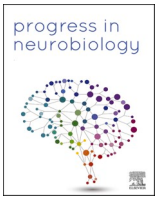
Progress in Neurobiology 228 (2023) 102491



Contents lists available at ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio





A recruitment through coherence theory of working memory

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ARTICLE INFO

Keywords:
Working memory
Feedback
Communication
Coherence
Oscillations
Phase coding

ABSTRACT

The interactions between prefrontal cortex and other areas during working memory have been studied for decades. Here we outline a conceptual framework describing interactions between these areas during working memory, and review evidence for key elements of this model. We specifically suggest that a top-down signal sent from prefrontal to sensory areas drives oscillations in these areas. Spike timing within sensory areas becomes locked to these working-memory-driven oscillations, and the phase of spiking conveys information about the representation available within these areas. Downstream areas receiving these phase-locked spikes from sensory areas can recover this information via a combination of coherent oscillations and gating of input efficacy based on the phase of their local oscillations. Although the conceptual framework is based on prefrontal interactions with sensory areas during working memory, we also discuss the broader implications of this framework for flexible communication between brain areas in general.

The relative contributions of prefrontal and sensory areas to working memory (WM) have long been the subject of debate (Emrich et al., 2013; Harrison and Tong, 2009; Lara and Wallis, 2015; Pasternak and Greenlee, 2005; Sreenivasan et al., 2014). Firing rate changes reflecting the content of WM during the delay period of tasks are more robust in prefrontal cortex (PFC) (Bruce and Goldberg, 1985; Funahashi et al., 1989; Fuster and Alexander, 1971; Miller et al., 1996; Rao et al., 1997; Romo et al., 1999), and indeed often absent in many earlier sensory areas (Chelazzi et al., 1998; Chelazzi et al., 2001; Fuster, 1990; Leavitt et al., 2017; Mendoza-Halliday et al., 2014; Zaksas and Pasternak, 2006); yet the stimulus selectivity of prefrontal neurons seems insufficient to support the level of detail which can be maintained in visual WM (Desimone et al., 1985), and lesions do not always abolish performance (Clark et al., 2014; D'Esposito and Postle, 1999; Rushworth et al., 1997). These challenges have led to the idea that the information maintained in WM needs to be stored in sensory areas, and such information can be recruited as needed (Emrich et al., 2013; Postle, 2006; Rose et al., 2016). This sensory recruitment theory of WM also faces its own challenges. Since the action potentials are the means of communication between brain areas, the lack of firing rate changes in sensory cortex raises the questions of exactly how WM recruits sensory areas. In light of the recent findings in our lab and others, we have developed a framework to describe the sequence of events needed for recruitment of sensory areas during WM. Briefly, in this framework, WM-driven oscillations in visual areas alter spike timing in a way which reflects the stored information. This information carried by spike timing is transferred to downstream areas through coherent oscillations and oscillation-dependent gating of inputs (Fig. 1). This framework was developed primarily to explain recent findings during WM, but may also apply to other tasks in which sensory areas receive top-down cognitive signals, such as covert attention.

1. A conceptual framework describing oscillation-based prefrontal modulation of sensory areas

First, the proposed framework is described in greater detail; a review of the literature supporting the various components of the framework will follow. During WM, PFC, and specifically the Frontal Eye Fields (FEF), sends a signal reflecting the content of WM to visual areas. Within visual areas, this top-down signal drives increased oscillatory activity in particular frequency bands, as reflected by power in the local field potential (LFP; #1 in Fig. 1), and as a result changes the timing of spikes relative to these oscillations to reflect the content of stored information within sensory areas (#2 in Fig. 1). In order for this information encoded in spike timing to be conveyed to downstream areas (such as PFC, which also receives visual input), they must have an oscillation coherent with

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https://doi.org/10.1016/j.pneurobio.2023.102491
Received 6 February 2023; Received in revised form 14 June 2023; Accepted 21 June 2023
Available online 29 June 2023
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the WM-induced oscillation in the visual areas. By gating the efficacy of visual input based on the phase of that local oscillation in the receiving area, information coded in the timing of visual spikes can be transformed back into a rate code (#3 in Fig. 1). Such phase-dependent representation of stored information could account for recruitment of sensory areas during WM. Moreover, it can also account for how WM facilitates the processing of sensory information matching the content of WM: visual neurons more strongly driven by the current visual stimulus will spike earlier in the oscillatory cycle. This also means that information about incoming visual stimuli is reflected in the timing of spikes relative to these oscillations; the implications of this framework for mechanisms of attention is also discussed.

Below, we will review existing evidence consistent with the proposed framework: that top-down signals are sent from prefrontal to sensory areas, that oscillations in sensory areas facilitate the expression of a hidden representation in these areas through the relative timing of spikes, that coherent oscillations across areas exist, and that local oscillation phase can gate the efficacy of incoming signals.

2. The functional and anatomical connectivity between prefrontal and extrastriate visual cortex

PFC has reciprocal anatomical connections with most extrastriate visual areas (Markov et al., 2014a). The FEF portion of PFC has direct projections to multiple extrastriate visual areas, including V4, middle temporal (MT), and inferotemporal cortex (Anderson et al., 2011; Barone et al., 2000; Markov et al., 2014a; Markov et al., 2014b; Pouget et al., 2009; Stanton et al., 1995; Ungerleider et al., 2008). The connections between FEF and V4 have been studied in the greatest anatomical detail. Both the projections from FEF to V4, and the projections from V4 to FEF, diverge from the stereotypical anatomical patterns associated with feedback vs. feedfoward projections (Rockland and Pandya, 1979), and are instead described as being of an 'intermediate' type (Ungerleider et al., 2008). FEF's projections to V4 arise predominantly in the supragranular layers (Barone et al., 2000; Markov et al., 2014b; Pouget et al., 2009; Ungerleider et al., 2008), and form synapses in all layers of V4 (Anderson et al., 2011; Stanton et al., 1995). V4 projections to FEF arise in the supragranular layers (Markov et al., 2014a; Markov et al., 2014b), and synapse in all layers of FEF (Ungerleider et al., 2008). Projections from FEF to V4 overwhelmingly synapse onto putatively excitatory neurons within V4 (~98% excitatory targets vs. 2% inhibitory targets, characterized based on electron microscopy (Anderson et al., 2011)). Despite accounting for such a small percentage of targets within V4, it is the putatively inhibitory neurons of extrastriate cortex that show larger firing rate changes than excitatory neurons during WM (Nesse et al., 2021), and are more consistently enhanced by attention (Mitchell et al., 2007). It is possible that these changes in inhibitory activity result from the small fraction of direct inputs, or that they are mediated through a subpopulation of excitatory neurons.

The information conveyed in FEF's projections to extrastriate cortex has been directly characterized. FEF contains a heterogenous mixture of visual, motor, and cognitive signals (Bruce and Goldberg, 1985; Lawrence et al., 2005; Lowe and Schall, 2018). A more recent study used electrical stimulation of V4 while recording from FEF to directly identify FEF neurons projecting to V4 and characterize their response properties during a classic spatial WM task, the memory-guided saccade task (Fig. 2 A) (Merrikhi et al., 2017). Activity reflecting the content of WM, rather than visual or motor responses, was the defining characteristic of FEF neurons projecting to V4. Thus, extrastriate visual cortex receives a top-down signal during the delay period of WM tasks. Although animals in this study directly identifying V4-projecting FEF neurons did not perform a covert attention task, a separate set of experiments found that the same FEF neurons displaying memory-related activity also reflect the location of covert attention (Armstrong et al., 2009), suggesting that visual areas will also receive top-down input directly from FEF neurons during these tasks. Despite receiving this WM signal, the firing rates of extrastriate neurons do not directly reflect the content of WM during the delay (Fig. 2D) (Bahmani et al., 2018). How this WM signal alters activity in visual areas will be reviewed in the following sections.

On the other side of the reciprocal projections, the efficacy of input from V4 to FEF has been shown to be modulated by the content of WM. Electrical stimulation of V4 was used to identify FEF neurons receiving input from V4, characterize their activity, and to test whether the effective strength of that input varied during WM (Noudoost et al., 2021). Although one might reasonably hypothesize that visual input from V4 would primarily target visually responsive neurons within FEF, instead it was neurons with a combination of both visual and motor activity which were more likely to receive V4 input (Fig. 2B), suggesting an important role for incoming V4 information in linking visual stimuli to behavior. The efficacy of the same V4 stimulation in driving FEF activity was greater when remembering a location corresponding the response fields (RFs) of the stimulation and recording sites (Fig. 2E); FEF neurons receiving V4 input were also more likely to fire together (within a narrow temporal window) when the content of WM matched their RF locations (Fig. 2 F). This shows that WM can modulate the strength of functional connectivity between areas, possibly by altering the oscillatory coherence between them, as discussed in more detail below.

