



Published in final edited form as:

Neuroimage. 2020 August 15; 217: 116927. doi:10.1016/j.neuroimage.2020.116927.

Multi-spectral oscillatory dynamics serving directed and divided attention

Marie C. McCusker^{a,b}, Alex I. Wiesman^{a,b,c}, Mikki D. Schantell^{a,b}, Jacob A. Eastman^{a,b}, Tony W. Wilson^{a,b,c,*}

^aCenter for Magnetoencephalography, University of Nebraska Medical Center, Omaha, NE, USA

^bCognitive Neuroscience of Development & Aging (CoNDA) Center, University of Nebraska Medical Center, Omaha, NE, USA

^cDepartment of Neurological Sciences, University of Nebraska Medical Center, Omaha, NE, USA

Abstract

Attention-related amplification of neural representations of external stimuli has been well documented in the visual domain, however, research concerning the oscillatory dynamics of such directed attention is relatively sparse in humans. Specifically, it is unknown which spectrally-specific neural responses are mainly impacted by the direction and division of attention, as well as whether the effects of attention on these oscillations are spatially disparate. In this study, we use magnetoencephalography and a visual-somatosensory oddball task to investigate the whole-brain oscillatory dynamics of directed (Experiment 1; $N=26$) and divided (Experiment 2; $N=34$) visual attention. Sensor-level data were transformed into the time-frequency domain and significant responses from baseline were imaged using a frequency-resolved beamformer. We found that multi-spectral cortical oscillations were stronger when attention was sustained in the visual space and that these effects exhibited informative spatial distributions that differed by frequency. More specifically, we found stronger frontal theta (4–8 Hz), frontal and occipital alpha (8–14 Hz), occipital beta (16–22 Hz), and frontal gamma (74–84 Hz) responses when visual attention was sustained than when it was directed away from the visual domain. Similarly, in the divided attention condition, we observed stronger fronto-parietal theta activity and temporo-parietal alpha and beta oscillations when visual attention was sustained toward the visual stimuli than divided between the visual and somatosensory domains. Investigating how attentional gain is implemented in the human brain is essential for better understanding how this process is degraded in disease, and may provide useful targets for future therapies.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

*Corresponding author. Cognitive Neuroscience of Development & Aging (CoNDA) Center, University of Nebraska Medical Center, Omaha, NE, USA. twwilson@unmc.edu (T.W. Wilson).

CRedit authorship contribution statement

Marie C. McCusker: Conceptualization, Formal analysis, Writing - original draft, Visualization. **Alex I. Wiesman:** Conceptualization, Methodology, Software, Writing - review & editing, Visualization, Funding acquisition. **Mikki D. Schantell:** Investigation. **Jacob A. Eastman:** Investigation. **Tony W. Wilson:** Conceptualization, Methodology, Writing - review & editing, Visualization, Supervision, Funding acquisition.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2020.116927>.

Keywords

Theta; Alpha; MEG; Magnetoencephalography; Occipital; Prefrontal

1. Introduction

Our daily interactions with the external environment require us to focus on salient stimuli and stimulus features, interpret these salient components, and respond efficiently (Pashler, 1998). Two of the most important abilities supporting these attentional capacities are directed and divided attention. Directed attention is the ability to voluntarily focus neural resources on relevant sensory stimuli or domains in isolation (Moriarty, 2015), while divided attention is the ability to focus on multiple stimuli or domains in parallel (Iaconi, 2005; Najdowski et al., 2014). Previous literature supports that there are both overlapping and separate brain regions involved in these attentional processes. For instance, using fMRI, Nebel and colleagues (2006) reported prefrontal, limbic, and parietal involvement in simple directed visual attention tasks, while activation in these areas plus occipital and cerebellar cortices was observed in more cognitively demanding single modality divided visual attention tasks. Further, goal-directed, top-down control of visual attention is known to activate the dorsal frontoparietal network, which consists of the superior frontal and intraparietal cortices (Corbetta and Shulman, 2002). Additionally, many studies have reported enhanced neural activity in the sensory cortices corresponding to processing of the attended modality, along with suppressed activity in the sensory cortex of any unattended modality (Ciaramitaro et al., 2007; Crottaz-Herbette et al., 2004; Degerman et al., 2007; Johnson and Zatorre, 2005, 2006; Laurienti et al., 2002; Loose et al., 2003; Mittag et al., 2013; Salo et al., 2013; Serences and Yantis, 2007; Shomstein and Yantis, 2004). These findings, together with a host of studies using other methodologies and model systems, have led to a working neurophysiological theory of attention. This theory proposes that attention is an increase in the synchronized firing of neurons in the sensory cortices representing the attended stimuli to influence downstream cortical processing (Buschman and Kastner, 2015).

Many studies have also suggested that spectrally-defined neural oscillations reflect mechanisms of sensory processing across multiple modalities. Specifically, processing of visual and tactile targets is thought to be reflected by multiple oscillations: synchronized gamma-band power, which is related to enhanced stimulus perception (Bhattacharya et al., 2002; Keil and Senkowski, 2018; Senkowski et al., 2005), desynchronized alpha-band power over occipital cortices (Bauer et al., 2012), and desynchronized beta-band power over the somatosensory cortices and supramarginal gyri (Bauer et al., 2012; Göschl et al., 2014, 2015). Polysensory processing also interacts robustly with attention (Macaluso et al., 2016) and task demands (Auksztulewicz et al., 2017; Mégevand et al., 2013), which has resulted in numerous studies comparing the direction and division of attention within and across sensory modalities, revealing a common pattern. The division of attention between the auditory and visual domains activates similar brain regions as directed attention tasks in each modality, but the activation of these regions is significantly reduced when cognitive resources are divided between the two modalities (Castiello and Umiltà, 1990, 1992; Eriksen

and St. James, 1986; Hopfinger et al., 2000; Johnson and Zatorre, 2006; Loose et al., 2003; Müller et al., 2003a; Müller et al., 2003b; Salo et al., 2015; Shaw and Shaw, 1977), suggesting resource processing limitations (Alais et al., 2006; Klingberg, 1998; Mowbray, 1953; Pashler, 1994; Roland and Zilles, 1998; Welford, 1952). In addition to these decreased activations during divided attention, there is also generally concurrent activation in components of the dorsal frontoparietal attention network (Corbetta et al., 2008; Corbetta and Shulman, 2002; Fagioli and Macaluso, 2009, 2016; Hopfinger et al., 2000; Johnson et al., 2007; Johnson and Zatorre, 2006; Loose et al., 2003; Moissala et al., 2015; Nebel et al., 2006; Salo et al., 2015, 2017; Santangelo et al., 2010; Schubert and Szameitat, 2003; Stelzel et al., 2006; Vohn et al., 2007).

While the spatial and, to a lesser degree, spectral correlates of directed and divided attention have been widely studied, the neural dynamics supporting active processing in these regions are less understood. Neural oscillatory activity is thought to support a diverse array of neural computational functions both within and across cortical regions, and thereby may underlie numerous cognitive and behavioral processes (Basar et al., 2001; Bonnefond and Jensen, 2012; Klimesch, 1999; Musall et al., 2014; Proskovec et al., 2018a, 2019). Regarding visual attention, previous research using electroencephalography (EEG) and magnetoencephalography (MEG) has found alpha activity (7–13 Hz) to be central to inhibitory processing (Bonnefond and Jensen, 2012; Klimesch, 2012; McDermott et al., 2017; Proskovec et al., 2018a, 2019; van Dijk et al., 2008; Wiesman et al., 2018; Wiesman and Wilson, 2019), theta activity (3–7 Hz) to index early stimulus recognition and top-down modulatory feedback (Basar et al., 2001; Busch et al., 2009; Klimesch et al., 2005; Landau and Fries, 2012; Landau et al., 2015; Proskovec et al., 2018a; Verbruggen et al., 2010; Wiesman et al., 2017b), and gamma activity (>30 Hz) to represent and possibly bind fine-grained stimulus features (Edden et al., 2009; Fries et al., 2001; Muthukumaraswamy and Singh, 2013; Swettenham et al., 2009; Tallon-Baudry, 2009; Womelsdorf et al., 2006). Studies have also shown that inter-sensory attention reduces alpha and beta power responses to visual stimuli, as well as beta power in primary somatosensory cortex when attending to tactile stimuli (Pomper et al., 2015). Despite these studies focusing on multi-spectral neural responses in information processing, very little is known regarding the spectro-temporal neural dynamics of directed and divided attention. Specifically, it remains uncertain which oscillatory responses are preferentially affected by the direction and division of attentional resources in visual space.

In this study, we utilized MEG and a visual-somatosensory oddball task to investigate the neural oscillatory dynamics that support directed (Experiment 1; $N = 26$) and divided (Experiment 2; $N = 34$) visual attention. Neural responses to visual stimulation were identified in the time-frequency domain and imaged using a frequency-resolved beamformer. In accordance with previous research, we hypothesized that neural responses in visual cortices would be significantly reduced when attention was directed away from the visual stimulus or divided between sensory modalities compared to when attention was sustained (Alais et al., 2006; Castiello and Umiltà, 1990, 1992; Eriksen and St. James, 1986; Hopfinger et al., 2000; Johnson and Zatorre, 2006; Klingberg, 1998; Loose et al., 2003; Mowbray, 1953; Müller et al., 2003a; Müller et al., 2003b; Pashler, 1994; Roland and Zilles, 1998; Salo et al., 2015; Shaw and Shaw, 1977; Welford, 1952). In addition, we hypothesized

that this effect would be most robust in oscillatory rhythms commonly associated with the allocation of attentional resources to the visual space (e.g., the theta and alpha bands), and that these effects would extend across the brain and involve major attention networks.

2. Methods

2.1. Participants

Experiment 1 enrolled 26 healthy young adults ($M_{age} = 24.00$; $SD = 3.10$; range = 19–31), and Experiment 2 enrolled 34 healthy young adults ($M_{age} = 26.34$; $SD = 4.00$; range = 19–36). The two participant groups were not mutually exclusive (overlap $N = 20$), thus no direct statistical comparisons were made between experimental sessions. Exclusionary criteria included any medical illness affecting CNS function, neurological and/or psychiatric disorder, history of head trauma, nonremovable metal implant that would adversely affect data acquisition, and current substance abuse. All participants had normal or corrected-to-normal vision. Each participant provided written informed consent and was compensated for their time and travel. The Institutional Review Board at the University of Nebraska Medical Center reviewed and approved this study, and all protocols were in accordance with the Declaration of Helsinki.

