



Alpha suppression indexes a spotlight of visual-spatial attention that can shine on both perceptual and memory representations

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Abstract

Although researchers have been recording the human electroencephalogram (EEG) for almost a century, we still do not completely understand what cognitive processes are measured by the activity of different frequency bands. The 8- to 12-Hz activity in the alpha band has long been a focus of this research, but our understanding of its links to cognitive mechanisms has been rapidly evolving recently. Here, we review and discuss the existing evidence for two competing perspectives about alpha activity. One view proposes that the suppression of alpha-band power following the onset of a stimulus array measures attentional selection. The competing view is that this same activity measures the buffering of the task-relevant representations in working memory. We conclude that alpha-band activity following the presentation of stimuli appears to be due to the operation of an attentional selection mechanism, with characteristics that mirror the classic views of attention as selecting both perceptual inputs and representations already stored in memory.

Keywords Alpha band activity · Attention · Working memory · Electrophysiology

Introduction

When Hans Berger first recorded the electroencephalogram (EEG) from his son Klaus, the most striking observation was that the amplitude of the ~10-Hz waves could be seen to visibly decrease when his son opened his eyes (Berger, 1929). This observation was subsequently replicated and legitimized by Edgar Adrian, having previously won the Nobel

Prize for his discovery of rate coding by neurons (Adrian & Matthews, 1934; Adrian & Yamagiwa, 1935). For decades researchers have sought to understand this decrease in alpha power, and what cognitive process elicits this signal that we can record on the surface of subjects' heads. Here we capitalize on this work and propose an account of these oscillations in which alpha power effects observed across different laboratory tasks can be understood as emanating from the same cognitive process of selection.

A great deal of work from the early period of EEG research focused on discovering the conditions that could quiet the alpha oscillations (Walter, 1938). Although Berger had initially thought that it was the closing of the eyelids that caused alpha oscillations to decrease in amplitude, Adrian first showed that it was not the position of the eyelids, but the presentation of visual stimuli that quieted the alpha oscillations (Adrian & Matthews, 1934; MacLean et al., 2019). Indeed, even the expectation of seeing a stimulus in a completely dark room was sufficient to quiet the alpha waves. Work from this period using multiple recording electrodes showed that the alpha waves appear to be synchronized across the posterior part of the head (Walter, 1938). These waves can be stopped by trying to see in a dark room, and by performing a mental math problem, but not by squeezing a lever with great force, suggesting to the researchers at the

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time that this alpha activity was due to activity in the visual system (Lindsley, 1969). This line of work also reported that the quieting of alpha was absent in blind subjects, providing further evidence that is consistent with the view that a normally functioning visual system is required for the suppression of alpha by stimuli or tasks (Adrian & Matthews, 1934). Although this qualitative work produced a large number of observations of interest to cognitive scientists, a review written when EEG activity was just beginning to be averaged into event-related potentials (ERPs) lamented the fact that we still did not understand the nature, source, or function of the 8- to 12-Hz oscillations in the EEG that Berger first identified decades before (Lindsley, 1969).

In the modern era, researchers continued to try to understand both the origin and the function of these obvious fluctuations that dominate the human EEG (Bollimunta et al., 2008; Jensen & Mazaheri, 2010; Klimesch, 2012; Lewis et al., 2016; Palva & Palva, 2007; Van Diepen et al., 2019). The phenomenon of *stimulus-induced alpha desynchronization*, *alpha suppression*, or simply *alpha blocking*, is the observation that posterior alpha power exhibits a prolonged decrease following the onset of a stimulus (Klimesch et al., 2006), often after an initial, brief increase in alpha power related to the evoked sensory activity typically measured with ERPs, such as the P1 and N1 that are dominated by 10-Hz activity (see Fig. 1). This phenomenon of alpha suppression has long been fertile ground in which to test a variety of hypotheses about human information processing (Sokolov, 1960, 1963), as it remains today. In this article, we focus on the riddle of what it is that our mind does that underlies this reduction in the amplitude of these 8- to 12-Hz oscillations around the time of stimulus presentation.

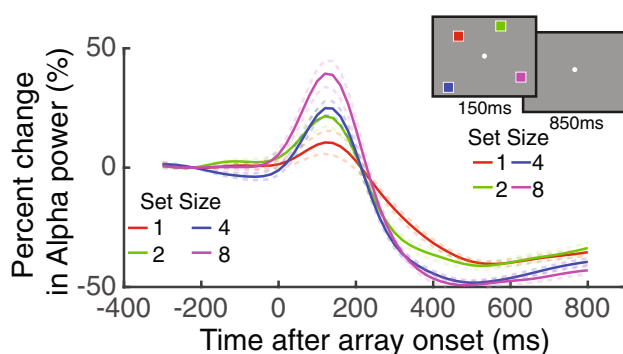


Fig. 1 Example of typical alpha-power profile elicited by the presentation of a stimulus array that varies in set size. The initial increase in alpha elicited by the amount of sensory stimulation is followed by a suppression of alpha activity. It is this subsequent valley of suppression that people have debated the meaning of. As observed in this example, the strength of alpha suppression appears to decrease until approximately set size 3. Adapted from Fukuda and Woodman (2017) *PNAS*

The brain in neutral

Until the last couple of decades, it seemed that the most obvious explanation for the modulation of alpha power was that alpha-band activity reflected the general state of arousal of the human brain, and not a specific mechanism of information processing (Lindsley, 1969; Palva & Palva, 2007). The idea was that alpha activity was strong when the brain was at rest, but when the brain began to work the alpha oscillations would decrease in amplitude. In this way, alpha power can be viewed as inversely proportional to the subject's state of arousal.

The idea that alpha waxes and wanes as the brain works less and more has been most clearly articulated by the idea that strong alpha activity may be due to the active inhibition of information-processing circuits in the brain (Klimesch, 2012). Under this account, a drop in alpha power is due to disinhibition of the circuitry needed to process the stimuli that are presented. However, both proponents and opponents recognize that this simple idea cannot explain the totality of the observations involving modulations of alpha-band activity (Deiber et al., 2012; Foster & Awh, 2018; Klimesch et al., 2007). Indeed, alpha-band modulations are unlikely to be a unitary phenomenon, but instead it seems clear that activity in this frequency band exists in the brain in the absence of cognitive activity (Kennard & Nims, 1942; Mehta et al., 2000), with some proportion of the alpha activity that we measure being related to tonic brain functions, not the punctate processing of information that we focus on during this discussion.

Although the simple idea that alpha power reflects brain idling was the modal perspective of alpha activity when the field was young (Walter, 1938), Berger entertained the hypothesis that the reduction in the size of the alpha waves indexes a particular cognitive mechanism, specifically *waves of attention* (Berger, 1929), as contemporaries referred to the phenomenon of mind wandering. During the last two decades, our field has witnessed a growing volume of research suggesting that the modulations of alpha-band power may provide a neurophysiological index of awareness (Benwell et al., 2017; Gallotto et al., 2017), implicit processing (Grasso et al., 2018), attention (Foster & Awh, 2018; Herring et al., 2015; Ikkai et al., 2016; Klimesch, 2012; Wildegger et al., 2017), or working memory (Fukuda & Woodman, 2017; Jensen et al., 2002; Palva et al., 2010; Reinhart et al., 2012; Reinhart & Woodman, 2014; Sauseng et al., 2009). But which is it? Or do the changes in our alpha-band activity measure a host of different cognitive operations? There appear to be both lateralized and broadly distributed alpha signals, and perhaps these different ways of measuring alpha suppression measure different brain mechanisms. The diversity

of findings and ways of measuring alpha might suggest that these 8- to 12-Hz oscillations are modulated by many independent cognitive operations. Alternatively, alpha oscillations might reflect a core cognitive operation that is common across many different tasks, namely, attentional selection. In this review, we propose that the entirety of the empirical evidence can be accounted for by proposing that alpha modulations are triggered by the operation of an attentional selection mechanism that selects important new inputs, as well as participating in the encoding and retrieval of visual memory representations.

In the following sections, we propose that the preponderance of the evidence in the literature indicates that alpha-band activity measures the selection of representations by attention, consistent with a foundational perspective regarding alpha (Klimesch, 2012), and not the other cognitive operations that may appear at times to be consistent with the patterns of alpha activity measured in a particular task. Specifically, we will describe how it is easy to mistake alpha-power modulations as indexing the buffering of representations in working memory.

