Traveling waves support rhythmic attentional search

Yue Kong[1,*], Kirsten Petras[1], Philippe Marque[2,3], Rufin VanRullen[4], David M. Alexander[1,#], Laura Dugué[1,5,#]

Affiliations

[1]Université Paris Cité, CNRS, Integrative Neuroscience and Cognition Center, F-75006 Paris, France

[2]Department of Physical and Rehabilitation Medicine, University Hospital of Toulouse, Toulouse, France

[3]ToNIC (Toulouse NeuroImaging Center), Inserm, University of Toulouse 3, Toulouse, France

[4]CerCo, CNRS, Universite de Toulouse, Toulouse, France

[5]Institut Universitaire de France (IUF), Paris, France

*Correspondence: yue.kong@u-paris.fr

[#]Shared senior authorship

Abstract

Brain activity unfolds across space and time, giving rise to spatiotemporal dynamics that can manifest as cortical traveling waves –smooth phase shifts propagating across the cortex. Although traveling waves have been observed across species and measurement scales, their functional role in human cognition remains largely inferred from correlational evidence. In healthy humans, large-scale neural dynamics must be studied non-invasively, which provides limited access to their neural origins. Here, we tested whether global traveling waves causally contribute to inter-areal communication during attention. Using transcranial magnetic stimulation (TMS), we induced long-range traveling waves detectable with electroencephalography and assessed their neural and behavioral consequences during a difficult attentional search task. Double-pulse TMS applied over the right frontal eye field transiently disrupted ongoing global waves and selectively induced direction- and frequency-specific traveling waves propagating toward the occipital visual cortex. These TMS-induced anterior-to-posterior theta traveling waves were periodically modulated by stimulation latency relative to search-trial onset. Critically, behavioral performance exhibited the same rhythmic pattern, with improved attentional search performance when TMS-induced traveling waves were more prominent. Together, these findings provide causal evidence that large-scale traveling waves support inter-areal communication during rhythmic visual attention.

Introduction

Traveling waves –smooth phase shifts across the cortex (Muller et al., 2018; Dugué & Chavane, 2025)– have been observed across species and scales and have been linked to cognitive processes (Zhang et al., 2018; Lozano-Soldevilla & VanRullen, 2019; Davis et al., 2020; Alamia et al., 2023; Fakche & Dugué, 2024; Fakche et al., 2024). In humans, electro- or magneto-encephalography (EEG, MEG) studies have reported wave-like patterns across the sensor array, but the significance of these observations is debated, partly due to uncertainties regarding their computational underpinnings (Grabot et al., 2025; Petras et al., 2025; Dugué & Chavane, 2025). This raises concerns about the functional relevance of these large-scale, non-invasively measured traveling waves. Here, we address this issue by using transcranial magnetic stimulation (TMS) to causally induce global traveling waves in EEG signals and examine their behavioral consequences.

Cortical traveling waves have been proposed as a canonical computation that organizes neuronal processing across space and time in a variety of cognitive functions, including attention (Dugué & Chavane, 2025). Attention itself is intrinsically spatiotemporal, and samples the sensory environment across space and time in a rhythmic manner, as reflected in low-frequency fluctuations in behavioral performance (VanRullen et al., 2007; Landau & Fries, 2012; Fiebelkorn et al., 2013; Senoussi et al., 2019; Galas et al., 2025; for review: Dugué & VanRullen, 2017; Fiebelkorn & Kastner, 2019; Kienitz et al., 2022). Such rhythmic modulations of performance can similarly be induced by time-locked perturbations such as with TMS. For example, when TMS is applied over the right frontal eye field (rFEF) at different latencies relative to task events, attentional performance is periodically modulated over time (theta frequency: Dugué et al., 2019; beta frequency: Veniero et al., 2021). The rhythmic nature of visual attention aligns with neuroimaging evidence linking it to local, stationary neural oscillations in frontal (i.e., rFEF, Buschman & Miller, 2009) and occipital regions (alpha: Worden et al., 2000; Sauseng, 2005; Thut, 2006; Händel, 2011; theta: Spyropoulos et al., 2018). The involvement of both frontal and occipital regions is consistent with two-stage

models suggesting inter-areal communication during attentional allocation between low-level and higher-level regions (Palmer et al., 1993; Treisman, 1998; Itti & Koch, 2001; Deco et al., 2002). Yet, the neural mechanisms supporting such long-range coordination remain unclear.

Here, we investigate whether global traveling waves support inter-areal communication in visual attention. We tested the hypothesis that anterior-to-posterior theta traveling waves have a causal, functional role in attentional search. We applied double-pulse TMS over rFEF (or over the vertex as a control site) at multiple stimulation latencies in a difficult, attentional search task while simultaneously recording EEG. TMS perturbed ongoing wave dynamics and selectively induced direction- and frequency-specific traveling waves. These TMS-induced traveling waves were periodically modulated by TMS latency, and attentional search performance varied accordingly with the same rhythm.

Results

We tested the hypothesis that anterior-to-posterior theta traveling waves have a causal functional role in attentional search. Participants performed a difficult search task with concurrent EEG recordings (Fig. 1a). Double-pulse TMS was applied over the rFEF at various latencies from search array onset. Stimulation of the vertex served as a control condition (Fig. 1b). We characterized global traveling wave activity in sensor space using a data-driven singular-value-decomposition (SVD)-based approach, complemented by time-frequency analyses and permutation-based statistical testing (Fig. 1c). We first assessed the prominence of global traveling waves in TMS–EEG recordings, then examined how TMS transiently disrupted ongoing wave activity while inducing frequency- and direction-specific traveling waves. Finally, we tested whether these TMS-induced waves were periodically modulated as a function of TMS latency, paralleling previously reported periodic interference of TMS on visual search behavioral performance (Dugué et al., 2019).