2.2. Experimental paradigm

For MEG recording, participants were seated in a custom-made nonmagnetic chair within a magnetically shielded room, with their heads positioned within the sensor array. During recording, each participant completed a visual-somatosensory oddball paradigm (Fig. 1; Wiesman and Wilson, 2020). Stimuli from the two sensory modalities were presented in alternation. A small proportion of these stimuli from each modality were temporal “oddballs,” which were utilized to monitor behavior and ensure that attention was directed towards either sensory domain. The somatosensory stimulus consisted of a paired-pulse delivered using unilateral electrical stimulation applied to the median nerve of the left hand. Mild electrical stimulation was delivered using external cutaneous stimulators connected to a Digitimer DS7A constant-current stimulator system (Digitimer Limited, Letchworth Garden city, UK). Each electrical pulse was comprised of a 0.2 ms constant-current square wave set to ten percent above the motor threshold needed to elicit a subtle thumb twitch, and the same stimulation amplitude was used in both blocks for each participant. Each participant received 80 paired-pulse somatosensory stimulation trials at 500 ms inter-stimulation intervals and eight “oddball” trials at 1000 ms inter-stimulation intervals per block. The visual stimulus consisted of a black circle centered on the horizontal axis to the right of a centrally-presented fixation crosshair, which subtended a visual angle of 1.0201° . Each participant also received 80 visual trials with a duration of 500 ms and eight “oddball” visual trials with a duration of 1000 ms per block. Thus, participants received a total of 176 trials of sensory stimulation per block (88 somatosensory and 88 visual). The inter-modality interval (IMI) between somatosensory and visual stimuli was 2400 ± 200 ms. Custom visual stimuli were programmed in Matlab (Mathworks, Inc., Massachusetts, USA) using Psychophysics Toolbox Version 3 (Brainard, 1997) and back-projected onto a semi-translucent non-ferromagnetic screen at an approximate distance of 1.07 m, using a Panasonic PT-D7700U–K model DLP projector with a refresh rate of 60 Hz and a contrast ratio of 4000:1.

In Experiment 1, participants performed two blocks of the experiment, with the blocks differing only by the instructions given. In the “attend visual” block, participants responded only to the visual oddballs and ignored the task-irrelevant somatosensory stimuli. In the “attend somatosensory” block, participants responded only to the somatosensory oddballs and ignored the task-irrelevant visual stimuli. Importantly, participants were required to fixate their vision on the centrally-presented crosshair and keep their left arm still for the entirety of both blocks. The order of the presentation of these blocks was counterbalanced across participants. Participants responded to oddball stimuli by pressing a button with their right index finger on a MEG-compatible five-finger response pad, and responses were counted as correct if they occurred before the onset of the next trial. The total MEG recording lasted approximately 10 min per block for a total of ~20 min per participant.

In Experiment 2, participants completed the same visual-somatosensory oddball paradigm as Experiment 1, only differing by the task instructions given. In the “attend visual” block, participants responded only to the visual oddballs and ignored the task-irrelevant somatosensory stimuli. In the “attend both” block, participants divided their attention between sensory domains and responded to both the visual and somatosensory oddballs. Any participant who correctly identified the oddballs with an average accuracy of less than 60%, in either experiment, was excluded from further analyses.

2.3. MEG data acquisition

MEG data acquisition, structural coregistration, preprocessing, and sensor-/source-level analyses for both experiments followed a similar pipeline as a number of previous manuscripts from our laboratory (Kurz et al., 2017; Proskovec et al., 2018a; Spooner et al., 2018, 2019; Wiesman et al., 2017a; Wiesman and Wilson, 2019, 2020). All recordings took place in a one-layer magnetically-shielded room with active shielding engaged for environmental noise compensation. A 306-sensor Elekta/MEGIN MEG system (Helsinki, Finland), equipped with 204 planar gradiometers and 102 magnetometers, was used to sample neuromagnetic responses continuously at 1 kHz with an acquisition bandwidth of 0.1–330 Hz. Participants were monitored by a real-time audio-video feed from inside the shielded room during MEG data acquisition. Each MEG dataset was individually corrected for head motion and subjected to noise reduction using the signal space separation method with a temporal extension (MaxFilter v2.2; correlation limit: 0.950; correlation window duration: 6 s; Taulu and Simola, 2006). Only the gradiometer data was used in further analyses.

2.4. Structural MRI acquisition

T1-weighted structural MRI were acquired for coregistration with the MEG data. Three different scanners were used for collection of these MRIs, however, these images were only used for coregistration with MEG data, spatial normalization of functional MEG images into standardized space, and visualization of results. Therefore, minor differences in MRI acquisition and image quality would not be expected to affect our MEG results. In addition, all of our relevant analyses were within-subjects, which mitigates concerns about any results being driven by a systematic bias between acquisition parameters. Three directed attention (Experiment 1) and four divided attention (Experiment 2) participants were collected on a

Philips Achieva 3T X-series scanner (Philips Healthcare) with an eight-channel head coil using a 3D fast field echo sequence with the following parameters: TE = 3.70 ms, TR = 8.09 ms, field of view (FOV) = 240 mm; slice thickness = 1 mm with no gap, and in-plane resolution = 1.0 × 1.0 mm. Seventeen directed attention and nineteen divided attention images were acquired using a Siemens Skyra 3T scanner (Siemens Medical Solutions) with a 32-channel head coil and a MP-RAGE sequence with the following parameters: TR = 2400 ms; TE = 1.94 ms; flip angle = 8°; FOV = 256 mm; slice thickness = 1 mm (no gap), and voxel size = 1 × 1 × 1 mm. Eleven divided attention images were collected using a Siemens Prisma 3T scanner (Siemens Medical Solutions) with a 32-channel head coil and a MP-RAGE sequence with the following parameters: TR: 2300 ms; TE = 2.98 ms; flip angle = 9°; FOV = 256 mm; slice thickness = 1.00 mm; voxel size = 1 × 1 × 1 mm. Lastly, MRIs for six directed attention participants were not acquired, and their data was fitted to a template MRI using the scalp surface points in BESA MRI (Version 2.0), prior to source-space analysis. Importantly, coregistering to individual structural MRIs and to a template MRI have been shown to yield similar results (Holliday et al., 2003). These data were aligned in parallel to the anterior and posterior commissures and transformed into standardized space.

2.5. Structural MRI processing and MEG coregistration

Prior to MEG acquisition, four coils were attached to the participants' heads and localized, together with the three fiducial points and scalp surface, using a 3-D digitizer (Fastrak 3SF0002, Polhemus Navigator Sciences, Colchester, VT, USA). Once positioned in the MEG, the coils produced an electrical current with a unique frequency label and an accompanying measurable magnetic field, which allowed each coil to be localized in reference to the MEG instrument sensors throughout recording. Since coil locations were also known in head coordinates, all MEG measurements could be transformed into a common coordinate system. With this coordinate system, each participant's MEG data were co-registered with structural T1-weighted MRI data using BESA MRI (Version 2.0) prior to source-space analysis. Structural MRI data were aligned parallel to the anterior and posterior commissures and transformed into standardized space. Following source analysis (i.e., beamforming), each participant's 4.0 × 4.0 × 4.0 mm functional images were also transformed into standardized space using the transform that was previously applied to the structural MRI volume and spatially resampled.

2.6. MEG preprocessing, time-frequency transformation, and sensor-level statistics

Cardiac and blink artifacts were identified in the raw MEG data and removed with signal-space projection (SSP), which was subsequently accounted for during source reconstruction (Uusitalo and Ilmoniemi, 1997). Briefly, SSP can be used to model and remove the topography of such artifacts at the level of the sensor data, which helps ensure that they are removed effectively. The continuous magnetic time series was then filtered between 0.5 and 200 Hz, plus a 60 Hz notch filter, and divided into 2500 ms epochs, with the baseline extending from -500 to 0 ms prior to the onset of the visual stimuli. Given the focus and hypotheses of the study, all analyses only considered the visual "short" (i.e., 500 ms) trials and disregarded the visual oddball and all somatosensory trials. Epochs containing artifacts were rejected using a fixed threshold method, supplemented with visual inspection. Briefly, in MEG, the raw signal amplitude is strongly affected by the distance between the brain and

the MEG sensors, as the magnetic field strength falls off sharply as the distance from the current source increases. To account for this source of variance across participants, as well as other sources of variance, we used an individually-determined threshold based on the within-subject signal distribution for both amplitude and gradient to reject artifacts. Across all participants, the average amplitude threshold for rejecting artifacts in Experiment 1 was 1080.77 ($SD = 258.09$) fT and the average gradient threshold was 170.38 ($SD = 76.13$) fT/s. Across the group, an average of 74.87 ($SD = 0.41$) out of 80 possible trials per participant per block were used for further analysis in this experiment, including an average of 75.15 ($SD = 1.93$) out of 80 trials per participant in the attend visual block and an average of 74.58 ($SD = 2.34$) out of 80 trials per participant in the attend somatosensory block. For Experiment 2, the average amplitude threshold was 1144.53 ($SD = 270.20$) fT and the average gradient threshold was 183.91 ($SD = 71.73$) fT/s. Across the group, an average of 76.30 ($SD = 0.29$) out of 80 possible trials per participant per block were used for further analysis, including an average of 76.50 ($SD = 1.80$) out of 80 trials per participant in the attend visual block and an average of 76.09 ($SD = 1.91$) out of 80 trials per participant in the attend both block. Importantly, none of our comparisons were compromised by differences in the number of accepted trials per condition, which can affect the signal to noise ratio, as this metric did not significantly differ across any of our attention conditions (all p 's > 0.20).

Complex demodulation (Kovach and Gander, 2016; Papp and Ktonas, 1977) was used to transform the artifact-free epochs into the time-frequency domain and the resulting spectral power estimations were averaged per sensor to generate time-frequency plots of mean spectral density. The time-frequency analysis was performed with a frequency-step of 2 Hz and a time-step of 25 ms between 4 and 100 Hz, using a 4 Hz lowpass finite impulse response (FIR) filter with a full-width half maximum (FWHM) in the time domain of ~115 ms. These sensor-level data were then normalized by each respective bin's baseline power for visualization purposes, calculated as the mean power during the -500 to 0 ms time period. The specific time-frequency windows used for source imaging were determined by statistical analysis of the sensor-level spectrograms, per experiment, across both conditions and the entire array of gradiometers. Each data point in each sensor-level spectrogram was initially evaluated using a mass univariate approach based on the general linear model. To reduce the risk of false positive results while maintaining reasonable sensitivity, a two-stage procedure was followed to control for Type 1 error. In the first stage, paired sample t -tests against baseline were conducted on each data point and the output spectrogram of t -values was thresholded at $p < 0.05$ to define time-frequency bins containing potentially significant oscillatory deviations across all participants. In stage two, the time-frequency bins that survived the threshold were clustered with temporally and/or spectrally neighboring bins (per sensor) that were also above the threshold ($p < 0.05$), and a cluster value was derived by summing all of the t -values of all data points in the cluster. Nonparametric permutation testing was then used to derive a distribution of cluster values and the significance level of the observed clusters (from stage one) were tested directly using this distribution (Ernst, 2004; Maris and Oostenveld, 2007). For each comparison, 1000 permutations were computed to build a distribution of cluster values. Based on these analyses, rectangular time-frequency windows within these significant clusters across all participants (per experiment) were subjected to a beamforming analysis.

2.7. MEG source analysis

Using a spherical head model, cortical networks were imaged through an extension of the linearly constrained minimum variance vector beamformer known as dynamic imaging of coherent sources (DICS; Gross et al., 2001), which applies spatial filters to time-frequency sensor data in order to calculate voxel-wise source power for the entire brain volume. Imaging of oscillatory responses was performed per condition, per participant for the time-frequency bins identified using the previously described statistical approach. The single images were derived from the cross-spectral densities of all combinations of MEG gradiometers averaged over the time-frequency range of interest, and the solution of the forward problem for each location on a grid specified by input voxel space. Following convention, we computed noise-normalized, source power per voxel using active (i.e., task) and passive (i.e., baseline) periods of equal duration and bandwidth. Such images are typically referred to as pseudo- t maps, with units (pseudo- t) that reflect noise-normalized power differences (i.e., active vs. passive) per voxel. This generated participant-level pseudo- t maps for each time-frequency-specific response identified in the sensor-level cluster-based permutation analysis. MEG preprocessing and imaging used the Brain Electrical Source Analysis (BESA version 6.1) software.

