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Recommended Citation

Capotosto, Paolo; Spadone, Sara; Tosoni, Annalisa; Sestieri, Carlo; Romani, Gian Luca; Penna, Stefania Della; and Corbetta, Maurizio, "Dynamics of EEG rhythms support distinct visual selection mechanisms in parietal cortex: A simultaneous transcranial magnetic stimulation and EEG study." *The New England Journal of Medicine*.34,2. 721-730. (2015).
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Dynamics of EEG Rhythms Support Distinct Visual Selection Mechanisms in Parietal Cortex: A Simultaneous Transcranial Magnetic Stimulation and EEG Study

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Using repetitive transcranial magnetic stimulation (rTMS), we have recently shown a functional anatomical distinction in human parietal cortex between regions involved in maintaining attention to a location [ventral intraparietal sulcus (vIPS)] and a region involved in shifting attention between locations [medial superior parietal lobule (mSPL)]. In particular, while rTMS interference over vIPS impaired target discrimination at contralateral attended locations, interference over mSPL affected performance following shifts of attention regardless of the visual field (Capotosto et al., 2013). Here, using rTMS interference in conjunction with EEG recordings of brain rhythms during the presentation of cues that indicate to either shift or maintain spatial attention, we tested whether this functional anatomical segregation involves different mechanisms of rhythm synchronization. The transient inactivation of vIPS reduced the amplitude of the expected parieto-occipital low- α (8–10 Hz) desynchronization contralateral to the cued location. Conversely, the transient inactivation of mSPL, compared with vIPS, reduced the high- α (10–12 Hz) desynchronization induced by shifting attention into both visual fields. Furthermore, rTMS induced a frequency-specific delay of task-related modulation of brain rhythms. Specifically, rTMS over vIPS or mSPL during maintenance (stay cues) or shifting (shift cues) of spatial attention, respectively, caused a delay of α parieto-occipital desynchronization. Moreover, rTMS over vIPS during stay cues caused a delay of δ (2–4 Hz) frontocentral synchronization. These findings further support the anatomo-functional subdivision of the dorsal attention network in subsystems devoted to shifting or maintaining covert visuospatial attention and indicate that these mechanisms operate in different frequency channels linking frontal to parieto-occipital visual regions.

Key words: attention; EEG rhythms; parietal cortex; TMS

Introduction

The allocation of spatial attention to salient environmental stimuli is controlled by a set of regions located in the frontal eye fields (FEFs) and dorsal parietal cortex [i.e., superior parietal lobe (SPL), intraparietal sulcus (IPS), and medial parietal cortex]. These regions form the so-called dorsal frontal-parietal attention network (DAN; Kastner et al., 2000; Corbetta et al., 2002; Serences et al., 2006). In recent years, several fMRI studies have provided evidence for a subdivision of the DAN into (1) medial regions of the SPL, which encode transient signals for shifting attention between spatial locations, and (2) lateral regions in the

posterior IPS, which encode sustained spatially selective signals for maintaining attention at an upcoming target location (Yantis et al., 2002; Shulman et al., 2009; Tosoni et al., 2013). Using repetitive transcranial magnetic stimulation (rTMS), we have recently provided crucial support for this hypothesis by showing a double dissociation between the behavioral effects produced by interference with lateral [right ventral IPS (vIPS)] and medial [right medial SPL (mSPL)] parietal regions (Capotosto et al., 2013). In particular, stimulation over right vIPS impaired target discrimination at contralateral locations, independently of whether the preceding cue instructed a shift of attention or maintenance to the same location (shift vs stay cues); in contrast, stimulation of mSPL impaired target discrimination following the presentation of shift cues independently of which visual field was attended.

Physiologically, the allocation of visuospatial attention is associated with modulations of neural synchronization in frontoparietal and occipital regions (Engel et al., 2001; Fries, 2005; Siegel et al., 2008), with a relative decrement of α/β synchronization and a relative increase of β/γ synchronization. Specifically a desynchronization of the occipitoparietal α rhythms is typically observed in the hemisphere contralateral to the attended visual field before target presentation (Worden et al., 2000; Yamagishi

Received May 21, 2014; revised Sept. 22, 2014; accepted Oct. 12, 2014.

Author contributions: P.C., A.T., C.S., S.D.P., and M.C. designed research; P.C. performed research; S.S. contributed unpublished reagents/analytic tools; P.C. and S.S. analyzed data; P.C., A.T., C.S., G.L.R., S.D.P., and M.C. wrote the paper.

This work was supported by the National Institute of Mental Health, Grant R01 1R01MH096482 (to M.C.). We are grateful to Mauro Gianni Perrucci for technical help.

The authors declare no competing financial interests.

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DOI:10.1523/JNEUROSCI.2066-14.2015

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et al., 2003; Kelly et al., 2006, 2009; Thut et al., 2006). Moreover, increased power at lower frequencies (i.e., δ , 2–4 Hz; θ , 4–8 Hz) has been reported over frontocentral regions following the presentation of attention cues (Klimesch, 2012; Daitch et al., 2013). Interestingly, recent work has suggested that the frontal δ modulates posterior α rhythms, which are instead more related to the tuning of sensory representations (Gomez-Ramirez et al., 2011; Jirsa and Müller, 2013).

Here we employ simultaneous rTMS and EEG methods to test the hypothesis that mechanisms for shifting and maintaining attention engage different patterns of neural synchronization and are selectively affected by interference with neural activity in different parietal regions. Specifically, interference with neural activity in right vIPS during the presentation of stay or shift cues should preferentially affect synchronization/desynchronization of neural oscillations in the contralateral hemisphere, which is consistent with the hypothesis that this region is involved in directing spatial attention at contralateral locations. In contrast, interference with activity of the right mSPL should affect synchronization/desynchronization of neural oscillations following shift cues regardless of spatial location, which is consistent with the hypothesis that this region is involved in shifting attention in a spatially independent manner (Yantis et al., 2002; Shulman et al., 2009; Capotosto et al., 2013).

