

Comparing the Effects of 10-Hz Repetitive TMS on Tasks of Visual STM and Attention

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Abstract

■ Numerous studies have demonstrated that visual STM (VSTM) and attention are tightly linked processes that share a number of neuroanatomical substrates. Here, we used repetitive TMS (rTMS) along with simultaneous EEG to examine the causal relationship between intraparietal sulcus functioning and performance on tasks of attention and VSTM. Participants performed two tasks in which they were required to attend to or remember colored items over a brief interval, with 10-Hz rTMS applied on some of the trials. Although no overall be-

havioral changes were observed across either task, rTMS did affect individual performance on both the attention and VSTM tasks in a manner that was predicted by individual differences in baseline performance. Furthermore, rTMS also affected ongoing oscillations in the alpha and beta bands, and these changes were related to the observed change in behavioral performance. The results reveal a causal relationship between intraparietal sulcus activity and tasks measuring both visual attention and VSTM. ■

INTRODUCTION

Over the past several years, numerous studies have attempted to identify the neural mechanisms that mediate the online maintenance of information in visual STM (VSTM). Critically, although it is clear that the amount of information that can be stored in VSTM is severely limited (Bays & Husain, 2008; Cowan, 2001), the factors that determine this limit remain elusive.

The Role of Intraparietal Sulcus in VSTM

Influential studies using fMRI identified activity in the intraparietal sulcus (IPS) as relating to the maintenance of information in VSTM. In these studies, BOLD signal was found to increase in the IPS as the number of to-be-remembered items increased (Xu & Chun, 2006; Todd & Marois, 2004). Importantly, this activity exhibited an asymptote around three to four items, which is consistent with the putative capacity limit of VSTM (Cowan, 2001), and correlated with individual differences in VSTM performance (Todd & Marois, 2005). Studies using EEG and magnetoencephalography have also observed low-frequency activity, isolated largely to regions of the IPS, that similarly seems to reflect the online maintenance of visual information (Mitchell & Cusack, 2011; Robitaille et al., 2010; Robitaille, Grimault, & Jolicoeur, 2009; Vogel

& Machizawa, 2004); this activity, referred to as the contralateral delay activity (CDA) or the sustained posterior contralateral negativity, appears to track with the number of items maintained in VSTM and correlates with individual differences in VSTM capacity (Vogel & Machizawa, 2004). Importantly, the fact that these signals do not continue to increase at loads beyond an individual's VSTM capacity has historically been used as evidence against attentional contributions to VSTM capacity limits, on the assumption that attentional demands continue to increase even if VSTM storage does not.

There have been a number of recent findings, however, that call into question whether these sustained increases in IPS activity mediate the representation of information in VSTM. For example, fMRI studies using multivoxel pattern analysis to decode the contents of VSTM have failed to find activity in the IPS that is associated with the specific contents of VSTM (Emrich, Riggall, Larocque, & Postle, 2013; Linden, Oosterhof, Klein, & Downing, 2012; Riggall & Postle, 2012; but see, Ester, Sprague, & Serences, 2015; Christophel & Haynes, 2014; Christophel, Hebart, & Haynes, 2012). Instead, these studies have observed content-specific activity in regions of sensory visual cortex (e.g., V1, V2, MT+), consistent with the idea that sensory regions may mediate STM processes (e.g., Postle, 2006; Pasternak & Greenlee, 2005).

Further evidence against a role for IPS that is specific to VSTM maintenance comes from the finding that similar capacity-limited increases in IPS activity are observed in tasks that have no explicit memory demands. In one study conducted by Mitchell and Cusack (2008), participants had

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to either maintain between one and eight colored items in VSTM over a retention interval, or, in a separate task, they monitored a set of continuously visible colored items for a change in luminance. Consequently, in the “extended spatial and temporal attention” task, participants had to attend to multiple visual objects over a period. Although there was no requirement in the latter task to maintain these items in VSTM (because they remained present in the display throughout the task), similar increases in activity were observed in both tasks; in other words, a capacity-limited increase in IPS activity was observed when multiple visual objects had to be attended but not remembered. Interestingly, a similar effect has recently been observed when examining the CDA, which is assumed to reflect the maintenance of information in VSTM (Tsubomi, Fukuda, Watanabe, & Vogel, 2013). Specifically, the amplitude of the CDA increased with increasing load up to around three to four items, even when those items remained present in the display, and thus, there was no requirement to store the information in VSTM. Together, these findings suggest that the load-dependent, capacity-limited activity observed in the IPS may be associated with attentional, rather than VSTM, constraints (Magen, Emmanouil, McMains, Kastner, & Treisman, 2009). Other studies have observed similar capacity limitations in the IPS during enumeration (Knops, Piazza, Sengupta, Eger, & Melcher, 2014) and multiple object tracking (Howe, Horowitz, Morocz, Wolfe, & Livingstone, 2009). Indeed, at a theoretical level, findings like these have been taken as evidence that mechanisms responsible for storage in VSTM tasks may be “nothing more” than covert attention directed to internal representations (e.g., Postle, 2015; Kiyonaga & Egner, 2013; Theeuwes, Olivers, & Chizk, 2005). (This perspective becomes more nuanced when one considers that items in VSTM can be held in different states of prioritization [e.g., LaRocque, Lewis-Peacock, & Postle, 2014], but considerations of the strategic control of the contents of VSTM are beyond the scope of this article.)

The Role of Alpha-Band Oscillations in VSTM

An additional mechanism that has been proposed to play a role in supporting the maintenance of information in VSTM is the modulation of neural activity in the alpha (8–12 Hz) frequency band. Specifically, a number of studies of VSTM have observed systematic variation in delay-period alpha-band power that relates monotonically to memory load (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). Alpha-band dynamics may also predict individual differences in VSTM performance (Palva, Monto, Kulashekhar, & Palva, 2010; Sauseng et al., 2009) and have been proposed as the neural basis of the CDA (van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010; but see Fukuda, Mance, & Vogel, 2015). Importantly, these VSTM-related changes in alpha-band power have been

shown to originate in the IPS, the region sometimes associated with VSTM maintenance (Palva et al., 2010).