Three-dimensional maps of functional brain activity were statistically evaluated using a multi-stage mass univariate approach based on the general linear model. Initially, paired sample t -tests were performed between attention conditions to identify regions generating differential oscillatory responses due to attentional load. A relatively strict initial alpha level of $p < 0.005$ and spatial extent threshold (cluster correction, $k = 300$ contiguous voxels) was utilized at this stage to mitigate the risk of false positives. Pseudo- t values corresponding to the peak voxel of each resulting cluster were extracted and used for visualization purposes. Next, we performed a secondary, more stringent, whole-brain correction for multiple comparisons, using a cluster-based permutation testing approach similar to the one employed for the sensor-level data, with an initial cluster threshold of $p < 0.005$. From the clusters that survived this stringent second-level correction, we then extracted amplitude values from the peak voxel for display purposes. To improve rigor, we also recomputed the relevant statistical contrasts between these peak values, with outliers (defined as being more than 1.5 times the interquartile range above or below the third and first quartiles, respectively) removed.

3. Results

3.1. Experiment 1: directed attention

3.1.1. Behavioral performance—All 26 participants performed well on the visual-somatosensory oddball task, with a mean accuracy of 97.60% correct ($SD = 1.36\%$) overall. The overall mean accuracy for responding to the temporal oddballs in the attend visual condition was 96.63% ($SD = 5.07\%$), while the overall mean accuracy for the identification of oddballs in the attend somatosensory condition was 98.56% ($SD = 3.22\%$). To parse these effects further, in the attend visual condition, participants identified and responded to the visual oddballs at a mean accuracy of 93.27% ($SD = 10.14\%$), and did not mistakenly respond to any of the somatosensory oddballs. In the attend somatosensory condition,

participants identified and responded to the somatosensory oddballs at a mean accuracy of 97.14% ($SD = 6.43\%$), and did not mistakenly respond to any of the visual oddballs. Participants were modestly but significantly more likely to identify the oddballs correctly when attending (and responding) to the somatosensory domain, compared to the visual domain ($t(25) = -2.132, p = 0.043$).

3.1.2. MEG sensor-level results—Statistical analysis of the sensor-level spectrograms indicated four significant clusters (Fig. 2). First, there was a strong increase in theta (4–8 Hz) activity in occipital sensors immediately after stimulus onset and this extended until about 250 ms post-stimulus onset. Second, there was a robust decrease in beta activity (i.e., a desynchronization; 16–22 Hz) across parietal and occipital sensors from 225 to 525 ms post-stimulus onset. Third, there was an alpha desynchronization (8–14 Hz; 300–800 ms) in a cluster of occipital sensors. Finally, there was an increase or synchronization in the gamma range (74–84 Hz; 300–550 ms) in sensors near the occipital cortices (see Fig. 2).

3.1.3. MEG imaging results—Each of the statistically-defined time-frequency responses was imaged using a beamformer and compared voxel-wise for conditional effects using paired-samples t -tests. Following permutation testing to control for Type 1 error, only significant clusters of attentional effects spanning the right anterior middle frontal gyrus for the theta-band, bilateral prefrontal and lateral occipital cortices for the alpha-band, and right lateral occipital cortex for the beta-band remained, indicating the robustness of these effects (Fig. 3). Importantly, exclusion of the outlier data points in Fig. 3 (defined as being more than 1.5 times the interquartile range above or below the third and first quartiles, respectively) did not alter these findings.

Significant clusters of directed attention effects that did not survive permutation testing were found for alpha responses encompassing bilateral prefrontal cortices, left precentral gyrus, and the left superior temporal gyrus; beta activity in the right parieto-occipital cortex, right paracentral lobule, and the left medial frontal gyrus; and gamma-band effects in the left superior frontal gyrus. For visualization of these less robust effects, see Figure S1.

Overall, with the exception of alpha responses in the bilateral prefrontal cortices, all conditional differences were such that responses were stronger (i.e., more positive for theta and gamma synchronizations and more negative for alpha and beta desynchronizations) when attention was sustained in the visual domain relative to when it was directed away.

3.2. Experiment 2: divided attention

3.2.1. Behavioral performance—Two participants were excluded from this analysis since they identified oddball stimuli with less than 60% accuracy. The remaining 32 participants performed well on the visual-somatosensory oddball task, with a mean accuracy of 94.43% correct ($SD = 3.73\%$) overall. The overall mean accuracy for responding to the oddballs in the attend visual condition was 97.07% ($SD = 4.20\%$), while the overall mean accuracy for the identification of oddballs in the attend both condition was 91.80% ($SD = 8.76\%$). To parse these effects further, in the attend visual condition, participants identified and responded to the visual oddballs at a mean accuracy of 94.53% ($SD = 8.36\%$), and disregarded the somatosensory oddballs at a mean accuracy of 99.61% ($SD = 2.21\%$). In the

attend both condition, participants responded to both the visual and somatosensory oddballs, with the mean accuracy for visual oddballs being 90.23% ($SD = 10.88\%$) and for somatosensory oddballs being 93.36% ($SD = 11.87\%$). Participants were significantly more likely to identify oddballs when attending to the visual domain, compared to when they attended to both domains ($t(31) = 3.54, p < 0.001$).

3.2.2. MEG sensor-level results—Non-parametric statistical analysis of the sensor-level spectrograms revealed three significant time-frequency responses that were notably similar to those identified in the previous directed attention experiment (Fig. 4). First, there was an increase or synchronization in the theta range (4–8 Hz) in occipital sensors that began at stimulus onset and lasted 250 ms. Second, there was a desynchronization in the beta range over posterior sensors (16–22 Hz; 225–525 ms). This beta response overlapped temporally and spatially with a desynchronization in the alpha band (8–14 Hz; 300–800 ms) in a cluster of occipital sensors. No significant gamma responses were detected.

3.2.3. MEG imaging results—Each of the statistically-defined time-frequency responses was imaged using a beamformer and compared voxel-wise for conditional effects using paired-samples t -tests. In this experiment, the right temporoparietal clusters of attentional effects in the alpha- and beta-bands survived stringent second-level multiple comparisons correction using nonparametric permutation testing (Fig. 5). Importantly, exclusion of the outlier data points in Fig. 5 (defined as being more than 1.5 times the interquartile range above or below the third and first quartiles, respectively) did not alter these findings. Additionally, activity levels during the prestimulus baseline period did not differ in these regions (see Fig. S2).

Significant clusters of divided attention effects that did not survive permutation testing were found in the left posterior insula, right posterior parietal cortex, and left cerebellum in the theta range, and in the right lateral occipital, left primary visual cortex, and left cerebellum in the beta range. For visualization of these less robust effects, please see Fig. S3.

To conclude, with the exception of the theta responses, all of the attentional effects reflected stronger oscillations (i.e., greater alpha and beta decreases) when attention was sustained in the visual domain relative to when it was divided between modalities.

4. Discussion

In this study, healthy adult participants underwent whole-brain MEG during a visual-somatosensory oddball attention paradigm, which enabled investigation of the spectro-temporal neural oscillatory dynamics serving directed and divided visual attention. Both of these experiments revealed a multi-spectral effect of attention on neural oscillatory activity, such that sustained attention towards the visual domain generally enhanced neural responses to the visual stimuli. More specifically, directing attention toward the visual domain increased theta synchronization in a cluster over the right anterior middle frontal gyrus, enhanced the alpha-band desynchronization responses (i.e., a stronger decrease from baseline) in a cluster encompassing the bilateral occipital cortices, and strengthened the beta desynchronization in a cluster over the right lateral occipital cortex. Additionally, dividing

attention between visual and somatosensory domains reduced alpha oscillatory activity in a cluster over the right TPJ and beta oscillations in a spatially-overlapping cluster, relative to when attention was sustained in the visual domain. The only exception to this general pattern was the increased alpha activity observed in a cluster over bilateral prefrontal cortices when attention was directed away versus toward the visual domain, which is consistent with prior work. Although numerous studies have examined the effects of directing and dividing attention on functional brain activity, the unique combination of high spatial, spectral, and temporal resolution available with MEG allowed us to determine the dynamics of specific oscillatory responses in local neural populations. These findings, as well as their implications in the context of previous literature and future research, are discussed next. Importantly, to enhance the rigor and robustness of the study, we focus our interpretations primarily on those effects that survived stringent cluster-based permutation testing.

Most broadly, this study provides novel information regarding the dynamics of directed and divided attention effects on neural oscillatory activity, which, within the context of previous literature, enhances our understanding of these essential cognitive processes. For instance, theta oscillations in early sensory regions are known to be involved in the processing of novel information (Cavanagh et al., 2010; Klimesch, 1999, 2012) and early stimulus recognition (Wiesman et al., 2017b), while frontal theta has been tightly linked to top-down executive control (Cavanagh and Frank, 2014; Cavanagh et al., 2010; Cohen and Donner, 2013; Fries et al., 2016; Ishii et al., 2014; Keller et al., 2017; Klimesch et al., 2005; Landau and Fries, 2012; Landau et al., 2015; Min and Park, 2010; Oehr et al., 2014; Sauseng et al., 2005; Verbruggen et al., 2010). We observed stronger theta oscillations in the right anterior middle frontal gyrus when attention was sustained towards the visual domain, relative to when it was directed away. This brain region has been theorized to act as a gateway between endogenous (top-down) and exogenous (bottom-up) control of attention (Corbetta et al., 2008; Fox et al., 2006; Japee et al., 2015), and therefore, our finding of a middle frontal theta effect during the sustained visual attention condition reinforces this interpretation. Interestingly, we found no such frontal theta effect when attention was divided between the visual and somatosensory domains, supporting the view that this response represents top-down influence in sustained visual attention.

In contrast to the theta band, we found significant effects of attention on the alpha oscillatory responses for both the directed and divided attention experiments. A widely accepted mechanism of alpha activity in the brain is the “gating by inhibition” framework (Bonnerford and Jensen, 2012; Hanslmayr et al., 2007; Händel et al., 2011; Jensen et al., 2002; Jensen and Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 2007; Spaak et al., 2014; Wiesman et al., 2018; Wiesman and Wilson, 2019), whereby higher levels of alpha oscillatory activity in posterior parieto-occipital cortices index the functional inhibition of incoming visual information. Within this framework, decreases from basal levels of alpha activity represent the *dis-inhibition* of these cortices towards the goal of visual stimulus processing. Therefore, as one might expect, stronger desynchronized alpha oscillations have often been found to facilitate heightened perception and attention. We found stronger desynchronized alpha oscillations in posterior cortices when attention was directed towards the visual domain relative to when it was directed away completely, as well as when it was divided between

sensory modalities, which again aligns with previous literature presenting more robust alpha activity in task-relevant regions during active processing (Haegens et al., 2011; Jones et al., 2010; McDermott et al., 2017; Proskovec et al., 2018a, 2019; Wiesman et al., 2017b, 2018; Wiesman and Wilson, 2019).