3. Top-down signals drive oscillations in sensory areas

Modulations in oscillatory power (reflected in the LFP) have been reported in sensory areas during WM and attention tasks. These modulations of LFP power during cognitive tasks have been reported in a variety of frequency bands; although the exact definitions of these frequency bins vary between individual publications, they are generally defined around delta (1–4 Hz), theta (5–8 Hz), alpha (8–12 Hz), beta (15–30 Hz), and gamma (>30 Hz) frequency ranges. Several studies have reported changes in LFP power during WM: in the dorsal stream,

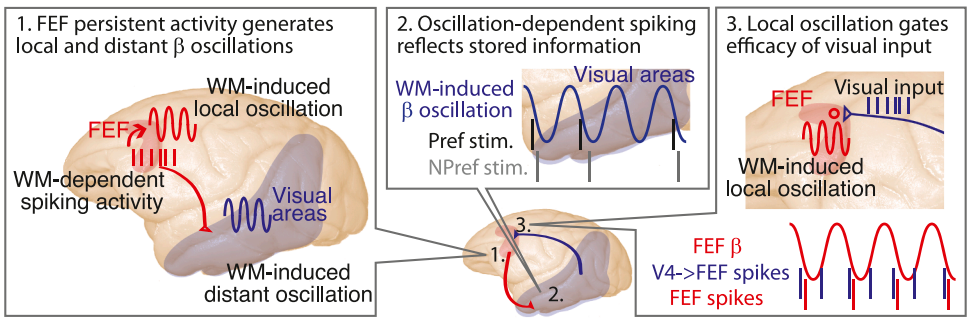

Fig. 1. A framework describing the role of coherent oscillations and spike timing in prefrontal-visual interactions during WM. 1) WM-related activity in FEF drives both local (within FEF) and distant oscillations (in visual areas). 2) Within visual areas, the WM-induced oscillations alter spike timing, so that the phase of spikes reflects the stored information. Spiking response of a visual neuron when remembering a preferred (black) and non-preferred (gray) stimulus relative to the local oscillation is schematically illustrated. 3) The efficacy of visual input sent to FEF is modulated by the phase of the FEF oscillation, which is coherent with the oscillation in visual areas. Thus, V4 spikes arriving at certain oscillatory phases are more likely to evoke spikes in FEF, turning spike timing differences in V4 into rate differences in FEF, illustrated schematically by V4 spikes (blue) arriving at various times relative to the FEF oscillation, and evoked FEF spikes (red).

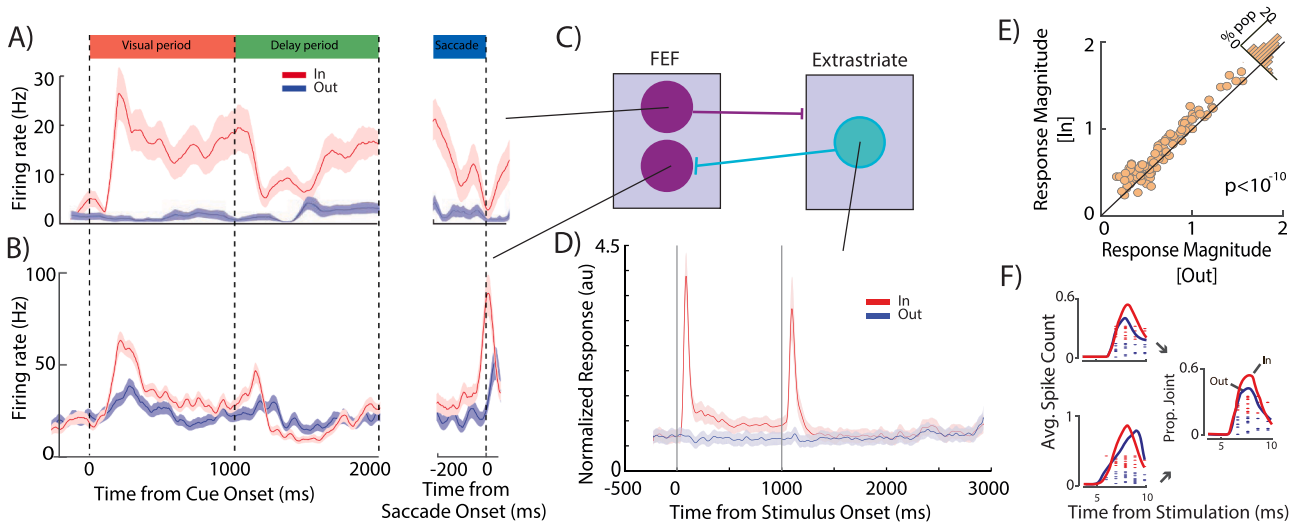

Fig. 2. Functional characteristics of the anatomical connections between FEF and extrastriate cortex. A) FEF neurons projecting to V4 are characterized by delay period activity. PSTH shows example V4-projecting FEF neuron during a spatial WM task, when remembering the RF location (In, red) or a location in the opposite visual hemifield (Out, blue). B) FEF neurons receiving V4 input display both visual and motor activity. PSTH shows example V4-receiving FEF neuron during the same spatial WM task. C) Schematic illustrating different neural populations represented by PSTHs (A, B, D). D) Extrastriate neurons show visual but no delay activity during a spatial WM task. PSTH shows normalized average activity of 107 MT neurons. E) WM increases the efficacy of V4 input into FEF. The magnitude of FEF responses evoked by V4 electrical stimulation is shown for memory In versus memory Out conditions. The histogram in the upper-right shows the distribution of differences across sessions. F) WM alters the likelihood of two FEF neurons receiving V4 input firing simultaneously. Mean V4 stimulation evoked spiking activity and raster plots for two example FEF neurons (left), and the probability of joint spiking (right) for memory In (red) and memory Out (blue). Figures from Merrikhi et al. (2017) (A), Noudoost et al. (2021) (B, E, F), and Bahmani et al. (2018) (D).

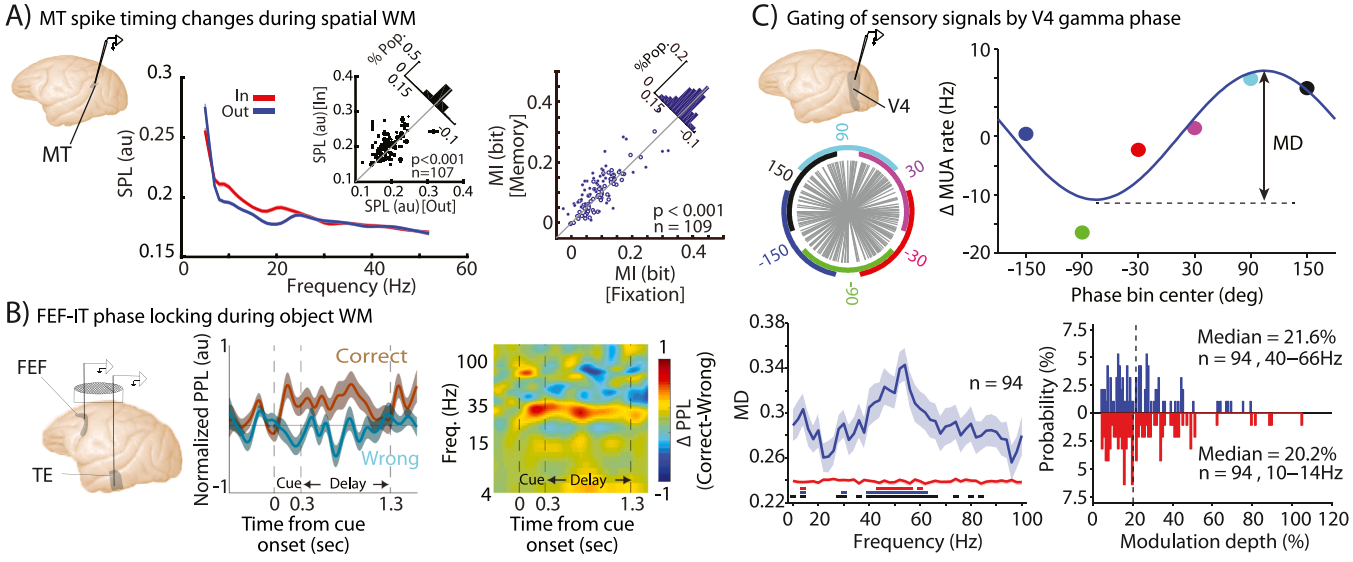

Fig. 3. Key experimental evidence supporting main aspects of the proposed framework. A) Changes in spike timing in visual area MT during WM. Middle: When remembering a location matching the RF of the recording site in MT, spikes are more strongly locked to alpha-beta oscillations. Plot shows SPL across frequencies during the delay period of a WM task, when remembering the RF location (In, red) or a location in the opposite visual hemifield (Out, blue). Inset shows scatter plot and histogram for SPL in the alpha-beta band, In vs. Out. Right: Information about the visual probe location encoded by the phase of spiking relative to the alpha-beta oscillation (measured as mutual information, MI), when remembering the RF location vs. during fixation. Histogram shows distribution of differences. B) Oscillatory coherence between prefrontal and visual cortex predicts WM performance. Left: schematic of simultaneous recordings from FEF and TE. Middle: Beta-band oscillatory coherence between areas (measured by phase-phase locking, PPL) during an object WM task, over time for correct (red) and wrong (blue) trials. Right: Difference in PPL between areas (Correct-Wrong), as a function of time and frequency. C) Modulation of sensory input efficacy by gamma phase, for an example V4 recording (top) and the population (bottom). Top left: Each gray line represents one trial, indicating the estimated gamma LFP phase just prior to input arrival in V4. Trials were grouped into six phase bins (colored segments), and the 75 trials closest to the center of each bin were used in subsequent analysis. Top right: Multiplicative response component of the V4 MUA of an example recording site as a function of gamma LFP phase. Blue curve shows a cosine fit; modulation depth (MD) is the difference between cosine peak and trough. Bottom left: Modulation depth for MUA at 94 V4 sites across two animals, as a function of LFP frequency (blue, ± SE). Red shows bias estimate. Bars at bottom show regions in which MD is significant (black $p < 0.05$; blue $p < 0.01$; red $p < 0.001$). Bottom right: histogram for MD across sites (expressed as percentage of pre-input MUA rate) in the gamma range (40–66 Hz, blue) and alpha-beta range (10–14 Hz, red). Dashed lines show medians of each distribution. Figures from Bahmani et al. (2018) (A), Rezayat et al. (2021) (B), and adapted with permission from Ni et al. (2016) (C).