Further evidence for the role of alpha-band oscillations in VSTM performance comes from the use of TMS. Specifically, previous studies using 10-Hz repetitive TMS (rTMS) during the maintenance period of VSTM tasks, combined with EEG, have found changes in VSTM performance that are associated with changes in delay-period alpha-band power. For example, Hamidi, Slagter, Tononi, and Postle (2009) applied 10-Hz rTMS to the superior parietal lobule during the delay period of a spatial and object working memory task. The resulting rTMS-related change in power predicted the change in accuracy in the spatial working memory task. Although it is possible that this change resulted from the local, phase-dependent entrainment of 10-Hz oscillations (Thut et al., 2011), a comparison of the EEG effects of 10-Hz flicker entrainment suggests a different mechanism for 10-Hz rTMS (Johnson, Hamidi, & Postle, 2010). Rather, we have proposed that 10-Hz rTMS, applied to the parietal lobe, may bias the power of endogenous ongoing oscillatory activity, resulting in changes in memory performance. In keeping with this possibility, we note that the frequency band affected by 10-Hz rTMS in the Hamidi et al. (2009) study (10–15 Hz) spanned the classical boundary between “high alpha” and “low beta” and that the task-related change in this band was evident in no-rTMS conditions.

Although these findings provide causal evidence that delay-period alpha-band dynamics contribute to capacity limits in VSTM, it is not clear whether these effects are specific to memory maintenance per se. That is, given the evidence for the potential role of IPS activity in attentional as well as memory tasks, it is possible that delay-period alpha-band power may similarly play a role in attentional tasks. Supporting this possibility, several studies have reported alpha-band power increases in attention tasks that include no explicit mnemonic component (see, e.g., Snyder & Foxe, 2010; Doesburg, Roggeveen, Kitajo, & Ward, 2008; Worden, Foxe, Wang, & Simpson, 2000). Most compellingly, two recent studies have shown that, with EEG data band-pass filtered to the alpha band, it is possible to reconstruct both the locus of spatial VSTM (Foster, Sutterer, Serences, Vogel, & Awh, 2016) and the locus of covert spatial attention (Samaha, Sprague, & Postle, 2016) using a multivariate inverted encoding modeling approach.

Whether the function of delay-period alpha-band dynamics relates to stimulus representation per se, or some other function, remains a topic of intense research. One influential account emphasizes a sensory inhibition role for alpha-band power during VSTM (Jensen & Mazaheri, 2010; Sauseng et al., 2009; Klimesch et al., 1999). Thus, as with the case of IPS activity observed in fMRI studies, alpha-band modulations may not reflect the direct representation of information in VSTM but may instead reflect processes associated with a number of tasks, including VSTM.

This Study

In this study, we used anatomically targeted TMS and simultaneous EEG to explore commonalities and possible differences in the contributions of the IPS and of low-frequency oscillatory dynamics to two nominally different classes of behavior—VSTM and visual attention. We applied rTMS to the left inferior IPS (iIPS) because this area has been most closely associated with the selection and maintenance of a limited number of objects in VSTM (Xu & Chun, 2006). We modeled our tasks after the VSTM and “extended spatial and temporal attention” tasks of Mitchell and Cusack (2008) because these had yielded similar patterns of behaviorally linked covariation in iIPS fMRI signal. We chose an rTMS protocol of “online” 10-Hz delay-period stimulation because this protocol has produced individual differences in delay-period power in the high-alpha/low-beta band of the EEG that covaries with its effects on behavior.

METHODS

Participants

Seventeen participants (eight women; age = 20–28 years, $M = 21.8$ years) were recruited from the University of Wisconsin-Madison community. All participants provided informed consent and were screened for the presence of neurological and psychiatric conditions as well as risk factors specific to the application of TMS. All study protocols were approved by the University of Wisconsin-Madison Health Sciences institutional review board. Three participants were not included in the analysis because of failing to complete all of the experimental blocks, failing to adequately understand task instructions, or having excessive amplifier/channel noise, resulting in 14 participants.

Stimuli and Procedures

Experimental Tasks

The main experimental procedure was adapted from two conditions used by Mitchell and Cusack (2008). Specifically, we used modified versions of their VSTM task and extended spatial and temporal attention task, referred to here as the attention task (Figure 1A).

Each trial began with the presentation of an instruction screen, presented for 2000 msec. The words “Remember” or “Detect” were presented and instructed the participant that the task for the following trial was to either remember the sample colors (the VSTM task) or detect a change to one of the colors presented on the screen (the attention task). After the instructions, a black fixation cross was presented against a gray background at the center of the display for 1000–1400 msec, randomly jittered on each trial. After the fixation, four colored circles were presented at 1 of 18 equally spaced locations equidistant from the fixation point. The sample stimuli subtended approximately $\sim 1^\circ$ visual angle and were presented 4.5° from the central fixation at a distance of ~ 57 cm. Colors were randomly selected from one of eight potential colors: red (RGB = 230, 0, 0), orange (230, 115, 0), yellow (230, 230, 230), dark blue (0, 0, 230), light blue (230, 115, 0), cyan (0, 230, 230), magenta (230, 0, 230), and green (0, 230, 0). Colors were generated from the Hue–Saturation–Value (HSV) color space and were set to be 90% of the maximal luminance value. The sample (color) stimuli were presented for 150 msec in the VSTM condition, followed by a 1450-msec delay period in which only the fixation was displayed. In the attention condition, the sample stimuli remained on the display for a full 1600 msec. During the attention task, on 50% of the trials, one of the colored circles would decrease in luminance for 32 msec (two frame refreshes). The change in

