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The role of alpha oscillations in spatial attention: limited evidence for a suppression account

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Covert spatial attention allows us to prioritize visual processing at relevant locations. A fast growing literature suggests that alpha-band (8–12 Hz) oscillations play a key role in this core cognitive process. It is clear that alpha-band activity tracks both the locus and timing of covert spatial orienting. There is limited evidence, however, for the widely embraced view that alpha oscillations suppress irrelevant visual information during spatial selection. Extant evidence is equally compatible with an account in which alpha activity enables spatial selection through signal enhancement rather than distractor suppression. Thus, more work is needed to characterize the computational role of alpha activity in spatial attention.

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Alpha-band activity tracks covert spatial attention

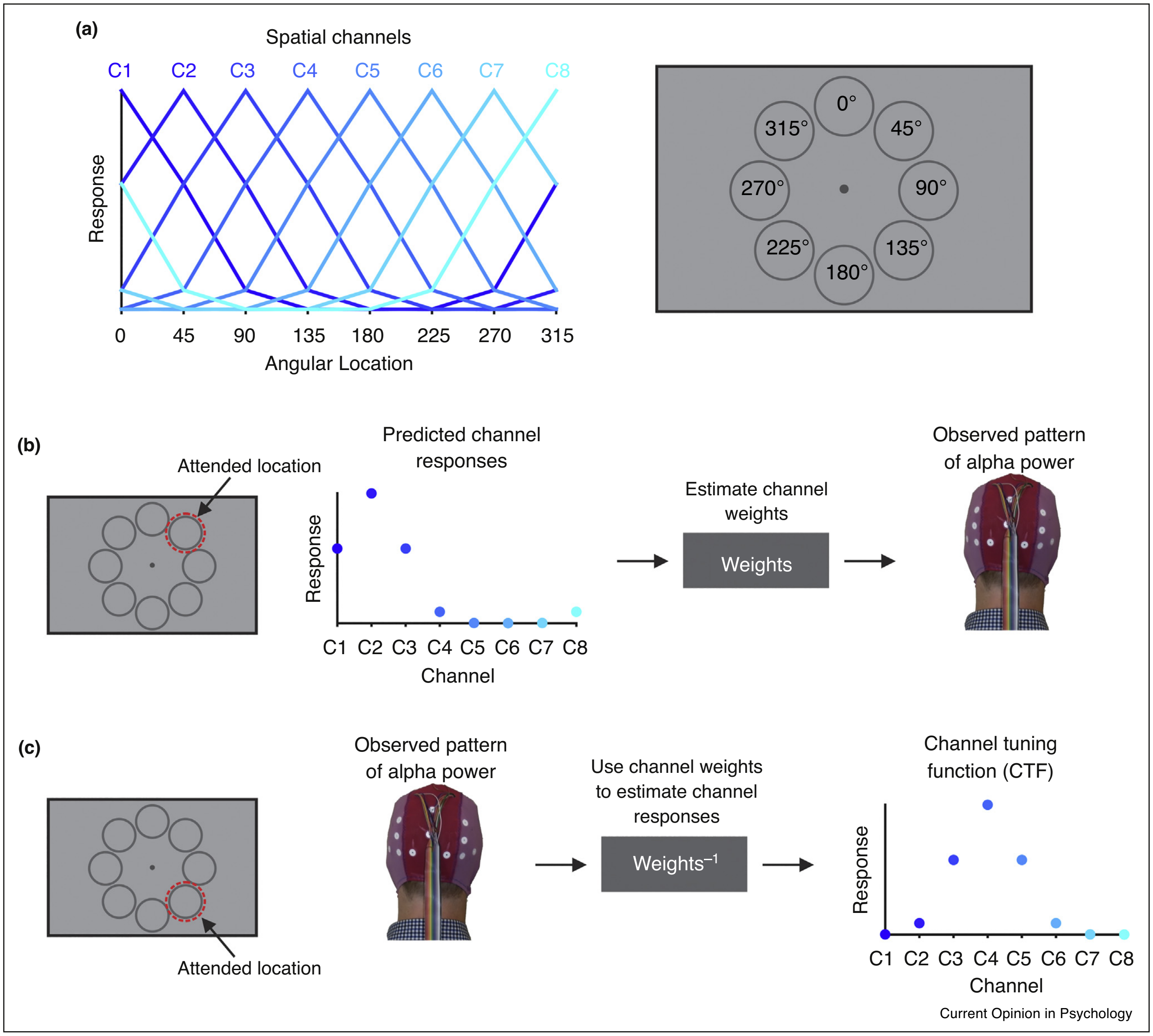
Our capacity to process visual information is limited. Thus, we must prioritize processing at relevant locations. Covert spatial attention allows us to select relevant locations without moving our eyes, enhancing processing at the attended location [1]. Human electroencephalogram (EEG) studies have long linked alpha-band (8–12 Hz) oscillations with covert spatial attention [2–7]. When attention is deployed to one side of space, posterior alpha-band power is reduced at electrodes over the contralateral hemisphere, which processes the attended side of space [4–6]. Further work has shown that the scalp topography of alpha power tracks more than just the relevant side of space [4,7]. For example, Rihs *et al.* [7] showed that the topography of alpha power on the scalp covaried with the specific location that was cued when observers were instructed to attend one of eight possible locations around a fixation point.