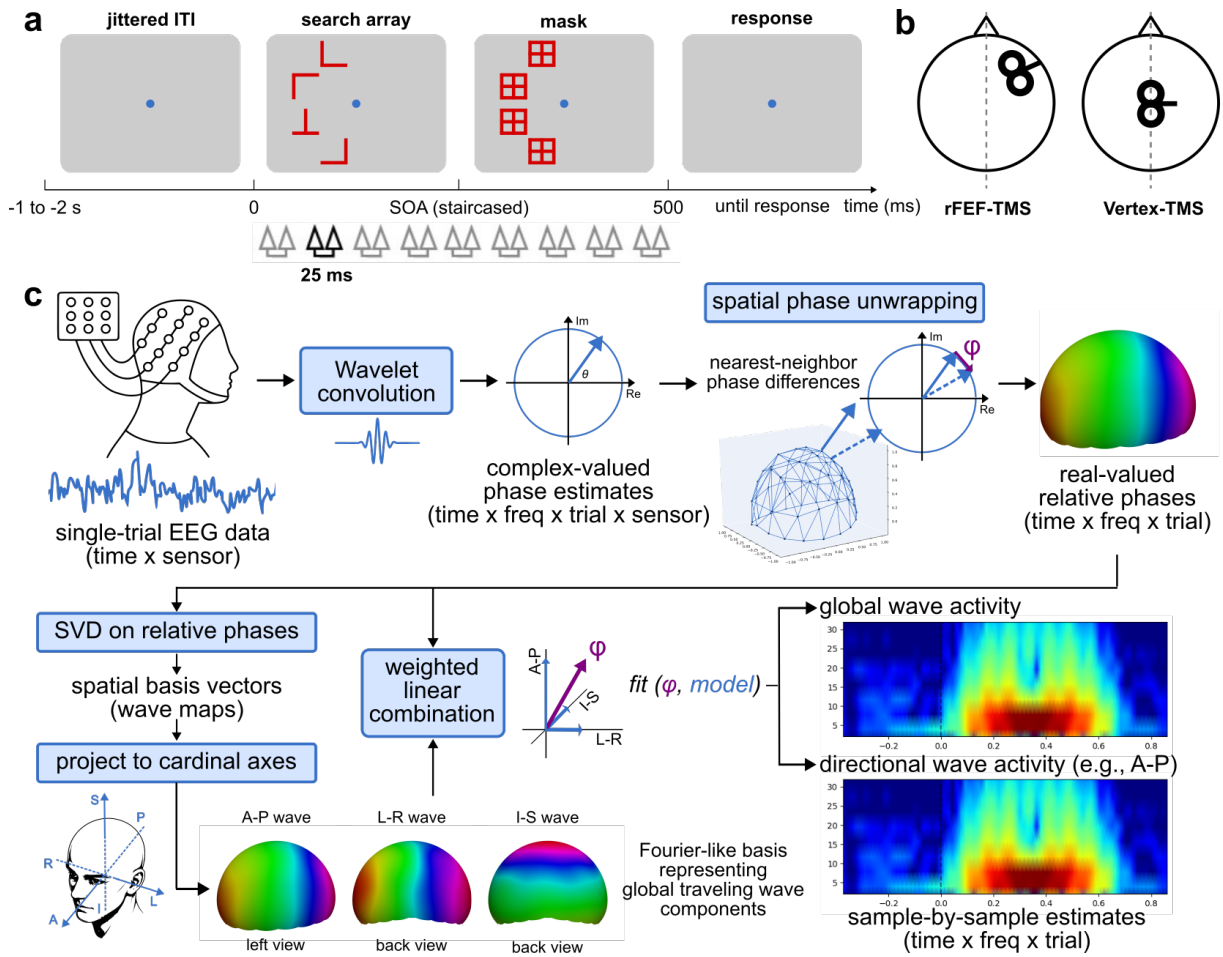

Fig. 1 Experimental paradigm, TMS sites, and traveling wave analysis. a Attentional visual search task. Each trial began with a 1-2 s jittered inter-trial interval (ITI). A four-item search array was briefly presented in the left visual field and masked after a staircase-determined stimulus-onset asynchrony (SOA), such that total visual stimulation lasted 500 ms. Participants reported the presence or absence of target "T" among distractor "L"s. A double-pulse TMS (25 ms inter-pulse interval) was delivered at one of nine delays during stimulus presentation. **b** TMS pulses were applied over the rFEF (left) or the vertex (right) as a control site. **c** Traveling wave analysis pipeline. Single-trial EEG data were wavelet-transformed to obtain complex-valued phase estimates, and then spatially unwrapped (via nearest-neighbor phase differences) into real-valued relative phases. Singular vector decomposition (SVD) was applied to the relative phases to extract spatial basis vectors (wave maps). The global wave maps were projected onto interpretable Cartesian dimensions of sensor space, yielding anterior-posterior (A-P), left-right (L-R), and inferior-superior (I-S) global traveling wave components. Relative phases were then reconstructed as a weighted linear combination of these components, providing sample-by-sample estimates of global or direction-specific wave activity across time and frequency.

Theta-band power is selectively enhanced following TMS

To demonstrate the frequency specificity and the power of TMS-evoked activity, we examined time-frequency representations and topographical distributions of induced power within trials in which TMS was applied at the latest latency (450 ms after search array onset). Grand-average power, computed across trials and sensors, revealed significant increases in the theta

band (4.76-5.66 Hz) at two distinct post-stimulus intervals: an early window around 104-204 ms and a later window around 436-536 ms following search array onset (Fig. 2a and 2c). These time-frequency windows corresponded to visually-evoked and TMS-evoked activity, respectively, as confirmed by their corresponding scalp topographies (Fig. 2b). Theta power peaked over right occipital electrodes during the early window (104-204 ms) in both rFEF-TMS and Vertex-TMS conditions, consistent with visual stimulation in the left visual field. During the later window (436-536 ms), right frontal power peaked in the rFEF-TMS condition, whereas power increases in the Vertex-TMS condition were localized near electrode Cz and did not reach statistical significance (Fig. 2b; permutation tests, see Methods section).

Importantly, the visually-evoked theta cluster fell outside the time-frequency cone of influence surrounding the TMS pulses confirming that it is not an artifact of the wavelet convolution. This cluster showed a clear temporal separation between visually-evoked and TMS-evoked activity; indicating the high temporal resolution of our time-frequency decomposition. Consistent with this interpretation, only the TMS-evoked activity exhibited systematic temporal shifts across TMS latencies, whereas visually-evoked theta power remained stable in both timing and magnitude across TMS latencies and stimulation conditions (Supplementary Fig. S1).

Direct comparison between conditions using cluster-based permutation testing further demonstrated significantly greater low-frequency power in the rFEF-TMS condition relative to the Vertex-TMS condition. These results demonstrate that TMS preferentially enhances theta-band activity, particularly following rFEF stimulation, providing a frequency-specific context for the subsequent observation of TMS-induced theta traveling waves.

