The Topography of Alpha-Band Activity Tracks the Content of Spatial Working Memory

Joshua J. Foster¹,²,⁴, David W. Sutterer¹,²,⁴, John T. Serences⁵,⁶, Edward K. Vogel¹,²,³,⁴ & Edward Awh¹,²,³,⁴

¹Department of Psychology, The University of Chicago, Chicago, Illinois, USA
²Institute for Mind and Biology, The University of Chicago, Chicago, Illinois, USA
³Grossman Institute for Neuroscience, The University of Chicago, Chicago, Illinois, USA
⁴Department of Psychology, University of Oregon, Eugene, Oregon, USA
⁵Department of Psychology, University of California, San Diego, La Jolla, California, USA
⁶Neuroscience Graduate Program, University of California, San Diego, La Jolla, California, USA

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Correspondence:
Joshua J. Foster
Institute for Mind and Biology
The University of Chicago
940 East 57th Street
Chicago, IL 60637
USA
Email: joshuafoster@uchicago.edu
Abstract

Working memory (WM) is a system for the online storage of information. An emerging view is that neuronal oscillations coordinate the cellular assemblies that code the content of WM. In line with this view, previous work has demonstrated that oscillatory activity in the alpha-band (8-12 Hz) plays a role in WM maintenance but the exact contributions of this activity have remained unclear. Here, we used an inverted spatial encoding model in combination with electroencephalography (EEG) to test whether the topographic distribution of alpha-band activity tracks spatial representations held in WM. Participants in three experiments performed spatial WM tasks that required them to remember the precise angular location of a sample stimulus for 1000-1750 ms. Across all three experiments, we found that the topographic distribution of alpha-band activity tracked the specific location that was held in WM. Evoked (i.e., activity phase-locked to stimulus onset) and total (i.e., activity regardless of phase) power across a range of low frequency-bands transiently tracked the location of the sample stimulus following stimulus onset. However, only total power in the alpha-band tracked the content of spatial WM throughout the memory delay period, which enabled reconstruction of location-selective channel tuning functions (CTFs). These findings demonstrate that alpha-band activity is directly related to the coding of spatial representations held in WM, and provide a promising method for tracking the content of this online memory system.
A range of evidence suggests that neuronal oscillations in the alpha-band (8-12 Hz) play a central role in the selection and storage of information in the brain (Fries, 2005; Canolty & Knight, 2010; Klimesch, 2012). For instance, many studies have shown that alpha-band activity covaries with the deployment of spatial attention, such that posterior alpha power is reduced contralateral to attended locations (e.g., Gould et al., 2011; Kelly et al., 2006; Thut et al., 2006). Indeed, the topographic distribution of alpha power not only tracks the attended visual hemifield, but also the specific retinotopic coordinates that are attended (Worden et al., 2000; Rihs et al., 2007). For example, Rihs and colleagues cued participants to attend one of eight placeholder locations around a central fixation point and found that the topography of alpha power systematically varied with the cued location, with more similar topographies associated with adjacent locations (Rihs et al., 2007). Extending these findings, others have decoded both horizontal and vertical shifts of attention from patterns of alpha power (Bahramisharif et al., 2010; van Gerven & Jensen, 2009), and shown that lateralized modulations of alpha power are sensitive to the eccentricity of the attended location (Bahramisharif et al., 2011). Thus, alpha-band activity enables tracking of the locus of spatial selective attention.

Here, motivated by past work positing a strong functional overlap between spatial attention and spatial working memory (WM; Awh & Jonides, 2001; Awh et al., 2006; Gazzaley & Nobre, 2012), we examined whether alpha-band activity tracks spatial representations held in WM. Consistent with this possibility, past work has already shown that alpha power is reduced contralateral to locations held in spatial WM (Medendorp et al., 2007; Van Der Werf et al., 2008; van Dijk et al., 2010). However, these contralateral modulations do not establish whether alpha-band activity – as in the case of spatial selective attention – tracks the specific locations that are stored. Instead, these modulations might reflect a lateralized memory operation (e.g., a top-down
control signal) that tracks the visual hemifield of the remembered location but not the exact location that is stored. Here, we tested whether alpha-band activity relates to the coding of the precise positions stored in WM, rather than a lateralized memory process that is not sensitive the specific content of spatial WM.

In three experiments, participants performed spatial WM tasks that required them to remember the precise angular location of a stimulus, sampled from a 360° space. Using an inverted spatial encoding model (IEM; Brouwer & Heeger, 2009, 2011; for review, see Sprague et al., 2015), we identified the oscillatory frequency bands in which the topographic distribution of power – measured using EEG – carried location-specific information. We found that the topographic distribution of both evoked (i.e., activity phase-locked to stimulus onset) and total (i.e., activity regardless of phase) power across a range of low-frequency bands transiently tracked stimulus location. However, only the topography of total power in the alpha-band tracked the content of spatial WM throughout the delay period, indicating that alpha-band activity is directly related to the coding of spatial representations held in WM. The IEM allowed us to reconstruct spatially specific response profiles (termed channel tuning functions, or CTFs) that tracked the stored location during both encoding and delay periods of WM tasks. Thus, alpha-band activity enables time-resolved tracking of spatial representations held in WM. These findings underscore the central role that alpha-band activity plays in coding the content of spatial WM, and provide new evidence for the functional overlap between spatial WM and spatial attention.