In the directed attention experiment, these alpha differences extended broadly across the bilateral primary and lateral occipital cortices. In contrast, these differences were much more spatially constrained to the right-lateralized TPJ/supramarginal region in the divided attention experiment. With visual stimuli in the right visual field, these significant right-lateralized responses may at first seem unusual considering the lateralization of visual processing. However, this finding can be explained by the theory of right-hemispheric dominance in attention, where alpha oscillations are more right-lateralized regardless of the attended hemifield (De Schotten et al., 2011; Heilman and Van Den Abell, 1980). In addition, the right supramarginal gyrus, and in particular the TPJ, has been tied robustly to goal-directed attentional (re-)orienting (Behrmann et al., 2004; Chang et al., 2013; Kucyi et al., 2012), which again is consistent with the current findings as our divided attention task required participants to re-orient towards/away from the visual space, whereas our directed attention task did not. In addition to attentional re-orienting, the TPJ is also established as being essential to multisensory processing, and specifically switching/re-orienting between sensory modalities (Bauer et al., 2012; Dugué et al., 2018; Göschl et al., 2014, 2015; Indovina and Macaluse, 2007). Since the visual and somatosensory stimuli were presented in alternation, participants would have been required to reorient their attention from one sensory modality to another in order to effectively perform the task. Finally, alpha differences also emerged in a cluster that spanned bilateral prefrontal cortices in the directed attention experiment, which are involved in attentional control (Corbetta et al., 2008; Fox et al., 2006; Japee et al., 2015) and reorienting to unexpected stimuli (Doricchi et al., 2010; Shulman et al., 2009). Neural activity in prefrontal cortices is also involved in sustained attention (Alho et al., 2015; Fagioli and Macaluso, 2016; Johnson et al., 2007; Loose et al., 2003; Nebel et al., 2006; Peelen et al., 2004; Salo et al., 2017; Santangelo, 2018; Santangelo et al., 2010; Serences and Yantis, 2007; Vohn et al., 2007; Wang et al., 2016), however, the spectral specificity of this finding to the alpha-band contributes an important nuance to these previous studies. Moreover, the direction of this difference was inconsistent with our other current findings (i.e., increased alpha amplitude/decreased desynchronization), but notably was consistent with a previous somatosensory study from our laboratory (Wilson et al., 2015). Future studies should further investigate the spectro-temporal dynamics of this response to identify the attentional parameters driving the effects.

Unexpectedly, we also observed robust attentional effects in the beta range for both the directed and divided attention experiments. Most notably, task-related beta perturbations are frequently observed within the somatomotor network and are linked to motor function (Cheyne et al., 2006; Engel and Fries, 2010; Gaetz et al., 2010; Heinrichs-Graham et al., 2017, 2018; Heinrichs-Graham and Wilson, 2015, 2016; Jurkiewicz et al., 2006; Wilson et al., 2014). However, other studies have also indicated that neural oscillations at this frequency may play a role in decision-making (Donner et al., 2007, 2009), cognitive control (Klimesch, 2012), and short-term or working memory (Proskovec et al., 2018a, 2018b; Tallon-Baudry et al., 1999). In contrast, the role of beta oscillations in visual processing and

attention is less clear. Although often reported, it is controversial whether these occipital beta effects are due to motor influences (Sacchet et al., 2015), are an extension of simultaneous alpha-frequency responses or spectral leakage (Bauer et al., 2014; Michalareas et al., 2016), or are indeed functionally- and spectrally-distinct from alpha (Gola et al., 2013; Sedley et al., 2016). In our experiments, no motor response was required of participants in the trials that were analyzed, and source analysis indicated that the origin of these significant attentional effects was the right lateral occipital and temporo-parietal cortices (i.e., TPJ), both regions commonly associated with visual attention. Additionally, the spectral and temporal constraints of the beta response were quite distinct from those of the alpha responses in the current study. For these reasons, we do not believe these effects to be due to motor confounds, nor “bleed through” from the alpha response. However, further research is certainly warranted to better understand the role of beta oscillations in visual attention.

Before closing, it is important to acknowledge the limitations of our research. One limitation of the current study was having overlapping, but not identical, participants across the two experiments. We opted to report the two experiments together, as the findings from each were highly complementary, but having identical samples would have strengthened the study. Of note, this limitation mainly affected the least interesting of the three possible comparisons, which was directing attention away from the visual domain versus dividing attention between visual and somatosensory domains. Such a comparison would have been difficult to interpret, and so we opted to move forward with the two experiments as reported here, although future work could further probe this. Another limitation is that the attentional load required for this multisensory oddball task was relatively low. Subsequent research ought to consider increasing attentional load in a step-wise manner in both directed and divided attention paradigms to see how this might affect oscillatory dynamics in a frequency-dependent manner. In addition, our use of a collapsed time-frequency localizer at the sensor-level likely biased our results towards those neural responses, modulated by directed and/or divided attention, that exhibited the strongest modulation from baseline. Although this approach may be less sensitive to sensor-level conditional differences that were weaker in amplitude or differed in their directionality, it is almost certainly preferable to performing the same conditional analyses at the sensor-level, where the positioning of the brain relative to the sensor array is not standardized across participants. Finally, although our accuracy results make us confident that participants were indeed directing/dividing their attention as instructed, the relatively coarse nature of these behavioral data (i.e., only the oddball stimuli required a behavioral response) made it difficult to extensively analyze reaction times on the task. Future research should develop experimental designs that allow for more advanced analyses to examine how the oscillatory effects found here relate to task performance. This would be particularly helpful in delineating the role of beta oscillations in visual attention. Despite these limitations, these experiments provide new information regarding the spectro-temporal evolution of neural oscillatory responses serving the direction and division of neural resources within the visual space. This information is essential, both in understanding the role of differing frequencies of neural oscillatory activity in the occipital and frontal cortices, and in developing novel therapeutic targets for disorders of attention.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

This research was supported by grants R01-MH103220 (TWW), R01-MH116782 (TWW), R01-MH118013 (TWW), R01-DA047828 (TWW), P20-GM130447 (TWW), U54-GM115458 (TWW), and F31-AG055332 (AIW) from the National Institutes of Health, and grant #1539067 from the National Science Foundation (TWW). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We would like to thank the participants for volunteering to participate in the study, as well as our staff and local collaborators for their contributions to the work. We would also like to specifically thank Nichole Knott for extensive help with the MEG recordings.

References

- Alais D, Morrone C, Burr D, 2006 Separate attentional resources for vision and audition. *Proc. Biol. Sci* 273, 1339–1345. [PubMed: 16777721]
- Alho K, Salmi J, Koistinen K, Salonen O, Rinne T, 2015 Top-down controlled and bottom-up triggered orienting of auditory attention to pitch activate overlapping brain networks. *Brain Res.* 1626, 136–145. [PubMed: 25557401]
- Auksztulewicz R, Friston KJ, Nobre AC, 2017 Task relevance modulates the behavioral and neural effects of sensory predictions. *PLoS Biol.* 15, e2003143. [PubMed: 29206225]
- Bauer M, Kennett S, Driver J, 2012 Attention selection of location and modality in vision and touch modulates low-frequency activity in associated sensory cortices. *J. Neurophysiol* 107, 2342–2351. [PubMed: 22323628]
- Bauer M, Stenner MP, Friston KJ, Dolan RJ, 2014 Attentional modulation of alpha/beta and gamma oscillations reflect functionally distinct processes. *J. Neurosci* 34, 16117–16125. [PubMed: 25429152]
- Ba ar E, Ba ar-Eroglu C, Karaka S, Schürmann M, 2001 Gamma, alpha, delta, and theta govern cognitive processes. *Int. J. Psychophysiol* 39, 241–248. [PubMed: 11163901]
- Behrmann M, Geng JJ, Shomstein S, 2004 Parietal cortex and attention. *Curr. Opin. Neurobiol* 14, 212–217. [PubMed: 15082327]
- Bhattacharya J, Shams L, Shimojo S, 2002 Sound-induced illusory flash perception: role of gamma band responses. *Neuroreport* 13, 1727–1730. [PubMed: 12395112]
- Bonneford M, Jensen O, 2012 Alpha oscillations serve to protect working memory maintenance against anticipated distractors. *Curr. Biol* 22, 1969–1974. [PubMed: 23041197]
- Brainard DH, 1997 The psychophysics toolbox. *Spatial Vis.* 10, 433–436.
- Busch NA, Dubois J, VanRullen R, 2009 The phase of ongoing EEG oscillations predicts visual perception. *J. Neurosci* 29, 7869–7876. [PubMed: 19535598]
- Buschman TJ, Kastner S, 2015 From behavior to neural dynamics: an integrated theory of attention. *Neuron* 88, 127–144. [PubMed: 26447577]
- Castiello U, Umiltà C, 1990 Size of the attentional focus and efficiency of processing. *Acta Psychol.* 73, 195–209.
- Castiello U, Umiltà C, 1992 Splitting focal attention. *J. Exp. Psychol. Hum. Percept. Perform* 18, 837–848. [PubMed: 1500879]
- Cavanagh JF, Frank MJ, 2014 Frontal theta as a mechanism for cognitive control. *Trends Cog. Neurosci* 414–421.
- Cavanagh JF, Frank MJ, Klein TJ, Allen JJ, 2010 Frontal theta links prediction errors to behavioral adaptation in reinforcement learning. *Neuroimage* 49, 3198–3209. [PubMed: 19969093]
- Chang CF, Hsu TY, Tseng P, Liang WK, Tzeng OJ, Hung DL, Juan CH, 2013 Right temporoparietal junction and attentional reorienting. *Hum. Brain Mapp* 34, 869–877. [PubMed: 22419442]