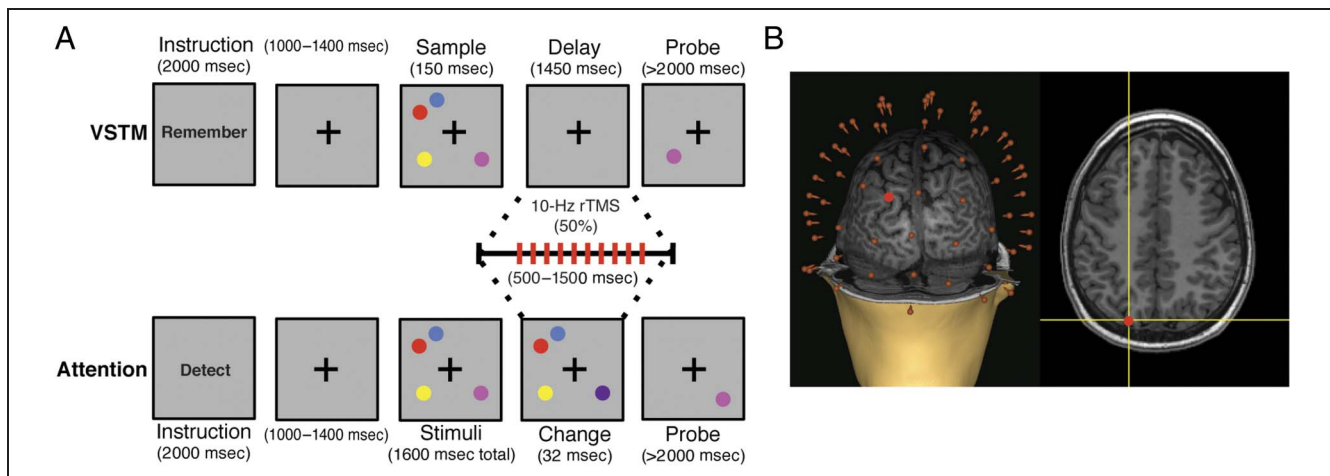


Figure 1. Experimental tasks and site of rTMS stimulation. (A) Schematic of experimental paradigms. In the VSTM task, participants were instructed to detect a change to the location of one of the items presented in the sample. In the attention task, participants had to indicate whether the item indicated in the probe display had briefly changed luminance during the trial. In both tasks, 10 pulses of rTMS were delivered at 10 Hz between 500 and 1500 msec on half of the trials. (B) The location of rTMS stimulation for a typical participant, as indicated by the red dot. For each participant, rTMS pulses were delivered to the left iIPS. The channel locations relative to the site of stimulation are indicated in the left.

luminance occurred randomly between 860 and 1360 msec, in 100-msec intervals, and the degree of luminance change varied across participants (see below). On half of the trials, orthogonal to the factor of stimulus change, participants received 10 TMS pulses between 500 and 1500 msec after the onset of the sample stimuli (see TMS Targeting and Stimulation procedures below). In both tasks, a probe display, which contained a single colored circle, was presented 1600 msec after the onset of the sample display. In the VSTM task, participants indicated whether the presented color was the same color that was presented in that location during the sample display. On 50% of the trials, a change occurred in which the probe color was sampled from one of the three other presented colors. This required memory for the bound item and location, which has been associated with greater alpha-band power at parietal electrodes than memory for only location (Johnson, Sutterer, Acheson, Lewis-Peacock, & Postle, 2011). In the attention task, participants indicated whether the luminance of the probed color had changed during the trial. The probe display remained on for 2000 msec or until a response, up to 3000 msec, after which no response was recorded. Each trial was followed by an 850-msec intertrial interval. Participants performed 20 trials of both tasks in each block (10 each with and without TMS stimulation), and each participant performed eight blocks for 80 trials per condition. Trial order was fully randomized within each block. An additional condition in which participants passively viewed a fixation cross and received TMS stimulation was also presented (10 trials per block, randomly assigned), although data from those trials will not be presented here.

Baseline Tasks

Before performing the experimental tasks, participants performed two tasks that were used to assess baseline performance and to attempt to equate performance on the attention task with that on the VSTM task. The first task was a change detection task that was similar to the VSTM task, with the following exceptions: Participants were instructed to remember the colors of all the items at the beginning of each block. Participants were presented with two, four, or six colored circles, and, after a 900-msec delay period, a probe display containing the same number of items as the sample display was presented. On 50% of the trials, one of the colors would be a new color (sampling without replacement), and participants would be required to indicate whether a change had occurred. Participants performed 50 trials of each set size, in blocks of 25 trials.

The second task was similar to the experimental attention task. This task was used to determine a threshold of luminance change that would prevent ceiling and floor effects during the experimental task. The task was identical to the attention task, with the following modifications: Four colored stimuli were presented for a total duration of 1417 msec. On half of the trials, one of the colors would

decrease in luminance for 32 msec at an unpredictable time between 750 and 1250 msec. As in the experimental task, participants indicated at the end of the trial whether the probe item changed luminance during the trial. Critically, the initial value (V in HSV color space) that the color decreased by was set to 0.1. A staircase procedure was used to identify an approximate 75% threshold. If participants correctly answered three trials in a row, the value was decreased by 0.01, and it was increased by 0.01 when participants answered incorrectly. After five reversals in a row, the task ended, and the upper value between the last reversal was used for the experimental trials. If no final value was obtained after 100 trials, the task was restarted, and the new starting value was used based on the final value from the last run. This method obtained an average change value of 0.076 (range = 0.04–0.12, $SD = 0.018$).

Stimuli were presented on the display surface of a 15-in. Dell Inspiron laptop placed approximately 57 cm from the participant. Stimuli were generated in MATLAB (The MathWorks, Natick, MA) and delivered using the Psychophysics Toolbox (Brainard, 1997).

Behavioral Analysis

Behavioral performance in both VSTM and attention tasks, as well as in the VSTM baseline task, was analyzed by calculating the capacity estimates, K , for each task using the formula $K = S \times (H - FA)$, where S is equal to the number of sample items and H and FA are the hit and false alarm rates, respectively (Cowan, 2001).

TMS Targeting and Stimulation

TMS was delivered using a focal bipulse, figure-of-eight 70-mm stimulating coil fit to a Magstim Standard Rapid magnetic stimulator (Magstim, Whitland, UK). TMS was targeted using an infrared-based frameless stereotaxy and Navigated Brain Stimulation system (Nexstim, Helsinki, Finland). The area targeted was the left iIPS, which was identified on the basis of individual anatomy from whole-brain T1-weighted anatomical MRIs acquired with a GE MR750 3-T MRI scanner before the experiment (176 axial slices, $1 \times 1 \times 1$ mm resolution). The iIPS was identified as the region in the sulcus running along the sagittal plane between the occipital and parietal lobes and immediately dorsal to the parieto-occipital fissure (Figure 1B). Stimulation intensity was set at 110% of the participant's resting motor threshold, which refers to the minimum intensity required to reliably elicit a muscle twitch after TMS of the hand area of the primary motor cortex. Stimulation intensity was corrected for each participant's head shape and scalp-to-cortex distance as well as coil position. Estimated stimulation intensity ranged from 54 to 128 V/m (35–82% of stimulator output, $M = 72\%$). The coil was oriented with the handle running caudally to the head, resulting in an induced current running in the anterior–posterior direction along the sulcus. Critically, coil position and orientation

were held constant within participants, and trial order was randomized within each block. Coil position was verified and corrected for a minimum of every two blocks (100 trials) or as needed. Participants were also presented with a masking noise delivered through earplugs to avoid contamination of the EEG by auditory artifacts produced by the TMS coil's discharge. The volume of the masking noise never exceeded 90 dB and was calibrated for each participant's own threshold for perceiving the TMS discharge.