alpha-beta power was elevated in MT during WM maintenance (Bahmani et al., 2018; Mendoza-Halliday et al., 2014). In the ventral stream, the inferotemporal (IT) cortex also had elevated alpha-beta power (Rezayat et al., 2021) during WM, while enhanced theta-band activity has been reported in area V4 (Lee et al., 2005). Similarly, human EEG recordings have also reported changes in oscillatory power during WM (Gevins et al., 1997; Howard et al., 2003; Mendoza-Halliday et al., 2014). Several hypotheses exist regarding the functional significance of and differences between various oscillatory frequencies (Bastos et al., 2018; Benchenane et al., 2011; Engel and Fries, 2010; Miller et al., 2018). One recent set of findings during covert attention tasks suggests that the gamma band is primarily associated with the feedforward flow of information, while the alpha-beta bands are associated with top-down, feedback signals (Bastos André et al., 2015a; Buffalo et al., 2011; Michalareas et al., 2016; van Kerkoerle et al., 2014a). Oscillatory activity in prefrontal and parietal areas is also modulated during WM and attention tasks (Kornblith et al., 2016; Lara and Wallis, 2014; Lundqvist et al., 2016). These stronger oscillations induced by WM may then exert greater control over the timing of spikes relative to the phase of the oscillations.

4. Top-down signals alter spike timing relative to oscillations in sensory areas

In addition to changes in oscillatory power during cognitive processing, the timing of spiking relative to these oscillations is also modulated by top-down WM and attention signals. The relationship between the time of spikes and LFP oscillations has typically been quantified using either spike-field coherence or spike-phase locking, both of which measure how reliably spikes occur at a particular phase of ongoing LFP oscillations. Multiple studies have reported changes in the relative timing of spikes in extrastriate cortex during the delay period of WM tasks, even in the absence of changes in overall firing rate. During WM, the timing of spikes relative to the theta band of V4 oscillations reflected the content of object WM (Lee et al., 2005). In MT, spikes of neurons with RFs matching the remembered location were more strongly phase-locked to local alpha-beta oscillations ((Bahmani et al., 2018); Fig. 3 A); this change in spike timing relative to oscillations occurred despite the lack of change in average firing rate (Fig. 2D). During covert attention tasks, spikes in V4 are more strongly locked to gamma-band oscillations (Fries et al., 2001; Gregoriou et al., 2014). Along the ventral visual stream, attention drives changes in spike-field coherence which vary across the cortical layers; superficial layers see coherence increase in the gamma-band, while deeper cortical layers of V1, V2, and V4 saw increased coherence in the alpha frequency range (Buffalo et al., 2011). Spike-field coherence in the gamma band in V4 also correlated with faster reaction times on an attention task (Womelsdorf et al., 2006). This change in spike timing based on the content of WM, or the location of covert attention, in turn means that spike timing carries information about these variables.

Bahmani and colleagues took this analysis of changes in spike timing during WM one step further, and looked at the responses of neurons to visual probes appearing during the delay period of the WM task (Bahmani et al., 2018). The alpha-beta phase of MT spiking in response to visual probes carried information about the location of the visual probe—i.e., there was phase coding of visual information. This phase coding of probe location was stronger during the memory period than during fixation (Fig. 3 A), and stronger when the remembered location was close to both the neuron's RF and the probe location. Although the evidence for modulation of such phase coding of sensory information by cognitive tasks remains limited, the existence of phase coding of sensory information has been previously reported in both visual (Montemurro et al., 2008) and auditory (Kayser et al., 2009) cortex. Thus, under the top-down influence of WM, the timing of spikes relative to WM-driven local oscillations could carry visual information as well as stored information.

Thus, there is evidence that the timing of spikes relative to LFP oscillations in visual areas carries both stored information and additional sensory information during WM. How could this information be transmitted to downstream areas, when the LFP signal itself is not conveyed by projecting axons? This information encoded by relative spike timing could be transformed back into a rate code in the downstream area if that downstream area 1) has a coherent oscillation with the sending area and 2) gates the efficacy of input based on the phase of the local oscillation. The next section reviews the evidence for both of these points. Many of these studies focus on the gamma frequency range, and this idea is often discussed as part of communication through coherence theory (Bastos et al., 2015b; Fries, 2005; Fries, 2015).

5. Coherence of oscillations between brain areas

Oscillations can become synchronized, or coherent, across brain areas, and the strength of this coherence can be modulated by a variety of factors. The simple onset of a visual stimulus is sufficient to induce synchronized gamma-band oscillations across multiple visual cortical areas (Brunet et al., 2014; Jia et al., 2013; Roberts et al., 2013). Considerable evidence also shows that oscillations can be flexibly synchronized across areas, particularly during cognitive tasks such as WM and attention; such dynamic modulation of inter-areal coherence could then be used to flexibly alter functional connectivity based on task demands. During WM, oscillatory coherence has been reported between prefrontal and visual areas in the theta-alpha band (Daume et al., 2017; Liebe et al., 2012) and the alpha-beta band (Mendoza-Halliday et al., 2014; Rezayat et al., 2021), between prefrontal and parietal areas in the beta band (Antzoulatos and Miller, 2016; Dotson et al., 2014; Salazar et al., 2012), between parietal and MT cortex in the alpha-beta band (Saalmann et al., 2007), and between PFC and the hippocampus in the alpha-beta band (Brincat and Miller, 2015). These inter-areal coherence measures are generally better predictors of WM performance than single-area spiking or LFP activity (Fig. 3B, and see (Rezayat et al., 2022) for review). During covert visual attention, at sites representing the attended stimulus or location, there is selective gamma-band coherence between FEF and V4 (Gregoriou Georgia et al., 2009), and between V1 and V4 (Bosman Conrado et al., 2012; Grothe et al., 2012), the latter of which predicts subsequent reaction times (Rohenkohl et al., 2018). An electrocorticography (subdural LFP recording) study from 28 areas simultaneously during an attention task revealed synchronization between areas in the theta, beta, and gamma bands (Bastos André et al., 2015a); combining these recordings with granger causality analysis and an anatomical measure of hierarchical level within the visual system led to the conclusion that inter-areal gamma synchrony is associated with feedforward processing, while beta frequency synchrony facilitates feedback signals. Consistent with this framework, prefrontal and parietal cortex synchronize at different frequencies for bottom-up vs. top-down attentional tasks (Buschman and Miller, 2007). Numerous human EEG and MEG studies likewise show flexible synchronization across brain areas depending on task demands (reviewed in (Fell and Axmacher, 2011)).

Indeed, the result of this combination of changes in spike timing relative to oscillations within an area and coherence of oscillations between areas can also be seen in the resulting changes in spike timing in one area relative to oscillations in a second area. Phase-locking between spikes in visual areas and oscillations in PFC have been reported during WM in multiple studies: between IT and FEF in the beta band (Rezayat et al., 2021), and between V4 and lateral PFC in the theta band (Liebe et al., 2012). There is also spike-phase coherence in the opposite direction, between lateral PFC spikes and alpha-beta oscillations in MT (Mendoza-Halliday et al., 2014). This inter-area spike phase locking often predicts task performance (Mendoza-Halliday et al., 2014; Rezayat et al., 2021; Verhoef et al., 2011). Changes in spike-phase coherence across areas have also been reported during covert attention (Gregoriou et al., 2012). Such changes in the timing of spikes relative to oscillations

in a connected area mean that, if input efficacy is gated by local oscillatory phase in the receiving area, the strength of functional connectivity between the regions can be modulated; the next section will review the evidence that such oscillation-based gating of inputs does occur.

6. Gating of input efficacy by local oscillatory phase

Several results provide indirect evidence that input efficacy might fluctuate with local oscillatory phase. For example, in the visual system such changes in input efficacy with phase would be expected to result in visual information which likewise fluctuates in magnitude as a function of local oscillatory phase. This dependence of visual information on oscillatory phase has been reported in the gamma band in V1 (Womelsdorf et al., 2012), and in the alpha-beta band in MT (Bahmani et al., 2018).

Paired recording data from Womelsdorf and colleagues provided early evidence that interactions between individual recording sites within or between visual areas may depend on their relative oscillation phase (Womelsdorf et al., 2007). They showed that the power correlation between sites varied based on the naturally occurring variations in the gamma-band phase offset between sites (defined relative to the average phase offset for each pair of sites); this was true across multiple datasets both within individual visual areas (cat area 17, monkey area V1 or V4), and between areas (areas 18 and 21 in cat). Optimal phase relationships preceded power correlations by 5 ms on average across all four datasets, suggesting a causal influence of phase offset on power correlation between sites, rather than a common factor causing both. These correlative data offer evidence that the strength of neuronal interactions between sites, as reflected by the power correlation, depend upon the phase relationship of their gamma oscillations; the authors hypothesize that this dependence is due to oscillation phase modulating the efficacy of synaptic input.