- Cheyne D, Bakhtazad L, Gaetz W, 2006 Spatiotemporal mapping of cortical activity accompanying voluntary movements using an event-related beamforming approach. *Hum. Brain Mapp* 34, 869–877.
- Ciaramitaro VM, B GT, Boynton GM, 2007 Spatial and cross-modal attention alter responses to unattended sensory information in early visual and auditory human cortex. *J. Neurophysiol* 98, 2399–2413. [PubMed: 17715196]
- Cohen MX, Donner TH, 2013 Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *J. Neurophysiol* 110, 2752–2763. [PubMed: 24068756]
- Corbetta M, Patel G, Shulman GL, 2008 The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324. [PubMed: 18466742]
- Corbetta M, Shulman GL, 2002 Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci* 3, 201–215. [PubMed: 11994752]
- Crottaz-Herbette S, Anagnoson RT, Menon V, 2004 Modality effects in verbal working memory: differential prefrontal and parietal responses to auditory and visual stimuli. *Neuroimage* 21, 340–351. [PubMed: 14741672]
- De Schotten MT, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, Murphy DG, Catani M, 2011 A lateralized brain network for visuospatial attention. *Nat. Neurosci* 14, 1245. [PubMed: 21926985]
- Degerman A, Rinne T, Pekkola J, Autti T, Jääskeläinen IP, Sams M, Alho K, 2007 Human brain activity associated with audiovisual perception and attention. *Neuroimage* 34, 1683–1691. [PubMed: 17204433]
- Donner TH, Siegel M, Fries P, Engel AK, 2009 Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Curr. Biol* 19, 1581–1585. [PubMed: 19747828]
- Donner TH, Siegel M, Oostenveld R, Fries P, Bauer M, Engel AK, 2007 Population activity in the human dorsal pathway predicts the accuracy of visual motion detection. *J. Neurophysiol* 98, 345–359. [PubMed: 17493916]
- Doricchi F, Macci E, Silvetti M, Macaluso E, 2010 Neural correlates of the spatial and expectancy components of endogenous and stimulus-driven orienting of attention in the Posner task. *Cerebr. Cortex* 20, 1574–1585.
- Dugué L, Merriam EP, Heeger DJ, Carrasco M, 2018 Specific visual subregions of TPJ mediate reorienting of spatial attention. *Cerebr. Cortex* 28, 2375–2390.
- Edden RA, Muthukumaraswamy SD, Freeman TC, Singh KD, 2009 Orientation discrimination performance is predicted by GABA concentration and gamma oscillation frequency in human primary visual cortex. *J. Neurosci* 29, 15721–15726. [PubMed: 20016087]
- Engel AK, Fries P, 2010 Beta-band oscillations - signaling the status quo? *Curr. Opin. Neurobiol* 20, 156–165. [PubMed: 20359884]
- Eriksen CW, St James JD, 1986 Visual attention within and around the field of focal attention: a zoom lens model. *Percept. Psychophys* 40, 225–240. [PubMed: 3786090]
- Ernst MD, 2004 Permutation methods: a basis for exact inference. *Stat. Sci* 19, 676–685.
- Fagioli S, Macaluso E, 2009 Attending to multiple visual streams: interactions between location-based and category-based attentional selection. *J. Cognit. Neurosci* 21, 1628–1641. [PubMed: 18823252]
- Fagioli S, Macaluso E, 2016 Neural correlates of divided attention in natural scenes. *J. Cognit. Neurosci* 28, 1392–1405. [PubMed: 27167404]
- Fox MD, Corbetta M, Snyder AZ, Vincent JL, Raichle ME, 2006 Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proc. Natl. Acad. Sci. U. S. A* 103, 10046–10051. [PubMed: 16788060]
- Fries P, Reynolds JH, Rorie AE, Desimone R, 2001 Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291, 1560–1563. [PubMed: 11222864]
- Friese U, Duane J, Göschl F, König P, Wang P, Engel AK, 2016 Oscillatory brain activity during multisensory attention reflects activation, disinhibition, and cognitive control. *Sci. Rep* 1–11. [PubMed: 28442746]
- Gaetz W, Macdonald M, Cheyne D, Snead OC, 2010 Neuromagnetic imaging of movement-related cortical oscillations in children and adults: age predicts post-movement beta rebound. *Neuroimage* 51, 792–807. [PubMed: 20116434]

- Gola M, Magnuski M, Szumska I, Wróbel A, 2013 EEG beta band activity is related to attention and attentional deficits in the visual performance of elderly subjects. *Int. J. Psychophysiol* 89, 334–341. [PubMed: 23688673]
- Gross J, Kujala J, Hämäläinen M, Timmermann L, Schnitzler A, Salmelin R, 2001 Dynamic imaging of coherent sources: study neural interactions in the human brain. *Proc. Natl. Acad. Sci. U. S. A* 98, 694–699. [PubMed: 11209067]
- Göschl F, Engel AK, Frieze U, 2014 Attention modulates visual-tactile interaction in spatial pattern matching. *PLoS One* 9, e106896. [PubMed: 25203102]
- Göschl F, Frieze U, Duame J, König P, Engel AK, 2015 Oscillatory signatures of crossmodal congruence effects: an EEG investigation employing a visuotactile pattern matching paradigm. *Neuroimage* 116, 177–186. [PubMed: 25846580]
- Haegens S, Händel BF, Jensen O, 2011 Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *J. Neurosci* 31, 5197–5204. [PubMed: 21471354]
- Hanslmayr S, Aslan A, Staudigl T, Klimesch W, Hermann CS, Bäuml KH, 2007 Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage* 37, 1465–1473. [PubMed: 17706433]
- Heilman KM, Van Den Abell T, 1980 Right hemisphere dominance for attention: the mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology* 30, 327–330. [PubMed: 7189037]
- Heinrichs-Graham E, Kurz MJ, Gehringer JE, Wilson TW, 2017 The functional role of post-movement beta oscillations in motor termination. *Brain Struct. Funct* 22, 3075–3086.
- Heinrichs-Graham E, McDermott TJ, Mills MS, Wiesman AI, Wang YP, Stephen JM, Calhoun VD, Wilson TW, 2018 The lifespan trajectory of neural oscillatory activity in the motor system. *Dev. Cog. Neurosci* 30, 159–168.
- Heinrichs-Graham E, Wilson TW, 2015 Coding complexity in the human motor circuit. *Hum. Brain Mapp* 36, 5155–5167. [PubMed: 26406479]
- Heinrichs-Graham E, Wilson TW, 2016 Is an absolute level of cortical beta suppression required for proper movement? Magnetoencephalographic evidence from healthy aging. *Neuroimage* 134, 514–521. [PubMed: 27090351]
- Holliday IE, Barnes GR, Hillebrand A, Singh KD, 2003 Accuracy and applications of group MEG studies using cortical source locations estimated from participants' scalp surfaces. *Hum. Brain Mapp* 20, 142–147. [PubMed: 14601140]
- Hopfinger JB, B MH, Mangun GR, 2000 The neural mechanisms of top-down attentional control. *Nat. Neurosci* 3, 284–291. [PubMed: 10700262]
- Händel BF, Haarmeier T, Jensen O, 2011 Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J. Cognit. Neurosci* 23, 2494–2502. [PubMed: 20681750]
- Iacoboni M, 2005 Divided attention in the normal and the split brain: chronometry and imaging In: Itti L, Rees G, Tsotsos JK (Eds.), *Neurobiology of Attention*. Academic Press, pp. 363–367.
- Indovina I, Macaluse E, 2007 Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. *Cerebr. Cortex* 17, 1701–1711.
- Ishii R, Canuet L, Ishihara T, Aoki Y, Ikeda S, Hata M, Katsimichas T, Gunji A, Takahashi H, Nakahachi T, Iwase M, Takeda M, 2014 Frontal midline theta rhythm and gamma power changes during focused attention on mental calculation: an MEG beamformer analysis. *Front. Hum. Neurosci* 8, 1–10. [PubMed: 24474914]
- Japee S, Holiday K, Satyshur MD, Mukai I, Ungerleider LG, 2015 A role of right middle frontal gyrus in reorienting of attention: a case study. *Front. Syst. Neurosci* 9, 1–16. [PubMed: 25709570]
- Jensen O, Gelfand J, Kounios J, Lisman JE, 2002 Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebr. Cortex* 12, 877–882.
- Jensen O, Mazaheri A, 2010 Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci* 4, 186. [PubMed: 21119777]
- Johnson JA, Strafella AP, Zatorre RJ, 2007 The role of the dorsolateral prefrontal cortex in bimodal divided attention: two transcranial magnetic stimulation studies. *J. Cognit. Neurosci* 19, 907–920. [PubMed: 17536962]

- Johnson JA, Zatorre RJ, 2005 Attention to simultaneous unrelated auditory and visual events: behavioral and neural correlates. *Cerebr. Cortex* 15, 1609–1620.
- Johnson JA, Zatorre RJ, 2006 Neural substrates for dividing and focusing attention between simultaneous auditory and visual events. *Neuroimage* 31, 1673–1681. [PubMed: 16616520]
- Jones SR, Kerr CE, Wan Q, Pritchett DL, Hämäläinen M, Moore CI, 2010 Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *J. Neurosci* 30, 13760–13765. [PubMed: 20943916]
- Jurkiewicz MT, Gaetz WC, Bostan AC, Cheyne D, 2006 Post-movement beta rebound is generated in motor cortex: evidence from neuromagnetic recordings. *Neuroimage* 32, 1281–1289. [PubMed: 16863693]
- Keil J, Senkowski D, 2018 Neural oscillations orchestrate multisensory processing. *Neuroscientist* 24, 609–626. [PubMed: 29424265]
- Keller AS, Payne L, Sekuler R, 2017 Characterizing the roles of alpha and theta oscillations in multisensory attention. *Neuropsychologia* 99, 48–63. [PubMed: 28259771]
- Klimesch W, 1999 EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res. Rev* 29, 169–195. [PubMed: 10209231]
- Klimesch W, 2012 Alpha-band oscillations, attention, and controlled access to stored information. *Trend Cog. Neurosci* 16, 606–617.
- Klimesch W, Sauseng P, Hanslmayr S, 2007 EEG alpha oscillations: the inhibitiontiming hypothesis. *Brain Res. Rev* 53, 606–617.
- Klimesch W, Schack B, Sauseng P, 2005 The functional significance of theta and upper alpha oscillations. *Exp. Psychol* 52, 99–108. [PubMed: 15850157]
- Klingberg T, 1998 Concurrent performance of two working memory tasks: potential mechanisms of interference. *Cerebr. Cortex* 8, 593–601.
- Kovach CK, Gander PE, 2016 The demodulated band transform. *J. Neurosci. Methods* 261, 135–154. [PubMed: 26711370]
- Kucyi A, Hodaie M, Davis KD, 2012 Lateralization in intrinsic functional connectivity of the temporoparietal junction with salience- and attention-related brain networks. *J. Neurophysiol* 108, 3382–3392. [PubMed: 23019004]
- Kurz MJ, Wiesman AI, Coolidge NM, Wilson TW, 2017 Children with cerebral palsy hyper-gate somatosensory stimulation of the foot. *Cerebr. Cortex* 28, 2431–2438.
- Landau AN, Fries P, 2012 Attention samples stimuli rhythmically. *Curr. Biol* 22, 1000–1004. [PubMed: 22633805]
- Landau AN, Schreyer HM, van Pelt S, Fries P, 2015 Distributed attention is implemented through theta-rhythmic gamma modulation. *Curr. Biol* 25, 2332–2337. [PubMed: 26279231]
- Laurienti PJ, Burdette JH, Wallace MT, Yen Y-Y, Field AS, Stein BE, 2002 Deactivation of sensory-specific cortex by cross-modal stimuli. *J. Cognit. Neurosci* 14, 420–429. [PubMed: 11970801]
- Loose R, Kaufmann C, Auer DP, Lange KW, 2003 Human prefrontal and sensory cortical activity during divided attention tasks. *Hum. Brain Mapp* 18, 249–259. [PubMed: 12632463]
- Macaluso E, Noppeney U, Talsma D, Vercillo T, Hartcher-O'Brien J, Adam R, 2016 The curious incident of attention in multisensory integration: bottom-up vs. top-down. *Multisensory Res.* 29, 557–583.
- Maris E, Oostenveld R, 2007 Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164, 177–190. [PubMed: 17517438]
- McDermott TJ, Wiesman AI, Proskovec AL, Heinrichs-Graham E, Wilson TW, 2016 Spatiotemporal oscillatory dynamics of visual selective attention during a flanker task. *Neuroimage* 156, 277–285.
- Michalareas G, Vezoli J, van Pelt S, Schoffelen J-M, Kennedy H, Fries P, 2016 Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. *Neuron* 89, 384–397. [PubMed: 26777277]
- Min BK, Park HJ, 2010 Task-related modulation of anterior theta and posterior alpha EEG reflects top-down preparation. *BMC Neurosci.* 11, 79. [PubMed: 20584297]