Materials and Methods

Subjects. Fifteen right-handed (Edinburgh Inventory Index: 0.78 ± 0.2 ; Oldfield, 1971) volunteers (age range: 19–29 years old; nine females), with no previous psychiatric or neurological history, participated in the experiment. Their vision was normal or corrected-to-normal. Participants gave written consent according to the Code of Ethics of the World Medical Association and the Institutional Review Board and Ethics Committee of the University of Chieti. All the subjects participated in our previous fMRI-rTMS study (Capotosto et al., 2013).

Stimuli. Stimuli (Fig. 1a) were generated using Psychtoolbox-3 (Brainard, 1997) and consisted of two drifting Gabor patches (3° diameter, 2 cycles/° spatial frequency, 0.7°/s drift rate) constantly presented on left and right locations at an eccentricity of 5.5° from central fixation over a light gray background. Targets consisted of a 150-ms-duration change in the orientation of one of the patches (clockwise/anticlockwise).

Participants were instructed to detect and discriminate orientation changes as fast as possible by pressing a right/left button on a response box with their right hand. Targets ($N = 108$) occurred on average every 11 s. At random intervals between 4 and 6 s, a 300 ms isoluminant change in color (cue, $N = 240$) was simultaneously applied to both patches (cyan, pink), indicating the to-be-attended location (left, right). The relevant and irrelevant colors were shown at the beginning of each run and counterbalanced across runs. Cue and target presentation was temporally independent except that a target could not occur in a temporal window extending from 2 s before to 1 s after a cue. The cue–target interval was on average 2.06 s. Cue location correctly predicted target location with 0.80 probability but provided no temporal prediction of target occurrence. A cue could appear in the same location as the previous one (stay cue) or in the opposite location (shift cue). A sample sequence of stimuli is shown in Figure 1a. The experimental design also included a 30 s period of fixation at the beginning and in the middle of each experimental run. This rest period was used as baseline for the analysis of the EEG signals.

Thirty subjects participated in a preliminary behavioral session in which performance and eye position (Iscan etl-400, RK-826 PCI) were monitored. Only subjects ($N = 15$) showing a significant validity effect on target discrimination accuracy ($p < 0.05$) and able to maintain central fixation were enrolled in the present study. Eye position in the 100 ms interval before each cue onset was used as a baseline to assess changes of eye position during the following 2 s. Subjects with eye movements $>1^\circ$ were excluded. Mean values of the experimental group of subjects were

$0.03 \pm 0.15^\circ$ (mean \pm SD) and $-0.10 \pm 0.14^\circ$ for right and left shifts, respectively. Participants completed 12 fMRI runs of 210 s duration, and eight TMS-EEG runs (four for each stimulation site), each 360 s long. Given the intensive experimental design, a limitation to the recording period, and therefore on the number of trials, was required to minimize fatigue and drops of attention.

Identification of stimulation sites and TMS procedure. Target stimulation sites were individually localized by fMRI (Fig. 1b) using the apparatus, acquisition procedure, and analysis methods described by Capotosto et al. (2013). Briefly, the right vIPS and mSPL target regions were identified on single-subject contrast maps between shift versus stay and left versus right regressors (Capotosto et al., 2013).

TMS stimulation was delivered through a focal figure-eight coil, connected with a standard Mag-Stim Rapid 2 stimulator (maximum output, 2.2 tesla). The individual resting excitability threshold for right motor cortex stimulation was preliminarily determined following standardized procedures (Rossini et al., 1994). The rTMS train was delivered 500 ms before cue onset in 60% of cue presentations with the following parameters: 150 ms duration, 20 Hz frequency, and intensity set at 100% of the individual motor threshold. The parameters are consistent with published safety guidelines for TMS stimulation (Rossi et al., 2009). Such stimulation has been shown to produce effects lasting for >3000 ms (Capotosto et al., 2013).

Participants performed two active rTMS conditions, one for each stimulation site, applied in different blocks and counterbalanced across subjects. A mechanical arm maintained the handle of the coil angled at $\sim 45^\circ$ away from the midline. The center of the coil wings was positioned on the scalp to deliver the maximum rTMS intensity over each site (individual activation peak). Stimulation sites were identified on each subject's scalp using the SofTatic navigator system (E.M.S.). The individual coordinates for the two parietal stimulation sites are reported in Table 1.

EEG recordings. To assess the physiological impact of rTMS on anticipatory neural activity, we recorded simultaneously EEG activity from the scalp. Specifically, we measured the effect of magnetic stimulation delivered over different cortical loci on the peak latency and amplitude of EEG rhythm synchronization/desynchronization measured over the parieto-occipital and frontocentral regions, a reliable physiological index of anticipatory spatial attention modulation (Worden et al., 2000; Yamagishi et al., 2003; Sauseng et al., 2005; Thut et al., 2006).

EEG data were recorded (bandpass, 0.05–100 Hz; sampling rate, 256 Hz; AC couple mode recording; BrainAmp, Brain Products) from 64 EEG electrodes placed according to an augmented 10–20 system, and mounted on an elastic cap resistant to magnetic pulses. Electrode impedance was set below 5 K. The artifact of rTMS on the EEG activity lasted ~ 10 ms and did not alter the EEG power spectrum. Two electrooculographic channels were used to monitor eye movements and blinking. The acquisition time for all data was set from -0.25 to $+3$ s after cue stimulus. The 30 s periods of fixation rest were segmented off-line in windows of 1 s duration and used as baseline to estimate the effects of rTMS on EEG rhythms in the cue–target period. EEG trials contaminated by eye movements, blinking, or other involuntary movements (e.g., mouth, head, trunk, or arm) were rejected off-line. To remove the effects of the electric reference, EEG single trials were re-referenced to the common average reference, which includes the averaging of amplitude values at all electrodes and the subtraction of the mean value from the amplitude values at each single electrode. Following artifact removal, an average number of $32 (\pm 3)$ trials per condition (i.e., stay right, stay left, shift right, and shift left) was available for the EEG analysis. One subject was excluded from the analysis because the corresponding profile of EEG power density spectra was clearly abnormal/artifactual in both TMS conditions.

EEG analysis. Task-related synchronization/desynchronization (TRS/TRD) of nonphase-locked rhythms was assessed following removal of the visual evoked potentials (VEPs) to the cue stimulus from the EEG's raw waveforms. This was performed using a standard procedure based on an adaptive algorithm with orthogonal projections (Samonas et al., 1997; Della Penna et al., 2004).