Recently, multivariate analysis techniques have enabled a more refined quantification of the spatial information present in alpha activity. We and others have used an inverted encoding model (IEM) [8–10] to track the spatial and temporal dynamics of covert attention [11••,12•]. This approach (Figure 1) assumes that alpha power at each electrode reflects the combined activity of a number of spatially selective channels (or neuronal populations). By first estimating the relative contribution of each of these spatial channels to the response measured at each electrode, it is then possible to *invert* the model to estimate the profile of activity across the channels from the pattern of alpha power across electrodes. This results in a graded profile of activity (a *channel tuning function* or CTF) that peaks at the channel tuned for the attended location. These alpha CTFs reflect the spatial selectivity of the population-level activity that is measured with EEG [13]. In spatial-cueing tasks, alpha CTFs track covert spatial orienting to the precise location that is cued, starting several hundred milliseconds after the onset of a central cue (Figure 2a) [11••,12•]. During visual search, the time-course of alpha CTFs tracks trial-by-trial variations in the latency of target selection, as measured with response times (Figure 2b) [11••]. Thus, alpha activity is tightly linked with both the locus and timing of covert spatial selection (also see Box 1).

Does alpha-band activity suppress irrelevant visual inputs? The jury is out

What computational role does alpha activity play in covert attention? The modal view is that alpha activity mediates the suppression or gating of irrelevant visual inputs [2,3••,14–16]. This view falls in line with the consensus that distractor exclusion is a critical component of visual attention [17]. However, it is broadly acknowledged that improved perception at a relevant location can also occur via *signal enhancement*, which directly improves processing at attended locations [1,18]. While many studies have shown that alpha activity tracks the attended positions in the visual field [4–6], even in the absence of irrelevant distractors [5,7,19], recent work has cast doubt on whether alpha activity tracks locations at which distractors are expected [20••]. At first glance, this may seem to point towards a role in signal enhancement rather than distractor suppression. However, a neural signal that suppresses interference at all unattended locations may also enable precise tracking of target position. Thus, the fact that