Materials and Methods

Participants
Fifteen volunteers took part in each experiment for monetary compensation ($10 per hour). The participants in each experiment were non-overlapping, with the exception of one participant who took part in both Experiments 1 and 3. Participants reported normal or corrected-to-normal vision, were between 18 and 35 years old, and provided informed consent according to procedures approved by the University of Oregon Institutional Review Board. Participants were replaced if more than 25% of trials were lost due to recording or ocular artifacts, and/or if the participants did not complete all trials during the session (five in Experiment 1, seven in Experiment 2, and three in Experiment 3).

**Stimulus displays**

Stimuli were generated in Matlab (Mathworks, Inc.) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and were presented on a 17-inch CRT monitor (refresh rate: 60 Hz) at a viewing distance of ~100 cm. All stimuli were rendered in dark gray against a medium gray background.

The spatial WM tasks required participants to remember the angular location of a sample stimulus. The stimulus was a circle (1.6° in diameter) centered 4° of visual angle from the central fixation point (0.2° in diameter). For each trial, the angular location of the stimulus was sampled from one of eight location bins spanning 0-315° (in angular location), in steps of 45°, with jitter added to cover all 360° of possible locations to prevent categorical coding of stimulus location. In all experiments, the location of the sample stimulus was drawn from each bin equally often, and in a random order, within each block of trials.

**Procedures**

After providing informed consent, participants were fitted with a cap embedded with 20 scalp electrodes before completing a spatial WM task (see below for details). Testing took place
in a dimly lit, electrically shielded chamber. In each experiment, the spatial WM task comprised 15 blocks of 64 trials, and took approximately 2-2.5 hours to complete.

**Delayed estimation task.** Participants in Experiments 1 and 2 performed a spatial delayed-estimation task (Wilken & Ma, 2004; Zhang & Luck, 2008; see Fig 1A). These experiments differed only in trial timing. Participants began each trial by pressing the spacebar. The trial began with a fixation display lasting between 600-1500 ms. A sample stimulus was then presented (250 ms in Experiment 1; 1000 ms in Experiment 2), followed by a delay period during which only the fixation point remained visible (1750 ms in Experiment 1; 1000 ms in Experiment 2). After the delay period, participants used a mouse to click on the perimeter of a probe ring (8° in diameter, 0.2° thick) to report the remembered location of the sample disc as precisely as possible. Before starting the task, participants completed a brief set of practice trials to ensure they understood the task.

**Spatial change detection task.** Participants in Experiment 3 performed a spatial change detection task (see Fig 1B). Rather than reporting the remembered location after the delay period with a mouse click, a test stimulus (identical to the sample stimulus) was presented for 250 ms. On half of trials, the test stimulus was presented in the same location as the sample stimulus (no-change trials), while on the other half of trials the test stimulus was shifted 20° clockwise or anticlockwise from the sample location (change trials). Participants indicated with a key press whether or not the location of the stimulus had changed. The timing of the task was identical to Experiment 1 (i.e., 250 ms sample stimulus, 1750 ms delay period). Before starting the task, participants completed a brief set of practice trials with feedback to ensure they knew the size of the change to expect for change of trials.

**Modeling Response Error Distributions**
In the delayed estimation experiments (Experiments 1 and 2), response error, the angular difference between the reported and presented locations, could range from -180° to 180°. The response error distribution for each participant was modeled as the mixture of a von Mises distribution and a uniform distribution, corresponding to trials in which the sample stimulus was successfully or unsuccessfully stored, respectively (see Zhang & Luck, 2008). Maximum likelihood estimates were obtained for three parameters: (1) the mean of the von Mises component (\(\mu\)), corresponding to response bias; (2) the dispersion of the von Mises distribution (s.d.), corresponding to mnemonic precision; and (3) the height of the uniform distribution (\(P_f\)), corresponding to the probability of forgetting the sample stimulus. Parameter estimates were obtained using the ‘MemFit.m’ function of MemToolbox (Suchow et al., 2013).

**EEG Acquisition**

We recorded EEG from 20 tin electrodes mounted in an elastic cap (Electro-Cap International, Eaton, OH). We recorded from International 10/20 sites F3, FZ, F4, T3, C3, CZ, C4, T4, P3, PZ, P4, T5, T6, O1, and O2, along with five nonstandard sites: OL midway between T5 and O1, OR midway between T6 and O2, PO3 midway between P3 and OL, PO4 midway between P4 and OR, and POz midway between PO3 and PO4. All sites were recorded with a left-mastoid reference, and were re-referenced offline to the algebraic average of the left and right mastoids. To detect horizontal eye movements, horizontal electrooculogram (EOG) was recorded from electrodes placed ~1 cm from the external canthus of each eye. To detect blinks and vertical eye movements, vertical EOG was recorded from an electrode placed below the right eye and referenced to the left mastoid. The EEG and EOG were amplified with an SA Instrumentation amplifier with a bandpass of 0.01 to 80 Hz and were digitized at 250 Hz using LabVIEW 6.1 running on a PC. Trials were visually inspected for artifacts, and we discarded
trials contaminated by blocking, blinks, detectable eye movements, excessive muscle noise, or
skin potentials. An average of 12.2% ($SD = 5.6\%$) of trials were rejected per participant across
all three experiments.