Alpha as an index of attentional selection

After Berger's early proposals that alpha power indexed the waxing and waning of attentiveness across time, one of the first rigorous tests in the modern era of this idea was performed by Worden and colleagues (Worden et al., 2000). As shown in Fig. 2a, spatial cues indicated the likely location of a target stimulus. The presentation of these cues induced the suppression of the alpha activity contralateral to the cued location during the protracted cue-to-target interval. This provided a clear demonstration that the orienting of visual-spatial attention was mirrored by a spatial pattern of alpha power change across the head. Since this demonstration, researchers have shown that the scalp distribution of alpha suppression shifts systematically as attention is shifted to different locations in the visual field (see Fig. 2b) (Rihs et al., 2007). Currently, the spatial distribution of alpha-band activity is what feeds most machine-learning analyses of EEG data during a variety of different tasks (Yannick et al., 2019). That is, this spatial pattern of alpha suppression across the head is used to test hypotheses about how information is processed (Sutterer, Foster, Adam, et al., 2019a).

Concluding that the alpha power suppression following a stimulus is due to attention and not a closely related cognitive mechanism, such as working memory, can be difficult (Fukuda & Woodman, 2017). The difficulty arises because theories of cognitive processing propose that mechanisms of attentional selection may be embedded in memory systems that store representations. Specifically, a long line of models have proposed that attending to a memory representation

brings that representation into a state that we call working memory, and that retrieval from long-term memory is little more than selecting that memory representation with attention (Cowan, 2016; James, 1890; Norman, 1968; Oberauer, 2019).

These models propose that the reason working memory has a capacity limit is because attention can only switch between representations fast enough to maintain about three of them across time (Camos et al., 2018). Either attention cannot be split between more than about three representations simultaneously, or the speed of an attentional shift is sufficiently slow that attention can only shift between three representations and be effective. When we try to shift attention between more representations, the fourth and fifth representations slip back into an inactive memory state before attention can return to this representation to refresh it, and this results in worse memory. Like spinning plates on poles, if attention does not return fast enough to refresh a representation, then that representation drops and disappears from the active set in working memory (Zhang & Luck, 2009). A closely related view is that attention might serve working memory storage by refreshing representations held in this temporary memory state (Awh & Jonides, 1998; Awh & Jonides, 2001), although attentional selection of a representation might not be necessary to establish storage in working memory.

This view of attention as a mechanism that selects important perceptual inputs, but also representations that are already stored in memory is the focus of our theoretical proposal. Specifically, the available evidence that we review in what follows makes it seem as though alpha suppression tracks exactly such a mechanism. That is, alpha suppression appears to implement a spatial mechanism that works to activate both the task-relevant perceptual inputs and the task-relevant memory representations needed at any given moment in time. However, given that attention-based refreshing is one model of working memory maintenance, how can we ever determine that alpha-band activity is due to the operation of attention and not the storage of the working memory representations themselves?

Alpha suppression looks like a spatial spotlight or zoom lens of attention

One way in which alpha-band suppression behaves like an attention mechanism is that it appears to have the defining characteristics of a spatial spotlight (Posner & Cohen, 1984). The spatial cuing results of Worden et al. (2000) are obviously consistent with the idea that alpha tracks the spatial deployment of attention across our visual field. Recent studies using decoding methods have shown that alpha-band activity following stimulus onset can decode the location

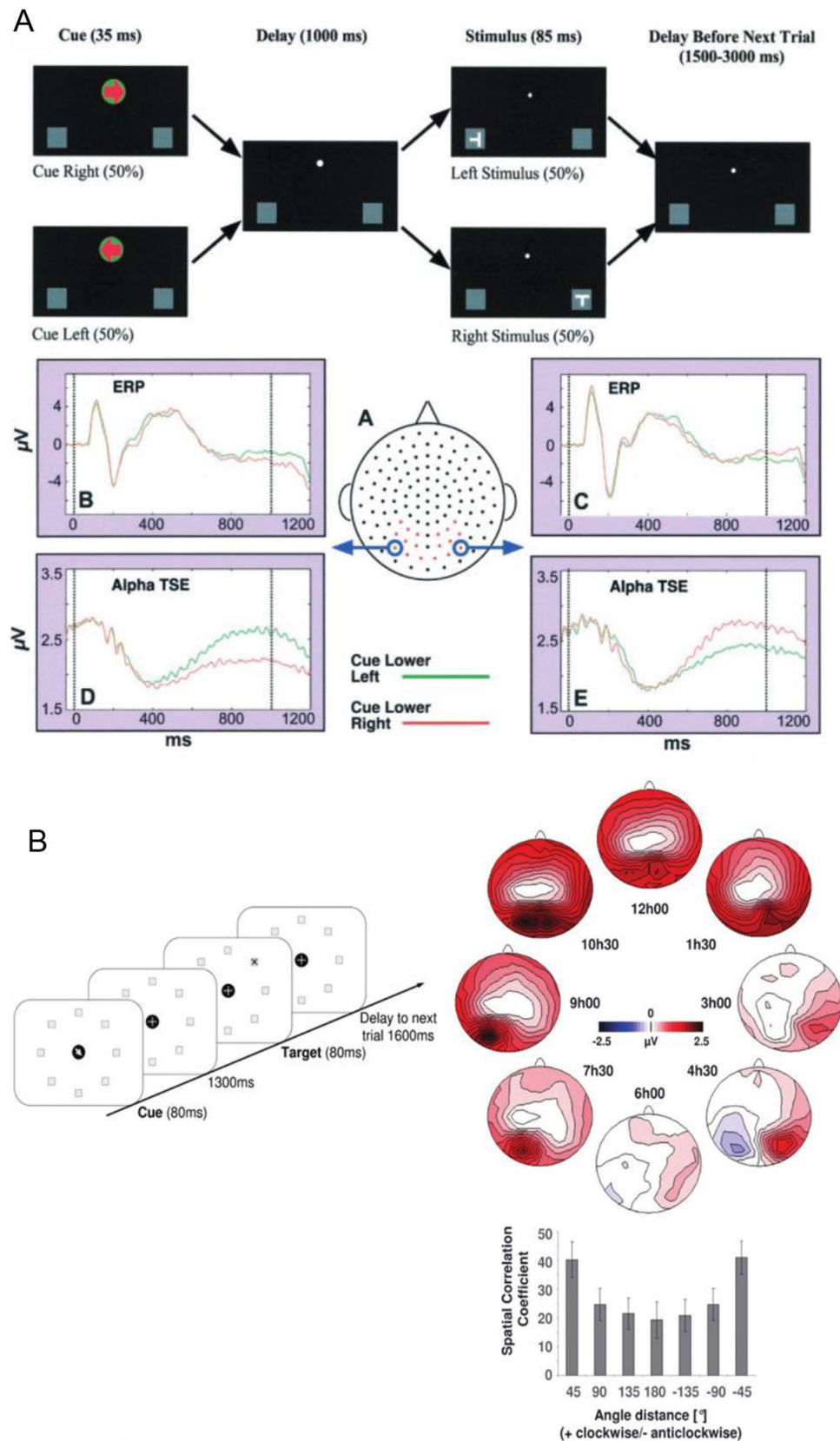


Fig. 2 Scalp distribution differences of alpha suppression following spatial cues to attend to certain locations in the visual field. **a** Results of an early study showing alpha suppression contralateral to a cued

location (Worden et al., 2000). **b** Results of a spatial cuing experiment showing the shift in the distribution of alpha suppression as attention is shifted to locations in a circular array (Rihs et al., 2007)

of the stimuli, but not the other features of these objects (Bae & Luck, 2018; Wolff et al., 2017). If alpha indexes a spatial spotlight of attention (Sutterer et al., 2021), then it would make sense that these oscillations would only carry information about where the object was. In contrast, if alpha were indexing the storage of those object representations in working memory, then we would expect these oscillations to carry information about object representations, such as the orientation, color, shape, or some other feature of the objects that people can easily remember. It appears that alpha only carries information about the locations of task-relevant objects, devoid of any other information about what is stored in memory. For example, Fig. 3 shows how

an inverted encoding model can be used to reconstruct the spatial location of a task-relevant stimulus from the distribution of alpha power (Foster et al., 2017), whereas we know that it is not possible to decode the orientation of the same objects (Bae & Luck, 2018). This is an important point to emphasize, because a reader might think that alpha looks spatially selective simply because people have used spatial manipulations to study it. However, when researchers have presented subjects with other kinds of information, human alpha activity appears to be unmodulated by stimulus features other than spatial location (Bae & Luck, 2018; Wolff et al., 2017). Thus, the spatial nature of alpha-band activity makes this signal look like the spotlight of attention that