EEG Recording

EEG was recorded with a 60-channel TMS-compatible amplifier (Nexstim). The amplifier prevents saturation by the TMS pulse with a sample-and-hold circuit that maintains a constant output from 100 μ sec before until 2 msec after the TMS pulse (Virtanen, Ruohonen, Näätänen, & Ilmoniemi, 1999). The impedance at each electrode was also kept below 5 k Ω to reduce residual TMS artifacts. The data were recorded with a right mastoid reference, and eye positions were recorded with two additional electrodes placed \sim 1 cm outside the external canthi of each eye. Data were sampled at 1450 Hz with 16-bit resolution.

Data Preprocessing

Data processing was conducted using the EEGLAB toolbox (Delorme & Makeig, 2004) and the ERPLAB toolbox (Lopez-Calderon & Luck, 2014). Data were rereferenced to the common average reference and down-sampled to 500 Hz. Data were band-pass filtered between 1 and 100 Hz. Noisy or bad channels were identified and reinterpolated with spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989). Data were then segmented into individual trials and subjected to independent component analysis to isolate and remove artifacts associated with muscle activity, eye movements, and blink-related activity as well as any residual TMS-related artifacts (Jung et al., 2000). This procedure has previously been shown to be effective at removing TMS-related artifacts while leaving the underlying EEG activity intact (Hamidi, Slagter, Tononi, & Postle, 2010).

Data Analysis

To examine the effect of TMS on delay-period alpha-band power, the spectral transform of the data was calculated using the FieldTrip toolbox (freely available at fieldtrip.fcdonders.nl/; Oostenveld, Fries, Maris, & Schoffelen, 2011). Oscillatory power was estimated using a frequency-dependent sliding window. The window length was six cycles/frequency of interest (1–60 Hz, in 1-Hz steps), applied in time steps of 25 msec throughout the 2500-msec trial (including a 500-msec prestimulus baseline period). The data from each time window were multiplied by a Hanning taper and Fourier-transformed, and the power spectral densities were averaged over trials. Baseline cor-

rection was done by subtracting the mean spectral power from the 500-msec prestimulus period on a trial-by-trial basis.

Of critical interest for this study was individual differences in alpha-band power and behavior in both the VSTM and attention tasks with and without TMS. Consequently, those channels that demonstrated significant ($p < .05$) change in rTMS-related alpha-band power were identified and examined for further analysis using cluster-based permutation testing (Maris & Oostenveld, 2007) implemented using the Fieldtrip toolbox in MATLAB. Cluster-based permutation testing is a nonparametric statistical procedure used for identifying differences between conditions in time, frequency, and space while controlling for the family-wise error rate. Clusters corresponding to significant differences ($p < .05$) between TMS-present and TMS-absent averaged over the alpha (8–12 Hz) range and over a window of 600–1600 msec after stimulus onset were identified using 500 random permutations.

RESULTS

Behavioral Results

To determine the effect of 10-Hz rTMS on performance, capacity estimates (K) for both the VSTM and attention tasks were examined with and without TMS. The results revealed that a similar number of items were remembered (VSTM) or attended (attention) in both tasks, independent of TMS condition (Figure 2A). This was confirmed by a 2 (Task) \times 2 (TMS condition) repeated-measures ANOVA, which revealed no significant effects or interaction (all F s $<$ 2.6, p s $>$.13).

Individual Differences

Relation between VSTM and Attention Performance

To examine whether performance on the two tasks was related, we correlated performance between tasks, both with and without rTMS. This analysis revealed no significant relation between capacity estimates on either the VSTM or attention tasks, r s $<$ $-.21$, p s $>$ $.47$. Thus, although performance on the two tasks was similar across the groups, this was not tied to individual performance. This finding is explored further in the Discussion.

Relation between Tasks with and without rTMS

Although the ANOVA failed to find evidence for an effect of 10-Hz rTMS on behavior at the group level, previous studies have demonstrated that the effect of TMS can vary between individuals. For example, we have previously reported, on a test of spatial VSTM, that the same rTMS protocol can produce improved performance in some participants and impaired performance in others and in a manner that is predicted by individual differences in the effects of rTMS on the delay-period EEG in the 10- to 15-Hz