- Mittag M, Inauri K, Huovilainen T, Leminen M, Salo E, Rinne T, Kujala T, Alho K, 2013 Attention effects on the processing of task-relevant and task-irrelevant speech sounds and letters. *Front. Neurosci* 231, 1–15.
- Moisala M, Salmela V, Salo E, Carlson S, Vuontela V, Salonen O, Alho K, 2015 Brain activity during divided and selective attention to auditory and visual sentence comprehension tasks. *Front. Hum. Neurosci* 9, 86. [PubMed: 25745395]
- Moriarty D, 2015 *Information Processing Practical Human Factors for Pilots*. Academic Press, pp. 11–75.
- Mowbray GH, 1953 Simultaneous vision and audition the comprehension of prose passages with varying levels of difficulty. *J. Exp. Psychol* 46, 365–372. [PubMed: 13109141]
- Musall S, von Pföst V, Rauch A, Logothetis NK, Whittingstall K, 2014 Effects of neural synchrony on surface EEG. *Cerebr. Cortex* 24, 1045–1053.
- Muthukumaraswamy SD, Singh KD, 2013 Visual gamma oscillations: the effects of stimulus type, visual field coverage and stimulus motion on MEG and EEG recordings. *Neuroimage* 69, 223–230. [PubMed: 23274186]
- Mégevand P, Molholm S, Nayak A, Foxe AA, 2013 Recalibration of the multisensory temporal window of integration results from changing task demands. *PLoS One* 8, e716608.
- Müller MM, Malinowski P, Gruber T, Hillyard SA, 2003a Sustained division of the attentional spotlight. *Nature* 424, 309–312. [PubMed: 12867981]
- Müller NG, Bartelt OA, Donner TH, Villringer A, Brandt SA, 2003b A physiological correlate of the “Zoom Lens” of visual attention. *J. Neurosci* 23, 3561–3565. [PubMed: 12736325]
- Najdowski AC, Persicke A, Kung E, 2014 Executive functions In: Granpeesheh D, Tarbox J, Najdowski AC, Kornack J (Eds.), *Evidence-Based Treatment for Children with Autism*. Academic Press, pp. 355–387.
- Nebel K, Wiese H, Stude P, de Greiff A, Diener H-C, Keidel M, 2006 On the neural basis of focused and divided attention. *Cognit. Brain Res* 25, 760–776.
- Oehrn CR, Hanslmayr S, Fell J, Deuker L, Kremers NA, Do Lam AT, Egler CE, Axmacher N, 2014 Neural communication patterns underlying conflict detection, resolution, and adaptation. *J. Neurosci* 34, 10438–10452. [PubMed: 25080602]
- Papp N, Ktonas P, 1977 Critical evaluation of complex demodulation techniques for the quantification of bioelectrical activity. *Biomed. Sci. Instrum* 13, 135–145. [PubMed: 871500]
- Pashler H, 1994 Dual-task interference in simple tasks: data and theory. *Psychol. Bull* 116, 220–244. [PubMed: 7972591]
- Pashler H, 1998 *The Psychology of Attention*. MIT Press, Cambridge, MA.
- Peelen MV, Heslenfeld DJ, Theeuwes J, 2004 Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage* 22, 822–830. [PubMed: 15193611]
- Pomper U, Keil J, Foxe JJ, Senkowski D, 2015 Intersensory selective attention and temporal orienting operate in parallel and are instantiated in spatially distinct sensory and motor cortices. *Hum. Brain Mapp* 36, 3246–3259. [PubMed: 26032901]
- Proskovec AL, Heinrichs-Graham E, Wiesman AI, McDermott TJ, Wilson TW, 2018a Oscillatory dynamics in the dorsal and ventral attention networks during the reorienting of attention. *Hum. Brain Mapp* 39, 2177–2190. [PubMed: 29411471]
- Proskovec AL, Wiesman AI, Heinrichs-Graham E, Wilson TW, 2018b Beta oscillatory dynamics in the prefrontal and superior temporal cortices predict spatial working memory performance. *Sci. Rep* 8, 8488. [PubMed: 29855522]
- Proskovec AL, Wiesman AI, Wilson TW, 2019 The strength of alpha and gamma oscillations predicts behavioral switch costs. *Neuroimage* 188, 274–281. [PubMed: 30543844]
- Roland PE, Zilles K, 1998 Structural divisions and functional fields in the human cerebral cortex. *Brain Res. Rev* 26, 1339–1345.
- Sacchet MD, LaPlante RA, Wan Q, Pritchett DL, Lee AKC, Hämäläinen M, Moore CI, Kerr CE, Jones SR, 2015 Attention drives synchronization of alpha and beta rhythms between right inferior frontal and primary sensory neocortex. *J. Neurosci* 35, 2074–2082. [PubMed: 25653364]

- Salo E, Rinne T, Salonen O, Alho K, 2013 Brain activity during auditory and visual phonological, spatial and simple discrimination tasks. *Brain Res.* 1496, 55–69. [PubMed: 23261663]
- Salo E, Rinne T, Salonen O, Alho K, 2015 Brain activations during bimodal dual tasks depend on the nature and combination of component tasks. *Brain Res.* 17, 733–746.
- Salo E, Salmela V, Salmi J, Numminen J, Alho K, 2017 Brain activity associated with selective attention, divided attention, and distraction. *Brain Res.* 1664, 25–36. [PubMed: 28363436]
- Santangelo V, 2018 Large-scale brain networks supporting divided attention across spatial locations and sensory modalities. *Front. Integr. Neurosci* 12, 1–11. [PubMed: 29456494]
- Santangelo V, Fagioli S, Macaluso E, 2010 The costs of monitoring simultaneously two sensory modalities decrease when dividing attention in space. *Neuroimage* 49, 2717–2727. [PubMed: 19878728]
- Sauseng P, Klimesch W, Stadler W, Schabus M, Doppelmayr M, Hanslmayr S, Gruber WR, Birbaumer N, 2005 A shift of visual spatial attention is selectively associated with human EEG alpha activity. *Eur. J. Neurosci* 22, 2917–2926. [PubMed: 16324126]
- Schubert T, Szameitat AJ, 2003 Functional neuroanatomy of interference in overlapping dual tasks: an fMRI study. *Cognit. Brain Res* 17, 733–746.
- Sedley W, Gander PE, Kumar S, Kovach CK, Oya H, Griffiths TD, 2016 Neural Signatures of Perceptual Inference. *eLife*, e11476. [PubMed: 26949254]
- Senkowski D, Talsma D, Herrmann CS, Woldorff MG, 2005 Multisensory processing and oscillatory gamma responses: effects of spatial selective attention. *Exp. Brain Res* 166, 411–426. [PubMed: 16151775]
- Serences JT, Yantis S, 2007 Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cerebr. Cortex* 17, 284–293.
- Shaw ML, Shaw P, 1977 Optimal allocation of cognitive resources to spatial locations. *J. Exp. Psychol. Hum. Percept. Perform* 3, 201–211. [PubMed: 864393]
- Shomstein S, Yantis S, 2004 Control of attention shifts between vision and audition in human cortex. *J. Neurosci* 24, 10702–10706. [PubMed: 15564587]
- Shulman GL, Astafiev SV, Franke D, Pope DL, Snyder AZ, McAvoy MP, Corbetta M, 2009 Interaction of stimulus-driven reorienting and expectation in ventral and dorsal frontoparietal and basal gangliacortical networks. *J. Neurosci* 29, 4392–4407. [PubMed: 19357267]
- Spaak E, de Lange FP, Jensen O, 2014 Local entrainment of alpha oscillations by visual stimulation causes cyclic modulation of perception. *J. Neurosci* 34, 3536–3544. [PubMed: 24599454]
- Spooner RK, Wiesman AI, Mills MS, O’Neill J, Robertson KR, Fox HS, Swindells S, Wilson TW, 2018 Aberrant oscillatory dynamics during somatosensory processing in HIV-infected adults. *Neuroimage Clinic* 20, 85–91.
- Spooner RK, Wiesman AI, Proskovec AL, Heinrichs-Graham E, Wilson TW, 2019 Rhythmic spontaneous activity mediates the age-related decline in somatosensory function. *Cerebr. Cortex* 29, 680–688.
- Stelzel C, Schumacher EH, Schubert T, Mark DE, 2006 The neural effect of stimulus-response modality compatibility on dual-task performance: an fMRI study. *Psychol. Res* 70, 514–525. [PubMed: 16175414]
- Swettenham JB, Muthukumaraswamy SD, Singh KD, 2009 Spectral properties of induced and evoked gamma oscillations in human early visual cortex to moving and stationary stimuli. *J. Neurophysiol* 10, 1241–1253.
- Tallon-Baudry C, 2009 The roles of gamma-band oscillatory synchrony in human visual cognition. *Front. Biosci* 14, 321–332.
- Tallon-Baudry C, Kreiter A, Bertrand O, 1999 Sustained and transient oscillatory responses in the gamma and beta bands in a visual short-term memory task in humans. *Vis. Neurosci* 16, 449–459. [PubMed: 10349966]
- Taulu S, Simola J, 2006 Spatiotemporal signal space separation method for rejecting nearby interface in MEG measurements. *Phys. Med. Biol* 51, 1759–1768. [PubMed: 16552102]
- Uusitalo MA, Ilmoniemi RJ, 1997 Signal-space projection method for separating MEG or EEG into components. *Med. Biol. Eng. Comput* 35, 135–140. [PubMed: 9136207]

- van Dijk H, Schoffelen JM, Oostenveld R, Jensen O, 2008 Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J. Neurosci* 28, 1816–1823. [PubMed: 18287498]
- Verbruggen F, Aron AR, Stevens MA, Chambers CD, 2010 Theta burst stimulation dissociates attention and action updating in human inferior frontal cortex. *Proc. Natl. Acad. Sci. U. S. A* 107, 13966–13971. [PubMed: 20631303]
- Vohn R, Fimm B, Weber J, Schnitker R, Thron A, Spijkers W, Willmes K, Sturm W, 2007 Management of attentional resource in within-modal and cross-modal divided attention tasks: an fMRI study. *Hum. Brain Mapp* 28, 1267–1275. [PubMed: 17315224]
- Wang W, Viswanathan S, Lee T, Grafton ST, 2016 Coupling between theta oscillations and cognitive control network during cross-modal visual and auditory attention: supramodal vs modality-specific mechanisms. *PLoS One* 11, 1–16.
- Welford AT, 1952 The ‘psychological refractory period’ and the timing of high-speed performance - a review and a theory. *Br. J. Psychol* 43, 219.
- Wiesman AI, Groff BR, Wilson TW, 2018 Frontoparietal networks mediate the behavioral impact of alpha inhibition in visual cortex. *Cerebr. Cortex* 29, 3505–3513.
- Wiesman AI, Heinrichs-Graham E, Coolidge NM, Gehringer JE, Kurz MJ, Wilson TW, 2017a Oscillatory dynamics and functional connectivity during gating of primary somatosensory responses. *J. Physiol* 595, 1365–1375. [PubMed: 27779747]
- Wiesman AI, Heinrichs-Graham E, Proskovec AL, McDermott TJ, Wilson TW, 2017b Oscillations during observations: dynamic oscillatory networks serving visuospatial attention. *Hum. Brain Mapp* 38, 5128–5140. [PubMed: 28714584]
- Wiesman AI, Wilson TW, 2019 Alpha frequency entrainment reduces the effect of visual distractors. *J. Cognit. Neurosci* 31, 1–12. [PubMed: 30240313]
- Wiesman AI, Wilson TW, 2020 Attention modulates the gating of primary somatosensory oscillations. *Neuroimage* 211, 1–12.
- Wilson TW, Heinrichs-Graham E, Becker KM, 2014 Circadian modulation of motor-related beta oscillatory responses. *Neuroimage* 102, 531–539. [PubMed: 25128712]
- Wilson TW, Heinrichs-Graham E, Becker KM, Aloji J, Robertson KR, Sandkovsky U, White ML, O’Neill J, Knott NL, Fox HS, Swindells S, 2015 Multimodal neuroimaging evidence of alterations in cortical structure and function in HIV-infected older adults. *Hum. Brain Mapp* 36, 897–910. [PubMed: 25376125]
- Womelsdorf T, Fries P, Mitra PP, Desimone R, 2006 Gamma-band synchronization in visual cortex predicts speed of change direction. *Nature* 439, 733. [PubMed: 16372022]