First, to compare the TRD/TRS mean amplitude between the two TMS conditions, we performed a stationary analysis, in which the frequency bands of interest were δ (2–4 Hz), θ (4–8 Hz), low α , and high α . We

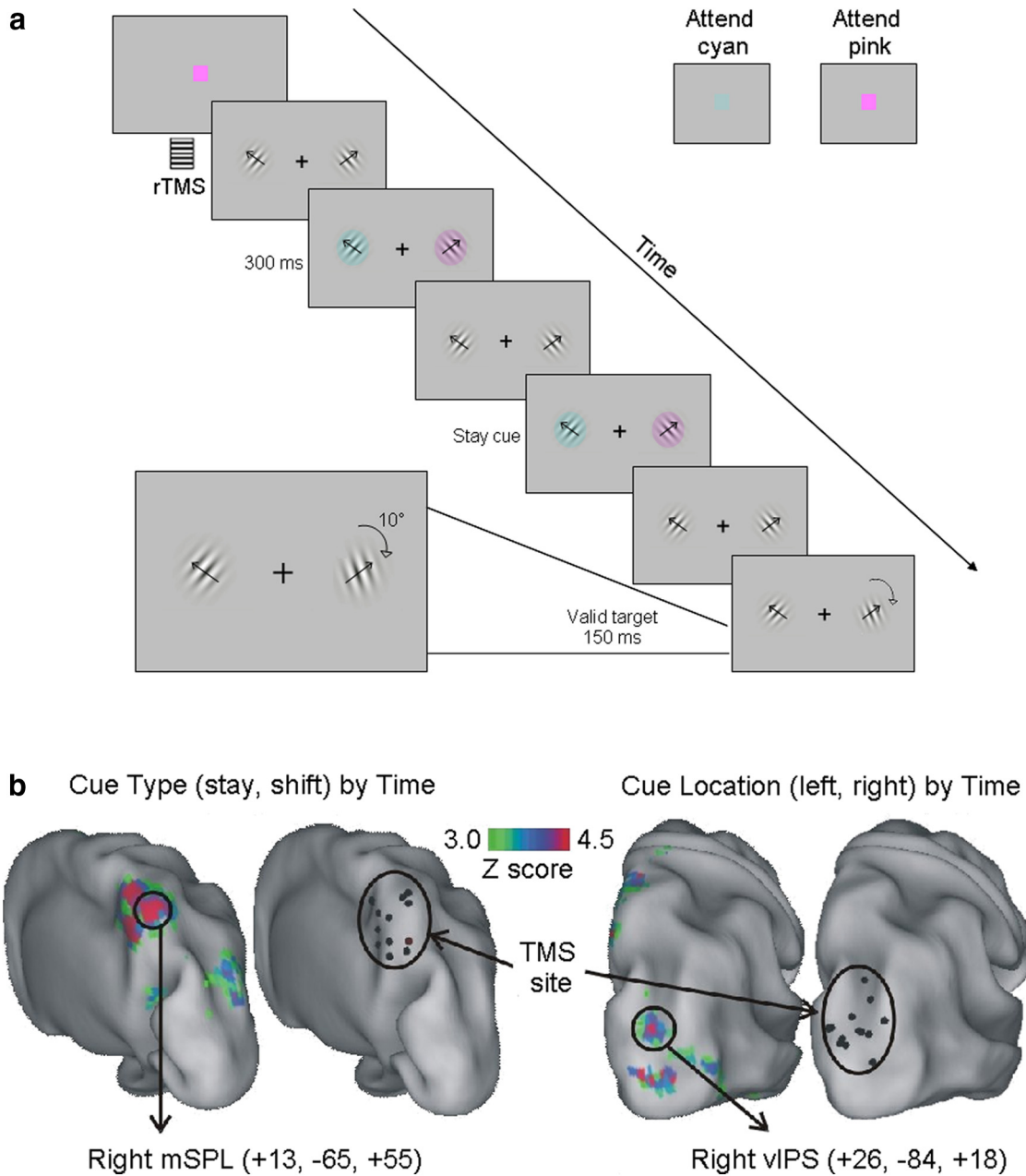


Figure 1. *a*, Example of the display sequence in the visual search task. *b*, Left, Voxels showing significantly group-wise different fMRI activation following shift versus stay cues, superimposed over an inflated cortical representation based on the Population-Average Landmark- and Surface-Based Atlas of the Human Cerebral Cortex (Van Essen, 2005), along with the corresponding individual sites of rTMS stimulation (black spheres). Right, Voxels showing significantly different fMRI activation following left versus right cues and the corresponding stimulation sites.

conducted separate analyses on low- α and high- α rhythms based on the widely accepted functional distinction between these two sub-bands (Steriade and Llinás, 1988; Pfurtscheller and Lopes da Silva, 1999). These α frequencies were determined according to a standard procedure based on the peak of individual α frequency (IAF; Klimesch et al., 1998), since the peak presents clear intersubject variability. These frequency bands were defined as follows: (1) low α , IAF - 2 Hz to IAF, and (2) high α , IAF to IAF + 2 Hz. This power spectrum analysis was based on the Welch technique and Hanning windowing function. EEG periods of 1 s duration were used as input for the analysis, with a resulting frequency resolution of 1 Hz. TRD/TRS of each EEG band of interest was obtained using the following equation: $TRD \% = (T - R)/R \times 100$, where T and R respectively indicate task-related and rest power density (each lasting 1 s). Notably, the task-related period represents the period starting at cue onset and lasting for 1 s. The length of this period, in which the cue prepares for target detection, was chosen to exclude target occurrence.