One of the more direct tests of this idea was conducted by Cardin and colleagues, using cell-type specific optogenetic stimulation in the barrel cortex of rodents (Cardin et al., 2009). They showed that optogenetic photostimulation of parvalbumin interneurons enabled them to specifically boost gamma-band LFP oscillations in barrel cortex. The efficacy of sensory input (vibrissa deflections) then depended on the timing of this input relative to the phase of the induced gamma oscillation. This is compelling evidence for oscillation-based gating of input efficacy; however, it was only shown for the artificially induced, rather than naturally occurring, LFP oscillations. Subsequent experiments also showed that behavioral detection of low-salience tactile stimuli depended on the timing of the stimulus relative to the phase of either evoked or endogenous gamma oscillations in barrel cortex (Siegle et al., 2014).

Similar results were reported in monkey V4 by Ni and colleagues (Ni et al., 2016). In this case, gamma oscillations were driven by the presence of a visual stimulus, while monkeys performed a change detection task. Sensitivity to visual input was measured by spiking responses to the change in the stimulus. They found that the magnitude of the visually-evoked response varied according to the oscillation phase at which visual input arrived in V4—this was true for both the gamma and alpha-beta frequency oscillations (Fig. 3 C). Only the gamma band phase, however, was significantly predictive of the animal's reaction time, and the same gamma phase corresponded with both the greatest visual response and the lowest reaction times. Because V1 spiking relative to its own gamma oscillation is likely co-varying with the coherent V4 gamma oscillation (Bosman Conrado et al., 2012; Grothe et al., 2012), this phase-dependent V4 visual response cannot be definitively attributed to changes in sensitivity of neurons within V4. To address this, Ni and colleagues turned to experiments using optogenetically-induced gamma oscillations in anesthetized cats, in area 21a (the homologue of V4). This optogenetic manipulation increased gamma power in area 21a but not in earlier visual area 17. The magnitude of area 21a visual responses again varied with local gamma phase, and by approximately the same magnitude as in the monkey V4 dataset. Together, these results strongly suggest that the phase of local gamma oscillations can modulate the gain of synaptic inputs to an area.

For gamma band oscillations, the circuit-level mechanisms which generate the oscillation, and by which the local oscillation phase could modulate sensitivity to synaptic input, have been extensively studied in systems ranging from rodent hippocampal slices to the cortex of primates performing covert attention tasks. The overall picture is one in which there is a narrow gamma phase window in which excitatory inputs to pyramidal neurons will be most effective, after which local inhibitory neurons are strongly activated, making pyramidal neurons less likely to fire (Atallah and Scanziani, 2009; Burchell et al., 1998; Buzsáki and Wang, 2012; Csicsvari et al., 2003; Haider et al., 2006; Hasenstaub et al., 2005; Salkoff et al., 2015; Vida et al., 2006; Vinck et al., 2013). Multiple computational modelling studies demonstrate that gamma synchronization can alter effective connectivity between sites based on the timing of spike arrival (Börgers and Kopell, 2008; Buehlmann and Deco, 2010; Knoblich et al., 2010; Palmigiano et al., 2017). Additionally, increases in gamma power within one area are also associated with greater synchronization between action potentials in the neurons providing input to a downstream area, increasing their ability to drive downstream neurons (Azouz and Gray, 2008; Jia et al., 2013; Zandvakili and Kohn, 2015); this synchronization of inputs is a distinct mechanism from oscillation phase-based changes in the sensitivity of the receiving neurons, although since changes in gamma synchronization within and between areas often occur in concert (e.g., (Jia et al., 2013)), both likely contribute to increased functional connectivity in many scenarios. Circuit mechanisms generating alpha-beta oscillations are comparatively less well-studied, but may also involve rhythmic local inhibitory activity (Jensen et al., 2005; Kopell et al., 2011; Lee et al., 2013; Nesse et al., 2021), with potentially analogous gating of sensitivity to excitatory inputs as a function of oscillatory phase.

We have reviewed evidence consistent with a proposed framework of sensory recruitment during WM, in which WM-driven oscillations in sensory areas enable spike timing relative to these oscillations to carry a 'hidden' representation of stored information. This phase-coded information is transmitted to downstream areas through a combination of a coherent oscillation and oscillation-dependent gating of input efficacy. Although the focus is on WM, this mechanism for controlling communication between areas could apply during many cognitive tasks in which sensory processing and behavior are modulated based on top-down signals such as context, task rules, or reward associations. The combination of changes in spike timing, oscillatory coherence, and oscillation-dependent gating of inputs could be a general mechanism to enable rapid, flexible changes in functional connectivity across regions, allowing dynamic changes in the routing of signals based on rapidly changing circumstances.

7. Implications of the proposed framework for communication between brain areas

In this framework, the role of top-down induced oscillations is to control the timing of action potentials relative to these oscillations in the recruited area. WM representations are 'hidden' in sensory areas, in that there is no change in firing rate based on the content of WM (Chelazzi et al., 1998; Chelazzi et al., 2001; Fuster, 1990; Leavitt et al., 2017; Mendoza-Halliday et al., 2014; Zaksas and Pasternak, 2006); there is, however, modulation of the oscillations in these areas, which will in turn facilitate the generation of action potentials at particular times, expressing the hidden representations. The timing of each individual spike relative to the reference oscillation will carry information about the stored representation.

pAs a general criticism to any phase code theory, the proposed framework must also address the issue of how the oscillatory code can be transmitted from one brain area to another. Oscillatory activity reflects the summation of many subthreshold synaptic interactions in the nearby neuronal population; these oscillations, unlike spiking activity, are not

directly transmitted from one brain area to another. As a solution to this issue, based on the literature reviewed in the previous section, in this framework, during times of phase-coded communication, the receiving area has a copy of the relevant oscillation in the sending area (i.e., an oscillation of the same frequency which is coherent, or phase-locked, with that in the sending area). In this mechanism, the issue of oscillations not being transmissible between locations is solved by the two communicating areas already oscillating in a synchronized manner, such that the information reflected in the phase-coded spikes could be directly transmitted. The common source of this coherent oscillatory activity is not known, but either a local source (e.g. PFC neurons maintaining a persistent activity to generate both local and distant oscillations) or another area serving as a hub coordinating both oscillations (e.g. the pulvinar nucleus of the thalamus as suggested by several studies (Saalmann et al., 2012a, Zhou et al., 2016)) could be the answer.

The proposed framework is built upon three pillars: the presence of a common oscillatory source, the oscillatory recruitment of sensory areas by prefrontal areas, and information gating between the two areas by phase-coding through the shared oscillations. The common oscillatory source serves to create and maintain the shared oscillatory reference with which communicating neuronal populations can share phase-coded information. The oscillatory recruitment of sensory areas shapes spike timing in the sensory neuronal populations without directly driving elevated spiking activity. This oscillation-dependent activity carries phase-coded information, which is then gated by the phase of the coherent oscillation in the receiving area.

8. Implications for theories of WM and attention

Within this framework, the WM representation is reflected in the timing of spikes relative to WM-induced oscillations, rather than changes in firing rate, and the role of a feedback signals is to induce a common oscillatory frame of reference to enable communication of phase-coded information during recruitment.

The proposed framework supports the idea of a distributed WM representation involving sensory areas, rather than a modular perspective in which memory maintenance occurs solely in higher associative areas. Under the assumption that the neural representation must involve spiking activity, the absence of persistent activity in sensory areas has often been interpreted as strong evidence against a distributed theory of WM (Leavitt et al., 2017); however, under the proposed framework, the lack of persistent activity does not mean that an area is not being recruited. (There is also psychophysical evidence against mnemonic information being represented in the exact same way as sensory signals (e.g., (Harrison and Bays, 2018)); however, involvement of sensory areas does not mean that sensory and memory representations are identical—see point 4 of 'Challenges' section.) The Noudoost lab has directly measured changes in the timing of spikes in MT (Bahmani et al., 2018) which reflect the content of WM, in the absence of firing rate changes. These subthreshold modulations may explain why the content of WM can be decoded using fMRI from many visual areas which do not exhibit delay activity in extracellular neurophysiological recordings (Christophel et al., 2012; Ester et al., 2009; Harrison and Tong, 2009; Serences et al., 2009). These changes in spike timing in earlier visual areas could also contribute to the delay period activity which emerges later in the visual hierarchy (e.g., in IT (Chelazzi et al., 1993) and MST (Mendoza-Halliday et al., 2014)), through the same type of changes in input efficacy demonstrated for V4 and FEF (Noudoost et al., 2021). Interestingly, inter-areal coherence is generally a better predictor of WM performance than firing rate (reviewed in (Rezayat et al., 2022)); however, the necessity of these WM-driven changes (either oscillatory changes or delay activity) in various visual areas for successful WM performance has yet to be causally tested, an important step in confirming the proposed framework.