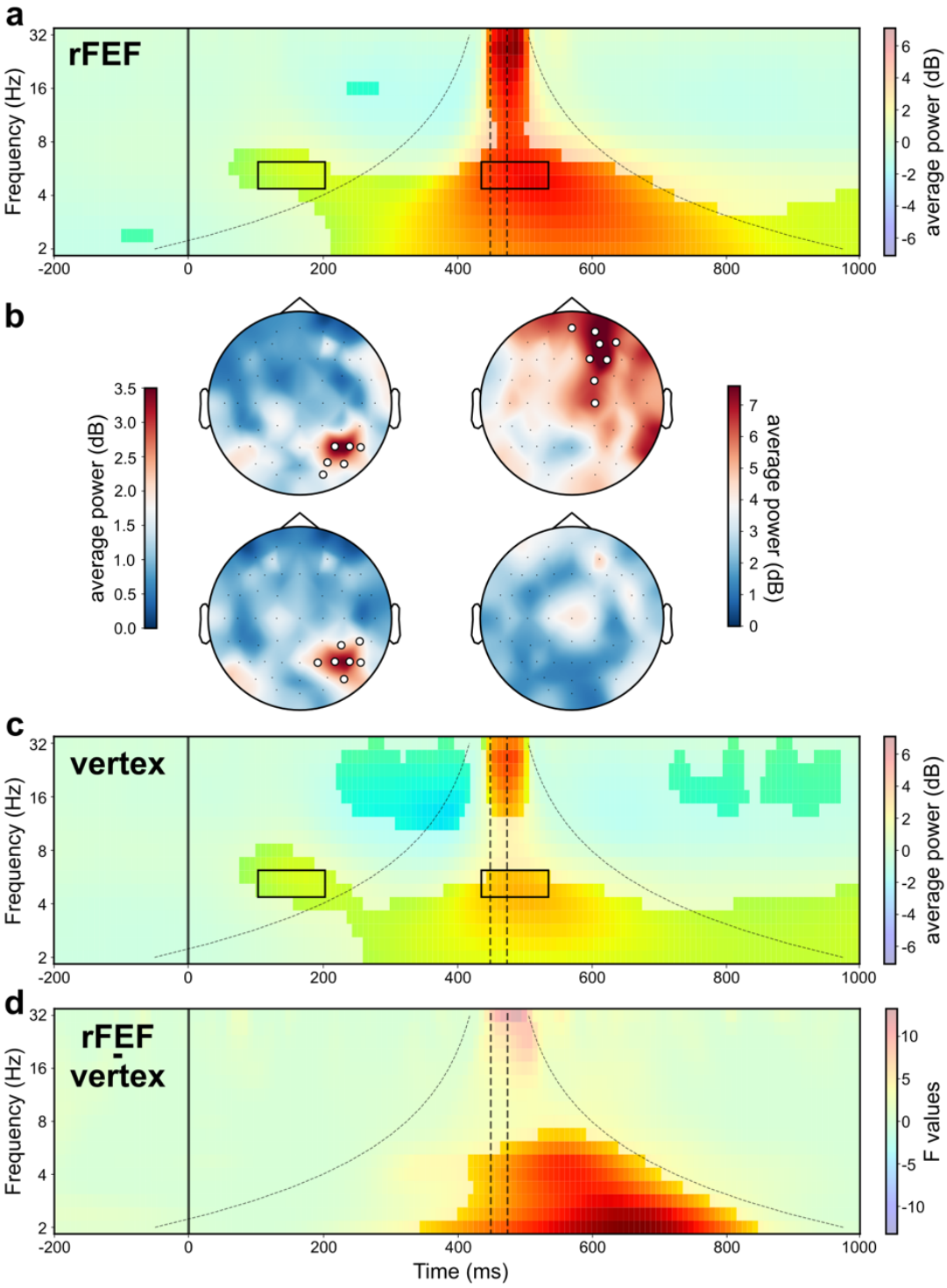

Fig. 2 Theta-band power is selectively enhanced following TMS. a Grand-average time-frequency power (across trials and sensors) in the rFEF-TMS condition. The solid black line marks search array onset; dashed vertical lines indicate TMS single-pulse onsets. The cone of influence is overlayed (area potentially impacted by artifactual spread of the TMS-evoked activity). Non-transparent regions denote significant clusters identified by permutation testing. **b** Scalp topographies averaged over the time-frequency windows outlined by black boxes in **a** (top row) and **c** (bottom row). Left column shows activity averaged over 104-204 ms; right column shows activity averaged over 436-536 ms. Black circles outline electrodes within clusters of significant positive difference to zero (permutation testing). **c** Same as **a**, but for the Vertex-TMS (control) condition. **d** Power differences between rFEF-TMS and Vertex-TMS conditions, expressed as F values.

Global traveling waves dominate EEG dynamics

To directly test our hypothesis, we first determined whether long-range cortical traveling waves constitute a dominant component of EEG dynamics in the context of concurrent TMS-EEG experiments. To this end, global traveling wave components were empirically extracted for each participant using an SVD-based approach.

Across participants, the first four spatial basis vectors explaining the largest proportion of variance consistently exhibited a low spatial frequency corresponding to approximately one cycle across the measurement array. Subsequent basis vectors showed higher spatial frequencies and explained substantially less variance. After projecting the low-frequency basis vectors onto interpretable cardinal axes, three global traveling wave components were identified, corresponding to anterior-posterior, inferior-superior, and left-right directions of propagation (Fig. 3a; see examples in Supplementary Fig. S2).

The proportion of variance explained by each component is shown in Fig. 3b. The anterior-posterior component accounted for the largest share of variance, followed by the left-right component. Low spatial-frequency global traveling waves account for the majority of EEG variance (58.13-69.76 %) and thus dominate cortical dynamics during concurrent TMS-EEG recordings. Notably, the summed variance explained by these three axes slightly exceeded 100 %, as the projection procedure renders the components marginally non-orthogonal.

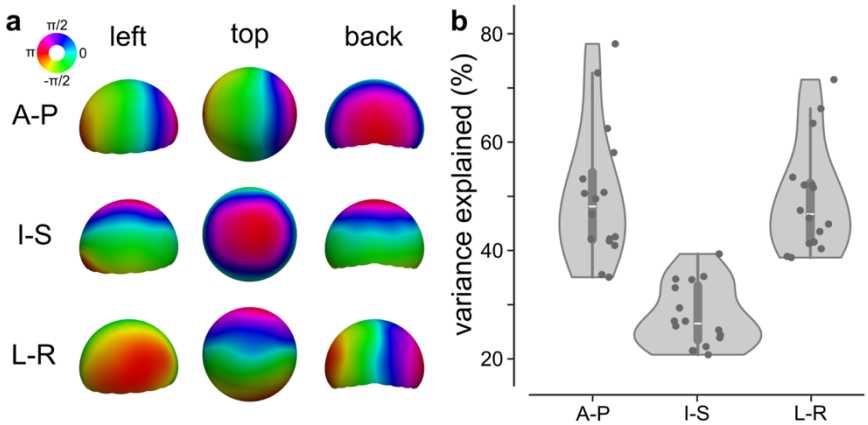

Fig. 3 Global traveling waves dominate EEG dynamics. a Global traveling wave components projected onto cardinal axes (collapsed for participants). **b** Variance explained by each global traveling wave component after cardinal transformation across individual participants. A-P: anterior-posterior; I-S: inferior-superior; L-R: left-right.

TMS transiently disrupts global wave activity

To assess the effect of TMS on ongoing traveling waves, single trials were realigned to TMS onset, and global wave activity –defined as the fit of the model wave to the relative phases – was computed as a function of time and frequency. Permutation testing revealed a significant transient reduction in global wave activity time-locked to TMS onset in both the rFEF-TMS (Fig. 4a) and Vertex-TMS conditions (Fig. 4b). This disruption was temporally specific to the TMS pulses, as evidenced by its systematic temporal shift across different TMS latencies (Supplementary Fig. S3), indicating that the observed effect reflects TMS-induced disruption of ongoing wave dynamics rather than task-related or spontaneous fluctuations.