**Time-Frequency Analysis**

Time-frequency analyses were performed using Matlab in conjunction with the Signal
Processing and EEGLAB toolbox (Delorme & Makeig, 2004). To isolate frequency-specific
activity, the raw EEG signal was bandpass filtered using a two-way least-squares finite impulse
response filter (‘eegfilt.m’ from EEGLAB Toolbox; see Delorme & Makeig, 2004). This
filtering method uses a zero-phase forward and reverse operation, which ensures that phase
values are not distorted, as can occur with forward-only filtering methods. A Hilbert Transform
(Matlab Signal Processing Toolbox) was applied to the bandpass-filtered data, producing the
complex analytic signal, $z(t)$, of the filtered EEG, $f(t)$ where $z(t) = f(t) + i\tilde{f}(t) =
A(t)e^{i\phi(t)}$, from which instantaneous amplitude, $A(t)$, was extracted; $\tilde{f}(t)$ is the Hilbert
Transform of $f(t)$ and $i = \sqrt{-1}$. The complex analytic signal was extracted for each electrode
using the following Matlab syntax:

```
 hilbert(eegfilt(data,F,f1,f2)')
```

where data is a 2D matrix of raw EEG (number of trials $\times$ number of samples), F is the sampling
frequency (250 Hz), f1 is the lower bound of the filtered frequency band, and f2 is the upper
bound of the filtered frequency band. For alpha-band analyses, we used an 8-12 Hz bandpass
filter, thus f1 and f2 were eight and twelve, respectively. For the time-frequency analysis, we
searched a broad range of frequencies (4-50 Hz, in increments of 1 Hz with a 1 Hz bandpass).
For these analyses f1 and f2 were four and five to isolate 4-5 Hz activity, five and six to isolate
5-6 Hz activity, and so on.
Total power was computed by squaring the complex magnitude of the complex analytic signal, and then averaging across trials. Thus, total power reflects ongoing activity irrespective of its phase-relationship to onset of the sample stimulus. In contrast, evoked power was calculated by first averaging the complex analytic signal across trials, and then squaring the complex magnitude of the averaged analytic signal. Evoked power reflects activity phase-locked to stimulus onset because only activity with consistent phase across trials remains after averaging the complex analytic signal.

Because calculating evoked power requires averaging across trials, artifact-free trials were partitioned into three blocks. To prevent bias in our analysis, we equated the number of observations across location bins within each block. To this end, we calculated the minimum number of trials for any given location bin $n$ for each participant, and assigned $n/3$ many trials for each location bin to each of the three blocks. Importantly, the blocks were independent (i.e., no trial was repeated across blocks) to prevent circularity in the cross-validation procedures used for the IEM routine (see Inverted Encoding Model). Evoked and total power was then calculated for each location bin for each block, resulting in an $l^*b \times m \times s$ matrix of both evoked and total power values, where $l$ is the number of location bins, $b$ is the number of blocks, $m$ is the number of electrodes, and $s$ is the number of time samples. For the analysis in which the IEM is applied across many frequency bands, we down-sampled the data matrix to a sample rate of 50 Hz (i.e., one sample every 20 ms) to reduce computation time. The data matrix was not down-sampled for analyses restricted to the alpha-band.

Finally, because we equated the number of trials across location bins within blocks, a random subset of trials were not included in any block. Thus, we randomly generated multiple block assignments (five for the full time-frequency analyses, and ten for the alpha-band).
analyses), each resulting in an $l \times b \times m \times s$ power matrix. The IEM routine (see Inverted
Encoding Model) was applied to the matrices of power values for each block assignment, and
their outputs (i.e., channel response profiles) were averaged. This approach better utilized the
complete data set for each participant and minimizes the influence of idiosyncrasies in estimate
of evoked and total power specific to certain assignments of trials to blocks.

**Inverted Encoding Model**

We used an IEM to reconstruct location-selective CTFs from the topographic distribution
of oscillatory power across electrodes. We assumed that power measured at each electrode
reflects the weighted sum of eight spatial channels (i.e., neuronal populations), each tuned for a
different angular location (c.f. Brouwer & Heeger, 2009, 2011; Sprague et al., 2013, 2014). We
modeled the response profile of each spatial channel across angular locations as a half sinusoid
raised to the seventh power, given by:

$$R = \sin(0.5 \theta)^7$$

where $\theta$ is angular location (ranging from $0^\circ$ to $359^\circ$), and $R$ is the response of the spatial
channel in arbitrary units. This response profile was circularly shifted for each channel such that
the peak response of each spatial channel was centered over one of the eight location bins (i.e.,
$0^\circ, 45^\circ, 90^\circ$ etc.). The predicted channel responses for each location bin were derived from these
basis functions (calculated using the angular location at the center of each bin).