The proposed framework also has potential implications for attention. Attention and WM are closely related (Knudsen, 2007). Psychophysical studies indicate that the two are naturally tightly linked, with attention both determining entry into WM and also being drawn to stimuli matching the content of WM (Awh et al., 2000; Awh et al., 2006; Olivers et al., 2011; Postle et al., 2004; Schmidt et al., 2002). In the presence of visual stimuli, the visual response is enhanced when the stimulus appears at the location held in WM (Merrikhi et al., 2017). The framework described here, in which the content of WM biases the efficacy with which incoming signals are passed to downstream areas (Noudoost et al., 2021), could also be described as a mechanism of attentional modulation, where changes in efficacy of input have also been reported (Briggs et al., 2013). As previously mentioned, changes in inter-areal coherence have also been reported during attention (Bastos André et al., 2015a; Bosman Conrado et al., 2012; Gregoriou Georgia et al., 2009; Grothe et al., 2012; Rohenkohl et al., 2018). Furthermore, changes in spike timing relative to oscillations, in the absence of rate changes, have also been reported to correlate with performance on an attention task (Fiebelkorn and Kastner, 2021), consistent with the proposed recruitment framework. Alternatively, some of these similarities between attention and WM effects may exist because WM typically also causes the deployment of attention; given the tight natural association between attention and WM, one cannot definitively attribute neurophysiological changes observed during WM tasks to that process alone, rather than the naturally linked deployment of attention. However, there is evidence that the neural substrates of attention and WM can be dissociated under certain circumstances. With training, it is possible to separate the focus of attention and WM using a dual-task structure (Lebedev et al., 2004; Messinger et al., 2009); using this dual-task paradigm, separate population-level representations of the attended and remembered locations can be found in the dorsolateral prefrontal cortex (dlPFC), with approximately a third of spatially selective dlPFC neurons 'multitasking' and showing selectivity for both attention and memory. A dissociation between sensory and mnemonic representations is also reported in this area (Mendoza-Halliday and Martinez-Trujillo, 2017). Such dissociations may form the basis for future experiments which more precisely attribute changes seen during WM to purely WM vs. attention-related processes. Thus, although the neural mechanisms of attention and WM are not entirely identical but difficult to fully dissociate, we propose that the oscillatory recruitment mechanism discussed here is one potential point of overlap between them.

9. Challenges and future directions

The communication through coherence theory (Bastos et al., 2015b; Fries, 2005; Fries, 2015) describes how coordinated oscillations can flexibly alter the efficacy of communication between brain areas. The "recruitment through coherence" model outlined in this paper specifically suggests that WM creates a shared oscillatory frame of reference to recruit sensory areas. Moreover, by incorporating the role of a phase code, it claims that the role of oscillations is to express the maintained representation in the differential timing of spikes. There remain several challenges to the feasibility of this model, some of which are specific to the phase coding aspect and some of which are shared with communication through coherence theory. This section highlights these challenges and suggests some avenues to address them.

1) Robustness: Although phase coding of information has been reported in many contexts (Kamiński et al., 2020; Kayser et al., 2009; Lee et al., 2005; Montemurro et al., 2008; O'Keefe and Burgess, 2005; Siegel et al., 2009; Turesson et al., 2012; Zarei et al., 2022), the magnitude of phase information overall is smaller than what is expected of the main neural code for sensory representation. However, a robust readout of a phase code requires identifying the specific oscillatory frame of reference. One experimental barrier to accurately measuring phase coding is that the recorded LFP will reflect a combination of multiple oscillatory and aperiodic signals. For example, if multiple areas recruiting a single area induce separate

oscillations to create their own channel of communication, the interference between these multiple oscillations may obscure an experimenter's ability to read out the phase code. A critical verification of the proposed model will be to show that isolating the specific oscillatory frame of reference (for example by decomposing the LFP signal using source separation techniques (Cohen, 2022, Makarov et al., 2010)) drastically improves the readout of phase coded information. In addition, it is important that measures of oscillatory coherence, power, and spike-phase locking check for confounding factors such as changes in oscillatory frequency (Haegens et al., 2014), contributions of aperiodic activity, and signal to noise ratio, and need to use methods that work with non-uniform distributions; fortunately awareness of these potential issues is increasing, and novel analytical approaches for addressing them are being developed (Cohen, 2017; Cohen, 2021; Donoghue et al., 2022; Keil et al., 2022).

2) Utility: An unresolved issue with phase coding has always been an explanation of how the information in this code can be utilized by another brain area. The timing of spikes relative to a specific local oscillation loses its meaning arriving in the next area if the appropriate oscillatory frame of reference is missing. In the proposed model, the role of coherent oscillations in the sending and receiving areas, generated by a common source (see point 5 below), is expected to resolve the issue of utility. It also requires that any changes in the exact frequency of oscillations (as have been reported for gamma oscillations, see (Ray and Maunsell, 2010)) are shared across areas, which has yet to be tested. In the case of spatial WM, in the proposed framework a spatially selective spiking activity straddling the period of WM maintenance, namely FEF persistent activity (Armstrong et al., 2009; Lawrence et al., 2005; Merrikhi et al., 2017; Sommer and Wurtz, 2001), drives both the local and distant oscillations. However, a causal manipulation of WM-related FEF activity, e.g. using pharmacological drugs known to alter PFC persistent activity (Noudoost and Moore, 2011; Williams and Goldman-Rakic, 1995), and assessing its impact on generating coherent FEF-V4 oscillations is needed to test this theory.
3) The primacy of oscillations: The proposed model suggests that the benefits of WM for sensory processing and maintenance are exerted via induced oscillations. A comprehensive model needs to take a stance regarding the relationship between these oscillatory changes and the non-oscillatory signatures of WM. As discussed earlier, the proposed model can be potentially applied to visuospatial attention as well. In the case of attention, there is as yet no unifying theory to account for the long list of neural signatures (surveyed e.g. in Table 1 of (Noudoost et al., 2010)). Importantly, many of these attentional signatures are also observed during WM; e.g. WM not only induces oscillations in visual areas, it changes the Fano factor (Merrikhi et al., 2017), RF profile (Merrikhi et al., 2017) and correlated variability of neurons (Merrikhi et al., 2018). Are these various signatures all byproducts of the induced oscillatory change, or are there separate oscillatory and non-oscillatory mechanisms in place to bring about the benefits of attention and WM for sensory processing? Answering this question may require manipulations of neural activity, to determine whether various signatures can be dissociated, along with computational modeling to understand the mechanisms linking various changes.
4) Interference between stored information and incoming sensory information: One important outstanding question is how maintained information and incoming sensory information can be simultaneously represented in sensory areas, without interfering with one another. This question is so far relatively unexplored, as almost all WM tasks used in neurophysiological recordings involve no sensory stimuli during the delay period (only occasionally with qualitatively distinct distractors (Suzuki and Gottlieb, 2013)). Indeed, even the question of how multiple visual stimuli within a single neuron's receptive field are represented is an ongoing topic of research (Jun et al., 2022). There is behavioral evidence that distracting visual stimuli can indeed interfere with memory maintenance (Hallenbeck et al., 2021); however, clearly both WM representations and sensory representations can coexist. How might the brain differentiate between the stored and sensory information? Several possibilities exist: 1) Oscillatory coherence in different frequencies, and timing of spikes relative to these oscillations, could guide the flow of stored vs. incoming information—for example, it has been suggested that gamma is used in feedforward processing, while alpha/beta reflects feedback signals (Bastos André et al., 2015a; Michalareas et al., 2016; Popov et al., 2017; van Kerkoerle et al., 2014b). 2) Phase and rate coding might carry different types of information; indeed, this type of dual coding for different variables has been reported in the hippocampus for speed and location (Huxter et al., 2003). 3) WM may recruit from a broader neural pool in visual areas- for example, object or feature WM may recruit neurons with a variety of RF locations (as suggested by fMRI decoding of stimuli from primary visual cortex (Ester et al., 2009), and spatial WM may recruit neurons with various feature selectivities, compared to those driven by an actual visual stimulus. This in turn could represent remembered stimuli in a different population subspace than sensory input (Ruff et al., 2018; Semedo et al., 2022; Semedo et al., 2019; Srinath et al., 2021). Further research will be needed to investigate these or other possible mechanisms.
5) Common source. The framework posits a common source for oscillations in the two areas, which seems necessary to ensure their coherence; more specifically, it proposes that persistent memory-related activity in FEF drives oscillations in both FEF and V4. This suggestion is as yet unproven, and can be tested with pharmacological or optogenetic manipulations of FEF activity. It is also possible that oscillations are coordinated by a third area; indeed, evidence for a role of the pulvinar nucleus of the thalamus in coordinating oscillations across cortical areas has been reported during attention (Fiebelkorn et al., 2019; Saalmann et al., 2012b).
6) Storage of multiple items. Previous findings show that within prefrontal cortex, multiple items held in WM are coded at different phases of gamma oscillations (Siegel et al., 2009). One possibility is that the same phase dependence exists in visual areas, either relative to the alpha-beta oscillation or perhaps to nested gamma cycles. The number of items held in WM may also alter the frequency of oscillations, as has been previously reported (Haegens et al., 2014). Further experiments will be needed to verify these phenomena, along with a more precise understanding of the neural circuits generating these oscillations to explain the change in frequency.

In conclusion, this framework provides a mechanistic explanation for multiple phenomena observed during visual WM, and points towards several avenues for further research. From where does the common oscillation in prefrontal and visual areas originate? To what extent is communication between other brain areas similarly modulated during WM? Does the same mechanism modulate the strength of functional connectivity between areas during covert attention? How does the brain differentiate between stored and sensory representations? How are multiple items stored? To what degree is the recruitment of various areas across the visual hierarchy necessary for successful WM performance? These questions remain important points for future investigation.

Funding

This work was supported by the National Institutes of Health [grant numbers EY026924 and NS113073 to B.N. and a training grant EY024234 to P.C.], a National Institutes of Health Core Grant [grant number EY014800], and an Unrestricted Grant from Research to Prevent Blindness, New York, NY, to the Department of Ophthalmology & Visual Sciences, University of Utah.