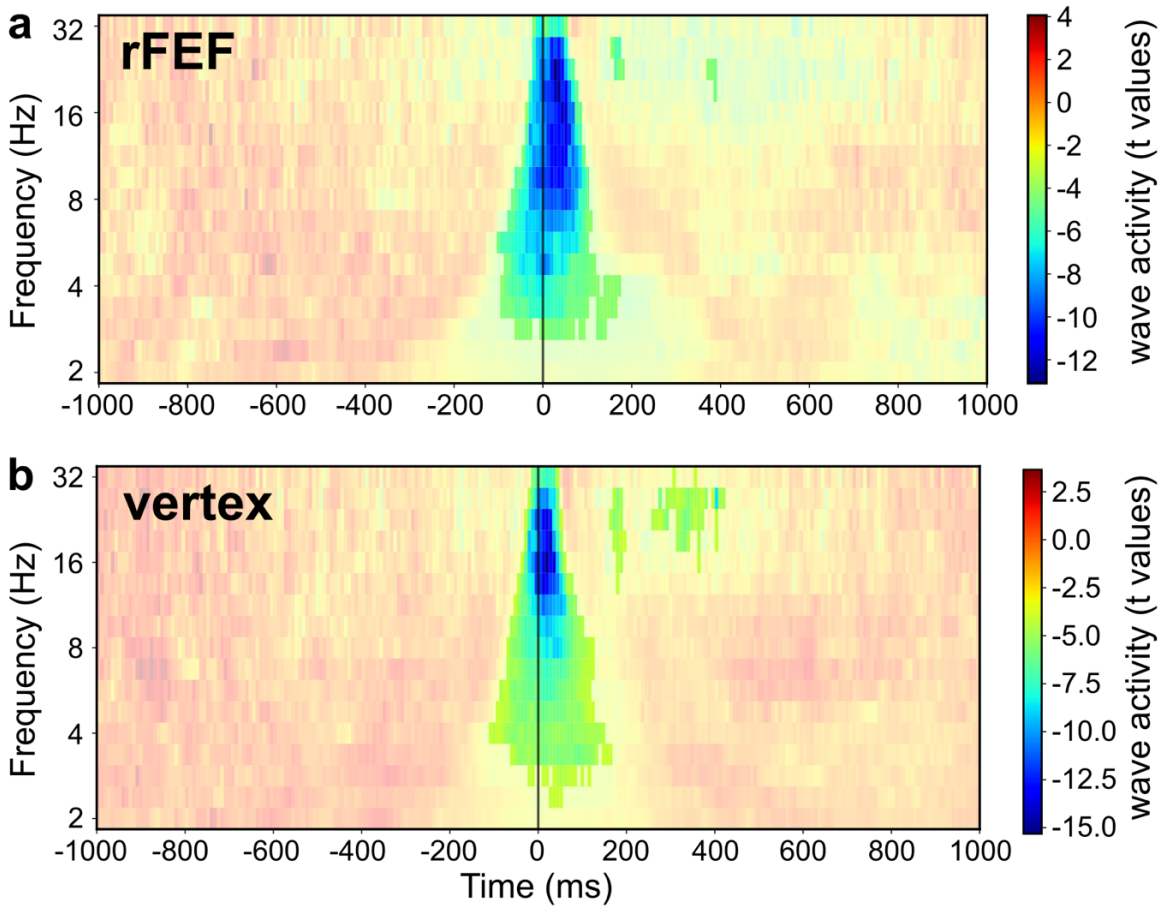

Fig. 4 TMS transiently disrupts global wave activity. a Global traveling wave activity (t values) across time and frequency in the rFEF-TMS condition. The solid black line marks TMS onset (first pulse). Non-transparent regions indicate significant clusters identified by permutation testing. **b** Same as **a**, but for the Vertex-TMS condition.

rFEF-TMS selectively induces anterior-to-posterior theta traveling waves

Based on our *a priori* hypothesis on anterior-to-posterior traveling waves, we specifically extracted traveling waves propagating from anterior to posterior direction across time and frequency. Despite the transient disruption of ongoing global traveling waves by TMS, stimulation of the rFEF led to a robust increase in anterior-to-posterior traveling wave activity in the theta frequency range (Fig. 5a). In contrast, vertex stimulation produced a more confined increase in anterior-to-posterior wave activity that was largely restricted to the immediate post-TMS period (Fig. 5b). Comparison between conditions revealed a significant cluster of enhanced anterior-to-posterior theta traveling wave activity following rFEF stimulation, centered in the theta band (4.0–5.7 Hz) and spanning approximately 60–220 ms after stimulation (Fig. 5c; cluster-based permutation test, $p < 0.05$). Together, these results demonstrate that TMS applied over the rFEF selectively induces theta-band traveling waves propagating along the anterior-to-posterior direction, presumably from the rFEF to occipital visual regions, beyond nonspecific effects of TMS on overall wave activity.

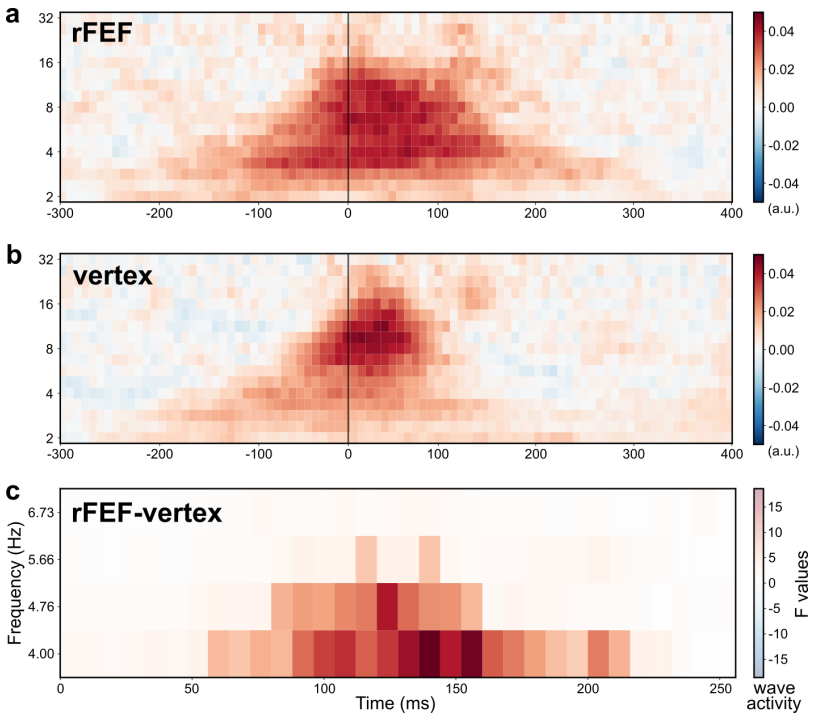

Fig. 5 rFEF-TMS selectively induces anterior-to-posterior theta traveling waves. a Anterior-to-posterior traveling wave activity across time and frequency in the rFEF-TMS condition. The solid black line marks TMS onset (first pulse). **b** Same as **a**, but for the Vertex-TMS condition. **c** Differences in anterior-to-posterior traveling wave activity between rFEF-TMS and Vertex-TMS conditions, expressed in F values. Non-transparent regions indicate significant clusters identified by permutation testing.

rFEF-TMS modulates theta traveling waves periodically at 6.7 Hz

Previous work has demonstrated that TMS over the rFEF periodically modulates attentional search performance (measured as dprime) as a function of stimulation latency (Dugué et al., 2019). We thus examined anterior-to-posterior theta traveling waves as a function of TMS latency and compared the results with our previous behavioral observations under the same condition (Dugué et al., 2019) to assess the causal functional role of TMS-induced theta traveling waves in attentional search.

Wave activity was first averaged within the previously identified significant cluster between 60-220 ms (Fig. 5c) for each TMS latency and condition. Two-way repeated-measure ANOVAs showed a significant main effect of TMS latency ($F(8) = 2.376$, $p = 0.021$), a significant main effect of TMS condition ($F(1) = 12.246$, $p = 0.003$), and a significant interaction between TMS latency and condition ($F(8) = 2.058$, $p = 0.045$). This result indicates that anterior-to-posterior theta wave activity varies as a function of TMS latency, and that this effect is different between stimulations of the rFEF and the Vertex.

Wave activity differences (rFEF-TMS minus Vertex-TMS) were then plotted as a function of TMS latency (Fig. 6a). Spectral analysis using Fast Fourier Transform revealed a significant peak at 6.7 Hz, indicating that TMS-induced anterior-to-posterior theta traveling waves are periodically modulated at this frequency (Fig. 6b). This modulation falls within the theta band and matches the periodicity previously reported for TMS effects on behavioral performance (Fig. 6a; note that more noise is expected in early latencies due to masking effects). Critically, the 6.7 Hz modulation was in phase across participants (Fig. 6b; Rayleigh test for circular data showed significant non-uniform distribution: $Z = 6.1$, $p = 0.001$).