An IEM routine was applied to each time-frequency point in the time-frequency analyses,
and to each time point in the alpha-band analyses. This routine proceeded in two stages (train
and test). In the training stage, training data $B_i$ were used to estimate weights that approximate
the relative contribution of the eight spatial channels to the observed response measured at each
electrode. Let $B_i$ ($m$ electrodes $\times n_i$ observations) be the power at each electrode for each
measurement in the training set, \( C_i (k \text{ channels} \times n_i \text{ observations}) \) be the predicted response of each spatial channel (determined by the basis functions) for each measurement, and \( W (m \text{ electrodes} \times k \text{ channels}) \) be a weight matrix that characterizes a linear mapping from “channel space” to “electrode space”. The relationship between \( B_1, C_i, \) and \( W \) can be described by a general linear model of the form:

\[
B_1 = WC_1
\]

The weight matrix was obtained via least-squares estimation as follows:

\[
\hat{W} = B_1 C_1^T (C_1 C_1^T)^{-1}
\]

In the test stage, with the weights in hand, we inverted the model to transform the observed test data \( B_2 (m \text{ electrodes} \times n_2 \text{ observations}) \) into estimated channel responses, \( C_2 (k \text{ channels} \times n_2 \text{ observations}) \):

\[
C_2 = (\hat{W}^T \hat{W})^{-1} \hat{W}^T B_2
\]

Each estimated channel response function was circularly shifted to a common center (i.e., 0° on the “Channel Offset” axes of the figures) by aligning the estimated channel responses to the channel tuned for the stimulus bin to yield CTFs. The IEM routine was performed separately for each sample point from 500 ms prior to stimulus onset through to the end of the delay period (2000 ms).

Importantly, we used a “leave-one-out” cross validation routine such that two blocks of estimated power values (see Time-Frequency Analysis) served as \( B_1 \) and were used to estimate \( \hat{W} \), and the remaining block served as \( B_2 \) and was used to estimate \( C_2 \). Thus, the training and test data were always independent. This process was repeated until each of the three blocks were held out as the test set, and the resulting CTFs were averaged across each test block.
Finally, because the exact contributions of each spatial channel to each electrode (i.e., the channel weights, $W$) will likely vary by subject, the IEM routine is applied separately for each subject, and statistical analyses were performed on the reconstructed CTFs. This approach allowed us to disregard differences in the how location-selectivity is mapped to scalp-distributed distributed patterns of power across subjects, and instead focus on the profile of activity in the common stimulus or “information” space (Sprague & Serences, 2015).

**Statistical Analysis**

To quantify the location selectivity of CTFs, we used linear regression to estimate CTF slope (i.e., slope of channel response as a function of location channels after collapsing across channels that were equidistant from the channel tuned to the location of the evoking stimulus), where higher CTF slope indicates greater location selectivity. To test whether CTF selectivity was reliably above chance, we tested whether CTF slope was greater than zero using a one-sample $t$ test. Because mean CTF slope may not be normally distributed under the null hypothesis, we employed a Monte Carlo randomization procedure to empirically approximate the null distribution of the $t$ statistic. Specifically, we implemented the IEM as described above but randomized the location labels within each block so that the labels were random with respect to the observed responses in each electrode. This randomization procedure was repeated 1000 times to obtain a null distribution of $t$ statistics. To test whether the observed CTF selectivity was reliably above chance, we calculated the probability of obtaining a $t$ statistic from the surrogate null distribution greater than or equal to the observed $t$ statistic (i.e., the probability of a Type 1 Error). Our permutation test was therefore a one-tailed test. CTF selectivity was deemed reliably above chance if the probability of a Type 1 Error was less than .01. This permutation testing
procedure was applied to each time-frequency point in the time-frequency analyses, and to each
time point in the alpha-band analyses.

**Quantifying Biases in Eye Position**

Although we discarded trials with detectable eye movements, small but systematic biases
in eye position towards the remembered location may still exist. Indeed, we found evidence for
very small but reliable biases in horizontal EOG amplitude that tracked stimulus location (see
Results). If eye position is biases towards stimulus location, then there should be a linear
relationship between the horizontal position of the stimulus and horizontal EOG amplitude.

Thus, we used linear regression to calculate an *eye bias score* to quantify the extent to which eye
position covaried with stimulus location. The eye bias score was calculate as the slope of the best
fitting linear function describing horizontal EOG amplitude (in µV) as a function of the
horizontal location of the stimulus (in degrees of visual angle). Higher eye bias scores therefore
reflect greater changes in eye position as a function of stimulus location. This eye bias score was
calculated across time for each participant separately.

**Results**

**Behavior**

Task performance confirmed that participants were engaged in the spatial WM tasks in
all three experiments. In the delayed-estimation experiments (Experiments 1 and 2), mnemonic
precision computed from a mixture model (Suchow et al., 2013; Zhang & Luck, 2008) was high,
indicated by low *s.d.* values (Experiment 1: $M = 6.6^\circ$, $SD = 1.8^\circ$; Experiment 2: $M = 5.2^\circ$, $SD =
1.6^\circ$), and the probability that the stimulus was forgotten, $P_f$, was extremely low (Experiment 1:
$M = .002$, $SD = .002$; Experiment 2: $M = .002$, $SD = .002$). In the spatial change detection task
(Experiment 3), change detection accuracy was high ($M = 90.1\%$, $SD = 4.7\%$).
Experiment 1: Identifying Frequency-Bands that Track the Content of Spatial Working Memory