Next, a nonstationary analysis was performed to compare the TRD peak latencies between TMS conditions. After the application of the VEP filter, the nonphase-locked rhythms of each EEG raw waveform was analyzed using a short-term Fourier transform (STFT) spectrogram, which provided the temporal dynamics of the power spectrum density for each EEG channel. This approach has already been used to study the event-related synchronization/desynchronization of low-frequency brain rhythms (Makeig et al., 2002). The STFT size was 128 points, the resulting frequency resolution was 2 Hz, and the temporal resolution was ~ 20 ms. Each time interval was processed by a Hanning window assuming local stationarity of source signal. For this analysis, we first estimated the average spectrograms of rest (i.e., 30 s before and 30 s in the middle of each run) and task periods (i.e., from 0 to 1 s after the cue stimulus). By using the average power of rest spectrograms as the baseline power level, we next computed the percentage power variation associated with task execution as a function of time and frequency bin (Pfurtscheller and

Table 1. Individual coordinates of stimulated sites

	mSPL			vIPS		
	x	y	z	x	y	z
Subject						
#1	1	−69	48	14	−87	20
#2	7	−56	47	25	−85	23
#3	7	−63	54	21	−93	19
#4	10	−49	54	17	−79	29
#5	9	−72	44	34	−83	22
#6	14	−61	57	24	−71	30
#7	12	−62	59	22	−88	13
#8	3	−57	54	24	−85	16
#9	8	−51	55	31	−74	23
#10	2	−55	41	28	−84	8
#11	9	−75	48	22	−82	12
#12	13	−66	60	14	−80	21
#13	1	−78	41	16	−90	21
#14	1	−56	43	23	−93	18
#15	15	−50	54	24	−81	11
Mean	7.467	−61.3	50.6	22.6	−83.7	19.07
SD	4.912	9.123	6.423	5.779	6.253	6.273

Lopes da Silva, 1999). The whole δ (2 Hz wide), θ (4 Hz wide), and α (6 Hz wide) bands were considered separately. Furthermore, for the computation of TRD/TRS time courses, we selected the frequency band (2 Hz span) with the largest modulation with respect to the baseline within each band of interest in each individual subject. This is the standard procedure to investigate the rhythm modulations following a stimulus (Pfurtscheller and Neuper, 2006). Of note this procedure was not possible for the δ band since it is only 2 Hz wide. Finally, individual latencies of TRD/TRS were extracted from the percentage power variations of the most reactive frequency band as the first local minimum/maximum of the corresponding time course, excluding the first 100 ms after the cue stimulus.

Statistical analyses. Statistical analyses were conducted using within-subject ANOVAs for repeated measures. Mauchley's test was used to evaluate sphericity assumption, the Green-house-Geisser procedure was used to correct for the degrees of freedom, and Duncan tests were used for *post hoc* comparisons ($p < 0.05$).

To test the influence of rTMS on EEG rhythms (i.e., δ , θ , low α , high α) in the cue–target period, we used the same statistical design for both the TRD/TRS peak latency and mean amplitude. In particular, we used the δ and θ mean amplitude of EEG TRS and α mean amplitude of EEG TRD as the dependent variable and TMS Condition (right vIPS, right mSPL), Cue Type (Stay, Shift), and Hemisphere (contralateral or ipsilateral to the cue stimulus) as the within-subject factors. The same statistical design was also computed separately for the three bands of interest using the TRD/TRS peak latency as the dependent variable. Since we were interested in discriminating posterior/frontocentral ipsilateral versus contralateral variations in δ/θ and α power, all statistical analyses were performed on the regional average of four parieto-occipital electrodes for each hemisphere (i.e., P2, P4, PO₄, and O₂ for the right hemisphere, and P1, P3, PO3 and O1 for the left hemisphere) and four frontocentral electrodes for each hemisphere (i.e., FC2, FC4, C2, and C4 for the right hemisphere, and FC1, FC3, C1 and C3 for the left hemisphere). To test whether the rTMS interference disrupted the relationships between δ and α bands, we computed the correlation (Pearson test, $p < 0.05$) between TRD/TRS peak latencies of the two bands (i.e., α TRD and δ TRS) for shift and stay cues, separately. Finally, an ANOVA conducted on power estimates during the fixation-rest period confirmed that rTMS delivered at different cortical sites did not affect the baseline power of each band of interest.

Results

Behavior

Behavioral results for the whole group of subjects were reported in our previous TMS study (Capotosto et al., 2013). Nevertheless, since one subject was excluded from the present study (see Ma-

terials and Methods), we examined whether in the present group rTMS differentially affected visual target discrimination when applied over either right mSPL or right vIPS. Right mSPL stimulation impaired target discrimination following shift cues compared with stay cues, whereas right vIPS stimulation impaired target discrimination following contralateral versus ipsilateral cues. These conclusions were supported by a significant interaction of TMS Site by Cue Type (stay, shift) ($F_{(1,13)} = 4.37$, $p = 0.057$), and a significant interaction between TMS site and Cue Location (left, right; $F_{(1,13)} = 4.67$, $p = 0.05$).

TRD/TRS amplitude

We examined whether rTMS interference delivered over distinct nodes of the DAN, i.e., right mSPL and right vIPS, before the presentation of a spatial cue indicating to shift or maintain attention at a location had a differential effect on the subsequent EEG rhythms over parieto-occipital and frontocentral regions. The rTMS train lasted for 150 ms and was delivered from -500 to -350 ms before cue onset. The cue duration was 300 ms, and the EEG rhythms were analyzed from 0 to 1000 ms after cue onset.

The signals chosen for the analysis of the EEG rhythms were free of rTMS artifacts, and the α frequency peak was clearly recognizable at all electrodes of interest. The stationary analysis on the mean amplitude of EEG low-frequency α TRD conducted over the parieto-occipital electrodes showed that vIPS stimulation, but not mSPL stimulation, disrupted the typical desynchronization observed over the hemisphere contralateral to the attended side. This observation was confirmed by a significant TMS Site–Hemisphere (contralateral, ipsilateral) interaction ($F_{(1,13)} = 10.57$, $p = 0.006$) and relevant *post hoc* tests ($p < 0.01$; Fig. 2a). Importantly, as indicated by the absence of a significant interaction of TMS Site by Cue Type, this spatial effect on the low α was independent of cue type, i.e., stay versus shift (Fig. 2b). In contrast, mSPL stimulation, compared with vIPS stimulation, disrupted the high-frequency α desynchronization following a shift of attention, independent of its direction. This observation was supported by a significant TMS site by Cue Type (stay, shift) interaction ($F_{(1,13)} = 5.65$, $p = 0.033$) and relevant *post hoc* tests ($p < 0.005$; Fig. 2d). No significant interaction of TMS Site by Hemisphere was observed for the high-frequency α TRD (Fig. 2c). Interestingly, rTMS significantly interfered with the α power of parieto-occipital but not frontocentral electrodes. Moreover, no statistically significant effect was observed for the δ and θ TRS over both frontocentral and parieto-occipital regions, supporting a frequency-specific and spatial-specific involvement of the α band. Importantly, after Bonferroni's correction (i.e., $p < 0.025$ for comparison between low and high α), statistical interaction of low-frequency α TRD amplitude was still significant, whereas statistical interaction of high-frequency α TRD tended to be significant.