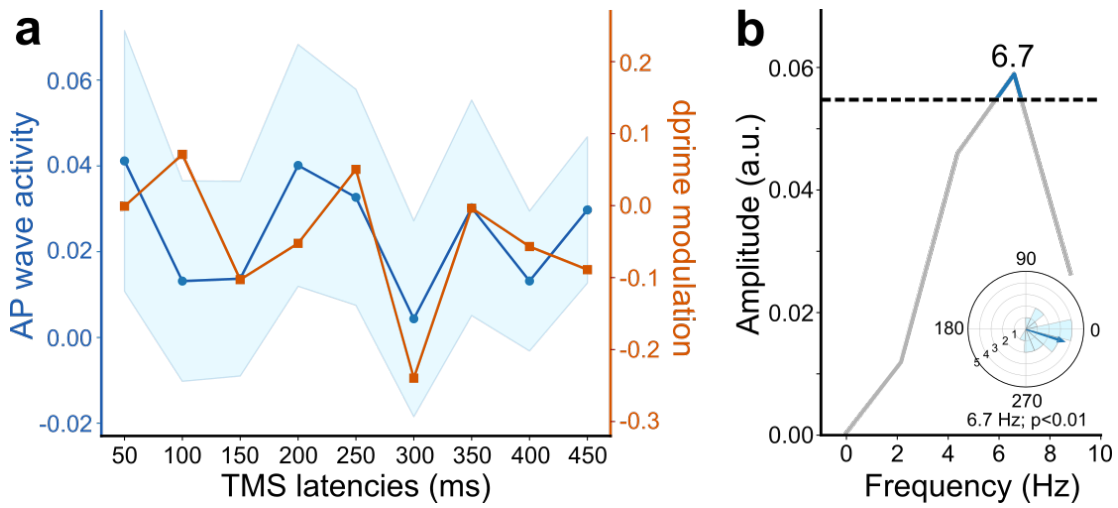

Fig. 6 rFEF-TMS modulates theta traveling waves periodically at 6.7 Hz. a Both anterior-to-posterior wave activity (blue lines) and dprime modulation (orange lines) are represented as a function of TMS latencies from the search array onset. Shaded area indicates 95% confidence interval. **b** Amplitude spectrum obtained from FFT of averaged anterior-to-posterior wave activity. Dashed line marks statistical threshold (p = 0.05) from permutation test. Polar histogram of individual participant phases (light bins) and their average (blue arrow) at the peak frequency (6.7 Hz).

Discussion

This study investigated the causal functional role of global traveling waves in inter-areal communication during visual attention. By applying double-pulse TMS over the rFEF at multiple latencies in a difficult attentional search task while recording EEG, we show that TMS pulses transiently interrupt ongoing global wave dynamics and selectively induce direction- and frequency-specific traveling waves. Critically, rFEF stimulation elicits anterior-to-posterior theta traveling waves that are rhythmically modulated as a function of TMS latency during the task, consistent with rhythmic fluctuations in attentional search performance.

Cortical traveling waves have been linked to cognitive functions, including visual attention (for review Muller et al., 2018; Dugué & Chavane, 2025). Specifically, a recent EEG study observed that during the allocation of spatial attention, alpha-band traveling waves propagate more from frontal to occipital electrodes than in the opposite direction along the same path (Alamia et al., 2023). To date, this remains the only study explicitly correlating visual attention with traveling waves. Recently, neural stimulation studies have demonstrated that external perturbations can evoke or modulate propagating activity patterns in the cortex (Wei et al., 2024; Campbell et

al., 2025). However, they have not established a causal link between traveling waves and cognition. Our results show that TMS can causally induce large-scale traveling waves that predict behavioral performance, providing direct evidence that traveling waves can have a causal functional role in attention.

Importantly, the traveling waves observed here are unlikely to reflect purely local activity generated at the stimulation site. Indeed, authors have raised concerns regarding the interpretability of apparent traveling waves observed in non-invasive recordings (for review Dugué & Chavane, 2025). A recent study analyzed the spatial-frequency spectrum of gray-matter activity in intra-cranial EEG recordings and demonstrated that low spatial frequencies dominate cortical dynamics (Alexander & Dugué, 2024). This argues against explanations based exclusively on localized sources or standing waves (Orsher et al., 2023; Zhigalov & Jensen, 2023). Instead, these results support the presence of large-scale traveling waves measurable at the scalp level, consistent with the present interpretation of global traveling waves coordinating inter-areal communication in visual attention.

Here, TMS was applied over the rFEF, which constrained the point of origin of the induced anterior-to-posterior traveling waves to that cortical region. The rFEF has long been shown to play a critical role in the attention network (for review Corbetta & Shulman, 2002; Corbetta et al., 2008) and be causally linked to endogenous attention (Fernandez et al., 2023). Stimulation of rFEF not only affects behavioral performance in visual attention tasks but also alters neural excitability and evoked responses in visual cortex (Taylor et al., 2007; Dugué et al., 2019; Veniero et al., 2021). This is consistent with other studies showing that the visual cortex is causally involved in such attentional tasks (Dugué et al., 2011; 2015). Although our analysis pipeline does not directly determine the ending site of the traveling waves, the anterior-to-posterior propagation observed here suggests that TMS-induced traveling waves propagate toward occipital visual areas. Future studies will test this hypothesis by probing the endpoint of waves, for example by combining the present TMS-EEG approach with a second TMS coil targeting the visual cortex.

Our findings are consistent with established theories of visual attention. Visual search has been postulated as a two-stage process involving feature extraction and attentional selection, supported by iterative communication between early visual areas and higher-order regions (Palmer et al., 1993; Treisman, 1998; Itti & Koch, 2001; Deco et al., 2002). Such exploratory behavior was more recently formalized in the rhythmic sampling theory of attention, which proposes that attention explores the sensory environment rhythmically (for review VanRullen, 2016; Fiebelkorn & Kastner, 2019; Kienitz et al., 2022). Numerous studies have reported theta-band fluctuations in behavioral performance and neural oscillations during attention tasks (VanRullen et al., 2007; Landau & Fries, 2012; Fiebelkorn et al., 2013, 2018; Song et al., 2014; Chota et al., 2018; Helfrich et al., 2018; Senoussi et al., 2019; Michel et al., 2022; Galas et al., 2025). Our observation of functionally relevant traveling waves within the same frequency range provides strong empirical support that theta traveling waves are the underlying neural substrates of rhythmic attentional sampling.

Several influential theories have been proposed to explain the neural mechanisms underlying inter-areal communication, e.g., binding-by-synchrony (Singer & Gray, 1995), communication-through-coherence (Bastos et al., 2015), gating-by-inhibition (Jensen & Mazaheri, 2010), nested oscillations (Bonnefond et al., 2017). While these theories account for key temporal characteristics of oscillatory activity across brain regions, they generally conceptualize brain oscillations as stationary or locally synchronized processes. Instead, the traveling wave perspective considers temporal changes of global patterns of activity over areas of cortex, here large-scale cortex accessible via EEG. Our findings argue in favor of traveling waves supporting inter-areal communication, and are consistent with the latest proposal (Dugué & Chavane, 2025) that they constitute a canonical computation underlying diverse brain functions.

Methods

All data were originally collected as part of a previously published study, for which the behavioral results along with a detailed description of the experimental protocol have been published by Dugué et al. (2019). Here, we analyzed the EEG data and describe only the relevant materials and methods.

Participants

Twenty-three participants (7 women, age range: 24-38 years) with normal or corrected-to-normal vision participated in the experiment. Two did not complete the experiment due to discomfort during stimulation, and the EEG could not be recorded for five other participants for technical reasons. The EEG data from 16 participants were included in the analysis. All participants met the inclusion criteria for TMS and provided written informed consent prior to participation. The study was conducted in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee (Sud-Ouest et Outre-Mer I; Protocol 2009-A01087-50).

Visual Search Task

Participants performed a difficult, attentional visual search task (Fig. 1a; same procedure as in Dugué et al., 2011; Dugué et al., 2015). Visual stimuli were displayed on a screen (36.5 × 27 degree of visual angle, °VA) positioned 57 cm from the participant in a dark room. On each trial, four stimuli of identical size (1.5 × 1.5°VA) were presented at a fixed eccentricity (6°VA) in the left visual field. The stimulus array consisted either of four distractors ('L's; target absent trials) or of three distractors and one target randomly in one of the four stimulus locations ('T'; target present trials). All items were randomly oriented (0, 90, 180, or 270° from upright).

After an individually determined stimulus-onset asynchrony (SOA; one-up-two-down staircase) to achieve approximately 70% correct performance (mean ± standard deviation: 85 ± 8 ms), the search array was masked, such that the total duration of visual stimulation was 500 ms.