Declaration of Competing Interest

None.

Data Availability

Data will be made available on request.

References

Anderson, J.C., Kennedy, H., Martin, K.A.C., 2011. Pathways of attention: synaptic relationships of frontal eye field to v4, lateral intraparietal cortex, and area 46 in macaque monkey. J. Neurosci. 31, 10872.

Antzoulatos, E.G., Miller, E.K., 2016. Synchronous beta rhythms of frontoparietal networks support only behaviorally relevant representations. eLife 5, e17822.

Armstrong, K.M., Chang, M.H., Moore, T., 2009. Selection and maintenance of spatial information by frontal eye field neurons. J. Neurosci. 29, 15621.

Atallah, B.V., Scanziani, M., 2009. Instantaneous modulation of gamma oscillation frequency by balancing excitation with inhibition. Neuron 62, 566–577.

Awh, E., Anllo-Vento, L., Hillyard, S.A., 2000. The role of spatial selective attention in working memory for locations: evidence from event-related potentials. J. Cogn. Neurosci. 12, 840–847.

Awh, E., Vogel, E.K., Oh, S.H., 2006. Interactions between attention and working memory. Neuroscience 139, 201–208.

Azouz, R., Gray, C.M., 2008. Stimulus-selective spiking is driven by the relative timing of synchronous excitation and disinhibition in cat striate neurons in vivo. Eur. J. Neurosci. 28, 1286–1300.

Bahmani, Z., Daliri, M.R., Merrikhi, Y., Clark, K., Noudoost, B., 2018. Working memory enhances cortical representations via spatially specific coordination of spike times. Neuron 97, 967-79.e6.

Barone, P., Batardiere, A., Knoblauch, K., Kennedy, H., 2000. Laminar distribution of neurons in extrastriate areas projecting to visual areas V1 and V4 correlates with the hierarchical rank and indicates the operation of a distance rule. J. Neurosci. 20, 3263.

Bastos, A.M., Vezoli, J., Fries, P., 2015b. Communication through coherence with inter-areal delays. Curr. Opin. Neurobiol. 31, 173–180.

Bastos, A.M., Loonis, R., Kornblith, S., Lundqvist, M., Miller, E.K., 2018. Laminar recordings in frontal cortex suggest distinct layers for maintenance and control of working memory. Proc. Natl. Acad. Sci. 115, 1117–1122.

Bastos André, M., Vezoli, J., Bosman Conrado, A., Schoffelen, J.-M., Oostenveld, R., et al., 2015a. Visual areas exert feedforward and feedback influences through distinct frequency channels. Neuron 85, 390–401.

Benchenane, K., Tiesinga, P.H., Battaglia, F.P., 2011. Oscillations in the prefrontal cortex: a gateway to memory and attention. Curr. Opin. Neurobiol. 21, 475–485.

Börgers, C., Kopell, N.J., 2008. Gamma oscillations and stimulus selection. Neural Comput. 20, 383–414.

Bosman Conrado, A., Schoffelen, J.-M., Brunet, N., Oostenveld, R., Bastos Andre, M., et al., 2012. Attentional stimulus selection through selective synchronization between monkey visual areas. Neuron 75, 875–888.

Briggs, F., Mangun, G.R., Usrey, W.M., 2013. Attention enhances synaptic efficacy and the signal-to-noise ratio in neural circuits. Nature 499, 476–480.

Brincat, S.L., Miller, E.K., 2015. Frequency-specific hippocampal-prefrontal interactions during associative learning. Nat. Neurosci. 18, 576–581.

Bruce, C.J., Goldberg, M.E., 1985. Primate frontal eye fields. I. Single neurons discharging before saccades. J. Neurophysiol. 53, 603–635.

Brunet, N.M., Bosman, C.A., Vinck, M., Roberts, M., Oostenveld, R., et al., 2014. Stimulus repetition modulates gamma-band synchronization in primate visual cortex. Proc. Natl. Acad. Sci. 111, 3626–3631.

Buehlmann, A., Deco, G., 2010. Optimal information transfer in the cortex through synchronization. PLoS Comput. Biol. 6.

Buffalo, E.A., Fries, P., Landman, R., Buschman, T.J., Desimone, R., 2011. Laminar differences in gamma and alpha coherence in the ventral stream. Proc. Natl. Acad. Sci. 108, 11262–11267.

Burchell, T.R., Faulkner, H.J., Whittington, M.A., 1998. Gamma frequency oscillations gate temporally coded afferent inputs in the rat hippocampal slice. Neurosci. Lett. 255, 151–154.

Buschman, T.J., Miller, E.K., 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science 315, 1860–1862.

Buzsáki, G., Wang, X.J., 2012. Mechanisms of gamma oscillations. Annu Rev. Neurosci. 35, 203–225.

Cardin, J.A., Carlén, M., Meletis, K., Knoblich, U., Zhang, F., et al., 2009. Driving fast-spiking cells induces gamma rhythm and controls sensory responses. Nature 459, 663–667.

Chelazzi, L., Miller, E.K., Duncan, J., Desimone, R., 1993. A neural basis for visual search in inferior temporal cortex. Nature 363, 345–347.

Chelazzi, L., Duncan, J., Miller, E.K., Desimone, R., 1998. Responses of neurons in inferior temporal cortex during memory-guided visual search. J. Neurophysiol. 80, 2918–2940.

Chelazzi, L., Miller, E.K., Duncan, J., Desimone, R., 2001. Responses of neurons in macaque area V4 during memory-guided visual search. Cereb. Cortex 11, 761–772.

Christophel, T.B., Hebart, M.N., Haynes, J.D., 2012. Decoding the contents of visual short-term memory from human visual and parietal cortex. J. Neurosci. 32, 12983–12989.

Clark, K.L., Noudoost, B., Moore, T., 2014. Persistent spatial information in the FEF during object-based short-term memory does not contribute to task performance. J. Cogn. Neurosci. 26, 1292–1299.

Cohen, M.X., 2017. Multivariate cross-frequency coupling via generalized eigendecomposition. Elife 6.

Cohen, M.X., 2021. A data-driven method to identify frequency boundaries in multichannel electrophysiology data. J. Neurosci. Methods 347, 108949.

Cohen, M.X., 2022. A tutorial on generalized eigendecomposition for denoising, contrast enhancement, and dimension reduction in multichannel electrophysiology. Neuroimage 247, 118809.

Csicsvari, J., Jamieson, B., Wise, K.D., Buzsáki, G., 2003. Mechanisms of Gamma oscillations in the hippocampus of the behaving rat. Neuron 37, 311–322.

Daume, J., Gruber, T., Engel, A.K., Friese, U., 2017. Phase-amplitude coupling and long-range phase synchronization reveal frontotemporal interactions during visual working memory. J. Neurosci. 37, 313.

Desimone, R., Schein, S.J., Moran, J., Ungerleider, L.G., 1985. Contour, color and shape analysis beyond the striate cortex. Vis. Res 25, 441–452.

D'Esposito, M., Postle, B.R., 1999. The dependence of span and delayed-response performance on prefrontal cortex. Neuropsychologia 37, 1303–1315.

Donoghue, T., Schaworonkow, N., Voytek, B., 2022. Methodological considerations for studying neural oscillations. Eur. J. Neurosci. 55, 3502–3527.

Dotson, N.M., Salazar, R.F., Gray, C.M., 2014. Frontoparietal correlation dynamics reveal interplay between integration and segregation during visual working memory. J. Neurosci. 34, 13600.

Emrich, S.M., Riggall, A.C., LaRocque, J.J., Postle, B.R., 2013. Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. J. Neurosci. 33, 6516.

Engel, A.K., Fries, P., 2010. Beta-band oscillations—signalling the status quo? Curr. Opin. Neurobiol. 20, 156–165.

Ester, E.F., Serences, J.T., Awh, E., 2009. Spatially global representations in human primary visual cortex during working memory maintenance. J. Neurosci. 29, 15258–15265.

Fell, J., Axmacher, N., 2011. The role of phase synchronization in memory processes. Nat. Rev. Neurosci. 12, 105–118.

Fiebelkorn, I.C., Kastner, S., 2021. Spike timing in the attention network predicts behavioral outcome prior to target selection. Neuron 109, 177-88.e4.

Fiebelkorn, I.C., Pinsk, M.A., Kastner, S., 2019. The mediodorsal pulvinar coordinates the macaque fronto-parietal network during rhythmic spatial attention. Nat. Commun. 10, 215.

Fries, P., 2005. A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn. Sci. 9, 474–480.

Fries, P., 2015. Rhythms for cognition: communication through coherence. Neuron 88, 220–235.

Fries, P., Reynolds, J.H., Rorie, A.E., Desimone, R., 2001. Modulation of Oscillatory Neuronal Synchronization by Selective Visual Attention. Science 291, 1560.

Funahashi, S., Bruce, C.J., Goldman-Rakic, P.S., 1989. Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. J. Neurophysiol. 61, 331–349.

Fuster, J.M., 1990. Inferotemporal units in selective visual attention and short-term memory. J. Neurophysiol. 64, 681–697.

Fuster, J.M., Alexander, G.E., 1971. Neuron activity related to short-term memory. Science 173, 652–654.

Gevins, A., Smith, M.E., McEvoy, L., Yu, D., 1997. High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cereb. Cortex 7, 374–385.

Gregoriou, G.G., Gotts, S.J., Desimone, R., 2012. Cell-type-specific synchronization of neural activity in FEF with V4 during attention. Neuron 73, 581–594.