We first sought to identify the frequency bands in which the topographic distribution of oscillatory power tracked the content of spatial WM. To this end, we used an IEM to reconstruct location-selective CTFs (see Materials and Methods). Using the IEM, we searched a broad range of frequencies (4-50 Hz, in increments of 1 Hz) across time to identify the frequency bands in which the topographic distribution of evoked and total power tracked the location of the sample stimulus. If the multivariate pattern of power across electrodes carries information about stimulus location, then the IEM should reveal a graded CTF profile, with a clear peak in the channel tuned for the remembered location. On the other hand, if the multivariate pattern of power does not carry information about stimulus location, then the IEM should produce a flat CTF profile, indicating no location tuning. Figure 2 shows location selectivity of reconstructed CTFs (as measured by CTF slope) as a function of time and frequency for both evoked and total power. We performed a permutation test at each time-frequency point to identify the points at which CTF slope was reliably above zero (see Materials and Methods). We found the topographic distribution of both evoked and total power transiently tracked the location of the sample stimulus across a range of low frequencies (~4-20 Hz; Fig 2A). In contrast, only total alpha power (~8-12 Hz) enabled sustained tracking of the stored location throughout the blank delay (Fig 2B). Thus, the topographic distribution of total alpha power tracked spatial representations held in WM.

Alpha power tracks the content of spatial WM with fine-grained spatial resolution.

Previous work has demonstrated that alpha power decreases contralateral to a location held in spatial WM (Medendorp et al., 2007; Van Der Werf et al., 2008; van Dijk et al., 2010). It is
possible that location-selectivity in the alpha-band, measured using CTF slope, simply reflects sensitivity of alpha power to the hemifield (or quadrant) of the remembered location. Such coarse location tuning could give rise to a graded CTF when shifted and averaged across location bins. To test this possibility, we examined the channel responses profiles reconstructed from total alpha (8-12 Hz) power in Experiment 1 for each of the eight location bins separately. If the topographic distribution of alpha power tracks the precise location held in WM, then the channel response profiles should differ for each of the eight location bins. Specifically, for each location bin, we should observe a graded tuning profile, with a peak response in the channel tuned for the remembered location. Figure 3 shows the channel responses (averaged across time from 0-2000 ms) for each of the eight location bins. Indeed, we found that the peak channel response was always seen in the channel tuned for the remembered location, providing clear evidence that the topography of alpha power tracked the specific angular location held in WM.

Examining the format of spatial representations tracked by alpha power. Next we examined the format of the spatial representations tracked by the topographic distribution of alpha power. Our standard basis set specified a “graded” channel response profile, with the peak response in the channel tuned for the remembered location, and with gradually diminishing response for channels tuned for other locations. This graded response profile across feature-selective cells is the hallmark of population coding of sensory variables (Pouget et al., 2000), rather than more abstracted (e.g., categorical) representations. We found that CTFs reconstructed from alpha-band activity showed this graded profile, suggesting that that modulations of alpha power follow a graded, sensory format (Fig 4A). However, using an IEM, it is always possible that the graded CTF profile reflects the graded basis function itself rather than truly graded location-selective activity (Ester et al., 2015; Saproo & Serences, 2014). To rule out this
possibility, we reconstructed CTFs with the IEM, this time with a modified basis set of eight orthogonal Kronecker delta functions, each centered on one of the eight location bins. These functions do not specify a graded profile of responses across channels. Thus, if a graded profile is observed using this basis function it must reflect a graded pattern in the data itself. In contrast, if the spatial representations tracked by alpha-band power does not follow this graded format, we would expect to recover a peak in the channel tuned for the remembered, and uniform responses across the rest of the channels. Using this orthogonal basis set, reconstructed CTFs had a graded profile (Fig 4B), confirming that graded location tuning is an intrinsic property of alpha activity and is not imposed by the graded basis function. Figure 4C shows that this graded profile was consistent across time. Therefore, alpha-band activity follows the expected format of a sensory code.

Ruling out biases in eye position. Eye movements generate electrical potentials that affect EEG recordings. We instructed participants to maintain fixation during the spatial WM task, and discarded trials with detectable eye movements. Nevertheless, small but systematic biases in eye position towards the remembered location may still exist. To examine this possibility, we inspected horizontal electrooculogram as a function of stimulus location. We found a reliable bias in eye position that tracked stimulus position. However, this bias was remarkably small (< 2 µV), corresponding to shifts from fixation of less than 0.15° of visual angle on average (Lins et al., 1993a, 1993b). We found that CTF slope in the alpha-band is greatest early in the trial, and decreased towards the end of the delay period (Fig 5A). In contrast, bias in eye position, quantified using an eye bias metric (see Materials and Methods), increased gradually as the delay period progressed (Fig 5B). Therefore, subtle biases in eye position cannot explain the link between alpha activity and the content of spatial WM.
In Experiment 1, we demonstrated that topographic patterns of alpha power track the content of spatial WM during the delay period of a WM task. Recent work suggests that WM is important not only for maintaining representations of stimuli that are no longer externally available but also for representing stimuli that remain within view (Chun, 2011; Tsubomi et al., 2013). In Experiment 2, we used an extended encoding period (1000 ms) to examine whether the topographic distribution of alpha power tracks the spatial representation of a stimulus that remains in view. We observed location-selective CTFs reconstructed from total alpha activity (Fig 6B). Importantly, robust CTFs were seen throughout both the stimulus (0-1000 ms) and delay (1000-2000 ms) periods, demonstrating that alpha activity tracks the location of a to-be-remembered stimulus, even when the stimulus remains in view. Thus, total alpha power tracks spatial representations both in the presence and absence of visual input.