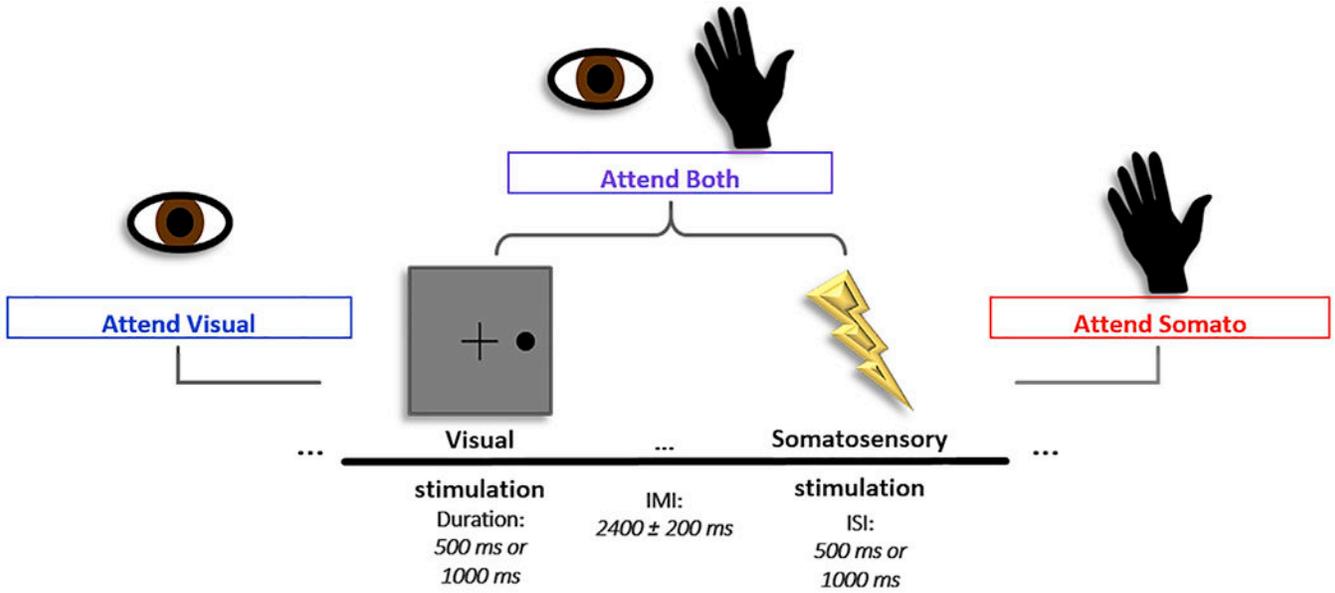


Fig. 1. Visual-Somatosensory Oddball Paradigm.

In each experiment, participants performed two pseudo-randomized, 88-trial blocks; the stimuli were the same, but the instructions differed between blocks. The task consisted of interspersed somatosensory paired-pulse stimulation (ISI: 500 ms) and visual stimuli (duration: 500 ms), separated by a variable inter-modality interval of 2400 ± 200 ms. Eight stimuli for each modality were temporal oddballs (somatosensory ISI: 1000 ms; visual duration: 1000 ms). In Experiment 1 (Directed Attention), participants responded to the oddballs in one domain per block (i.e., “respond to visual oddballs (“attend visual”)” or “respond to somatosensory oddballs (“attend somato”)”, with the order counterbalanced across participants. In Experiment 2 (Divided Attention), participants responded to either the visual oddballs (“attend visual”) or both the visual and the somatosensory oddballs (“attend both”), and again the order of blocks were counterbalanced and only differed by the instructions given. The visual fixation cross was present for the entirety of the task. ISI: inter-stimulus interval, IMI: inter-modality interval.

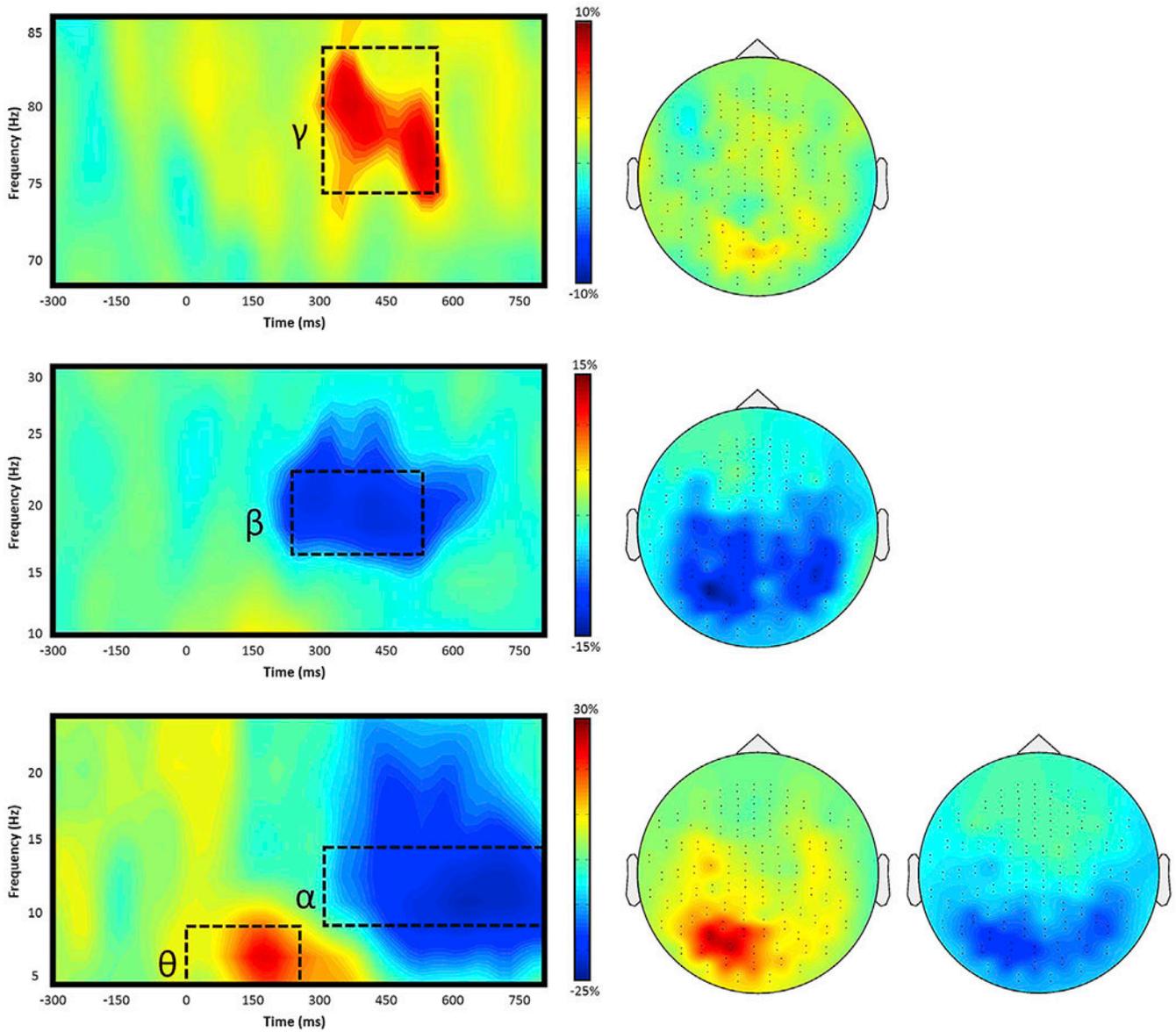


Fig. 2. Sensor-level Spectrograms and Topographical Maps for Directed Attention Experiment. (Bottom) Spectrogram from a MEG sensor near the occipital cortices (M2512) shows the significant synchronization or increase in theta activity (4–8 Hz; 0–250 ms) and the desynchronization or decrease in alpha activity (8–14 Hz; 300–800 ms). (Middle) Spectrogram from a representative sensor (M0222) near the parietal cortices showing the significant desynchronization in the beta band (16–22 Hz; 225–525 ms). (Top) Spectrogram showing the significant synchronization or increase in gamma activity (74–84 Hz; 300–550 ms) in a sensor (M2343) near the occipital cortices. Across all spectrograms, time (in ms) is denoted on the x-axis and frequency (in Hz) denoted on the y-axis. The dashed rectangles frame the time-frequency bins that were imaged for sourcelevel analysis. To the right of each spectrogram is its corresponding topographical map(s). In between the two, is a color scale bar denoting percent change from baseline.