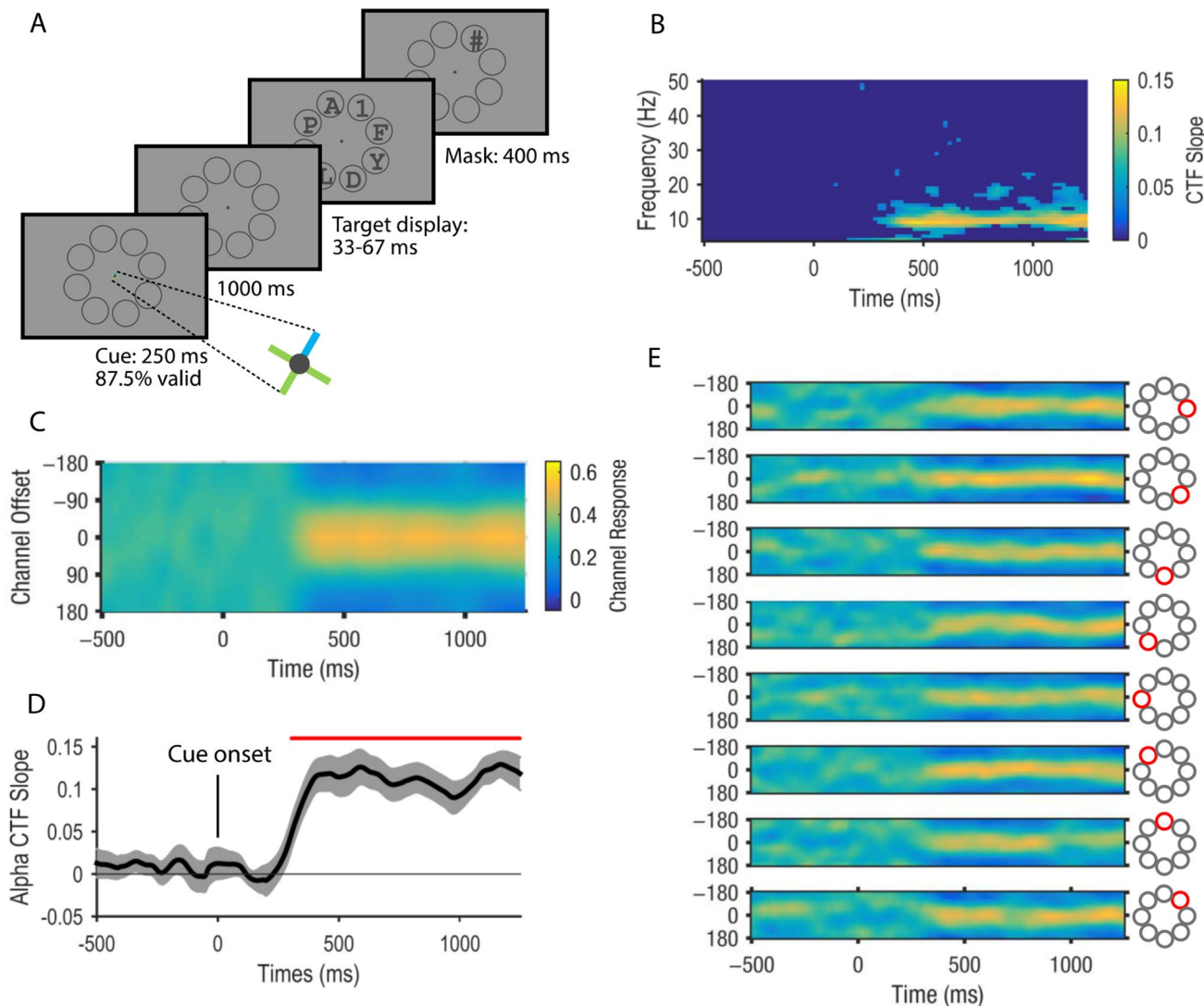


Fig. 3 Alpha suppression used to reconstruct the location cued by a spatial pre-cue using an inverted encoding model. **a** The spatial pre-cuing paradigm. **b** The channel-tuning functions of the model are used to derive a slope indicating where the information content is changing across channels. **c** The spatial precision of this model to

reconstruct the cued location. **d** The onset of these signals in time, showing that they appear well before the target array. **e** The reliability of the model to reconstruct each cued location, as shown with the red circle in the cartoon of the array. Adapted from Foster, Sutterer, et al. *Psych Sci* (2017)

cognitive psychologists have hypothesized the existence of for decades (Eriksen & St. James, 1986; Posner, 1980; Treisman & Gormican, 1988; Wolfe, 1998).

One long-standing proposal about the spatial nature of attentional selection is that such selection may operate less like a spotlight with a fixed size and more like a zoom lens that can change the size of its field of view (Eriksen & St. James, 1986). This idea accounts for findings suggesting that attention can either be strongly focused on a small region of space, or can be weakly focused across a much larger region of space. It should be noted that such a deployment of visual attention could be brought about either by the probabilistic movement of an attentional beam or spotlight, or by the simultaneous deployment of a limited attentional resource across increasingly large regions of space (Shulman et al., 1979). Current evidence makes it appear that alpha exhibits exactly the pattern expected of a spatial attention mechanism that operates like a zoom lens, in that the spatial extent of a to-be-attended region modulates the depth of alpha suppression (Wang et al., 2021), and findings from alpha-fed machine learning approaches that show that the spatial tuning of alpha-band activity broadens when observers are asked to attend to multiple locations (Feldmann-Wüstefeld & Awh, 2019; Sutterer, Foster, Adam, et al., 2019a).

Recall that the hypothesis that is in competition with the attentional selection explanation is that alpha-band suppression tracks working memory. One prediction of this account is that alpha power should change with each additional representation that needs to be stored in working memory, but not change when task-irrelevant stimuli are presented that attention filters out. Recent empirical work suggests that this prediction is not confirmed. Figure 4 shows that the alpha suppression that follows the onset of arrays with distractors that require filtering is stronger than arrays with only to-be-remembered color targets. When the array contains a distractor that needs to be filtered, then the alpha suppression increases, and is stronger with each additional distractor in each array. But alpha power does not increase with each additional target that needs to be stored in working memory as with each new array the *list* of targets increases in length. In contrast with the pattern of alpha-band suppression, we find that the contralateral delay activity (CDA) component of subjects' ERPs does increase with each target that needs to be stored in memory. A large volume of empirical work has experimentally linked the CDA with storage in working memory (Luria et al., 2016), so this ERP waveform provides a useful way of cross-validating the sensitivity