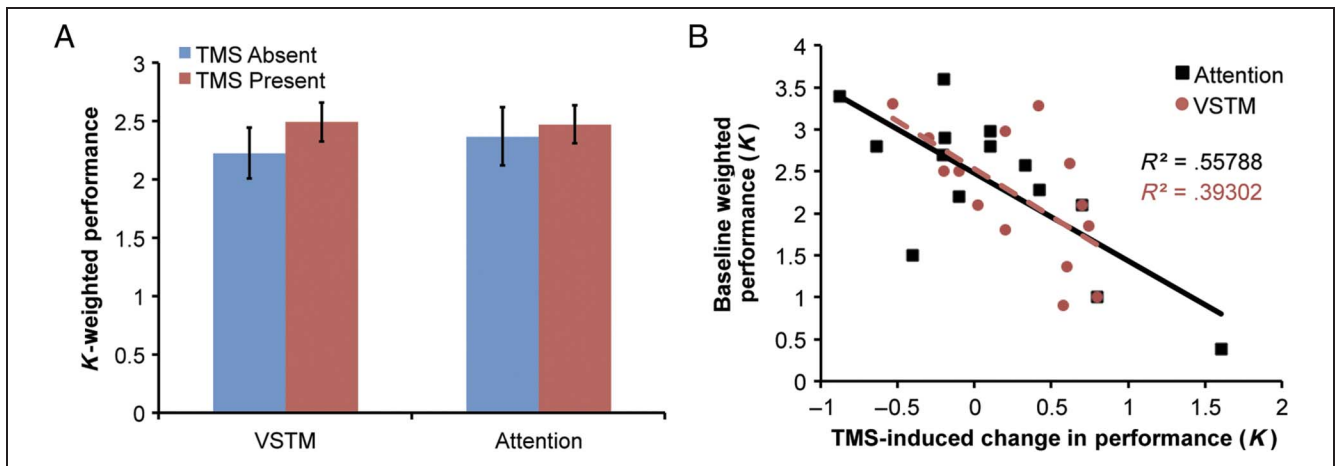


Figure 2. Behavioral results. (A) Mean K -weighted performance on the VSTM and attention tasks with and without 10-Hz rTMS. (B) Relation between baseline (no-TMS) K estimates and the resulting change in K estimates.

range (Hamidi et al., 2009). Consequently, to examine potential individual differences in the effect of rTMS on performance, we correlated capacity in the no-rTMS condition with the TMS-related change in performance (rTMS minus no-rTMS). This analysis revealed significant interindividual differences in the effect of rTMS on behavior for both tasks: VSTM, $r(12) = -.63, p = .016$; attention, $r(12) = -.75, p = .002$ (Figure 2B). That is, for both tasks, individuals whose baseline capacity was high tended to show decreases in performance when 10-Hz rTMS was applied, whereas those participants who started off with a lower capacity tended to show improvements. (Note that the K estimates derived from the rTMS-absent condition of the experimental

VSTM task correlated with K estimates derived from the baseline VSTM task, $r(12) = .627, p = .016$, suggesting stable estimates of individual differences in capacity.)

Given these observed relationships, most of the EEG analyses focus on individual differences—specifically, those related to rTMS-related changes.

EEG Results

Time-Frequency Analysis

No-rTMS trials. As illustrated in Figure 3A, both tasks produced marked changes in power in the 10- to 13-Hz

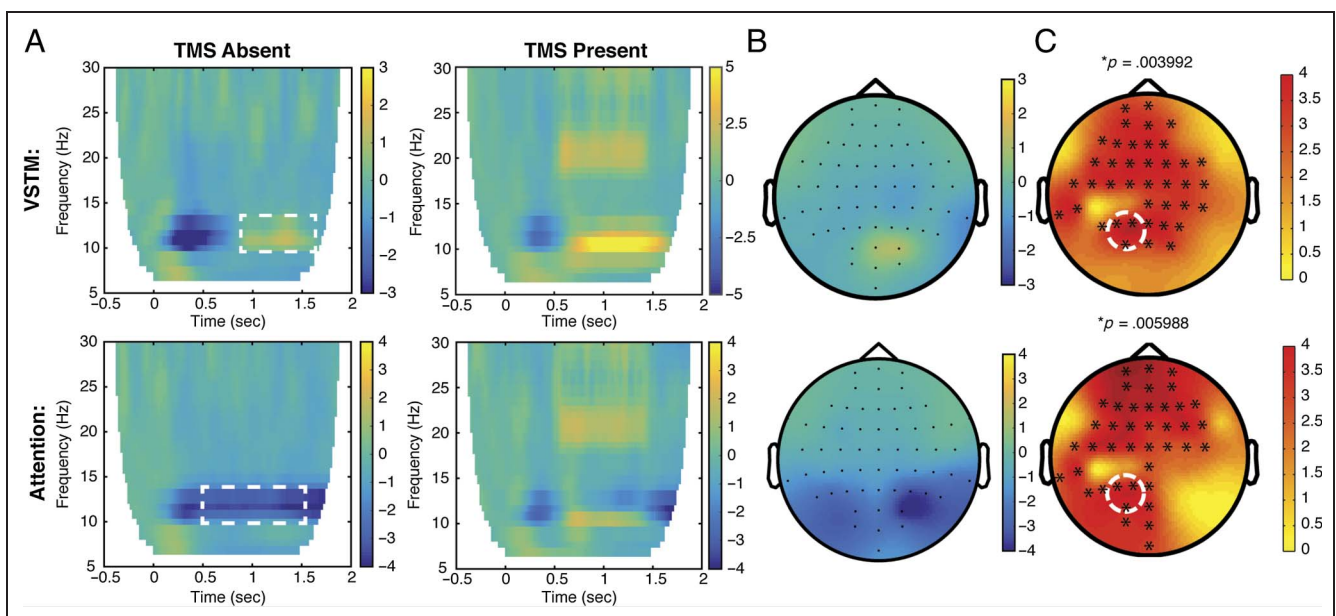


Figure 3. Time-frequency spectra, topographies, and cluster-based tests for the VSTM (top) and attention (bottom) tasks. (A) Time-frequency spectra over the posterior channels for TMS-absent (left) and TMS-present (right) trials. White lines indicate windows for generating topographies. Color denotes power in decibels. (B) Topographical plot of the high-alpha/low-beta (10–13 Hz) power window in the TMS-absent conditions between ~900 and 1500 msec (in decibels) in the VSTM task (top) and between ~500 and 1500 msec in the attention task (bottom). (C) Topographies of cluster-based permutation tests between the TMS-present and TMS-absent conditions within the alpha 8- to 12-Hz range. Starred channels indicate significant differences.

range (“high alpha/low beta”) across posterior electrodes, although the pattern differed across the two. In the absence of rTMS during the VSTM task, after an initial decrease in power in this range, there was a clear increase in the 10- to 13-Hz range from around 900 msec to the end of the trial. This increase was observed primarily over posterior channels (Figure 3B), consistent with previous studies (Johnson et al., 2011; Sauseng et al., 2009; Jensen et al., 2002). In contrast, there was no observable increase in the 10- to 13-Hz range in the attention task. Instead, a significant decrease in 10- to 13-Hz power was observed throughout the trial, with a distribution that was more extensive and included more lateral channels. These results suggest that the VSTM and attention tasks may be supported by different patterns of oscillatory dynamics: Whereas the online maintenance of information in the VSTM task is associated with increases in high-alpha/low-beta power, sustained attention to a visual array is associated with decreases in the same range of frequencies. It is important to note, however, that we cannot rule out the possibility that, despite these differences at the level of measurement from individual electrodes, different (and/or dynamic) patterns can nonetheless underlie a common, stable representation at the population level (e.g., Stokes, 2015; Churchland et al., 2012). An analysis such as multivariate inverted encoding modeling (e.g., Foster et al., 2016) would be necessary to assess this possibility.