In Experiment 2, we again found that evoked alpha power generated reliable CTFs following stimulus onset (Fig 6A). However, weak but reliable CTF selectivity was also seen following stimulus offset (at 1000 ms). This second burst of location-specific evoked activity may reflect resynchronization of low-frequency activity caused by abrupt visual transient of stimulus offset (Gruber et al., 2005; Hanslmayr et al., 2007). However, further work is necessary to test this possibility.

**Experiment 3: Ruling out Response Confounds**

In our first two experiments, we used a delayed-estimation task in which participants used a mouse to click on a ring around fixation to report the remembered location (Fig 1A & 1B). Consequently, the remembered location covaried with the required response. In Experiment
3, we sought to rule out the possible contribution of preparatory motor activity to the location-selective CTFs that we observed in the delayed-estimation task. To this end, participants performed a spatial change detection task, in which they remembered the precise location of a sample stimulus, and reported whether the location of a test stimulus – presented after the delay period – differed from that of the sample stimulus (Fig 1C). Critically, participants could not plan their response (“change” vs. “no change”) until the test stimulus was presented. Therefore, any location-selective delay activity cannot reflect a planned response. As in Experiment 1, evoked CTFs only transiently tracked stimulus location (Fig 7A), while the topographic distribution of total alpha power tracked the remembered location, allowing for the reconstruction of reliable CTFs throughout the delay period (Fig 7B). Thus, findings from Experiment 3 solidify our conclusion that alpha activity tracks the contents of spatial memory, rather than the trajectory of a planned response.

**Location-Selective Activity is Specific to the Alpha-Band: A Cross-Experiment Analysis**

In our analyses of Experiments 2 and 3 so far, we focused exclusively on the alpha-band (8-12 Hz) because this frequency band was implicated in WM storage in Experiment 1. These analyses replicated the finding that the topographic distribution of alpha power tracks the content of spatial WM. However, because we focused on the alpha-band, these analyses did not replicate the finding that sustained, location-selective activity is *specific* to the alpha-band. Next, we sought to identify the frequency bands in which oscillatory power tracked stimulus location across all three experiments. To this end, we used the IEM to search time-frequency space for frequencies that carried location-specific information in Experiments 2 and 3 (as we previously reported for Experiment 1) to obtain maps of CTF slope across time and frequency (4-50 Hz, in increments of 1 Hz) for each experiment (Fig 8A-C). With these maps in hand, we then
identified the points in time-frequency space that showed reliable CTF selectivity across all three experiments to create a cross-experiment map of location-selective oscillatory activity (Fig 8B). This simple but conservative analysis revealed that evoked and total power across a range of frequency bands (~4-20 Hz) transiently tracked stimulus location, while only total alpha power tracked the remembered location throughout the delay period. The cross-experiment maps combined data from three independent experiments, with non-overlapping groups of participants.\(^1\) Therefore, this analysis provides clear evidence that location-selective oscillatory activity during WM maintenance, as reflected in the topographic distribution of oscillatory power, is specific to the alpha-band.

Our results provide decisive evidence that the topography of power tracks the location held in spatial WM, suggesting that alpha-band activity is related to the coding of spatial representations in WM. However, it is less clear whether other frequency bands play similar roles. Theta- and gamma-band activity (i.e., 4-7 Hz and ~30-100 Hz, respectively) are of particular interest because they have been proposed to play a central role in coordinating cellular assembles that code the content of WM (Lisman, 2010; Roux & Uhlhaas, 2014). Given that we observed no evidence of sustained location-selectivity in the topographic distribution of theta or gamma power, it is tempting to conclude that the frequency bands do not contribute to the coding of spatial representations in WM. However, it is possible that these frequency bands contribute to the coding of spatial WM representations in ways that do not result in location-specific patterns of EEG power across the scalp. For example, location-specific patterns of theta-band activity may exist in hippocampal local field potentials (e.g., Agarwal et al., 2014). However, such location-selectivity might not necessarily produce location-specific patterns of theta power on

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\(^1\) One participant took part in both Experiments 1 and 3. This subject was excluded from the Experiment 3 dataset for the purpose of the cross-experiment map to ensure that the data from each experiment were independent.
the scalp. Thus, our results do not rule out potential roles for oscillatory activity outside the alpha-band in coding the content of spatial WM.

**Discussion**

Previous work has demonstrated that alpha power is reduced contralateral to locations held in spatial WM (Medendorp et al., 2007; Van Der Werf et al., 2008; van Dijk et al., 2010). However, those studies left it unanswered whether the topographic distribution of alpha activity tracked the precise location held in WM, or whether alpha activity reflected a lateralized memory process (e.g., a contralateral control signal) that is insensitive to the specific location that is stored. Here, we provide clear evidence that the topographic pattern of total alpha-band power precisely tracks the angular location maintained in WM. We used an inverted encoding model (IEM) to reconstruct CTFs from the pattern of EEG power across the scalp, which provided an assay of location-selective activity across the neuronal populations reflected in EEG activity. A clear pattern of results emerged over three independent experiments: while evoked and total power across a range of frequency bands transiently tracked the location of the sample stimulus, only total alpha power tracked the remembered location throughout the delay period. Furthermore, these location-specific patterns of alpha power showed the hallmark graded profile of a sensory population code. This result clearly demonstrates that alpha activity coordinates location-tuned neuronal populations rather than populations that code for more abstract variables, such as top-down control signals or categorical representations of location. Together, these results demonstrate that alpha activity is related to the *sensory coding* of spatial representations in WM.