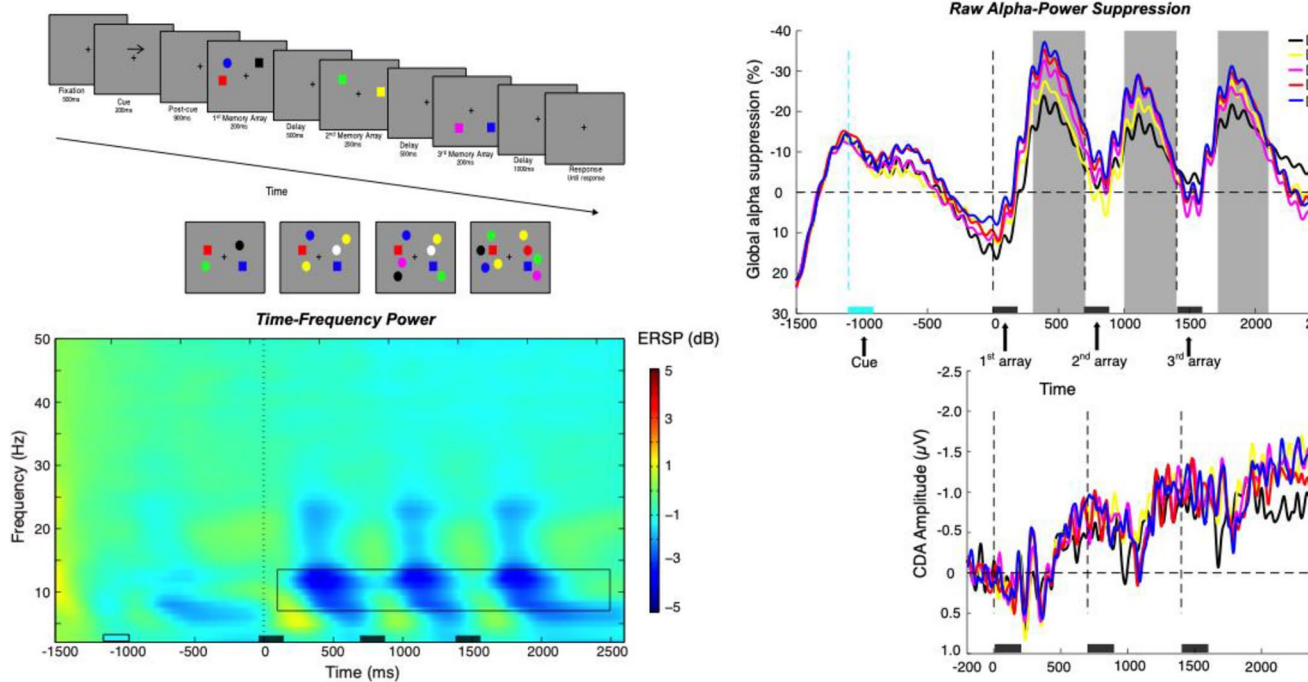


Fig. 4 Alpha suppression tracking the presence and number of distractor objects, while the contralateral delay activity (or CDA) tracked the number of targets people needed to remember. The upper left panel shows the stimuli in which the number of distractors was manipulated across trials (D0 = 0 distractors, D1 = 1 distractor, D2 = 2 distractors, etc.), and the bottom left panel show the power across frequencies from a representative posterior parietal channel.

The plot in the upper right panel shows the change in alpha power relative to baseline following each event in the task. The bottom right panel shows the currently measured posterior CDA amplitude. We found that mean alpha power was sensitive to the set size of distractors in each array, whereas the CDA amplitude was only sensitive to the number of targets held in visual working memory. Adapted from Wang et al. (2021)

of the alpha power that we measure at the same time. These findings are hard to reconcile with the view that alpha indexes a mechanism that is storing target representations in working memory. Instead, this pattern suggests that alpha power tracks the operation of attention, as it filters out distractors from subsequent processing (Wang et al., 2021).

The fact that alpha carries only location information and does not increase with working memory load still means that this mechanism could be vital for the storage and maintenance of spatial information in memory. Indeed, one of the primary models of spatial working memory is that attentional rehearsal keeps spatial representations active (Awh & Jonides, 1998). Our point here is simply that given the evidence that this mechanism is purely spatial, we believe when this mechanism is interacting with memory representations it performs the kind of spatial selection and refreshing described previously (Awh & Jonides, 2001; MacLean et al., 2019), and does suggest that we are studying a mechanism with its origins in the dorsal visual processing stream (Freud et al., 2016).

Our proposal that alpha suppression tracks a mechanism of visual-spatial attention that looks like a spatial spotlight is related to a contrasting proposal that alpha suppression is actually due to gating inhibition. Jensen and Mazaheri (2010) proposed an account in which spatially-specific networks are inhibited to prevent their representations from propagating through the rest of the brain. The idea is that alpha really indexes an inhibitory gating function. From this perspective, power is high when information is being actively suppressed within a sensory system, such as the visual hemifield containing an unattended item (Händel et al., 2011). Theoretically, this idea is a possible implementation of the classic filter models in cognitive psychology (Broadbent, 1957), in which perceptual attention serves to gate sensory inputs by keeping out unattended information. The literature is currently assessing whether this account is consistent with the available data (Foster & Awh, 2019). This idea provides a nice contrast to the present proposal in which we hypothesize that alpha suppression tracks a spatial spotlight of attention that enhances targets and is sensitive to the spatial extent of the attended region, while the number of task-relevant inputs was held constant (Wang, et al., 2020). We believe that our proposal will help spur definitive experiments in this active area of cognitive neuroscientific investigation.

Here we have emphasized how the spatial characteristics of alpha suppression exhibit the defining characteristics of a spatial attention mechanism, not working memory storage. Next, we turn to the temporal characteristics of the alpha-suppression signal.

Lateralized alpha suppression is elicited by spatial attention cues, not memory arrays

Another crucial feature of alpha-band suppression that ties it to attention and not working memory is its timing. Figure 5 shows that lateralized alpha suppression is elicited by the onset of the spatial cue indicating the location of targets that subjects need to remember, but not the to-be-remembered stimuli themselves. In addition, it appears that the time course of alpha suppression tracks both internally generated shifts of attention and stimulus-driven shifts (Keefe & Störmer, 2021). Clearly this is problematic for the view that the alpha oscillations themselves are the reverberations of the working memory representations.

The time locking of lateralized alpha-band modulations to visual-spatial cues, but not memoranda, links alpha-band activity to the shift in visual-spatial attention preceding visual working memory storage, not visual working memory storage itself, because there is no information yet to store. As shown in the lower panel of Fig. 5, if we present an attentional pre-cue showing the spatial location of the to-be-encoded information, followed by the to-be-remembered information, we can see that the spatial pre-cue strongly suppresses the alpha activity. In contrast, the memoranda that follow the cue elicit weak modulations of lateralized alpha activity, never reaching the level that we observed following the visual-attention cue. Thus, the timing of lateralized alpha suppression is locked to when attention needs to shift through space, not when information needs to be encoded or maintained in working memory.

There is a puzzle when it comes to the timing of alpha activity related to the mechanism it may index. That is, the timing of alpha-band activity may lag the cognitive mechanisms that trigger its oscillations. Specifically, attention is thought to be an early mechanism in the course of information processing in the brain dating back to the earliest theories (Broadbent, 1957). Neurophysiological demonstrations of early selection have shown that spatial pre-cues can result in attention-changing activity in the earliest stages of processing in the brain, such as in area V1 of the visual system (Luck et al., 1997; Motter, 1993). As a result, we would expect alpha-suppression signals to be fast and early, like we believe attentional selection to be itself. Instead, the alpha-suppression signal appears to be a temporally slow signal, after an initial transient sensory signal (MacLean et al., 2019). One that can continue to be measured for hundreds of milliseconds after the effects of attentional shifts are evident with other neuroscientific measures (Woodman & Luck, 1999, 2003). Although the timing of alpha suppression is more consistent with it indexing attention than memory storage, its sluggishness

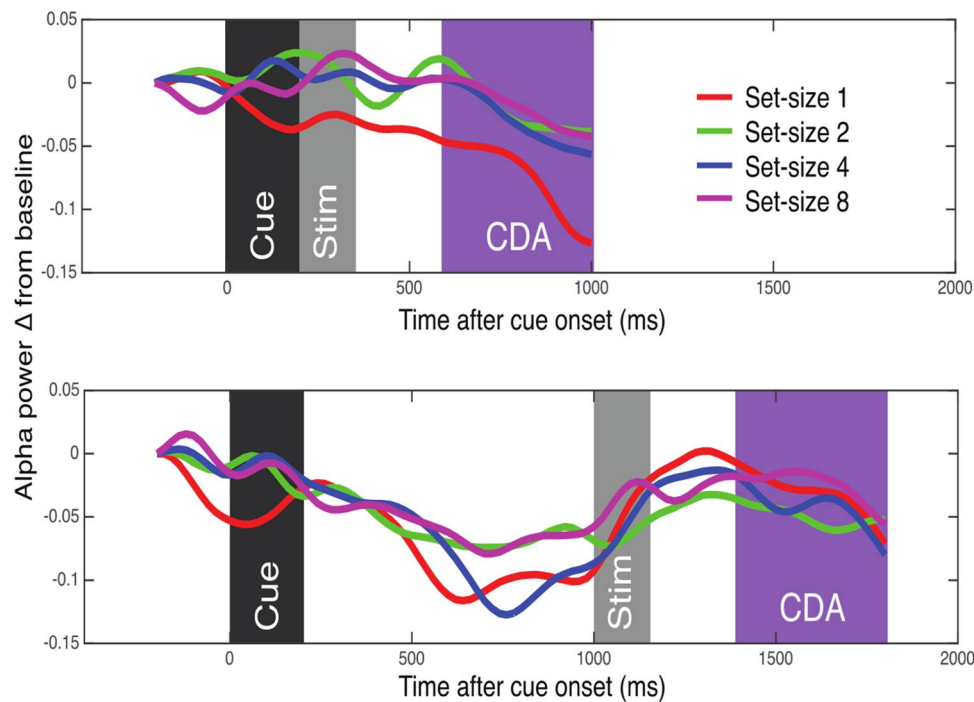


Fig. 5 Lateralized alpha power relative to a pre-trial baseline across two different cue-to-stimulus onset asynchronies (SOAs). The top panel shows the alpha power suppression when the cue immediately precedes an array of to-be-remembered items that varied in set size. At short SOAs (top panel) the alpha suppression appears to be in response to the target array (the gray Stim box marks this presenta-

tion); however, at long SOAs it becomes evident that the alpha suppression was in response to the spatial pre-cue (the black Cue box marks this presentation), not the Stimulus array of varying set sizes. The purple CDA box indexes the time window of the memory storage component-CDA. Adapted from Fukuda et al. (2016)

relative to the assumed speed of shifts of attention is a topic that demands further study, as we discuss in our concluding remarks.