Effect of rTMS on low-frequency oscillations. Although, at the group-aggregate level, the VSTM and attention tasks exhibited different patterns of alpha-band dynamics throughout the trials, analyses of the behavioral data indicated that delay-period 10-Hz rTMS affected behavior on the two tasks similarly. To explore whether a similar effect might have been at play in the EEG data, we used a cluster-based permutation approach (see Methods) to identify those channels that demonstrated a significant change in 8- to 12-Hz synchronization—the traditional alpha band—with rTMS compared with no-rTMS in a window from 600 to 1600 msec after the stimulus onset (100 msec offset from the delivery of rTMS pulses). Consistent with previous findings, we observed that 10-Hz rTMS produced a clear increase in 10-Hz power relative to the TMS-absent conditions (Figure 3A, right). Consistent with this finding, in both the VSTM and attention tasks, we observed significant and widespread increases in 8- to 12-Hz oscillations in this window (Figure 3C), confirming that ongoing alpha-band oscillations were affected by rTMS.

Individual Differences Analyses

The primary question of interest for this study was whether rTMS would produce similar changes in both behavior and ongoing oscillations for both the VSTM and attention tasks. Specifically, we aimed to identify whether the observed changes in behavior were associated with individual differ-

ences in changes to the underlying time–frequency spectra. To examine this question, the rTMS-related change in behavior was correlated with the rTMS-related change in power in each time–frequency window, for both tasks. This analysis focused on the electrode sites immediately adjacent to the location of stimulation (CP1, P1, P3) for three reasons: (1) These channels, being directly adjacent to the site of stimulation, should most closely reflect activity in the area of interest—the iIPS; (2) these channels were identified as exhibiting significant changes in alpha-band power from the cluster-based permutation test (Figure 3C); and (3) as noted before, we have previously observed correlations between 10-Hz rTMS-related changes in behavior and changes in power in the 10- to 15-Hz range, in similar channels (Hamidi et al., 2009).

The correlation of rTMS-related changes in EEG power versus behavior revealed significant effects in both the VSTM and attentional tasks. For VSTM, there was an epoch of significant correlation in the 11- to 13-Hz range from ~600 to 800 msec (Figure 4A). Examining the spatial extent of this relationship revealed that the effects were localized primarily to those channels around the site of stimulation (Figure 4B). Extracting the mean power change in this window and correlating it with the change in VSTM performance revealed greater increases in VSTM performance associated with larger increases in alpha power, $r(12) = .655, p = .011$ (Figure 4C). For attention (Figure 4D–F), at the same cluster of electrodes, the epoch of significant rTMS-related EEG behavior correlation was from 1100 to 1200 msec, and the frequency range was 15–17 Hz ($r(12) = .705, p = .005$).

Next, to evaluate the possible relationship of this pattern in the EEG with what we observed in behavior, we conducted a second analysis to determine whether the observed change in alpha-band power was predicted by rTMS-absent baseline VSTM capacity (Figure 5). To do this, we correlated the mean change in 11- to 13-Hz power over the 600- to 800-msec time window with K estimates obtained from performance on rTMS-absent tasks, and this indicated that the changes in 11- to 13-Hz power were predicted by baseline VSTM capacity, $r(12) = -.573, p = .032$ (Figure 5A). Similarly, for the attention task, the baseline estimate of capacity predicted the rTMS-related change observed at 15–17 Hz in the 1100- to 1200-msec window, $r(12) = -.531, p = .051$ (Figure 5B).

DISCUSSION

The aim of this experiment was to examine whether 10-Hz rTMS delivered to the iIPS would affect behavioral performance and neural activity similarly for tasks of VSTM and attention. The results revealed two primary findings. First, 10-Hz rTMS had a similar effect on behavioral performance for the attention and VSTM tasks. Specifically, in both tasks, rTMS produced changes in performance that were tied to individual differences in baseline performance: Participants with a lower baseline performance

exhibited rTMS-related increases in VSTM or attentional capacity, whereas participants with a higher baseline performance exhibited modest rTMS-related decreases in performance. Second, the changes in behavior as a result of rTMS were correlated with changes in neural activity centered on the site of rTMS (i.e., the iIPS). Although these changes occurred in different frequency bands and at different time points, they followed the same pattern, in that, in both conditions, increases in power were positively, linearly related to improvements in behav-

ioral performance, and in both conditions, these effects were larger for individuals with lower baseline capacity estimates.

The Relation between VSTM and Attention Performance

One interesting outcome from these results is the absence of a correlation between the capacity estimates of the VSTM and attention tasks. A study published after