Our findings build on a foundation of human neuroimaging work demonstrating that the feature content of visual WM can be recovered from voxel-wise patterns of activity (e.g.,
While stimulus-specific activity measured with functional magnetic resonance imaging (fMRI) allows for reconstruction of feature-selective CTFs (e.g., Ester et al., 2013, 2015), the temporal precision of this approach is limited by the sluggish haemodynamic response. In a recent study, Garcia and colleagues reconstructed time-resolved CTFs that from patterns of power evoked by a flickering stimulus, highlighting the potential of combining IEMs with EEG recordings to obtained temporally-resolved stimulus-specific activity (Garcia et al., 2013). Here, we find that total alpha power tracks the content of spatial WM throughout a delay period, in the absence of rhythmic visual stimulation. Thus, the intrinsic role that alpha-band activity plays in spatial WM storage enables moment-by-moment tracking of location-specific activity, without the need for a flickering stimulus. Given that the topography of alpha power covaries with attended locations (Bahramisharif et al., 2010, 2011; Rihs et al., 2007; van Gerven & Jensen, 2009), we expect that this approach should also provide a powerful tool for tracking the dynamics of covert attention.

The IEM approach allowed us to reconstruct CTFs, providing an assay of location-specific activity across large populations of neurons (Serences & Saproo, 2012). While single neurons are the building block for sensory codes, it is the joint activity of a population of cells that guide behavior (Butts & Goldman, 2006; Jazayeri & Movshon, 2006). Thus, population-level encoding models provide a good approach for linking brain and behavior (Sprague et al., 2015). This approach has already enjoyed some success. For example, Sprague and colleagues (Sprague et al., 2014) used a spatial encoding model to obtain population-level reconstructions of stimulus location from patterns of activity measured with fMRI during a spatial WM task. Sprague and colleagues found that amplitude of spatial reconstructions tracked the decline in
mnemonic precision that is seen with increasing set size in a WM tasks. The location-specific patterns of alpha power we report here provide a new window onto population-level coding. Although we do not demonstrate it here, we expect that the topography of alpha activity should also track changes in the quality of population codes and predict behavior. Furthermore, because of the temporal resolution that EEG affords, this approach may be sensitive to rapid changes in the quality of population codes. Further work is necessary to test these predictions.

What are the cortical origins of the topographic pattern of alpha power that track the content of spatial WM? In studies of spatial attention, changes in topographic patterns of alpha power are thought to reflect synchronization of posterior visual areas tuned for unattended locations, reflecting suppression of processing in these regions (Kelly et al. 2006; Rihs et al., 2007; Thut et al., 2006). While it is tempting to conclude that the location-specific modulations of alpha activity reflect synchronization within visual cortex, it is difficult to infer the cortical source of oscillations based on EEG recordings alone. Neuroimaging studies have revealed location-specific activity in frontal, parietal, and occipital cortex during spatial attention and WM tasks (Sprague & Serences, 2013; Sprague et al., 2014; Silver & Kastner, 2009). Thus, it is possible that location-specific patterns of alpha power might reflect synchronization within or between any of the location-selective regions.

We found that alpha activity tracked stimulus location not only during the delay period, but also while the stimulus remained in view throughout an extended encoding period. Traditionally, visual WM has been characterized as a system for the maintenance of visual inputs that are no longer present. However, recent work has challenged this view, instead suggesting that WM also constrains representation of externally available stimuli (Chun, 2011; Tsubomi et al., 2013). For example, Tsubomi and colleagues demonstrated that memory-load dependent
contralateral delay activity (CDA) – an electrophysiological marker of maintenance in visual
WM– showed a similar profile across both stimulus-absent and stimulus-present periods under
the same task demands (Tsubomi et al., 2013). Here, we show that the alpha-band activity, like
the CDA, plays a role in maintaining active spatial representations in both the presence and
absence of visual input.

Our finding that the topography of alpha power tracks the content of spatial WM is
consistent with the broad hypothesis that neuronal oscillations synchronize the cellular
assemblies that code for mental representations (Fell & Axmacher, 2011; Hebb, 1949; Nicolelis
et al., 1997; Sejnowski & Paulsen, 2006; Singer & Gray, 1995; Singer, 1999; Watrous et al.,
2015). Applied to WM, this view predicts that patterns of oscillatory activity should not only
track spatial representations held in WM, but also non-spatial representations (e.g., color and
orientation). Indeed, Salazar and colleagues found content-specific synchronization between
frontal and parietal local field potentials in monkeys, peaking at 15 Hz. Fronto-parietal
synchronization tracked both the location and identity (i.e., shape) of a remembered stimulus in a
delayed-match to sample task, suggesting that both identity and location are encoded in patterns
of synchronization (Salazar et al., 2012). However, evidence for the role of oscillations in
coordinating the code of non-spatial features is sparse, and further work is needed to examine
whether neuronal synchrony plays a general role in coordinating feature-selective cellular
assemblies that code the content of WM.