If alpha tracks spatial attention, why do we see alpha suppression during long-term memory retrieval?

Readers who are familiar with the literature in which alpha is used to study different cognitive processes may be aware of the work that argues that alpha can track long-term memory storage and retrieval (Fellner et al., 2013; Hanslmayr et al., 2009; Hanslmayr et al., 2016; Hanslmayr & Staudigl, 2014). That is, previous empirical studies appear to show that alpha-band suppression can track what is encoded into and retrieved from long-term memory (Fukuda & Woodman, 2017; Hanslmayr et al., 2009; Sutterer, Foster, Serences, et al., 2019b). Figure 6 provides one concrete example in which subjects learned arrays of colored squares that varied in their set size (i.e., each array consisted of one, two, four, or eight colored squares in randomly selected locations), and had to report the color at a location in the array during the test phase at the end of the experiment. Subjects' alpha

power decreased as the set size of the array increased during encoding. During retrieval, the same pattern was found in which alpha power decreased when more information needed to be retrieved from long-term memory. How can we reconcile our account of alpha tracking attention with these effects in which alpha tracks memory storage and retrieval?

As mentioned above, there is an entire class of models of human memory that have no problem reconciling the view of alpha as attentional selection with the observation that this mechanism should be at work during long-term memory encoding and retrieval. These are sometimes known as the embedded-process models in which attention is a mechanism that is inherently embedded in the memory structures of the brain (e.g., Cowan, 1999). According to such a view, attention is the mechanism that encodes a representation into long-term memory, as well as the mechanism that reactivates representations so that they can be retrieved.

But then why would alpha suppression be deeper when there is more to encode or retrieve? It appears that this is due to the spatial sensitivity of alpha that we described above. Recall that when a larger array becomes the focus of attention, then alpha suppression is stronger. It is likely that this same *array-size effect* underlies the observation of stronger alpha suppression when more objects need

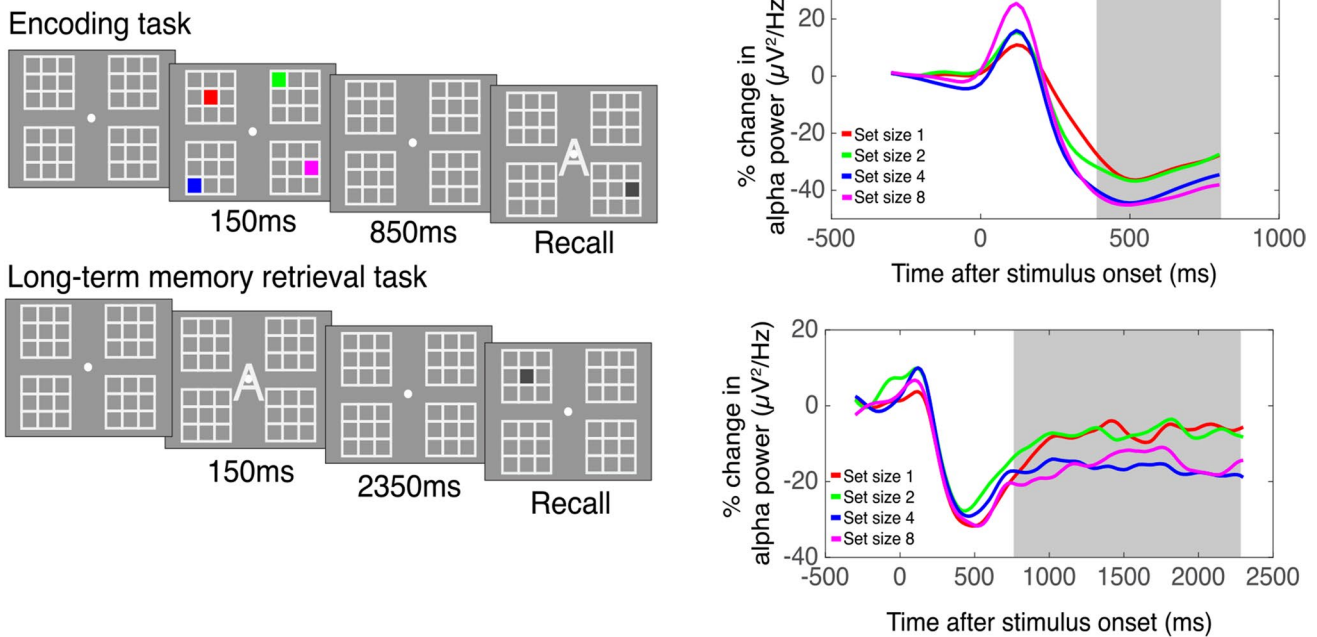


Fig. 6 Alpha suppression results from both the encoding and the retrieval phases of a long-term memory task in which subjects were probed to recall the color of the square in an array that varied in set size. The gray shaded regions show the array set size effect was

to be encoded or retrieved (i.e., Fukuda & Woodman, 2017). That is, when we need to retrieve our memories of an entire room that was the scene of a crime, we will need to attentively select a much larger spatial region than when we try to retrieve just the knife that was on the floor in the corner of the room. Recent work has shown that when subjects attend to larger regions of their visual field, alpha power is more suppressed (Wang et al., 2021), and it appears that alpha is also more deeply suppressed when subjects select memory representations that were spread across a larger region of the visual field (Fukuda & Woodman, 2017; Sauseng et al., 2009).

Our proposal, that alpha modulations are actually a result of the role that visual-spatial attention plays in long-term memory encoding and retrieval, is not the only idea of how alpha activity is related to long-term memory. One viable mechanistic account of the neural circuitry involved proposes that learning is due to the synchronization of theta activity in the hippocampus and the desynchronization of alpha in the neocortex (Hanslmayr et al., 2016; Parish et al., 2018). According to this idea, when there is more information to encode into long-term memory, then neocortical alpha will need to be further suppressed to enable that function. As we discuss near the end of the paper, the relationship between theta oscillations and posterior alpha power is one of the topics most in need of understanding.

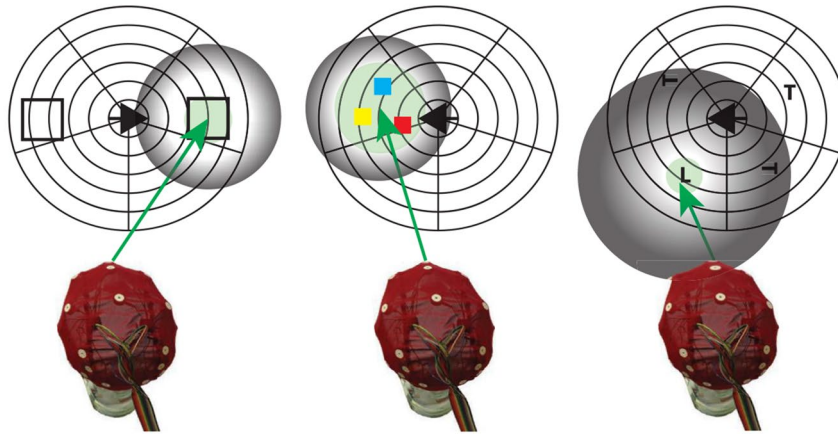
observed on alpha power both during encoding and while the subjects retrieved arrays from memory. Adapted with permission from Fukuda and Woodman (2017)

Alpha suppression measures the attentional selection of new perceptual inputs and memory representations

The evidence that we have just reviewed suggests that alpha suppression may index a cognitive mechanism of attention that not only works to select new, important inputs from our visual field, but also operates to activate memory representations through a spatial pointer-like map. That is, we can see this mechanism working on the front end when information needs to be encoded (see Fig. 7, top row). But we can also see it working on the back end when information needs to be retrieved from long-term memory (see Fig. 7, bottom row).

