.* (2017) Top-down beta enhances bottom-up gamma. *J. Neurosci.* 37, 6698–6711
128. Jensen, O. *et al.* (2014) Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. *Trends Neurosci.* 37, 357–369
129. Alekseichuk, I. *et al.* (2016) Spatial working memory in humans depends on theta and high gamma synchronization in the prefrontal cortex. *Curr. Biol.* 26, 1513–1521
130. Sauseng, P. *et al.* (2018) Does cross-frequency phase coupling of oscillatory brain activity contribute to a better understanding of visual working memory? *Br. J. Psychol.* 110, 245–255