312 Participants were instructed to report the absence or presence of target 'T' by key press, with
313 an emphasis on accuracy and no time pressure. The intertrial interval (ITI) was jittered between
314 1000 and 2000 ms to minimize cumulative effects of stimulation. Participants completed 26
315 blocks of 72 trials each, including one practice block, one staircase block, four blocks without
316 TMS, ten blocks with TMS applied over the rFEF (rFEF-TMS) and ten control blocks with TMS
317 applied over the Vertex (Vertex-TMS). The present study focuses the analyses on the rFEF-
318 TMS and Vertex-TMS blocks.

319 **TMS procedure**

320 TMS pulses were delivered using a Magstim Rapid^2 stimulator (biphasic; Magstim Company,
321 Whitland, UK) equipped with a 70-mm figure-of-eight coil. Stimulation was remotely triggered
322 via Matlab R2014 from the stimulus presentation computer (Mathworks Inc., Natick, MA).
323 Stimulation intensity was initially set at 50% of maximal output and individually adjusted to just
324 below the threshold for facial and temporal muscle activation (mean ± standard error to the
325 mean: 52 ± 2%). The coil was positioned tangentially to the scalp, with its handle oriented
326 about 45° backward and laterally.

327 The stimulation target over the rFEF was defined based on averaged Talairach coordinates (x
328 = 31, y = −2, z = 47). For 11 participants, coil positioning was guided by individual T1-weighted
329 anatomical MRIs (3T Philips) using these coordinates. For the remaining participants, for
330 whom anatomical MRI scans were not available, the stimulation site was defined as the
331 barycenter (between electrodes F2 and FC4) of the rFEF locations identified in the MRI-guided
332 participants. To control for nonspecific TMS effects (i.e., clicking noise and tapping sensation),
333 TMS was also applied over the vertex as the control condition (block-designed,
334 counterbalanced), which was individually defined as the location of electrode Cz (O'Shea et
335 al., 2004).

Double-pulse TMS (inter-pulse interval: 25 ms) was delivered at one of nine possible latencies relative to search array onset (50-450 ms, in 50-ms increments). Double-pulse TMS was used instead of single-pulse stimulation because paired pulses have been shown to produce stronger and more reliable behavioral effects, particularly in visual search (Juan & Walsh, 2003; Kalla et al., 2008; Dugué et al., 2011, 2015; Yan et al., 2016).

EEG recording and pre-processing

EEG data were recorded using a TMS-compatible 64-channel EEG cap (standard antiCAP snap; 10–20 system; EasyCap GmbH, Herrsching, Germany). Electrodes Fpz and FCz served as ground and reference, respectively. Signals were sampled at 5000 Hz and acquired with an online low-pass filter at 1000 Hz.

EEG data were preprocessed using custom scripts in combination with the MNE-Python toolbox (Gramfort et al., 2013), following recommendations from the TESA pipeline for TMS-EEG analysis (Rogasch et al., 2017). TMS-related artifacts in the raw EEG time series were removed (-1 to 15 ms relative to each pulse) and replaced using cubic interpolation based on five samples (1 ms) on each side of the interpolated window. Bad channels were identified by visual inspection and interpolated using MNE-Python's spline interpolation. Data were then lowpass filtered at 330 Hz (finite impulse response, FIR, Hamming window) and down-sampled to 1000 Hz.

Continuous data were epoched from -2 to 5 s relative to search array onset, followed by manual rejection of bad epochs. To remove large-amplitude artifacts (i.e., TMS-evoked muscle artifacts), independent component analysis (FastICA, 15 components) was performed on concatenated runs separately for rFEF-TMS and Vertex-TMS conditions. Cubic interpolation around TMS pulses was then applied again using the same parameters. After high-pass filtering at 0.1 Hz (FIR, Hamming window), a second ICA was performed to remove residual

artifacts (i.e., blinks, eye movements, and muscle activity). Cubic interpolation around TMS pulses was subsequently applied once more.

Finally, EEG data were re-referenced to the common average. Channels TP9, TP10 and Iz were excluded due to their distance from the remaining electrodes leaving a total of 59 electrodes for the analysis. To equalize trial counts across conditions and participants, analyses were restricted to the first 400 trials for each of the rFEF-TMS and Vertex-TMS conditions.

Time frequency decomposition

Time-frequency representations were computed using Morlet wavelet convolution. Phase and amplitude were estimated using two-cycle Morlet wavelets at 17 logarithmically spaced center frequencies ranging from 2 to 32 Hz. To reduce computational load, the resulting time-series of phase and power were down-sampled by a factor of eight.

Grand-average power was first computed by averaging across all 59 electrodes and trials. Power values were then normalized into decibels relative to a pre-stimulus baseline (−1000 to −600 ms from search array onset). Significant clusters of induced power against baseline activity were identified using a cluster-based permutation test (5000 permutations, two-tailed), with a cluster-forming threshold of $p = 0.001$ and a cluster-level significance threshold of $p = 0.05$. Differences in induced power between the rFEF-TMS and Vertex-TMS conditions were assessed using cluster-based permutation test (5000 permutations, two-tailed, cluster-level $p = 0.05$).

Topographic maps of induced power (decibel-normalized) were computed by averaging power within selected time-frequency windows defined from the grand-average data. Peak frequencies were identified from power spectra averaged across time, and for each frequency, a 100-ms time window centered on the peak latency was selected (outlined in Fig. 2a and 2c). After within-participant topographic normalization, significant power increase was identified

using threshold-free cluster enhancement permutation tests (5000 permutations, one-tailed, $p = 0.05$).

Traveling Wave Analysis

Cortical traveling waves were analyzed in single-trial EEG data using an SVD-based approach (Alexander et al., 2013). Complex-valued phase estimates (Φ) obtained from wavelet convolution were first converted, at each sample (time × frequency × trial × sensor), into real-valued relative phases (Ψ) by computing nearest-neighbor phase differences across the electrode array and then reintegrating these differences in radians. Specifically, for neighboring electrodes *i* and *j* (determined by Delaunay triangulation), their phase difference was defined as:

$$\Delta\theta_{ij} = \arg(\Phi_i) - \arg(\Phi_j) + 2\pi k_{ij},\ k_{ij} \in Z, \qquad (1)$$

with integer k_{ij} chosen such that $\Delta\theta_{ij} \in [-\pi, \pi)$. The relative phase ($\Psi$) at each electrode was then reconstructed by cumulatively adding these nearest-neighbor differences ($\Delta\theta$) according to:

$$\Psi i = \Psi j + \Delta\theta_{ij} \quad (2)$$

starting from an arbitrary reference electrode. These nearest-neighbor phase differences were sequentially integrated into an initially edgeless graph, in ascending order of $|\Delta\theta_{ij}|$. When the condition $|\Delta\theta_{ij}| << \pi$ is not satisfied everywhere, inconsistencies may arise such that $\Psi i - \Psi j = \delta\Phi ij + 2k\pi$ for some integer $k \neq 0$. In data where phase varies smoothly across electrodes, the number of such inconsistencies is small relative to the total number of nearest neighbors. These inconsistencies may reflect either genuine phase discontinuities or measurement noise (Spagnolini, 1995). Integrating phase differences by increasing $|\Delta\theta_{ij}|$ preferentially localizes such errors to regions exhibiting the largest phase differences, corresponding to legitimate discontinuities or elevated noise.

At the single-participant level, SVD was applied to the relative phase data to reduce dimensionality and extract dominant spatial patterns of phase dynamics across the scalp. For each participant, relative phase values were arranged into a matrix $A \in R^{Ne \times Ns}$, where N_e denotes the number of electrodes and N_s the number of samples collapsed across time, frequency, trial, and TMS condition. The matrix A was decomposed by SVD as

$$A = U\Sigma V^T, \qquad (3)$$

where U contains the left singular vectors (LSVs), Σ is a diagonal matrix of singular values σ_r ordered in descending magnitude, and V contains the right singular vectors. The LSVs represent orthogonal spatial basis vectors that capture dominant phase gradients across the electrode array, while the corresponding singular values σ quantify the proportion of the variance explained by each component. By definition, these empirically-derived components are orthogonal and can be treated as independent modes of the system; thus, weighted linear combinations of the LSVs can recover the original phase data without loss.