A control analysis ruled out the possibility that the observed modulations of the EEG power in each band of interest during the cue–target period reflected a corresponding power modulation in the baseline period ($p > 0.5$ for each frequency band; see Materials and Methods).

TRD/TRS latency

The spectrograms of the nonstationary analysis of EEG activity in parieto-occipital cortex showed a clear TRD in the α rhythms (i.e., 8–14 Hz) in each individual subject. Figure 3a displays the spectrograms of a representative subject in the frequency range between 6 and 22 Hz for both rTMS conditions, computed separately for Cue Type (Stay, Shift) and Hemisphere (contralateral

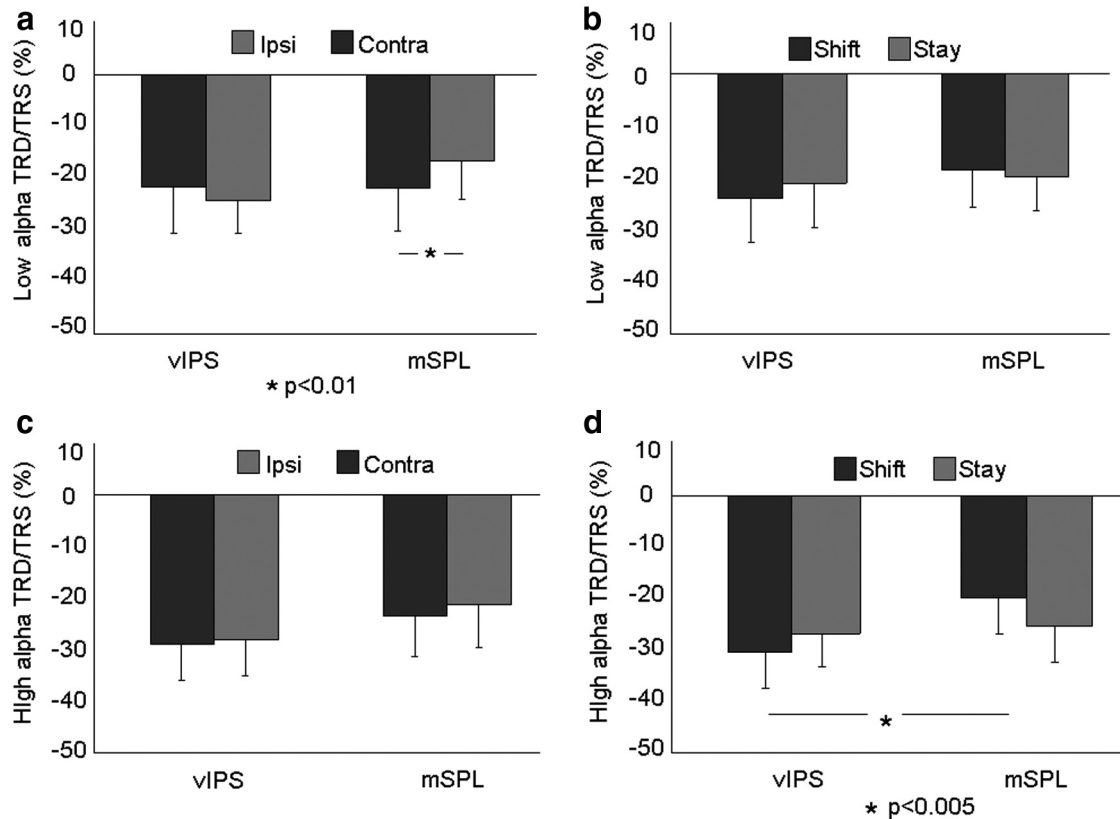


Figure 2. *a*, Group means of the low- α TRD for the two rTMS Conditions (right mSPL, right vIPS) as a function of Hemisphere [ipsilateral (Ipsi), contralateral (Contra)]. Duncan *post hoc* tests, * $p < 0.01$. *b*, Group means of the high- α TRD for the two rTMS Conditions (right mSPL, right vIPS) as a function of Hemisphere (Ipsi, Contra). *c*, Group means of the low- α TRD/TRS for the two rTMS Conditions (right mSPL, right vIPS) as a function of Cue Type (Shift, Stay). *d*, Group means of the high- α TRD/TRS for the two rTMS Conditions (right mSPL, right vIPS) as a function of Cue Type (Shift, Stay). Duncan *post hoc* tests, * $p < 0.005$.

or ipsilateral). Note the power decrement in the α band following the presentation of the cue (time 0) for the different cue types (stay, shift), spatial location (ipsilateral, contralateral to rTMS), and brain region (vIPS, mSPL). The asterisk denotes the latency of the peak of α desynchronization across subjects and conditions is shown in Figure 3*b* (i.e., top: vIPS and mSPL stay; bottom: vIPS and mSPL shift). The time against which the α TRD latency peaks were calculated is the onset of the cue. For vIPS-rTMS the latency is longer for stay than shift cues (469 vs 357 ms averaged over subjects); in contrast, for mSPL-rTMS the latency is longer for shift than stay cues (439 vs 373 ms averaged over subjects).

This result was confirmed by a significant interaction of TMS Site by Cue Type on the TRD latency ($F_{(1,13)} = 8.2$, $p = 0.013$; Fig. 3*c*). While the α TRD peak latency was longer after stay versus shift cues in the vIPS condition ($p < 0.03$), the pattern tended to be reversed in the mSPL condition, suggesting that mSPL and vIPS stimulation affected the shifting and maintenance of attention, respectively. No significant interaction of TMS Site by Hemisphere was observed. In agreement with the results of the stationary analysis, rTMS interfered with α TRD peak latencies over parieto-occipital, but not frontocentral, regions.