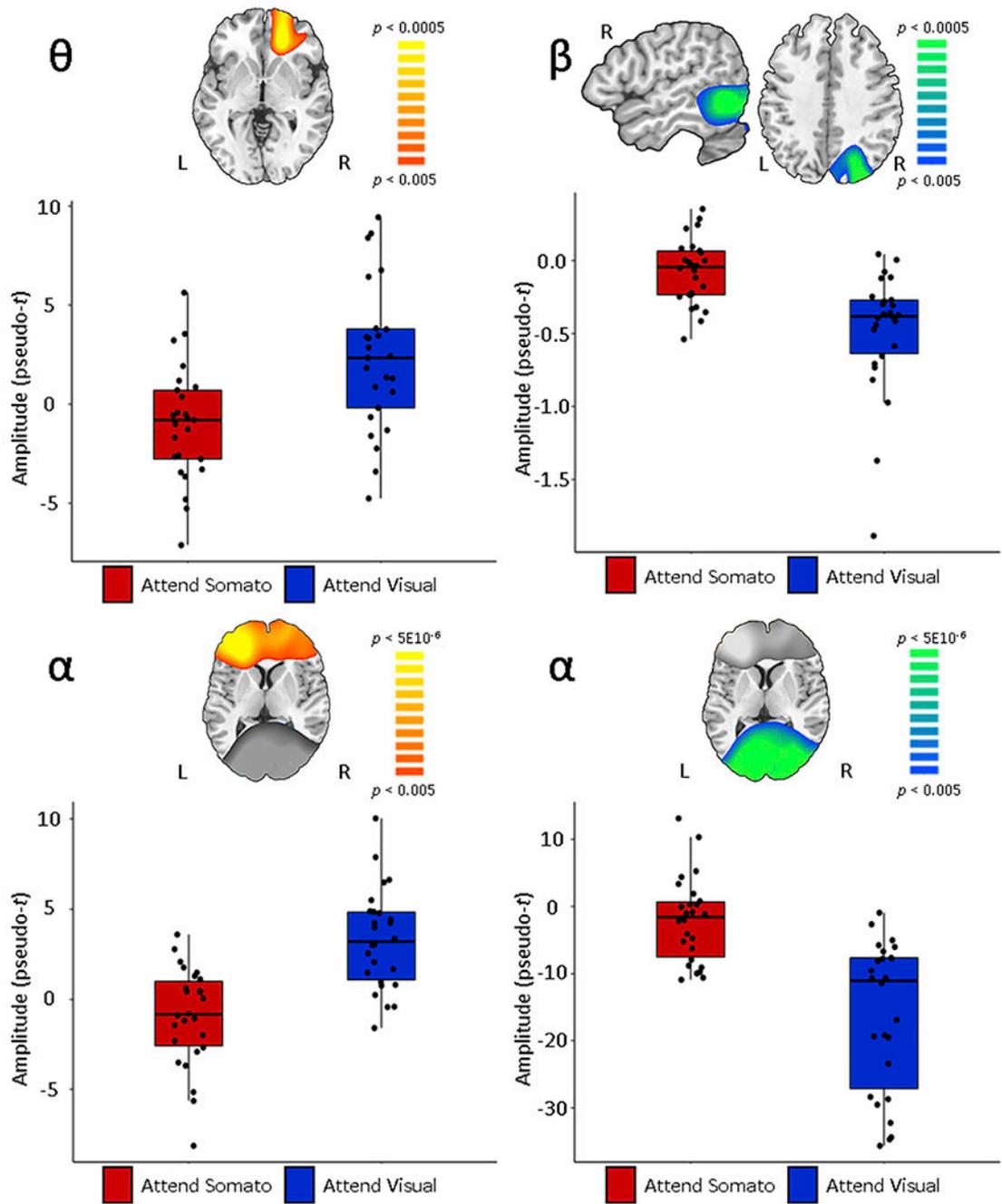


Fig. 3. Effects of Directed Attention on Neural Oscillatory Responses.

Directing attention toward the visual domain, relative to away from the visual domain, significantly altered oscillatory responses in the theta, alpha, and beta bands, and these differences survived stringent cluster-based permutation testing. The images above are statistical maps (paired t-tests) between the “attend somatosensory” and “attend visual” conditions, with corresponding p -values shown using the color scale bars to the right of each image. Box and whisker plots below each map show amplitude data extracted from the peak voxel for each of these effects, with amplitude denoted (in pseudo- t) on the y-axis. Each plot

includes the individual data points, median (horizontal line), first and third quartile (box), and local minima and maxima (whiskers). Points falling outside of the whiskers are more than 1.5 times the interquartile range above or below the third and first quartiles, respectively, and are plotted as such for visualization purposes.

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

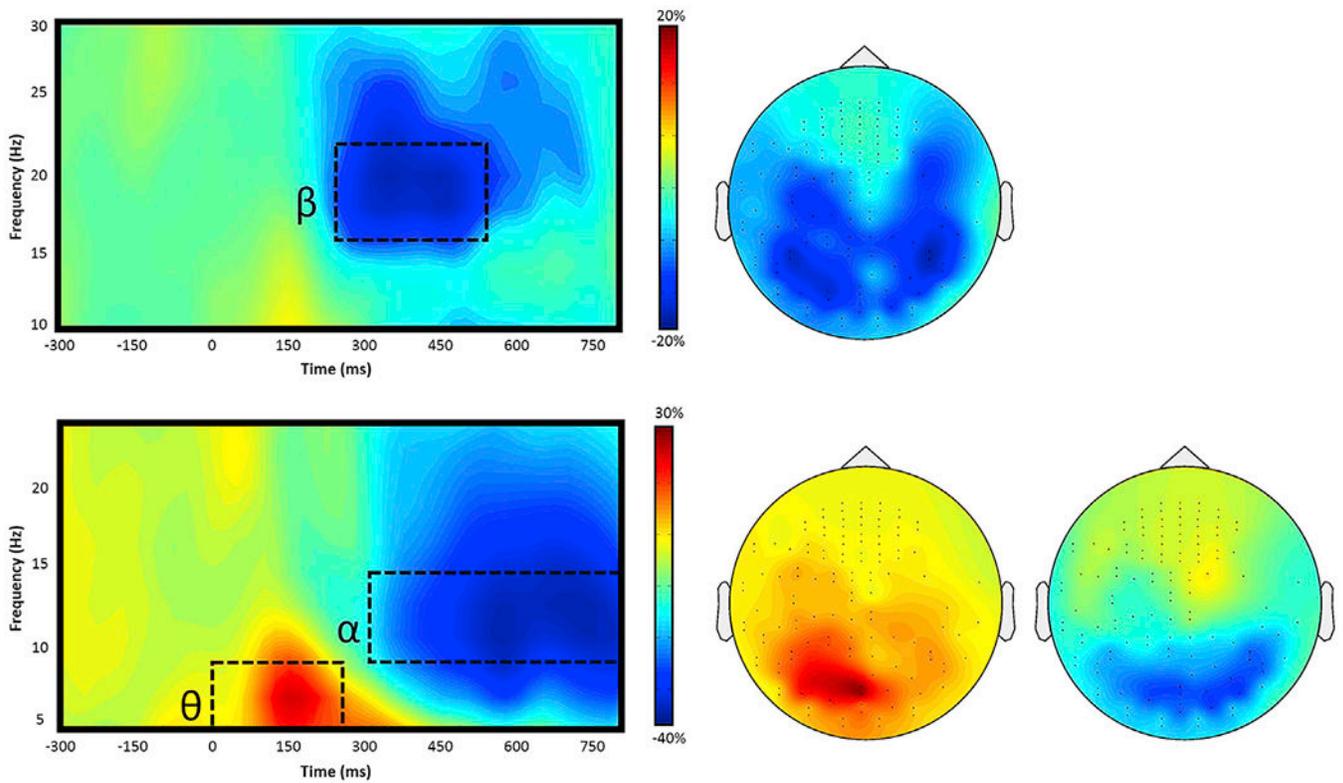


Fig. 4. Sensor-level Spectrograms and Topographical Maps for Divided Attention Experiment. (Bottom) Spectrogram of occipital sensor M2512 showing the significant posterior synchronization of theta (4–8 Hz; 0–250 ms) and desynchronization of alpha (8–14 Hz; 300–800 ms) activity. (Top) Spectrogram from a representative parietal sensor (M0222) showing the significant desynchronization in posterior beta activity (16–22 Hz; 225–525 ms). Across both spectrograms, time (in ms) is denoted on the x-axis and frequency (in Hz) is denoted on the y-axis. The dashed rectangles frame the time-frequency bins that were imaged for sourcelevel analysis. To the right of each spectrogram is its corresponding topographical map(s). In between the two, is a color scale bar denoting percent change from baseline.

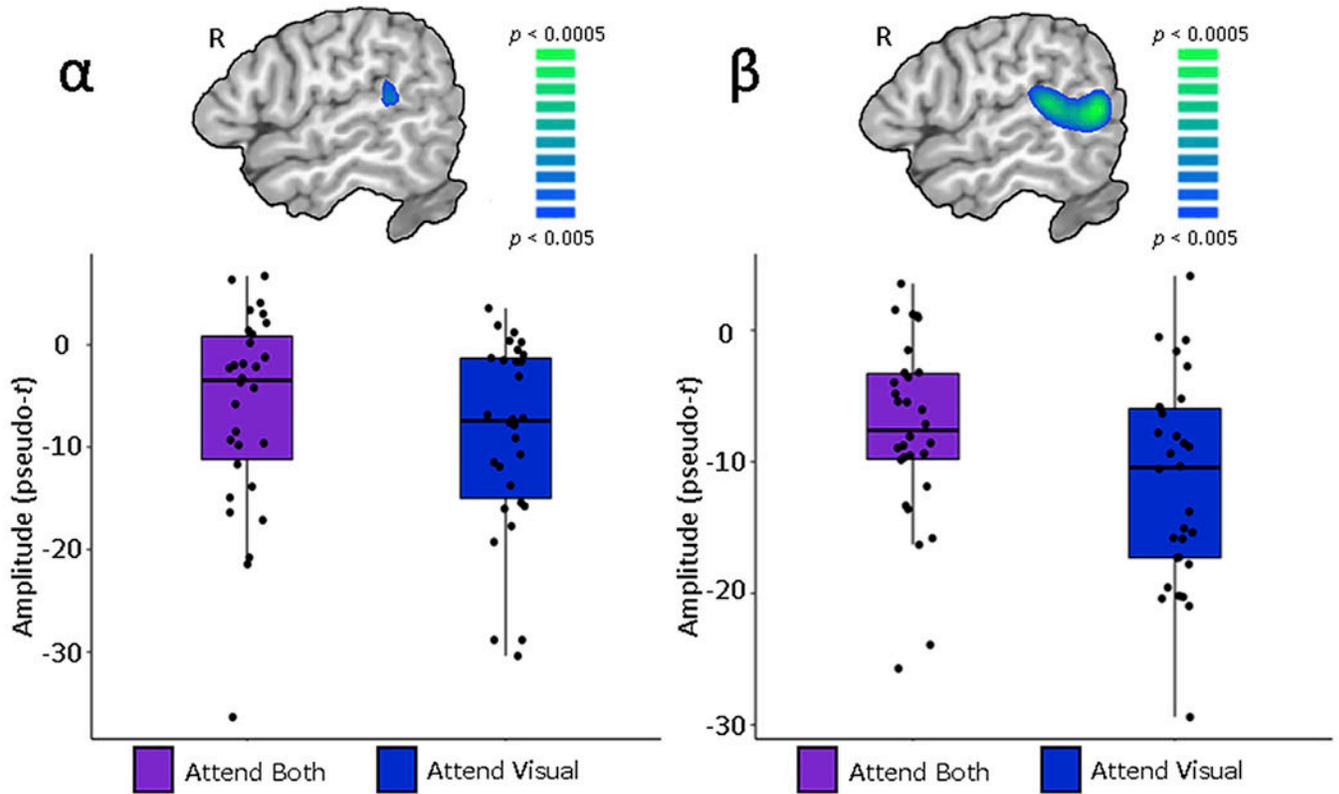


Fig. 5. Effects of Divided Attention on Neural Oscillatory Responses.

Dividing attention between visual and somatosensory domains compared to focusing on the visual domain significantly modulated oscillatory responses in the alpha and beta frequencies at the right temporoparietal junction, and these differences survived stringent cluster-based permutation testing. The images above reflect statistical maps following voxel-wise paired *t*-tests between the “attend both” and “attend visual” conditions, with corresponding *p*-values shown using the color scale bars to the right. Box and whisker plots below represent the extracted peak voxel amplitudes for each of these effects, with amplitude denoted (in pseudo-*t*) on the y-axis. The box and whisker plots follow the same design as was described in Fig. 3.