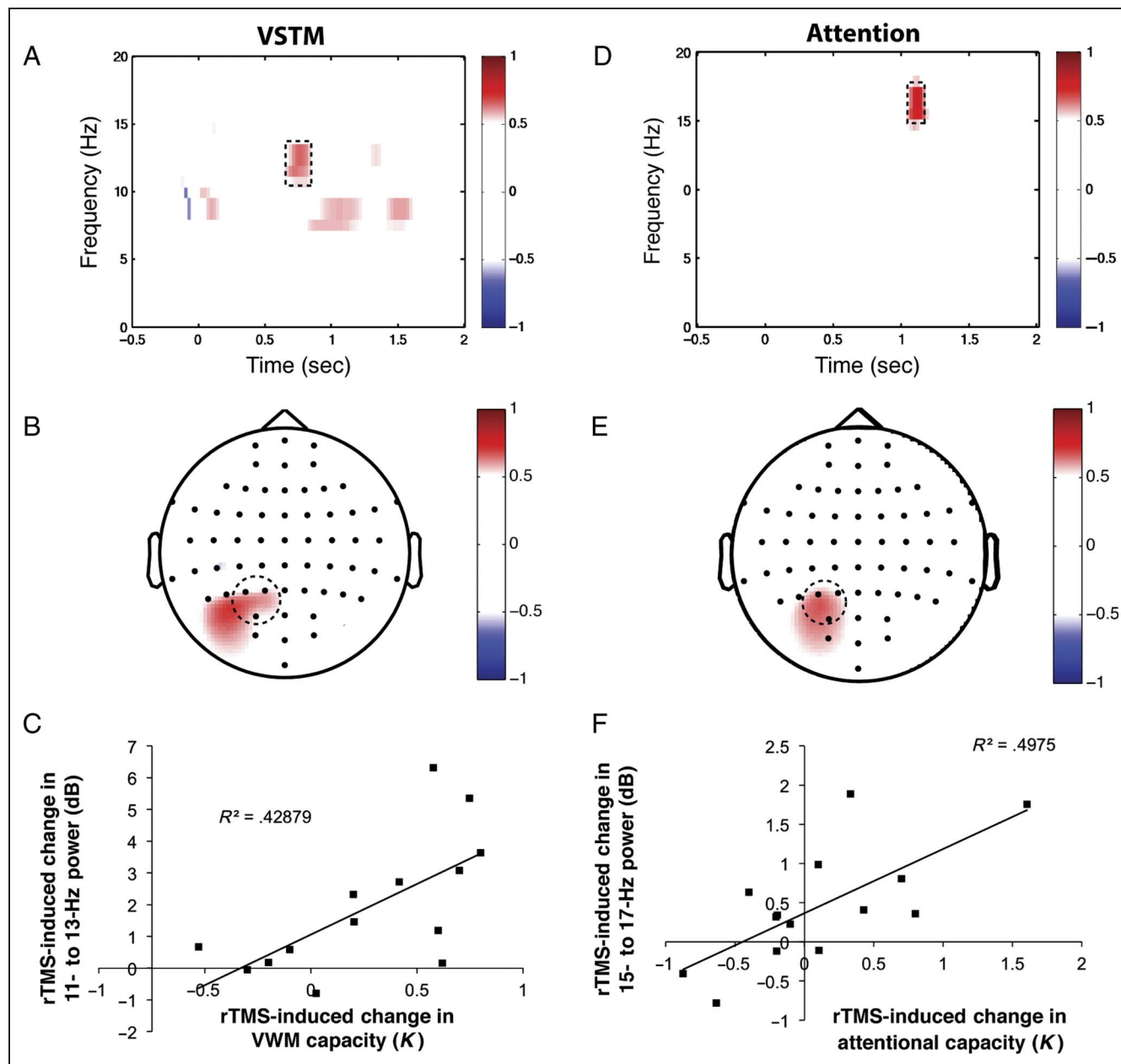


Figure 4. Correlations between rTMS-induced changes in oscillatory power and behavior for the VSTM (A–C) and attention (D–F) tasks. (A) Correlation (r value) between oscillatory power and the rTMS-related change in VSTM (A) and attention (D) capacity estimates as a function of time and frequency over posterior channels of interest (see text). Color bars are thresholded at $p < .05$. (B, E) Topography of peak r values observed in A (i.e., 11–13 Hz between ~600 and 800 msec in the VSTM task) and D (i.e., 15–17 Hz between ~1100 and 1200 msec in the attention task). Channels used in the analysis are highlighted. (C, F) Extracted correlation plot between TMS-related change in VSTM (C) and attention (F) capacity estimates and TMS-related changes in high-alpha/low-beta band power in the channels and time range defined by A and B.

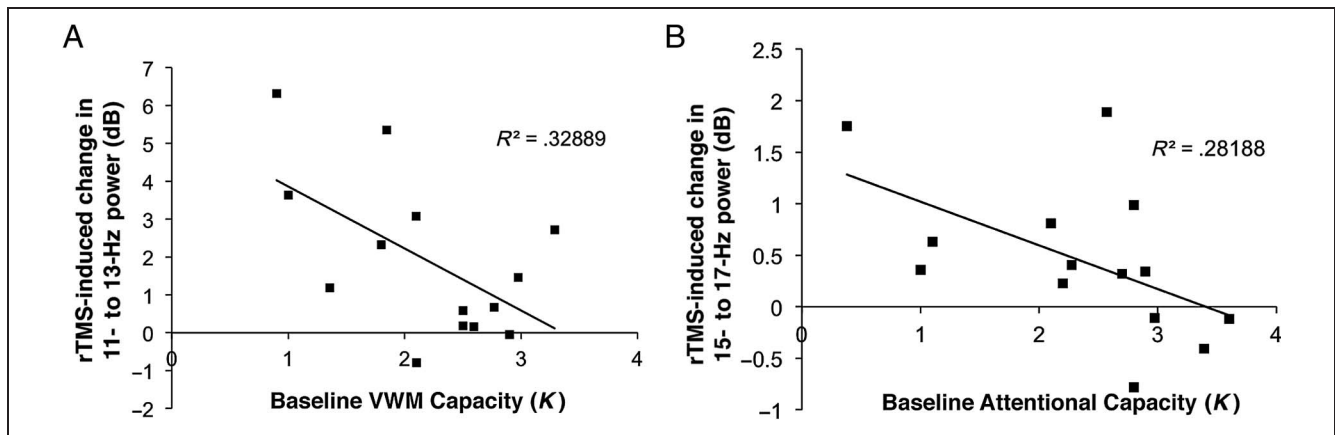


Figure 5. Correlations between baseline capacity and rTMS-induced change in behavior. (A) Correlation between baseline VSTM capacity estimates and change in 11- to 13-Hz power (see Figure 4). (B) Correlation between baseline attention capacity estimates and the change in the 15- to 18-Hz power (see Figure 4).

this study was designed used a different paradigm to compare CDA activity in a VSTM task and in a task without mnemonic demands (Tsubomi et al., 2013). In that study, strong correlations were observed between the number of items that were recalled in the VSTM task and the number of correctly reported items when items remained present in the display. However, in that study, the identities of items had to be reported in both tasks, whereas the attention task used here only required that objects be monitored for a luminance change. Moreover, our task involved a staircase procedure applied to the attention task, which was used to prevent ceiling or floor effects. Consequently, it is possible that different response biases applied to the staircase procedure could have resulted in different baseline performances across the two tasks, thereby uncoupling performance from specific individual capacity limitations. It is possible that, if we had used a task similar to that of Tsubomi et al. (2013), we may have found a stronger relationship between performance on the two tasks. Importantly, although there was no relationship observed between the two tasks, the overall effect of rTMS on behavior, and on neural activity, was similar across both tasks, suggesting that TMS may have affected a similar mechanism contributing to both tasks.