When the analysis was extended to the δ frequency, an effect of rTMS interference was measured over the frontocentral region, but not over the parieto-occipital region. Specifically, we observed that the latency of the synchronization of δ rhythms differed between TMS Site and Cue Type ($F_{(1,13)} = 6.38$, $p = 0.025$; Fig. 4*b*). The significant interaction reflected a prolongation of δ power TRS during vIPS stimulation following stay cues ($p <$

0.02), whereas no difference was observed in the mSPL condition ($p = 0.5$). Individual δ TRS latency peaks for each Condition and Cue Type are reported in Figure 4*a* (i.e., top: vIPS and mSPL stay; bottom: vIPS and mSPL shift). No statistically significant effect was observed for the θ band over frontocentral or parieto-occipital regions. Of note, after Bonferroni's correction (i.e., $p < 0.025$), statistical results of δ and θ TRS latency were still significant.

The prolongation of parieto-occipital α power desynchronization and frontocentral δ synchronization after vIPS stimulation following stay cues suggests that both mechanisms may be related to the allocation of spatial attention. To examine this hypothesis, a Pearson correlation analysis was conducted between frontal δ TRS and parieto-occipital α TRD latency peaks, separately for each Cue Type. Interestingly, we observed a significant negative correlation ($r = -0.73$, $p < 0.003$) between α and δ latency peaks only following shift cues during vIPS stimulation, thus suggesting that rTMS over vIPS disrupts the δ/α correlation during the maintenance of attention at a specific location (see Discussion; Fig. 4*c*).

Discussion

We used a combined fMRI-EEG-TMS approach to study the neurophysiological basis of the recently described functional-anatomical dissociation between visual selection mechanisms for shifting attention between locations and attending to contralateral locations in human posterior parietal cortex (Capotosto et al., 2013). The results show that rTMS delivered over individually selected right mSPL and vIPS during the period following the cue

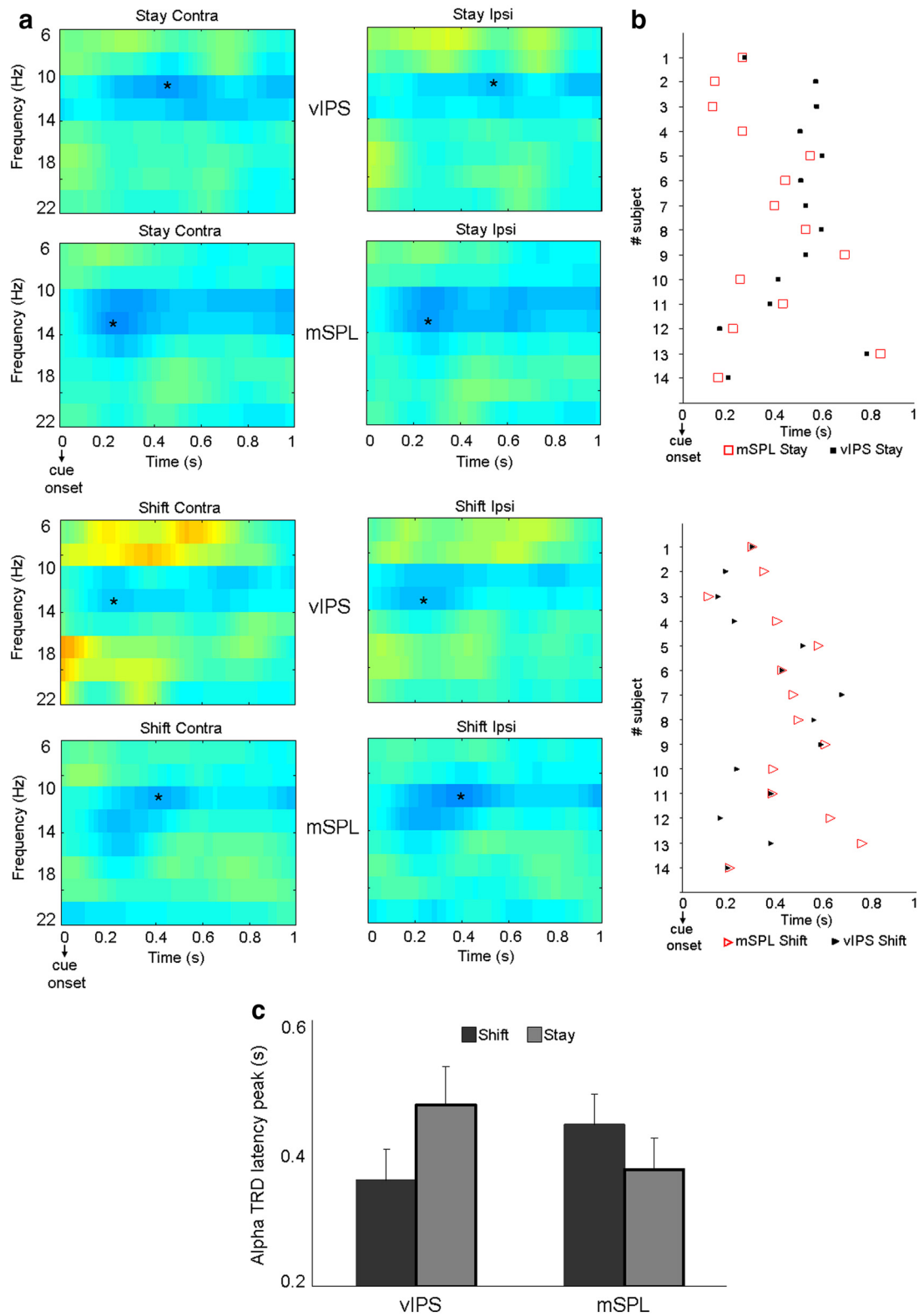


Figure 3. *a*, Typical time-frequency pattern for the α band in the vIPS and mSPL rTMS conditions from a representative subject. The left and right columns display activity from contralateral and ipsilateral electrodes with respect to cue location. The first two rows refer to maintenance (stay cues) whereas the last two rows refer to shifting (shift cues) of attention. *b*, Individual α TRD peak latencies for each Condition and Cue Type (i.e., top: vIPS and mSPL Stay; bottom: vIPS and mSPL Shift). *c*, Group mean α peak latencies (\pm SE) for the two rTMS Conditions (right mSPL, right vIPS) as a function of Cue Type (Shift, Stay). The time against which the α TRD latency peaks were calculated is the cue onset, corresponding to the zero time point for the x-axis.