Components were retained in order of explained variance, with the first three to four components typically corresponding to spatial frequencies of approximately one cycle across the electrode array. These participant-specific basis vectors, referred to as *wave maps*, represent global traveling wave components, each corresponding to an orthogonal direction of phase propagation across the scalp. Linear combinations of these wave maps reconstitute all possible global TW components.

To facilitate interpretation and comparison across participants, the basis vectors were projected onto a common set of axes defined by electrode coordinates in three Cartesian dimensions (anterior-posterior, inferior-superior, and left-right; Fig. 3a). This procedure effectively rotates each individual's wave maps to a shared cardinal reference frame, enabling direct cross-participant comparison. Prior to projection, phase values were normalized according to:

$$C_{norm} = (C_{x,y,z} - \min(C_{x,y,z})) / (\max(C_{x,y,z}) - \min(C_{x,y,z})) * R_{mean}, \quad (4)$$

where $C_{x,y,z}$ denotes the phase values expressed in electrode coordinate space and R_{mean} defines the mean range of the retained basis vectors. Projection coefficients were then computed as

$$\beta = U_R^T C_{norm}, \quad (5)$$

where U_R contains the first R basis vectors obtained from SVD, with R determined by the number of global traveling wave components retained (here R = 4, corresponding to approximately one spatial cycle across the electrode array). Reconstructed phase dynamics were obtained as:

$$C_{rec} = U_R \beta, \quad (6)$$

yielding sample-by-sample estimates of wave activity, aggregated across all bases (global *wave activity*; Fig. 4) or, for direction specific measures restricted to individual cardinal bases (i.e., anterior-to-posterior waves; Fig. 5).

Single-trial global wave activity was re-aligned to TMS onset and averaged across trials, followed by baseline correction using a pre-TMS interval (−1000 to −600 ms). For each condition, significant modulations of wave activity were assessed using two-tailed cluster-based permutation tests (5000 permutations), with a cluster-forming threshold of p = 0.001 and a cluster-level significance threshold of p = 0.05.

TMS-related anterior-to-posterior wave activity was then compared between the rFEF-TMS and Vertex-TMS conditions using cluster-based permutation testing (5000 permutations, two-tailed, p = 0.05). Statistical testing was restricted to a pre-defined time-frequency window (4-7 Hz, 0-250 ms relative to TMS onset). The theta frequency band was selected based on the *a priori* hypothesis that theta traveling waves have a causal functional role in attentional search;

the temporal window was chosen based on previous time-frequency analyses showing maximal grand-average power in this interval (Fig. 2a and 2c).

To characterize the periodic modulation of TMS on anterior-to-posterior traveling waves, wave activity was averaged within the significant cluster identified above, and differences between rFEF-TMS and Vertex-TMS conditions were computed as a function of TMS latency. Periodicity was assessed by applying a fast Fourier transform (FFT) to the detrended time series (Kienitz et al., 2022). Statistical significance at each frequency was evaluated using a bootstrapping procedure. Specifically, TMS latency labels were randomly permuted within participants (100,000 iterations). For each surrogate spectrum, the maximum amplitude across frequencies was retained to correct for multiple comparisons. The empirical spectrum was considered significant if it exceeded the 95th percentile of the surrogate distribution ($p < 0.05$). Finally, for the frequency showing a significant amplitude peak, phase values were extracted for each participant to verify that the observed periodicity was in phase across participants, and the circular distribution of these phases was assessed using a Rayleigh test for non-uniformity.

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Author contributions

L.D. and Y.K. designed the research. Y.K. and D.M.A. performed the analysis of the data. Y.K., D.M.A. and L.D. interpreted the data. Y.K. wrote the first version of the manuscript. All authors revised and edited subsequent versions of the manuscript.

Declaration of interests

The authors declare no competing interests.

Data and code availability

All data and analysis code will be made publicly available upon acceptance of the manuscript. The MEG_Chicken toolbox (https://github.com/DugueLab/MEG_Chicken) was used by the first author as a training program for artifact detection (combined with training from the senior authors).