Figure 1

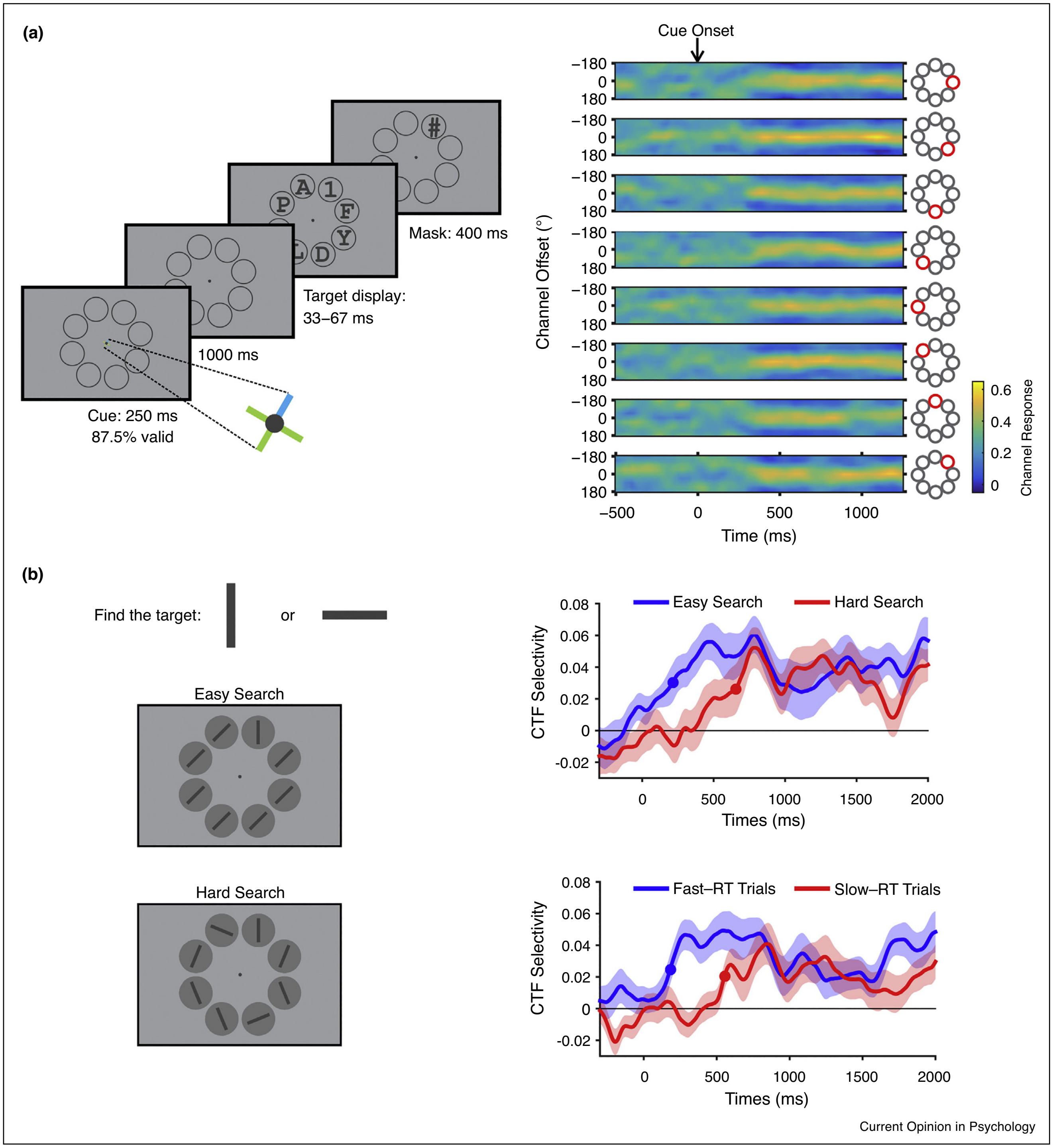


Reconstructing alpha channel tuning functions with an inverted encoding model. Inverted encoding models (IEMs) are a powerful tool for reconstructing population-level representations from aggregate measures of neural activity (e.g. EEG or fMRI). We and others have used the IEM approach to reconstruct spatially selective channel tuning functions (CTFs) from the scalp distribution of alpha-band power [11••,12•]. This approach assumes that alpha-band power at each electrode reflects the combined activity of a number of spatially tuned channels (or neuronal populations), each tuned for a different spatial position. Each curve shown in (**a**) shows the predicted response of each of eight spatially selective channels (C1–C8) across eight possible attended locations (right). The IEM analysis proceeds in two stages. In the training phase (**b**), we estimate the relative contribution of each channel to the response measured at each electrode (called channel weights). For a given attended location, the predicted response of each channel can be derived from the functions in (a). The example shown here is for an attended location at 45°. Because the predicted channel responses vary as a function of the attended location, by varying the attended location it is possible to estimate how strongly each channel contributes to activity measured at each electrode (i.e. the channel weights). In the test phase (**c**), using an independent set of data, we use the channel weights obtained in the training phase to estimate the profile of channel responses given the observed pattern of activity across the scalp. The example shown here is for an attended location at 135°. The resulting CTF reflects the spatial selectivity of population-level alpha-band activity. Adapted from Ref. [11••].

alpha activity precisely tracks the selected locations — but not the locations of distractors — still leaves open the question of *how* alpha activity supports selective attention (also see Box 2).

In support of the distractor suppression account, past work has emphasized the finding in spatial-cueing tasks that alpha power *decreases* contralateral to the cued location and/or *increases* contralateral to the uncued location [4–7].

Figure 2



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Alpha-band oscillations enable spatially and temporally resolved tracking of covert spatial attention. (**a**) Alpha CTFs precisely track where attention is deployed following an attentional cue. Observers performed a spatial-cueing task (left). A central cue (a cross with one uniquely colored arm) directed observers to attend one of eight place holders. After delay, a target digit was presented among distractor letters and then masked with a pound sign. The plot on the right shows the reconstructed alpha CTFs across time for each of eight locations. A channel offset of 0° corresponds to the channel tuned for the cued location. The yellow band in each subplot shows the peak channel response, which tracked the cued location start around 300 ms after cue onset. (**b**) The time course of alpha-band CTFs track the latency of target selection during visual search. Observers searched for a target (a vertical or horizontal bar) among distractors and reported the orientation of the target (left). The plots on the right show the selectivity of target-related CTFs as for easy and hard search (upper) and as a function of response times regardless of search condition (lower). Spatially selective activity that tracked the target position emerged earlier during easy search than during hard search, and earlier on trials with fast RTs than on trials with slow RTs. Adapted from Ref. [11••].