The Relation between VSTM- and Attention-related EEG

In terms of addressing the question of whether delay-period alpha-band power dynamics are similar across VSTM and attention tasks, the results remain mixed. First, a decrease, rather than an increase, in alpha-band power was observed during the delay period in the attention task. This differed dramatically from the activity observed during the VSTM task, in which increased alpha-band power was observed. This observed difference between the two tasks might reflect the fact that the two tasks reflect different processes. By definition, VSTM requires

the selection, encoding, and maintenance of visual information. Consequently, when the items remain on the screen, participants may be engaging the same processes (i.e., selection and encoding), as reflected in the similar early desynchronization in alpha-band power; when the task requirements of the VSTM task change, requiring the maintenance of information no longer present in the display, this is reflected by a change in the resulting neural activity (i.e., an increase in alpha-band synchronization in the VSTM task).

One account of alpha-band power is that it relates to sensory inhibition (Jensen & Mazaheri, 2010; Sauseng et al., 2009; Klimesch et al., 1999). According to this account, information may be “gated” through the use of inhibitory alpha-band synchronization. Accordingly, increased alpha-band power observed during the VSTM task may reflect the sensory gating of potentially distracting events in the environment, whereas the decreases in alpha-band power observed in the attention task may reflect the need to actively monitor and attend to this information (as in the early stages of the VSTM task). Alternatively, decreased alpha in the attention task may reflect the coordination of the parietal and occipital lobes in anticipation of the changing stimulus (Foxe, Simpson, & Ahlfors, 1998). The degree of alpha-band power can also be affected by aspects of the to-be-remembered features, such as whether both shapes and locations are relevant (Johnson et al., 2011). Thus, the role of 10-Hz activity may be dynamic and varied even within tasks, depending on the specific cognitive demands.

In addition, the rTMS-related changes in synchronization occurred in different frequency bands across the two tasks, suggesting that these tasks rely on different patterns of brain activity. It is possible, however, that these differences may be accounted for by the differences between the nature of the two tasks. Previous studies have demonstrated that the effects of TMS on cortical excitability and effective connectivity are task dependent (Johnson, Kundu, Casali, & Postle, 2012) and subject to

individual differences (Kundu, Johnson, & Postle, 2014). Thus, the effects of rTMS on the iIPS may have been affected by the different behavioral requirements of the two tasks. Moreover, although the iIPS may play a role in both tasks, successfully performing the two tasks may require this region to exert its effects on other brain regions in different ways. For example, whereas activity in the alpha-band range may be linked to the role of spatial attention (e.g., Grimault et al., 2009), inhibition (e.g., Jensen & Mazaheri, 2010), or binding (Johnson et al., 2011) in VSTM, successfully perceiving an event may depend on long-range synchronization in the alpha and/or beta band between posterior parietal cortex and frontal and/or extrastriate regions (Kundu, Chang, Postle, & Van Veen, 2015; Gross et al., 2004).

The Effects of 10-Hz rTMS on Task-related EEG

Previously, we have argued that 10-Hz rTMS can influence behavior by biasing endogenous oscillations (Hamidi et al., 2009), rather than by imposing an exogenous rhythm, entraining, or otherwise somehow disrupting brain function (Johnson et al., 2010). For this study, because the functional effects of rTMS were at frequencies that differed from the frequency of stimulation (and its harmonics), we believe that the “biasing” characterization is apt. That is, the effects of 10-Hz rTMS may have been to enhance or otherwise interact with iIPS processes that naturally cycle in the high-alpha/low-beta range. Consistent with this view is the fact that, at rest, the “natural frequency” of anatomically adjacent Brodmann’s area (BA) 7 has been estimated, via EEG responses to single pulses of TMS, to be 18.3 ± 2 Hz. (By contrast, the natural frequency of extrastriate BA 19 has been estimated at 11 ± 1.5 Hz; and that of BA 6 in the precentral gyrus, to be 29 ± 2.0 ; Rosanova et al., 2009). Although our methods do not permit us to measure the circuit-level biophysics of rTMS, the hypothesized “enhancement of ongoing activity” could result from increased levels of stochastic resonance in the iIPS circuits that are experiencing the periodic magnetic flux produced by rTMS (Chanes, Quentin, Vernet, & Valero-Cabré, 2015; Miniussi, Harris, & Ruzzoli, 2013; Schwarzkopf, Silvanto, & Rees, 2011). For this or other accounts, further research will be needed to understand why the enhancing effects of rTMS are greater for lower-performing individuals (as reflected by their low baseline *K*).

Implications for Models of IPS Function

The present findings provide important causal evidence that iIPS is associated with attentional mechanisms in a task that is closely matched to VSTM tasks for which iIPS also plays an important role. Indeed, the present results add to the growing body of studies suggesting that load-dependent activity observed in the IPS during VSTM tasks may reflect the operation of mechanisms that are fundamentally attentional in nature, rather than specific to

VSTM maintenance (Tsubomi et al., 2013; Magen et al., 2009; Mitchell & Cusack, 2008). Indeed, some have suggested that iIPS delay-period activity during tests of VSTM may not reflect the maintenance of information per se (Emrich et al., 2013; Linden et al., 2012; Riggall & Postle, 2012; but see, Christophel & Haynes, 2014; Christophel et al., 2012) but rather an attentional selection mechanism that is common to tasks that involve the selection and enhancement of a limited number of objects. Other such tasks would include enumeration (Knops et al., 2014) and multiple object tracking (Howe et al., 2009).

It is important to note that the results presented here do not speak to the question of functional heterogeneity among different subregions of the IPS. For example, one prominent model holds that the iIPS and superior IPS play different roles in VSTM: Whereas the iIPS may play a role in the selection of a limited number of locations, the superior IPS may play a role in the maintenance of a limited number of object features (Xu & Chun, 2006; cf. Naughtin, Mattingley, & Dux, 2016). From this perspective, our results may be consistent with the role of the iIPS being involved in tasks that require the selection of a limited number of locations or objects.

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