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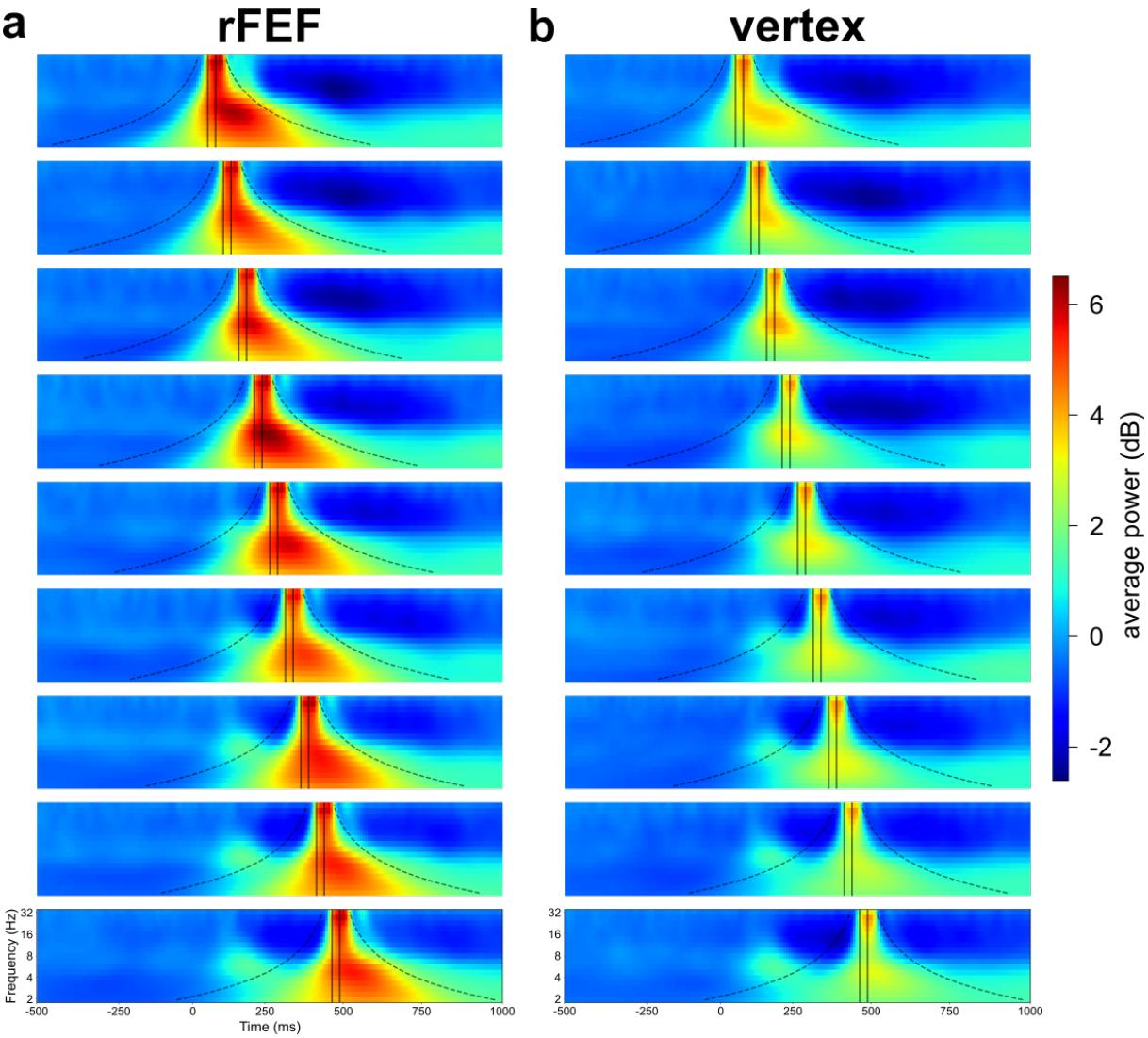
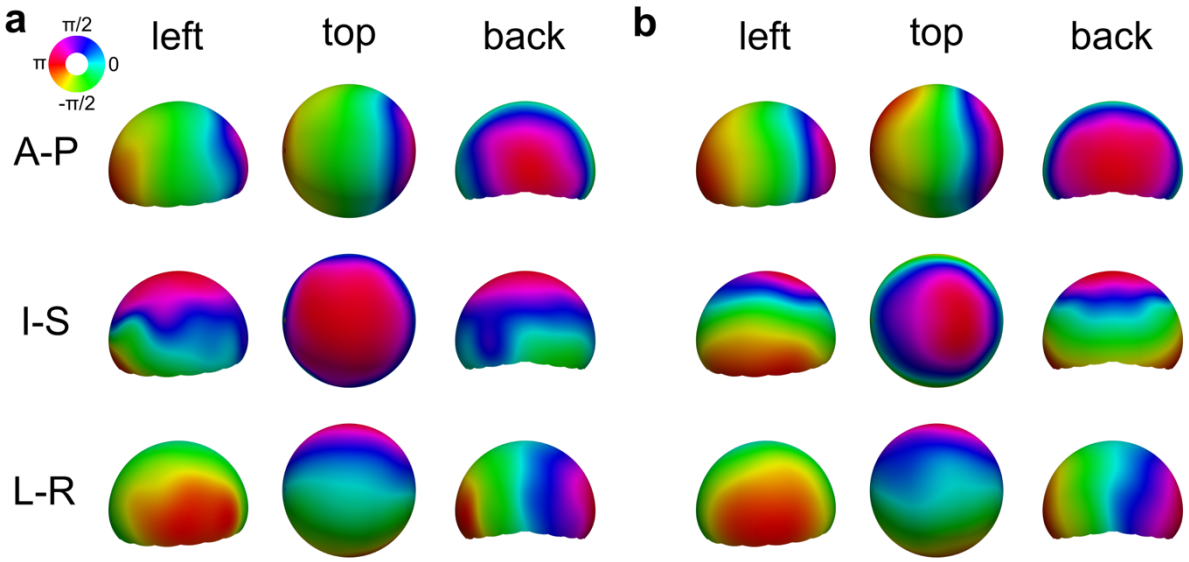
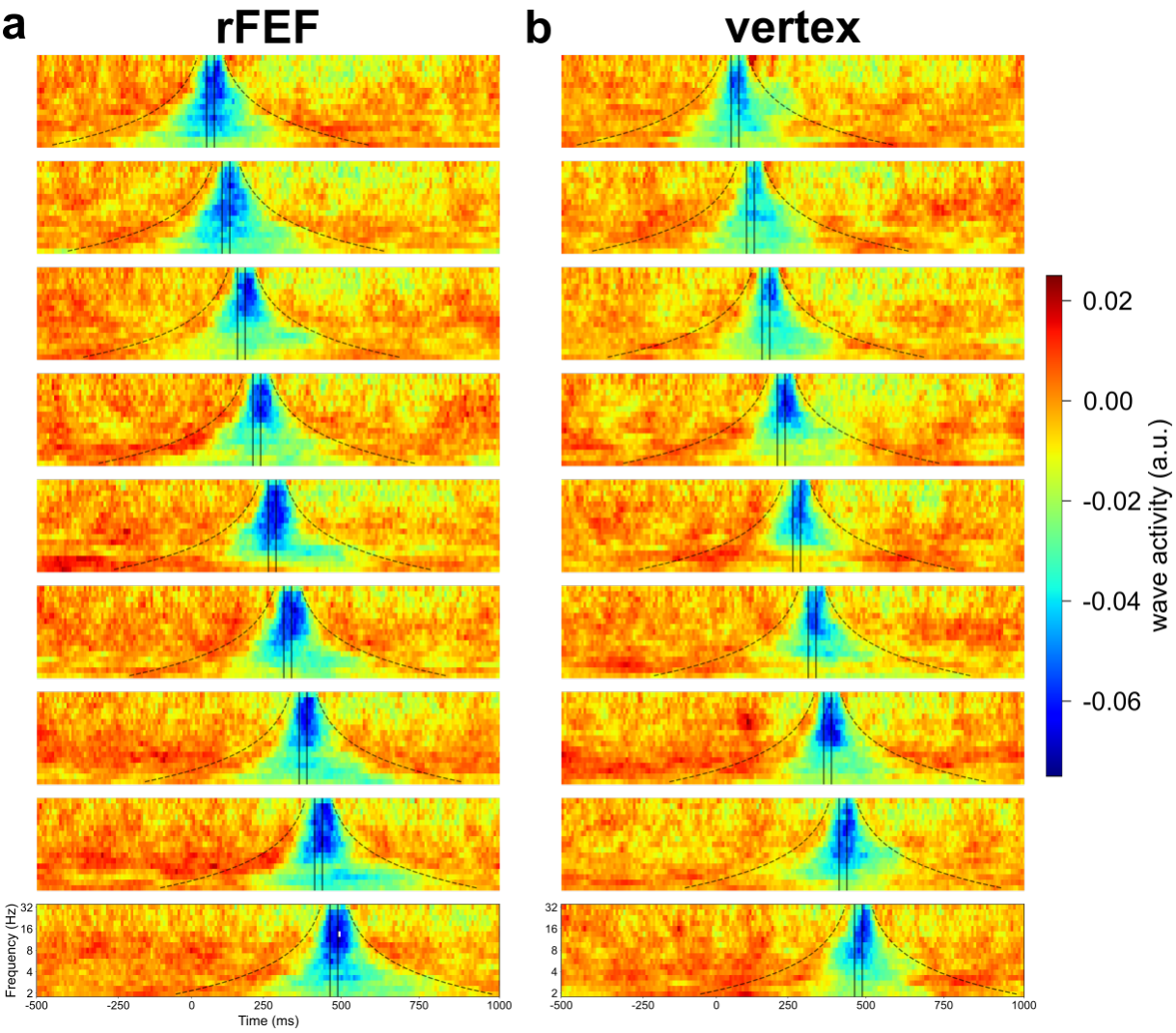
Supplementary Information



Supplementary Fig. 1 TMS-evoked power systematically shifts across TMS latencies. a Grand-average time-frequency power (across participants, trials and sensors) in the rFEF-TMS condition. The solid black line marks search array onset. Dashed vertical lines indicate single-pulse TMS onsets. The cone of influence is overlayed (area potentially impacted by artifactual spread of the TMS-evoked activity). Only the TMS-evoked activity exhibited systematic temporal shifts across TMS latencies, whereas visually-evoked theta power (around 100-200ms) remained stable in both timing and magnitude across TMS latencies and stimulation conditions. **b** Same as **a**, but for the Vertex-TMS (control) condition.



Supplementary Fig. 2 Global traveling waves components for two example participants. **a** Global traveling wave components projected onto cardinal axes for an example participant. A-P: anterior-posterior; I-S: inferior-superior; L-R: left-right. **b** Same as **a**, for another example participant.



Supplementary Fig. 3 Disruption of global wave activity shifts across TMS latencies. a Global traveling wave activity across time and frequency in the rFEF-TMS condition. The solid black lines mark TMS pulse onsets. The cone of influence is overlayed. TMS transiently disrupts global wave activity, and this disruption is temporally specific to the TMS pulses, as evidenced by its systematic temporal shift across different TMS latencies. **b** Same as **a**, but for the Vertex-TMS condition.