Deployments of attention during spatial cuing, change detection, and visual search tasks are represented in the top row of Fig. 7. As we discussed previously, alpha suppression indexes both the spatial extent of the region selected for preferential input (shown with the size of the green shaded region) (Fukuda & Woodman, 2017; Wang et al., 2019), but also the size of the region surrounding these attended inputs that need filtering out (shown with the gray shaded surrounding regions) (Wang et al., 2021). Although it is particularly useful to observe attention shifting in these canonical laboratory paradigms, we think that the alpha suppression mechanism may really provide a computational advantage when we forage in our surrounding environments.

Attentional deployment during attention and working memory tasks



Attentional deployment during memory encoding and retrieval

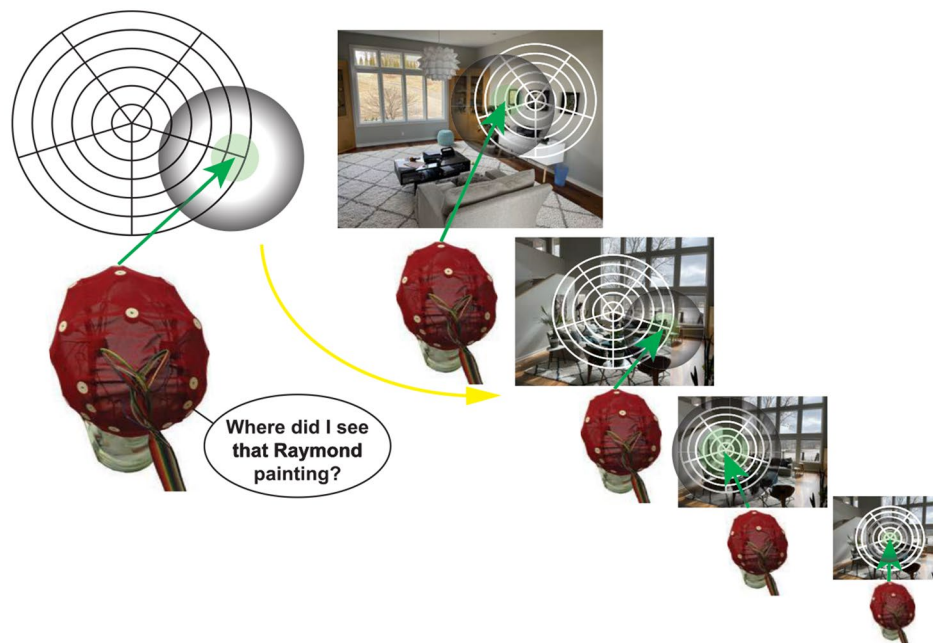


Fig. 7 Illustration of the deployment of visual-spatial attention tracked by alpha suppression across tasks and time. Covert attention shown with green arrows and green circles signifying the enhanced areas and the gray inhibitory surround. Overt attention is shown with the polar plot overlay indicating the fovea magnification of space. Both the size of the attended region and the size of the inhibited region appear to determine the strength of alpha suppression across spatial cuing (upper left), change detection (upper middle), and visual

search (upper right) tasks in the laboratory. The lower panel illustrates how visual spatial attention can operate during encoding to distinguish episodes in the same environment, and then help retrieval by providing an endogenously controlled retrieval cue that can serve to reconstruct the episodic context, as shown with the yellow arrow activating the memory of the scene with the same pattern of attentional deployment

We think one of the primary functions of this alpha mechanism is to support and supplement overt attentional mechanisms (i.e., shifting gaze to specific regions of space, represented with the polar grid in Fig. 7, shifts of covert attention represented with the green attended regions flanked by inhibitory surrounds in Fig. 7). This is useful as we think about how induced alpha suppression allows

humans interacting adaptively in the real world (Posner & Cohen, 1984). Fortunately, having two spatial gradients across our visual fields, one due to the acuity of vision and one due to the resolution of covert attention, provides our brains with two spatial pointers that can help distinguish different episodes in the same environment. That is, by having two independent spatial pointers that can be

placed at different locations in each environment, we can further separate the neural representations of events that take place in the same physical environment. Given the centrality of context reinstatement in mainstream models of memory (Polyn et al., 2009), we propose that the spatial pointer of the fovea and covert spatial attention are endogenously controlled levers of cognitive reactivation that can reinstate a subset of the neural activity present at encoding, serving to spread activation to the other representations encoded during that context (e.g., surfaces, objects, emotional reactions, etc.).

As we describe next, the components of our theoretical proposal are not new; however, our combination of these ideas when viewing the alpha suppression literature does provide a novel perspective. We note that this perspective links alpha suppression to theoretical ideas in cognitive psychology, instead of proposing an account of how ionic gradients or electrical fields in the brain interact to generate the alpha activity that we measure.

Decades of basic and translational cognitive science have examined how attention guides information processing in the brain by selecting specific regions of the visual field from which to preferentially process stimuli (Eriksen & Hoffman, 1972; Eriksen & Hoffman, 1974; Posner, 1994; Posner & Driver, 1992; Posner & Gilbert, 1999; Posner & Petersen, 1990). Our reference to visual-spatial attention should activate in the mind of the reader the spatial cuing paradigm used to study how regions of the visual field are selected by attention (Posner, 1980). Findings from this long line of work emphasize the ability of our minds to select information from a spatial map of locations, with the ability to attend to a location where no information is yet present (Fig. 7, upper left).

The findings we reviewed in previous sections indicate that the attention mechanism tracked with alpha suppression exhibits a novel feature relative to previous conceptualizations. Specifically, that both the size of the attended region of space (illustrated with green circles in Fig. 7) and the size of the ignored region of space (illustrated with gray annuli around the attended green circles in Fig. 7) are controlled independently. This would be necessary in a world like ours where the characteristics of targets and distractors vary independently across time and episodes. Although existing experiments could explain variations in the size of these enhancement and suppression windows through bottom-up factors (Wang et al., 2019; Wang et al., 2021), it is possible that these regions are independently adjustable via top-down control. This is a feature of the mechanism indexed by alpha suppression that will need to be examined in future research. Next we turn to how these spatial deployments of attention could interact with memory processes, providing an account of the ubiquity of alpha suppression across a large variety of laboratory tasks.

Here we propose that the same spatial orienting of attention to a location studied in visual-spatial attention tasks (see Fig. 7, upper panel) may also serve as a memory cue to aid in linking spatial layouts in our visual field to episodes of our lives that are continuously streamed to the hard disk in our brains. Although a reader might not think of attentional cuing research as discussing how attentional selection may guide memory processes (Deutsch & Deutsch, 1963), it is nonetheless true that studies of visual-spatial attention have discussed the possibility that attention is necessary for us to encode information into long-term memory and retrieve it when needed (Posner, 1994).

The proposal that attention operates to encode and retrieve memories is not a new idea. For over a century, brain scientists have proposed that attending to locations may be vital for us to form the memories that we store (Fernandes & Moscovitch, 2000; Muzzio et al., 2009). We believe that alpha suppression observed during long-term memory encoding and retrieval is caused by the operation of just the kind of selective attention mechanism that is focused on locations, or perhaps the object structure at a location (Vecera et al., 2000), in service of creating spatial structure in which to contextualize the objects and events that fill our memories. Here we attribute the idea that attention works to aid encoding and retrieval to the well-articulated views of Moscovitch (Ciarumelli et al., 2008; Fernandes & Moscovitch, 2000). However, the idea that attention to representations may be necessary for their encoding and retrieval has a long history in cognitive science (Chun et al., 2011; Cowan, 1997; James, 1890; Norman, 1968).

The hippocampus, which is such a vital region for human memory (Squire et al., 2004), appears to also be inherently spatial in a number of mammalian species (Moser et al., 2014; Moser et al., 2015). If we remove medial-temporal lobe tissue due to medical necessity, including the hippocampus, then the individual is likely to be densely amnesic, with an impaired ability to encode new memories that can later be retrieved (Scoville & Milner, 1957). However, if we record from neurons in the hippocampus of a non-human animal, what we tend to find is that the neurons seem to code for where in the environment an animal is when they encounter an object or event (Muzzio et al., 2009). It appears that key memory structures of our brain may be inherently spatial. This makes sense if spatial information is being used to tag each memory, providing for another type of retrieval cue. This spatial tag is affixed by the deployment of attention across the otherwise stable environment to provide an endogenously controlled pointer overlaid on the exogenous environmental cues that helps retrieve past episodes. There is ample evidence that people exhibit this kind of overt shift of attention when retrieving visual or linguistic information from long-term memory (Ferreira et al., 2008; Holm & Mäntylä, 2005; Mäntylä & Holm, 2006). When we spend long

periods in the same environment, such as when we work from home during an illness, snowstorm, or pandemic, then these endogenous spatial cues may be particularly important in distinguishing between episodes we want to retrieve.