Gregoriou, G.G., Rossi, A.F., Ungerleider, L.G., Desimone, R., 2014. Lesions of prefrontal cortex reduce attentional modulation of neuronal responses and synchrony in V4. Nat. Neurosci. 17, 1003–1011.

Gregoriou Georgia, G., Gotts Stephen, J., Zhou, H., Desimone, R., 2009. High-frequency, long-range coupling between prefrontal and visual cortex during attention. Science 324, 1207–1210.

Grothe, I., Neitzel, S.D., Mandon, S., Kreiter, A.K., 2012. Switching neuronal inputs by differential modulations of gamma-band phase-coherence. J. Neurosci. 32, 16172.

Haegens, S., Cousijn, H., Wallis, G., Harrison, P.J., Nobre, A.C., 2014. Inter- and intra-individual variability in alpha peak frequency. Neuroimage 92, 46–55.

Haider, B., Duque, A., Hasenstaub, A.R., McCormick, D.A., 2006. Neocortical network activity in vivo is generated through a dynamic balance of excitation and inhibition. J. Neurosci. 26, 4535.

Hallenbeck, G.E., Sprague, T.C., Rahmati, M., Sreenivasan, K.K., Curtis, C.E., 2021. Working memory representations in visual cortex mediate distraction effects. Nat. Commun. 12, 4714.

Harrison, S.A., Tong, F., 2009. Decoding reveals the contents of visual working memory in early visual areas. Nature 458, 632–635.

Harrison, W.J., Bays, P.M., 2018. Visual working memory is independent of the cortical spacing between memoranda. J. Neurosci. 38, 3116–3123.

Hasenstaub, A., Shu, Y., Haider, B., Kraushaar, U., Duque, A., McCormick, D.A., 2005. Inhibitory postsynaptic potentials carry synchronized frequency information in active cortical networks. Neuron 47, 423–435.

Howard, M.W., Rizzuto, D.S., Caplan, J.B., Madsen, J.R., Lisman, J., et al., 2003. Gamma oscillations correlate with working memory load in humans. Cereb. Cortex 13, 1369–1374.

Huxter, J., Burgess, N., O'Keefe, J., 2003. Independent rate and temporal coding in hippocampal pyramidal cells. Nature 425, 828–832.

Jensen, O., Goel, P., Kopell, N., Pohja, M., Hari, R., Ermentrout, B., 2005. On the human sensorimotor-cortex beta rhythm: sources and modeling. Neuroimage 26, 347–355.

Jia, X., Tanabe, S., Kohn, A., 2013. Gamma and the coordination of spiking activity in early visual cortex. Neuron 77, 762–774.
Jun, N.Y., Ruff, D.A., Kramer, L.E., Bowes, B., Tokdar, S.T., et al., 2022. Coordinated multiplexing of information about separate objects in visual cortex. Elife 11.
Kamiński, J., Brzezicka, A., Mamelak, A.N., Rutishauser, U., 2020. Combined phase-rate coding by persistently active neurons as a mechanism for maintaining multiple items in working memory in humans. Neuron 106, 256-64.e3.
Kayser, C., Montemurro, M.A., Logothetis, N.K., Panzeri, S., 2009. Spike-phase coding boosts and stabilizes information carried by spatial and temporal spike patterns. Neuron 61, 597–608.
Keil, A., Bernat, E.M., Cohen, M.X., Ding, M., Fabiani, M., et al., 2022. Recommendations and publication guidelines for studies using frequency domain and time-frequency domain analyses of neural time series. Psychophysiology 59, e14052.
Knoblich, U., Siegle, J., Pritchett, D., Moore, C., 2010. What do we gain from Gamma? Local dynamic gain modulation drives enhanced efficacy and efficiency of signal transmission. Front. Hum. Neurosci. 4.
Knudsen, E.I., 2007. Fundamental components of attention. Annu Rev. Neurosci. 30, 57–78.
Kopell, N., Whittington, M.A., Kramer, M.A., 2011. Neuronal assembly dynamics in the beta1 frequency range permits short-term memory. Proc. Natl. Acad. Sci. 108, 3779–3784.
Kornblith, S., Buschman, T.J., Miller, E.K., 2016. Stimulus load and oscillatory activity in higher cortex. Cereb. Cortex 26, 3772–3784.
Lara, A.H., Wallis, J.D., 2014. Executive control processes underlying multi-item working memory. Nat. Neurosci. 17, 876–883.
Lara, A.H., Wallis, J.D., 2015. The role of prefrontal cortex in working memory: a mini review. Front Syst. Neurosci. 9, 173.
Lawrence, B.M., White, R.L., Snyder, L.H., 2005. Delay-period activity in visual, visuomovement, and movement neurons in the frontal eye field. J. Neurophysiol. 94, 1498–1508.
Leavitt, M.L., Mendoza-Halliday, D., Martinez-Trujillo, J.C., 2017. Sustained activity encoding working memories: not fully distributed. Trends Neurosci. 40, 328–346.
Lebedev, M.A., Messinger, A., Kralik, J.D., Wise, S.P., 2004. Representation of attended versus remembered locations in prefrontal cortex. PLoS Biol. 2, e365.
Lee, H., Simpson, G.V., Logothetis, N.K., Rainer, G., 2005. Phase locking of single neuron activity to theta oscillations during working memory in monkey extrastriate visual cortex. Neuron 45, 147–156.
Lee, J.H., Whittington, M.A., Kopell, N.J., 2013. Top-down beta rhythms support selective attention via interlaminar interaction: a model. PLOS Comput. Biol. 9, e1003164.
Liebe, S., Hoerzer, G.M., Logothetis, N.K., Rainer, G., 2012. Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. Nat. Neurosci. 15, 456–462.
Lowe, K.A., Schall, J.D., 2018. Functional categories of visuomotor neurons in macaque frontal eye Field. ENEURO 5: ENEURO 0131–18, 2018.
Lundqvist, M., Rose, J., Herman, P., Brincat Scott, L., Buschman Timothy, J., Miller, Earl K., 2016. Gamma and Beta bursts underlie working memory. Neuron 90, 152–164.
Makarov, V.A., Makarova, J., Herreras, O., 2010. Disentanglement of local field potential sources by independent component analysis. J. Comput. Neurosci. 29, 445–457.
Markov, N.T., Ercsey-Ravasz, M.M., Ribeiro Gomes, A.R., Lamy, C., Magrou, L., et al., 2014a. A weighted and directed interareal connectivity matrix for macaque. Cereb. Cortex. *Cereb. Cortex* 24, 17–36.
Markov, N.T., Vezoli, J., Chameau, P., Falchier, A., Quilodran, R., et al., 2014b. Anatomy of hierarchy: Feedforward and feedback pathways in macaque visual cortex. J. Comp. Neurol. 522, 225–259.
Mendoza-Halliday, D., Martinez-Trujillo, J.C., 2017. Neuronal population coding of perceived and memorized visual features in the lateral prefrontal cortex. Nat. Commun. 8, 15471.
Mendoza-Halliday, D., Torres, S., Martinez-Trujillo, J.C., 2014. Sharp emergence of feature-selective sustained activity along the dorsal visual pathway. Nat. Neurosci. 17, 1255–1262.
Merrikhi, Y., Clark, K., Albarran, E., Parsa, M., Zirnsak, M., et al., 2017. Spatial working memory alters the efficacy of input to visual cortex. Nat. Commun. 8, 15041.
Merrikhi, Y., Clark, K., Noudoost, B., 2018. Concurrent influence of top-down and bottom-up inputs on correlated activity of Macaque extrastriate neurons. Nat. Commun. 9, 5393.
Messinger, A., Lebedev, M.A., Kralik, J.D., Wise, S.P., 2009. Multitasking of attention and memory functions in the primate prefrontal cortex. J. Neurosci. 29, 5640–5653.
Michalareas, G., Vezoli, J., van Pelt, S., Schoffelen, J.M., Kennedy, H., Fries, P., 2016. Alpha-Beta and Gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. Neuron 89, 384–397.
Miller, E.K., Erickson, C.A., Desimone, R., 1996. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. J. Neurosci. 16, 5154.
Miller, E.K., Lundqvist, M., Bastos, A.M., 2018. Working memory 2.0. Neuron 100, 463–475.
Mitchell, J.F., Sundberg, K.A., Reynolds, J.H., 2007. Differential attention-dependent response modulation across cell classes in macaque visual area V4. Neuron 55, 131–141.
Montemurro, M.A., Rasch, M.J., Murayama, Y., Logothetis, N.K., Panzeri, S., 2008. Phase-of-firing coding of natural visual stimuli in primary visual cortex. Curr. Biol. 18, 375–380.
Nesse, W.H., Bahmani, Z., Clark, K., Noudoost, B., 2021. Differential contributions of inhibitory subnetwork to visual cortical modulations identified via computational model of working memory. Front Comput. Neurosci. 15, 632730.
Ni, J., Wunderle, T., Lewis Christopher, M., Desimone, R., Diester, I., Fries, P., 2016. Gamma-rhythmic gain modulation. Neuron 92, 240–251.
Noudoost, B., Moore, T., 2011. Control of visual cortical signals by prefrontal dopamine. Nature 474, 372–375.
Noudoost, B., Chang, M.H., Steinmetz, N.A., Moore, T., 2010. Top-down control of visual attention. Curr. Opin. Neurobiol. 20, 183–190.
Noudoost, B., Clark, K.L., Moore, T., 2021. Working memory gates visual input to primate prefrontal neurons. eLife 10, e64814.
O'Keefe, J., Burgess, N., 2005. Dual phase and rate coding in hippocampal place cells: theoretical significance and relationship to entorhinal grid cells. Hippocampus 15, 853–866.
Olivers, C.N., Peters, J., Houtkamp, R., Roelfsema, P.R., 2011. Different states in visual working memory: when it guides attention and when it does not. Trends Cogn. Sci. 15, 327–334.
Palmigiano, A., Geisel, T., Wolf, F., Battaglia, D., 2017. Flexible information routing by transient synchrony. Nat. Neurosci. 20, 1014–1022.
Pasternak, T., Greenlee, M.W., 2005. Working memory in primate sensory systems. Nat. Rev. Neurosci. 6, 97–107.
Popov, T., Kastner, S., Jensen, O., 2017. FEF-controlled alpha delay activity precedes stimulus-induced gamma-band activity in visual cortex. J. Neurosci. 37, 4117–4127.
Postle, B.R., 2006. Working memory as an emergent property of the mind and brain. Neuroscience 139, 23–38.
Postle, B.R., Awh, E., Jonides, J., Smith, E.E., D'Esposito, M., 2004. The where and how of attention-based rehearsal in spatial working memory. Brain Res Cogn. Brain Res 20, 194–205.
Pouget, P., Stepniewska, I., Crowder, E., Leslie, M., Emeric, E., et al., 2009. Visual and motor connectivity and the distribution of calcium-binding proteins in macaque frontal eye field: implications for saccade target selection. Front. Neuroanat. 3.
Rao, S.C., Rainer, G., Miller, E.K., 1997. Integration of what and where in the primate prefrontal cortex. Science 276, 821–824.
Ray, S., Maunsell, J.H., 2010. Differences in gamma frequencies across visual cortex restrict their possible use in computation. Neuron 67, 885–896.
Rezayat, E., Dehaqani, M.-R.A., Clark, K., Bahmani, Z., Moore, T., Noudoost, B., 2021. Frontotemporal coordination predicts working memory performance and its local neural signatures. Nat. Commun. 12, 1103.
Rezayat, E., Clark, K., Dehaqani, M.-R.A., Noudoost, B., 2022. Dependence of working memory on coordinated activity across brain areas. Front Syst. Neurosci. 15.
Roberts, Mark J., Lowet, E., Brunet Nicolas, M., Ter Wal, M., Tiesinga, P., et al., 2013. Robust gamma coherence between macaque V1 and V2 by dynamic frequency matching. Neuron 78, 523–536.
Rockland, K.S., Pandya, D.N., 1979. Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Res. 179, 3–20.
Rohenkohl, G., Bosman, C.A., Fries, P., 2018. Gamma synchronization between V1 and V4 improves behavioral performance. Neuron 100, 953-63.e3.
Romo, R., Brody, C.D., Hernández, A., Lemus, L., 1999. Neuronal correlates of parametric working memory in the prefrontal cortex. Nature 399, 470–473.
Rose, N.S., LaRocque, J.J., Riggall, A.C., Gosseries, O., Starrett, M.J., et al., 2016. Reactivation of latent working memories with transcranial magnetic stimulation. Science 354, 1136–1139.
Ruff, D.A., Ni, A.M., Cohen, M.R., 2018. Cognition as a window into neuronal population space. Annu Rev. Neurosci. 41, 77–97.
Rushworth, M.F.S., Nixon, P.D., Eacott, M.J., Passingham, R.E., 1997. Ventral prefrontal cortex is not essential for working memory. J. Neurosci. 17, 4829.
Saalmann, Y.B., Pigarev, I.N., Vidyasagar, T.R., 2007. Neural mechanisms of visual attention: how top-down feedback highlights relevant locations. Science 316, 1612–1615.
Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012a. The pulvinar regulates information transmission between cortical areas based on attention demands. Science 337, 753–756.
Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012b. The pulvinar regulates information transmission between cortical areas based on attention demands. Science 337, 753–756.
Salazar, R.F., Dotson, N.M., Bressler, S.L., Gray, C.M., 2012. Content-specific fronto-parietal synchronization during visual working memory. Sci. (N. Y., N. Y.) 338, 1097–1100.
Salkoff, D.B., Zagha, E., Yüzgeç, Ö., McCormick, D.A., 2015. Synaptic mechanisms of tight spike synchrony at gamma frequency in cerebral cortex. J. Neurosci. 35, 10236.
Schmidt, B.K., Vogel, E.K., Woodman, G.F., Luck, S.J., 2002. Voluntazy and automatic attentional control of visual working memory. Percept. Psychophys. 64, 754–763.
Semedo, J.D., Zandvakili, A., Machens, C.K., Yu, B.M., Kohn, A., 2019. Cortical areas interact through a communication subspace. Neuron 102, 249-59.e4.
Semedo, J.D., Jasper, A.I., Zandvakili, A., Krishna, A., Aschner, A., et al., 2022. Feedforward and feedback interactions between visual cortical areas use different population activity patterns. Nat. Commun. 13, 1099.
Serences, J.T., Ester, E.F., Vogel, E.K., Awh, E., 2009. Stimulus-specific delay activity in human primary visual cortex. Psychol. Sci. 20, 207–214.
Siegel, M., Warden, M.R., Miller, E.K., 2009. Phase-dependent neuronal coding of objects in short-term memory. Proc. Natl. Acad. Sci. USA 106, 21341–21346.
Siegle, J.H., Pritchett, D.L., Moore, C.I., 2014. Gamma-range synchronization of fast-spiking interneurons can enhance detection of tactile stimuli. Nat. Neurosci. 17, 1371–1379.
Sommer, M.A., Wurtz, R.H., 2001. Frontal eye field sends delay activity related to movement, memory, and vision to the superior colliculus. J. Neurophysiol. 85, 1673–1685.
Sreenivasan, K.K., Curtis, C.E., D'Esposito, M., 2014. Revisiting the role of persistent neural activity during working memory. Trends Cogn. Sci. 18, 82–89.