Conclusions

Using an inverted spatial encoding model, we demonstrated that the topographic
distribution of alpha power tracks spatial representations held in WM. These findings show that
alpha-band activity plays a role in coding for spatial information held in WM, and this approach provides a time-resolved tool for tracking the content of spatial WM.
References


Saproo S, Serences JT. Attention improves transfer of motion information between V1 and MT. *J Neurosci* 34: 3586-3596, 2014.


Figure Captions

**Figure 1.** Spatial WM tasks. A: In Experiments 1 and 2, participants performed a delayed estimation task. Participants maintained fixation while they remembered the angular location of a sample stimulus, which they reported after a delay period by clicking on the perimeter of a rim. Experiments 1 and 2 differed only in trial timing. B: In Experiment 3, participants performed a change detection task. Rather than report the location of the sample stimulus, a test stimulus was presented after the delay period and participants reported whether or not the location of the stimulus had changed. Stimuli not perfectly to scale.

**Figure 2.** Identifying the frequency bands that track the content of spatial WM in Experiment 1. An IEM was used to reconstruct location-selective CTFs from the topographic distribution of evoked (A) or total (B) power across a broad range of frequencies (4-50 Hz, in increments of 1 Hz) and time. Evoked and total power transiently tracked stimulus location after stimulus onset across a broad range of frequencies (4 to ~20 Hz). However, only total alpha power tracked the content of spatial WM throughout the delay period. Color represents CTF slope, a measure of CTF selectivity that quantifies the location-specific activity in the topographic distribution of power. Points at which CTFs slope was not reliably above zero as determined by a permutation test are set to zero (dark blue).

**Figure 3.** Unshifted channel responses reconstructed from total alpha power after stimulus onset (averaged from 0-2000 ms) shown for each of the eight stimulus location bins in Experiment 1.
For all location bins, the peak response is seen in the channel tuned for that stimulus location, confirming that the topography of alpha power tracked the precise location held in spatial WM.

**Figure 4.** CTFs reconstructed from total alpha (8-12 Hz) power after stimulus onset (averaged from 0-2000 ms) using the standard, “graded” basis set (A) and using a basis set of eight orthogonal Kronecker delta functions (B) for Experiment 1. CTFs reconstructed using the orthogonal basis set still showed a smooth, graded profile, demonstrating that the intrinsic tuning properties of alpha power are well-described by the graded basis function of the spatial encoding model. Shaded error bars reflect bootstrapped standard error of the mean. C: Time-resolved CTF reconstructed using the orthogonal basis set, showing that the graded CTF profile was consistent across time points.

**Figure 5.** Alpha CTF selectivity and small biases in eye position towards the remembered location show different time courses. A: Location-selectivity of CTFs reconstructed from total alpha (8-12 Hz) power across time. Although CTF selectivity is robust throughout the delay period, it gradually declines across time. B: Eye bias score quantifying bias in eye position towards (positive values) or away (negative values) from the remembered location. This score reflects the change in HEOG amplitude (in µV) seen when the horizontal stimulus position changes by one degree of visual angle. In contrast to CTF selectivity, bias in eye position towards the remembered location increases across time, demonstrating that location-selective patterns of alpha power are not accounted for by small but reliable biases in eye position. Shaded error bars reflect bootstrapped standard error of the mean.
Figure 6. Total alpha activity tracks stimulus location when the stimulus remains in view. Location CTFs reconstructed from evoked (A) and total (B) alpha (8-12 Hz) activity during the spatial WM task with a long encoding period (1000 ms; Experiment 2). Despite the stimulus remaining in view from 0 to 1000 ms, total alpha power tracked stimulus location during this period, demonstrating that total alpha power tracks spatial representations both in the presence and absence of visual input. Evoked alpha power showed reliable but weaker location selectivity during the delay period. White markers along the top of the panels indicate the points at which CTF slope was reliably above chance as determined by a permutation test.

Figure 7. Ruling out response confounds. Location CTFs reconstructed from evoked (A) and total (B) alpha (8-12 Hz) power during a spatial change detection task (Experiment 3). Because participants could not anticipate the response (“change” vs. “no change”) during the delay period, this task eliminated any contribution of preparatory motor activity to the location CTFs. Nevertheless, total alpha power tracked location held in spatial WM throughout the delay period, whereas evoked alpha power only transiently tracked stimulus position. White markers along the top of the panels indicate the points at which CTF slope was reliably above chance as determined by a permutation test.

Figure 8. Location-selective activity in specific to the alpha band. A: Slope of CTFs reconstructed from the topographic distribution of evoked and total power across a broad range of frequencies (4-50 Hz, in increments of 1 Hz) and time for Experiments 1-3. Points at which CTFs slope was not reliably above zero as determined by a permutation test are set to zero (dark blue). B: Cross-experiment map of the points for which CTF slope was reliably above chance for
across all three experiments. Reliable points are shown in light blue. Across three experiments, evoked and total power transiently tracked stimulus location after stimulus onset across a broad range of frequencies (4 to ~20 Hz) while only total alpha power tracked the content of spatial WM throughout the delay period.
A. Delayed Estimation (Exp 1 & 2)

- Exp 1: 250 ms
- Exp 2: 1000 ms

B. Change Detection (Exp 3)

- 250 ms
- 1750 ms
- 250 ms