stimuli of a difficult spatial attention task produced different effects on the patterns of EEG TRS/TRD. In particular, we found that interference with mSPL, compared with vIPS, reduced the mean amplitude of parieto-occipital high α desynchronization

following shifts of attention, independent of their direction (left to right or vice versa), whereas interference with vIPS altered the typical contralateral topography of low- α TRD in parieto-occipital cortex. We additionally found that the latency of the α

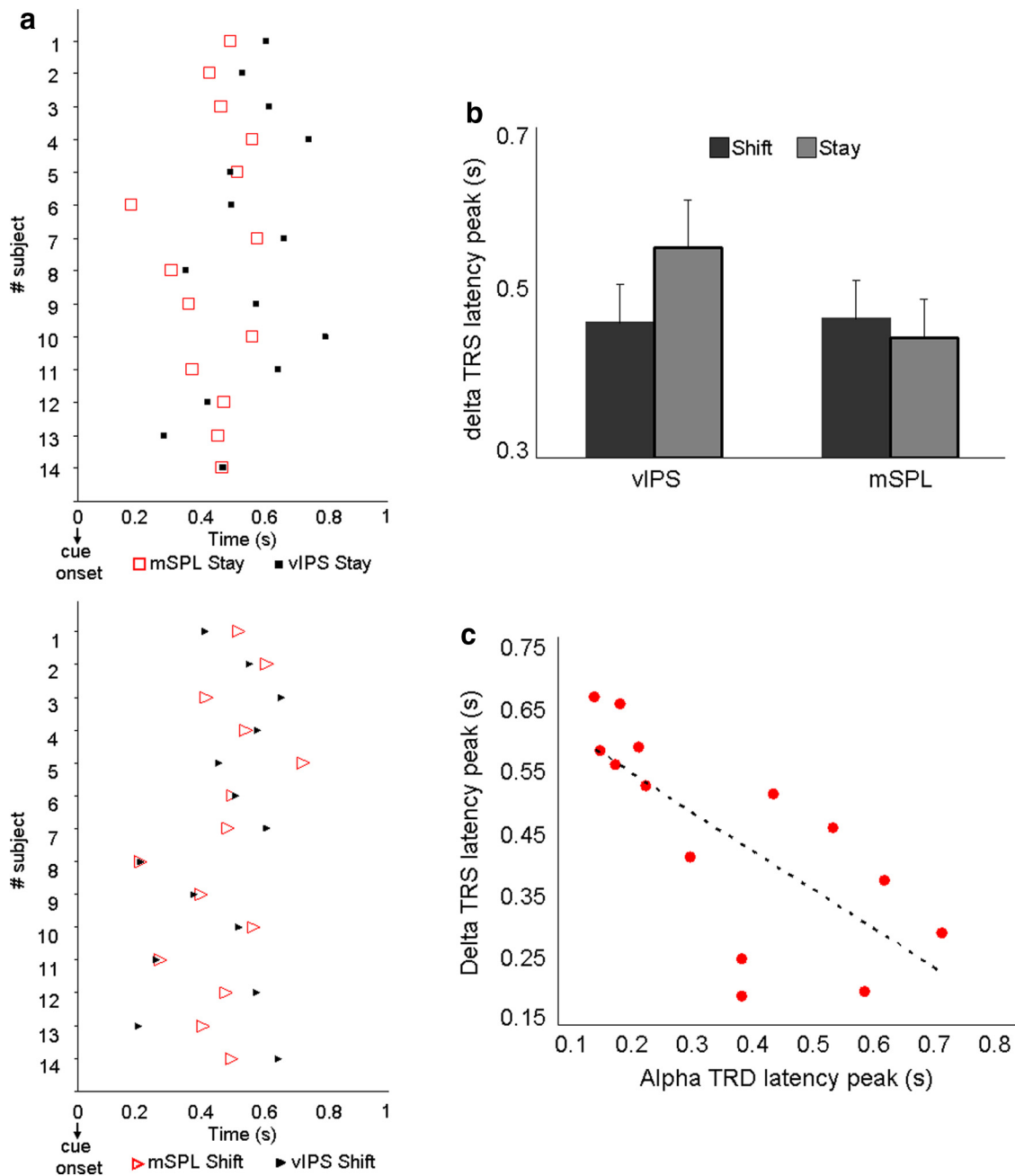


Figure 4. *a*, Individual δ TRS peak latencies for each Condition and Cue Type (i.e., top: vIPS and mSPL Stay; bottom: vIPS and mSPL Shift). *b*, Group mean δ peak latencies (\pm SE) for the two rTMS Conditions (right mSPL, right vIPS) as a function of Cue Type (Shift, Stay). *c*, Scatter plot showing the (negative) linear correlation between frontal δ and parieto-occipital α TRD latency peaks. Peak latencies were estimated with respect to the cue onset, corresponding to the zero time point for the x-axis.

TRD peak in parieto-occipital regions was longer following stay compared with shift cues when rTMS was delivered over the vIPS, while a tendency for the reversed pattern was observed when stimulating the mSPL. A similar effect was also observed for the latency of the δ TRS peak over frontocentral regions, while no rTMS effect was found on the peak latency of the θ band.