This finding has been presented as suggesting that higher alpha power contralateral to the uncued location reflects increased suppression of irrelevant stimuli [2,3••,14–16]. But this empirical pattern is equally compatible with the view that reduced alpha-band power reflects signal enhancement. Another finding that has motivated a suppression account of alpha activity is the inverse relationship between alpha power and other neural signals such as spiking activity [21] and gamma-band oscillations [22]. However, these findings do not establish whether alpha activity influences the quality of *sensory representations* because the information content of neural activity can be disconnected from the overall amount of neural activity (e.g. Ref. [23]). For example, inhibition of specific neural units could improve the fidelity of a sensory representation. Thus, it is unclear whether these inverse relationships reflect an inverse relationship between alpha power and the strength of sensory representations. Even though there is some evidence for an inverse relationship between alpha power and the strength of sensory representations measured via BOLD responses in visual cortex [24], these data are still compatible with the hypothesis that decreased alpha power reflects a relative increase in signal enhancement over the attended regions.

In our view, a more diagnostic approach for distinguishing between suppression and enhancement accounts is to use experimental designs that selectively manipulate the process of interest. If the degree of distractor suppression can be manipulated while signal enhancement is held constant, this provides an opportunity to link-specific neural signals with suppression *per se*. For example, Serences *et al.* [25] used this approach to test whether preparatory activity measured with fMRI reflected distractor exclusion. Spatial attention increases baseline activity measured with fMRI in visual cortex tuned for the attended location [26,27]. To test whether this preparatory activity reflects distractor exclusion, Serences *et al.* varied the probability that distractors accompanied visual targets, a manipulation that has been shown to increase resistance to distractor interference without affecting performance with distractor-free displays [28]. The selective effect of the probability manipulation suggests a specific effect on distractor exclusion, because changes in that process should not affect performance when there are no distractors to exclude. Critically, Serences *et al.* found that preparatory activity, measured via retintopic changes in the amplitude of the BOLD signal, was greater when the probability of distractors was higher, suggesting that this preparatory activity plays a specific role in distractor exclusion. Therefore, this work provides a clear example of how preparatory activity can be unambiguously linked with distractor exclusion.

Box 1 Alpha-band activity tracks spatial working memories.

Working memory allows us to hold goal-relevant information in an ‘online’ state. It is thoughts that there is considerable functional overlap between spatial attention and spatial working memory [33,34]. Consistent with this view, recent work has shown that alpha activity also precisely tracks spatial locations maintained in working memory [35••,36•,37,38,39•]. Interestingly, alpha activity encodes the location of memoranda even when spatial position is irrelevant to the task [36•,39•], suggesting that space may be an integral component of visual working memories. These findings provide further evidence that alpha oscillations play a central role in spatial cognition.

Of the substantial body of work that links alpha-band power with covert attention, only a few studies have attempted to selectively manipulate distractor suppression [19,20••,29,30•]. In one study, Kelly *et al.* [19] cued the location of an upcoming target. In some blocks, the target appeared alone, while in others a distractor appeared in the uncued hemifield. Kelly *et al.* reasoned that if spatially-specific alpha-band power reflects distractor exclusion, then lateralized alpha-band should be stronger when observers expect a distractor than when no distractor is expected. Interestingly, lateralization of alpha-band power was *weaker* when distractors were expected (also see Ref. [29], which found no effect of the strength of distractors on the lateralization of alpha-band power in a somatosensory task). However, one caveat here is that there was no behavioral evidence that distractor exclusion was increased in blocks that contained distractors. Thus, the failure to find stronger alpha lateralization when a distractor was expected may not provide strong evidence against a distractor exclusion account.

Box 2 Pre-stimulus alpha power and perception.