Given the inherently spatial nature of neurons in the medial-temporal lobe of the brain that are particularly important for human memory, it seems like we should expect there to be a selective mechanism that focuses on spatial locations that is intimately involved in the encoding and reinstatement of information into memory. We term this the *Attentional Selection and Memory Activation* (or ASMA) account of alpha suppression. This account proposes that the mechanism that we measure with alpha suppression is a mechanism of attentional selection, but that this mechanism operates on both perceptual inputs as well as memory representations, consistent with classic ideas of central attentional selection in which the work we perform on inputs determines their memorability (Craik & Lockhart, 1972 ; James, 1890 ; Pillsbury, 1908).

In sum, our proposal that alpha indexes an attention mechanism combines two ideas: a spatial selection mechanism that filters perceptual inputs, and one that also links spatial layouts to representations of episodes in memory. Consistent with this theoretical perspective, it appears that attending to the location in which you saw an object does help you retrieve its representation (Spivey & Geng, 2001). Here we propose that the strong alpha suppression we observe during our perception and memory experiments is tracking just this kind of operation in the brain. For example, when I want to remember where I left my coffee cup while walking around the house, I reconstruct my recent views of each room by remembering what I was doing in each room, triggering a replay of the shifts of attention in that environmental context. The proposal that attending to spatial locations is intimately intertwined with memory storage has been noted more in the neuroscientific literature than in psychology (Muzzio et al., 2009), but this again represents a combination of current ideas more than an introduction of some unheard of mechanism.

We note that this role of attention, in selecting representations from memory, is the major way that our discussion deviates from the foundational proposals out of which ours has grown. Specifically, keen readers may have noticed that we borrowed much from the view of Klimesch (2012). However, our perspective is novel in proposing that posterior alpha power modulations are a purely spatial pointer. The idea being that this spatial pointer is associated with the other information encountered there, so attending to that location activates the associated memories.

In the next section, we discuss potential neural generators for this internal and external information selecting mechanism. Although such invasive neuroscientific findings might reveal the true nature of the computation performed during

the suppression of alpha, such findings do not exist in the literature yet. However, how such a selective mechanism is implemented is less important than understanding the calculations that it affords the brain (Marr, 1982). Our hope is that our conceptualization of alpha suppression as the kind of mechanism that psychologists have posited for decades will spur decisive experiments that test our ASMA account of alpha-suppression.

What is the neural generator of the alpha oscillations?

If clues about the network that generates the alpha suppression signal are not inherently indicative of the computation that the brain is performing, then perhaps if we could localize the generator or generators of the posterior alpha, we could infer what it is doing based on the properties of the neurons that give rise to the activity. This was the goal of a number of neuroscientists who sought to understand the alpha-band activity following its discovery. One such program of research sought to eliminate the brain's alpha waves by applying lesions to different regions, and demonstrated that the destruction of subcortical structures permanently changed the oscillations recorded from the cortex (Kennard, 1943; Kennard & Nims, 1942). However, these techniques of complete ablation were accompanied by visual inspection of the animals' EEG, instead of the kind of frequency-specific analyses that are conducted now, as we discuss below.

As with any cognitive function, the brain is unlikely to only use neurons in one part of the brain to perform attentional selection. This means that alpha suppression is likely to be due to activity in a diverse set of brain regions. Based on the available evidence, this appears to be the case.

Several recent studies have shown that the posterior alpha suppression that we have been discussing here is frequency coupled to a frontal low-frequency oscillation (in the delta-to-theta range, i.e., ~1–8 Hz) (de Vries et al., 2019; Reinhart & Woodman, 2014). Coupling means that one oscillation appears to drive another. The communication by coupling hypothesis has been a popular way for scientists to think about how large groups of neurons in regions spread across the brain might be functionally linked through oscillations to perform a given cognitive operation (Fries, 2005), with this coupling allowing for dynamic organization and reorganization of computational mechanisms as task demands change.

Figure 8 provides an example of the frontal theta and the posterior alpha coupling that has been observed during a task in which subjects were cued to look for a certain object in an array of objects that followed (Reinhart & Woodman, 2014). As you can see, alpha power was coupled with the power of the frontal theta as subjects searched for target objects in an array of possible targets. In addition, you can

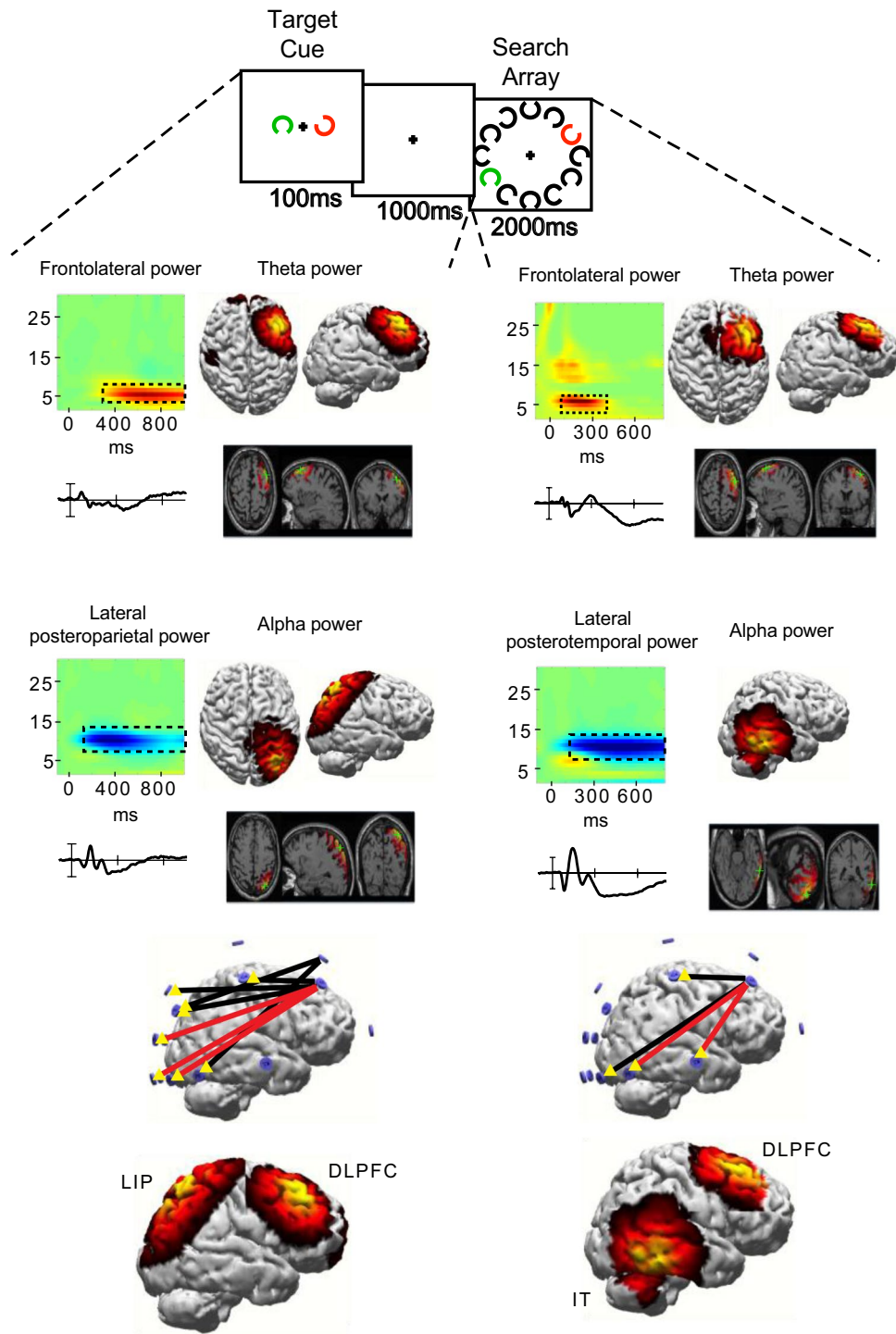


Fig. 8 Findings from a memory-guided visual search task adapted from Reinhart and Woodman (2014). The subjects remembered what to look for in an upcoming array (left column) and after the onset of the visual search array in which attention covertly selects the target (right panel). Grand average cue-locked frontolateral (F3/4, top left data panels) and lateral posteroparietal power (OL/R, bottom left panels) contralateral to the remembered location of the target. Insets show the event-related potentials. Current density estimates are pro-

jected onto the cortical surface for frontolateral theta (4–6 Hz, top panels) and lateral posteroparietal alpha (8–12 Hz, middle panels) 100–1,000 ms post-target cue. Significant theta (without triangle) and alpha (with triangle) coupling (red line, $q = 0.01$; black line, $q = 0.05$) while subjects remember the target they are about to look for. The right panels show the pattern of coupled oscillations triggered by the demand to search for the cued target in the array using the same conventions as the left panels

see that the distribution of the frontal-posterior coupling changes across the phases of the experiment.