Previous studies have shown that parieto-occipital α activity is strongly modulated by attention (Foxe et al., 1998). Although its generators are still not well known, the α power is most consistently localized in parieto-occipital cortex (Vanni et al., 1997), as well as in the ventral visual stream (Snyder and Foxe, 2010). Spontaneous oscillations of α power have been also recently associated with excitability of occipital cortex to visual stimulation

(Romei et al., 2008). In particular, when attention is directed to a peripheral spatial location, α EEG rhythms in parieto-occipital cortex desynchronize contralaterally to the attended location (Worden et al., 2000; Yamagishi et al., 2003; Thut et al., 2006; Jensen et al., 2012). Moreover, a recent study suggested a role of anticipatory α oscillations in establishing and maintaining an active task set, with the contralateral posterior α activity as a neural marker of the on-line maintenance of the stimulus–response association (Grent-’t-Jong et al., 2013). Using simultaneous EEG/rTMS methods, we have recently demonstrated that interference with bilateral IPS activity, one of the regions involved in the control of spatial attention (Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Serences and Yantis,

2006), leads to a disruption of parieto-occipital α topography (Capotosto et al., 2009, 2012). The current results extend our previous findings by showing that disruption of the typical contralateral bias in the α topography is evident only when causal interference is exerted over lateral (i.e., vIPS) but not over medial (i.e., mSPL) parietal regions. Thus, the present study not only provides additional support for a functional subdivision of the dorsal attention network but also identifies a putative neural mechanism through which lateral parietal regions control the maintenance of attention to the contralateral hemifield. Moreover, future studies will also investigate medial versus lateral parietal distinction during the deployment of other forms of attentional orienting (i.e., auditory spatial attention), since there were recently reported differences in scalp topographies of α activity depending on the sensory system within which spatial attention was deployed (Banerjee et al., 2011).

Another important result is the demonstration that interference with mSPL activity affects both the power and peak latency of α TRD following shifts of attention in addition to impairing behavioral performance (Capotosto et al., 2013). Importantly, a neurophysiological signature in the α band of shift-related activity has been recently shown in the context of task set reconfigurations (Foxe et al., 2014). By combining EEG with TMS, we provide here strong neurophysiological support for the idea put forth by neuroimaging studies that the medial part of SPL is a key region for shifting attention (Yantis et al., 2002; Kelley et al., 2008; Shulman et al., 2009). Since the TRS/TRD technique used in the present study to quantify brain oscillatory responses does not allow the possibility of distinguishing between evoked (phase-locked) and induced (not phase-locked) oscillatory activity (Basar et al., 1997), VEPs to the cue stimulus were removed from the corresponding EEG raw waveforms. As a consequence, the mean TRD amplitude in the first second after the cue stimulus only refers to induced activity. Nevertheless, it has been previously shown that there is a correlation between the latency of the evoked activity and the amplitude of the α desynchronization (Mazaheri and Jensen, 2008). On this basis, it could be speculated that mSPL interference affected both evoked and induced oscillatory activities, producing weaker TRD when subjects were asked to shift their attention to the opposite hemifield.

The present results also provide evidence for a specific role of different α frequency sub-bands in visuospatial attention, which may be related to the different temporal scales in which the maintaining and reorienting of attention occur. Interestingly, a recent study has provided evidence that visuospatial attention involves corticothalamic in addition to corticocortical interactions within the α band, highlighting the role of the pulvinar in the brain's attentional network (Saalmann et al., 2012). Older studies have also proposed a neurophysiological model in which different sub-bands of the α rhythms reflect different functional modes (global brain arousal/tonic alertness vs elaboration of event-specific information; Klimesch et al., 1998) of thalamocortical and corticocortical loops (Steriade and Llinás, 1988; Pfurtscheller and Lopes da Silva, 1999). On the basis of these studies, we speculate that in the present task, low- α rhythms (~ 8 – 10 Hz) reflect a more tonic attention mode related to the maintenance of attention to a location before target detection, a form of sustained attention, while high- α rhythms (~ 10 – 12 Hz) may reflect a more phasic mode related to the reorienting of the current focus of processing to a novel location.

Finally, our results suggest a functional role of δ -band synchronization in visual selection. Specifically, a delay of δ synchronization was observed only after vIPS stimulation following shift

cues. The functional significance of δ oscillations is not yet fully understood. While oscillations in the δ band have been usually associated with slow-wave sleep (Hobson and Pace-Schott, 2002), a long tradition has associated slow potentials in the range of the δ band (contingent negative variation) with anticipatory preparation for sensory events (Walter, 1950). Based on PET glucose studies and quantitative EEG, δ power has been associated with medial frontal cortical metabolism (Alper et al., 2006). δ Rhythms have been measured at rest (He et al., 2008) and a recent MEG study has shown that resting state interactions of key nodes of the DAN (i.e., FEF and IPS) specifically involve δ and α bands (Marzetti et al., 2013). When measured during task execution, δ rhythms have been associated with attentional task demands (Lakatos et al., 2008), attentional stimulus selection (Fries et al., 2008), and decision making (Nácher et al., 2013). Moreover, under conditions in which stimuli can be temporally predicted, strong entrainment of δ rhythms has been observed in sensory (visual/auditory) cortices (Schroeder and Lakatos, 2009; Cravo et al., 2013; Daitch et al., 2013), associative cortex (Besle et al., 2011), and frontoparietal regions of the DAN (Daitch et al., 2013). Interestingly, a negative correlation between δ and α power has been reported during attentionally demanding tasks, suggesting that power increases of δ oscillations may be an index of cortical inhibition (Knyazev, 2012; Harmony, 2013). Furthermore, Fiebelkorn and colleagues showed that during a sustained attention cross-frequency coupling of δ/θ with α/β band activity present profound effects on subsequent visual target detections (Fiebelkorn et al., 2013).

The present study shows frequency-specific effects in δ and α power over frontocentral and parieto-occipital regions, respectively. Specifically, interference with vIPS during maintenance of spatial attention (stay cues) caused a delay of both α parieto-occipital TRD and δ frontocentral TRS. These findings indicate that vIPS inactivation, which behaviorally produces a deficit of contralateral target detection (Capotosto et al., 2013), causes a disruption of the α – δ rhythm relationship during maintenance of spatial attention. The negative correlation between α -desynchronization and δ -synchronization latencies indicates that δ synchronization plays a potentially inhibitory effect on preparatory processes for visual selection indexed by α desynchronization. Recent work clearly shows a predominant role of δ synchronization during endogenous spatial attention in dorsal frontoparietal regions (Daitch et al., 2013); our work shows an interesting interaction with parieto-occipital α rhythms related to encoding of the locus of attention. This interpretation is consistent with resting state observations on the phase-to-phase δ – α coupling between frontal and parieto-occipital regions (Jirsa and Müller, 2013; Marzetti et al., 2013).

Conclusions

The current results describe different neurophysiological mechanisms supporting the distinction formulated in previous fMRI and TMS studies between parietal regions mediating shifting and maintenance of visuospatial attention.

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