Srinath, R., Ruff, D.A., Cohen, M.R., 2021. Attention improves information flow between neuronal populations without changing the communication subspace. Curr. Biol. 31, 5299-313.e4.
Stanton, G.B., Bruce, C.J., Goldberg, M.E., 1995. Topography of projections to posterior cortical areas from the macaque frontal eye fields. J. Comp. Neurol. 353, 291–305.
Suzuki, M., Gottlieb, J., 2013. Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. Nat. Neurosci. 16, 98–104.
Turesson, H.K., Logothetis, N.K., Hoffman, K.L., 2012. Category-selective phase coding in the superior temporal sulcus. Proc. Natl. Acad. Sci. USA 109, 19438–19443.
Ungerleider, L.G., Galkin, T.W., Desimone, R., Gattass, R., 2008. Cortical connections of area V4 in the Macaque. Cereb. Cortex 18, 477–499.
van Kerkoerle, T., Self, M.W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., et al., 2014a. Alpha and Gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. Proc. Natl. Acad. Sci. 111, 14332–14341.
van Kerkoerle, T., Self, M.W., Dagnino, B., Gariel-Mathis, M.A., Poort, J., et al., 2014b. Alpha and Gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. Proc. Natl. Acad. Sci. USA 111, 14332–14341.
Verhoef, B.E., Vogels, R., Janssen, P., 2011. Synchronization between the end stages of the dorsal and the ventral visual stream. J. Neurophysiol. 105, 2030–2042.
Vida, I., Bartos, M., Jonas, P., 2006. Shunting inhibition improves robustness of gamma oscillations in hippocampal interneuron networks by homogenizing firing rates. Neuron 49, 107–117.
Vinck, M., Womelsdorf, T., Buffalo Elizabeth, A., Desimone, R., Fries, P., 2013. Attentional Modulation of Cell-Class-Specific Gamma-Band Synchronization in Awake Monkey Area V4. Neuron 80, 1077–1089.
Williams, G.V., Goldman-Rakic, P.S., 1995. Modulation of memory fields by dopamine D1 receptors in prefrontal cortex. Nature 376, 572–575.
Womelsdorf, T., Fries, P., Mitra, P.P., Desimone, R., 2006. Gamma-band synchronization in visual cortex predicts speed of change detection. Nature 439, 733–736.
Womelsdorf, T., Schoffelen, J.-M., Oostenveld, R., Singer, W., Desimone, R., et al., 2007. Modulation of neuronal interactions through neuronal synchronization. Science 316, 1609.
Womelsdorf, T., Lima, B., Vinck, M., Oostenveld, R., Singer, W., et al., 2012. Orientation selectivity and noise correlation in awake monkey area V1 are modulated by the gamma cycle. Proc. Natl. Acad. Sci. 109, 4302–4307.
Zaksas, D., Pasternak, T., 2006. Directional signals in the prefrontal cortex and in area MT during a working memory for visual motion task. J. Neurosci. 26, 11726.
Zandvakili, A., Kohn, A., 2015. Coordinated neuronal activity enhances corticocortical communication. Neuron 87, 827–839.
Zarei, M., Jahed, M., Dezfouli, M.P., Daliri, M.R., 2022. Sensory representation of visual stimuli in the coupling of low-frequency phase to spike times. Brain Struct. Funct. 227, 1641–1654.
Zhou, H., Schafer Robert, J., Desimone, R., 2016. Pulvinar-cortex interactions in vision and attention. Neuron 89, 209–220.