Researchers have proposed that this frontal-posterior coupling is due to the maintenance of representations in working memory (de Vries et al., 2019; Reinhart & Woodman, 2014). That logic is based on the idea that neurons in both the prefrontal and posterior visual areas have been shown to participate in working memory storage. However, the same is true of attentional selection. That is, we already know that attentional selection involves the coordination of neurons in prefrontal and posterior visual areas (Buschman & Miller, 2007; Cohen et al., 2009). Thus, the scalp distribution of the frequency-coupled network that includes the alpha suppression signal does not provide useful diagnostic information about the cognitive processes at work. But the coupling of alpha suppression to a broader network does indicate that the work performed by the alpha suppression signal, for example, the filtering of distractors, may occur because another control region of the brain directs it to.

Several groups have made theoretical claims about the role that alpha-band activity plays in coordinating neural events in the brain based on recent intracranial recordings. One of these perspectives is that the brain switches between two different rhythmic states. In one state, perceptual processing is focused on a location or object, and in the second state, attention is shifted to a new spatial location or target (Fiebelkorn & Kastner, 2020). This perspective links the first state to decreases in alpha-band activity and increases in cortical gamma-band activity, while the second state is marked by the opposite pattern of neural activity (an increase in alpha and a decrease in gamma). These findings appear consistent with recordings of neural activity in both cortical and subcortical areas of the brain of macaque monkeys (Fiebelkorn et al., 2013; Fiebelkorn et al., 2019). Clearly, this view from inside the primate brain is entirely consistent with the general perspective that we advocate for here, in which alpha waves appear to track where and when the brain shifts attention.

However, another perspective is that the decrease in alpha-band activity that we discussed here is not about focusing attention on a location, but is instead due to the feedforward versus feedback flow of information that dominates the cortex at a given moment. Specifically, it has been proposed that decreases in alpha-band activity are an index of feedback dominating the activity of neurons in a given area of cortex (Bastos et al., 2015; Bosman et al., 2012). Given that researchers have proposed that attention likely is implemented in the brain via feedback connections (Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000), this view could be seen as consistent with the alpha-is-attention story. However, working memory has also been thought of as a feedback-driven brain mechanism (Lamme & Roelfsema, 2000), so additional wet-laboratory research will be needed

to determine if the nature of alpha across layers of the brain reveals why it appears that alpha measured at the scalp tracks the operation of spatial attention.

What lies ahead?

Do the modulations of alpha power track the operation of attention in the human brain? We have been on the other side of this debate in our own work, concluding that alpha was indexing working memory (Fukuda & Woodman, 2017), so we feel that we were skeptics from the outset. But this does not mean that we have worked out all of the wrinkles in the story. In this section we provide a set of questions that we see as central in understanding the nature of human alpha activity, and what it measures, as was the goal of Berger, and all the cognitive scientists who have followed.

Do lateralized alpha suppression and global alpha suppression measure different cognitive operations, or does the laterality simply reflect the spatial nature of the attention mechanism that alpha generally measures? Several papers have reported that the alpha activity measured contralateral to an attended object exhibits power modulations that are distinct from the power measured across posterior electrode channels (Fukuda et al., 2016; Gallotto et al., 2020; Medendorp et al., 2007; Wildegger et al., 2017). However, it has not always been observed that lateralized and global alpha power differ in their patterns (Kasten et al., 2020; Wang et al., 2021; Wright et al., 2015), thus it is an empirical question whether these different ways of measuring alpha activity reveal distinct mechanisms in the brain.

The question above raises a related question regarding the variety of biophysical processes that may contribute to the oscillations that we measure in the frequency band from 8 to 12 Hz. Does alpha measure a single cognitive operation? Almost surely not, as a number of studies have proposed that the alpha-activity they measured appears inconsistent with it measuring attentional selection (Antonov et al., 2020; Gundlach et al., 2020; Keitel et al., 2019; MacLean et al., 2019; Mössing & Busch, 2020; van Ede et al., 2012). For example, using an attentional cuing paradigm, van Ede et al. (2012) showed that magnitude of alpha suppression only accounted for about 30% of the reaction time effect. This could be because alpha suppression indexes a perceptual attention mechanism, with subsequent processing stages injecting additional variance unrelated to attentional selection (e.g., Donders, 1868/1969). However, it is also possible that modulations of alpha activity are generated by a host of cognitive mechanisms and biophysical processes. With the broadest perspective, it is clear that the 8–12 Hz alpha band is special, in that it evidences a peak in power, but this may simply be due to the geometry of the tissue in the head (Nunez & Srinivasan, 2006). We may see a peak in power in

the alpha band because gray matter in the brain that produces electrical fields has a finite thickness, with this thickness defining the fundamental frequency that it exhibits (Nunez & Srinivasan, 2006). From this perspective, we should find that much of the information processing performed by the brain is measured at the scalp as modulations of alpha. Consistent with this geometric perspective about why alpha is pervasive, we see changes in both evoked alpha power that is tightly time locked to the onset of stimuli (e.g., Fig. 8 in Foster et al., 2016), and the elicited alpha power that appears to lag the stimuli by more time (Foster et al., 2017). Here we have taken a fairly broad view, however, it will be important for researchers to clearly define which aspects of alpha activity are due to true ongoing oscillations versus changes in power that are sensory evoked at a low level.

What is the time course of the alpha suppression if it is indexing perceptual attention? For example, if you examine the figures in this paper, you will note that the alpha-power suppression lasts for many milliseconds, typically hundreds of milliseconds. Research in neuroscience suggests that perceptual processing is completed extremely quickly (Fabre-Thorpe et al., 2001), and that even perceptual attention can shift between objects within 100 ms or less (Wolfe, 2007). This feature of the alpha-suppression phenomenon may not fit as neatly with the ASMA account that we propose here in which alpha suppression indexes early perceptual attention, as well as late memory selection.

How is the mechanism indexed by alpha power changes related to the activity measured in other frequency bands using electrophysiology? Above we mentioned that several groups have proposed that posterior alpha and frontal theta power are inherently linked (e.g., Reinhart & Woodman, 2015). However, decades-old experiments using words as stimuli concluded that posterior alpha and frontal theta index completely different memory systems, with frontal theta hypothesized to index the storage of information in episodic memory, while alpha indexes access to semantic memory (Klimesch et al., 1994; Kroll & Klimesch, 1992). Interestingly, our view could be seen as essentially the opposite, in which posterior alpha activity is related to episodic memory in that attending to the location of objects as they are encoded or retrieved helps to build up the representation of the episode with rich spatial detail about the layout of the information in the world. Clearly this issue will require definitive experiments focused on distinguishing between these competing views of the nature of the relationship between frontal theta and posterior alpha during information processing.

Are there additional features of the alpha-band activity that contain information and have been missed as we have focused on the large modulations of power? Sine waves are characterized by their phase and frequency, in addition to their power. Work that we have not focused on here has

suggested that it may be possible to observe differences in the peak frequency of alpha-band activity that are related to individual differences in cognitive processing (Samaha & Postle, 2015), as well as the possibility that we can change the speed of alpha oscillations with top-down control (Wutz et al., 2018). Similarly, the phase of alpha activity has been proposed to determine whether subjects become aware of near-threshold stimuli (Mathewson et al., 2009). Thus, although we feel that we may be close to answering Berger's original question about the relationship of alpha power to attention, there are additional features of these prominent oscillations that may be related to other aspects of cognition.

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Declarations

Competing interests The authors declare no competing financial interests.

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