To directly examine how alpha-band power influences visual processing, researchers have tested whether pre-stimulus alpha power predicts perceptual outcomes. Early studies found that near-threshold stimuli are more readily detected when alpha power is low [40,41], which was taken as evidence that low alpha power improves stimulus perception [40,42]. However, recent work has challenged this view. Two recent studies [43••,44••] used a signal detection analysis to show that fluctuations in alpha power predict *response bias* (i.e. how likely the observer is to report a stimulus) instead of perceptual *sensitivity* (i.e. the degree to which signal and noise can be discriminated during perception). Thus, alpha power predicted a shift in response thresholds rather than changes in the sensitivity of visual encoding. Consistent with this view, others have found that alpha power does not predict performance in visual discrimination tasks [44••,45–47]. A key limitation of these findings, however, is that they focused on fluctuations in power without manipulating the attended location, in contrast to the work that we review in this article that focused on *spatially selective* modulations of alpha power following spatial cues. These two approaches may not tap into the same process, given the likelihood that alpha oscillations reflect more than a single aspect of cognitive processing (e.g. Ref. [48•]). For example, fluctuations in pre-stimulus alpha power could be tracking global changes in visual processing rather than something directly linked with spatial attention *per se*. Future work that combines these approaches to examine pre-stimulus fluctuations in spatially selective alpha activity could help to determine whether these pre-stimulus effects are directly linked with changes in spatial selection.

Händel *et al.* [31] took a different approach. Rather than manipulating the degree of distractor exclusion, they sought to test whether the degree of lateralization of alpha-band activity predicted individual differences in distractor exclusion. The authors reasoned that if lateralized alpha-band activity predicted processing of the stimulus in the uncued hemifield (on invalidly cued trials) but not processing of the stimulus in the cued hemifield (on validly cued trials), then this would provide evidence in favor of the distractor exclusion account of alpha-band power. Their results followed this pattern, but there was considerably more variability in performance for the uncued stimulus than for the cued stimulus. Thus, the failure to detect a relationship between alpha-band lateralization and processing of the cued stimulus may reflect a restriction of range for performance at the cued position.

In another study, Noonan *et al.* [20••] successfully manipulated distractor exclusion. Observers responded to a target stimulus. Noonan *et al.* varied whether or not the target was accompanied by a distractor in different blocks of trials, and found that the presence of a distractor reliably slowed response times. In some blocks, Noonan *et al.* cued the location of the target or the distractor in advance. Unsurprisingly, a spatial cue indicating the target location speeded responses (compared to trials with no cue). Interestingly, a spatial cue indicating the *distractor* location also speeded responses (again, compared to trials with no cue). Critically, this distractor-cueing benefit was not seen when the distractor was absent, providing clear evidence that cues indicating the location of a distractor selectively enabled distractor exclusion. Strikingly, Noonan *et al.* found that alpha-band activity tracked the cued location when the target location was cued but not when the distractor location was cued, suggesting that alpha-band activity plays a role in signal enhancement but providing no evidence for a role in distractor exclusion.

To summarize, while it is clearly the modal view that alpha activity reflects the suppression of irrelevant visual information, the evidence is equivocal. Extant work linking alpha activity with spatial attention is compatible with an account in which alpha supports target selection via signal enhancement. Thus, there is strong motivation for further work in which alpha-band activity is assessed during selective manipulations of different aspects of spatial selection, preferably with analytic approaches that focus on spatially selective alpha-band activity rather than overall power in that frequency band (see Box 2). For example, given prior work that has reported covariations of alpha power and BOLD activity [32], it may be worthwhile to use an approach similar to that of Serences *et al.* [25] to examine how alpha activity is affected by selective changes in distractor exclusion. Until such work is conducted, our view is that the jury is still out regarding the computational role played by alpha activity during spatial selection.

Conflict of interest statement

Nothing declared.

Acknowledgement

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- • of special interest
- •• of outstanding interest

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Fosteret *al.* used an inverted encoding model (IEM) to reconstruct alpha channel tuning functions (CTFs) that precisely tracked where spatial attention was deployed. During visual search, the time course of alpha CTFs tracked trial-by-trial variations in the latency of covert orienting toward the search target. This work highlights the potential of alpha CTFs as a method for spatially and temporally resolved tracking of covert attention.

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Noonanet *al.* showed that observers can suppress processing of an irrelevant distractor when provided with a pre-cue indicating the distractors locations. Interestingly, Noonan *et al.* found evidence for distractor suppression only when the location of the distractor was fixed across a block of trials (and not when the distractor location varied trial-to-trial), suggesting that selection history is critical to this form of distractor suppression. Furthermore, the authors found that alpha-band activity tracked the cued location when the cue indicated the location of the forthcoming target but not when it indicated the location of the forthcoming distractor. This finding clearly links alpha-band activity with spatial selection, but provides no evidence for a link with distractor suppression.

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