Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations

Ian C. Gould, Matthew F. Rushworth, and Anna C. Nobre
Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom

Submitted 26 July 2010; accepted in final form 1 January 2011

Gould IC, Rushworth MF, Nobre AC. Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. J Neurophysiol 105: 1318 –1326, 2011. First published January 12, 2011; doi:10.1152/jn.00653.2010.—Lateralization in the desynchronization of anticipatory occipitoparietal alpha (8–12 Hz) oscillations has been implicated in the allocation of selective visuospatial attention. Previous studies have demonstrated that small changes in the lateralization of alpha-band activity are predictive of behavioral performance but have not directly investigated how flexibly alpha lateralization is linked to top-down attentional goals. To address this question, we presented participants with cues providing varying degrees of spatial certainty about the location at which a target would appear. Time-frequency analysis of EEG data demonstrated that manipulating spatial certainty led to graded changes in the extent to which alpha oscillations were lateralized over the occipitoparietal cortex during the cue-target interval. We found that individual differences in alpha desynchronization contralateral to attention predicted reaction times, event-related potential measures of perceptual processing of targets, and beta-band (15–25 Hz) activity typically associated with response preparation. These results support the hypothesis that anticipatory alpha modulation is a plausible neural mechanism underlying the allocation of visuospatial attention and is under flexible top-down control.

beta; electroencephalography; spatial certainty

THE ABILITY TO SELECT and process relevant sensory stimuli flexibly underlies our ability to maintain goal-directed behavior within a noisy environment. A major goal of modern neuroscience research has therefore been to understand the neural mechanisms underlying the allocation of selective attention. Selective visuospatial attention has been extensively characterized as modulating baseline and target-evoked neural activity in cortical areas involved in processing attended vs. unattended stimuli (Chawla et al. 1999; Chelazzi et al. 1993; Hillyard et al. 1998; Kastner et al. 1999; Luck et al. 1997; McAdams and Maunsell 1999; McMains et al. 2007; Moran and Desimone 1985; Ress et al. 2000; Reynolds et al. 2000; Stokes et al. 2009). Some of these effects may reflect modulation of thalamic input to cortex (Crick 1984; McAlonan et al. 2008). Recently, anticipatory modulation of occipitoparietal alpha-band (8–12 Hz) oscillations during cue-target delays has also been identified as a possible neural mechanism underlying the allocation of selective visuospatial attention (Foxe et al. 1998; Worden et al. 2000). Similar to attention, alpha oscillations have been related to thalamocortical interactions (Hughes and Crunelli 2005; Lopes da Silva 1991). Occipitoparietal alpha oscillations are attenuated when visual information is attended compared with auditory information (Foxe et al. 1998; Fu et al. 2001). When visuospatial attention is covertly allocated, topographically organized modulation of alpha activity is also observed (Rihs et al. 2007; Worden et al. 2000). Increased anticipatory alpha synchronization is typically observed ipsilateral to the locus of attention, perhaps reflecting suppression of processing of unattended locations (Kelly et al. 2006; Rihs et al. 2007; Rihs et al. 2009; Worden et al. 2000), while decreased synchronization has been observed contralateral to attention, perhaps reflecting enhancement of processing for attended locations (Kelly et al. 2009; Rihs et al. 2009; Sauseng et al. 2005; Thut et al. 2006; Yamagishi et al. 2008).

This pattern of effects is disrupted by transcranial magnetic stimulation of parietal and frontal regions implicated in top-down control of attention (Capotosto et al. 2009).

Selective attention is advantageous to the extent it can be flexibly allocated. For example, attention can allow perceptual processing to be optimized given knowledge of probabilities of events occurring at different spatial locations within the visual environment (Eckstein et al. 2004; Eckstein et al. 2002; Egner et al. 2008; Kingstone 1992; Yantis and Jonides 1990). Ideally, it should be possible to understand the flexibility with which attention can be allocated across space in terms of its neural underpinnings. In this regard, it is interesting to note that trial-to-trial variability in alpha power can predict accuracy and reaction times on visual judgment tasks (Dockree et al. 2007; Ergenoglu et al. 2004; Kelly et al. 2009; Mathewson et al. 2009; O’Connell et al. 2009; Thut et al. 2006; Van Dijk et al. 2008) and that alpha power is inversely related to the probability that applying transcranial magnetic stimulation pulses to occipital cortex will result in perception of phosphenes (Romei et al. 2008a). Importantly, however, the evidence that trial-to-trial variability in alpha power is correlated with behavioral changes does not constitute evidence for flexible, voluntary control over alpha modulation. The covariance between small changes in alpha power and behavior may merely reflect that this measure provides an index of intrinsic variability in cortical excitability.

To investigate directly how flexibly anticipatory alpha lateralization is linked to voluntary attentional goals, we presented participants with spatially predictive cues of varying validity and examined whether the magnitude of anticipatory alpha rhythm lateralization covaried with the degree to which attention was allocated to a particular location. We hypothesized that, to the extent that the lateralization of alpha oscillations is a neural mechanism underlying the top-down allocation of attention, the lateralization of alpha rhythms should vary parametrically with graded changes in the allocation of voluntary spatial attention. We also examined the functional rele-
vance of observed alpha modulation by investigating, at a within-subject level, how attentional modulation of alpha-band activity was related to modulation of behavioral accuracy and reaction time measures of performance, to early sensory event-related potentials (ERPs) reflecting perceptual analysis of target stimuli, and to beta-band (15–25 Hz) activity over motor cortex electrodes providing a neural index of motor preparation (Donner et al. 2009; Doyle et al. 2005; Tzagarakis et al. 2010; van Wijk et al. 2009).

MATERIALS AND METHODS

Participants. Fourteen paid volunteers (6 females; mean age of 28) participated after giving informed written consent. All participants were right-handed (Oldfield 1971) and reported having normal or corrected-to-normal visual acuity and no history of neurological disorders. The methods and procedures used in the study were noninvasive and had ethical approval from the University of Oxford Central University Research Ethics Committee.

Task and stimuli. Participants were asked to discriminate the orientation of a peripheral target stimulus, which was preceded by a spatial cue. A schematic of the display sequence is shown in Fig. 1A. Participants were instructed to maintain central fixation throughout experimental trials and completed the task seated comfortably in a dimly lit room with their head position stabilized by a chin rest. Stimuli were presented at 60 Hz on a 22-inch Sony Trinitron CRT monitor at a viewing distance of 100 cm, with stimulus presentation and response acquisition controlled using Presentation 13.0 (Neurobehavioral Systems).

All stimuli were presented against a uniform mid-gray background. Trials commenced with a 1,500-ms presentation of a fixation cross consisting of two 0.3° × 0.06° black lines. A central cue stimulus was then presented for 500 ms. The cue on each trial was drawn randomly from a set of six cue shapes (Fig. 1B), each of which had a diameter of ~2.3° and a line width of 0.02°. Cues indicated that target stimuli would appear on the left or right side of the screen with a “spatial certainty” (i.e., probability) of 60, 80, or 100%. Participants were explicitly informed about the cued direction and validity associated with each cue shape. The cued direction and validity associated with specific cue shapes were randomized across participants.

Target stimuli were presented following a cue-target interstimulus interval (ISI) of 750 ms (50% of trials), 1,850 ms (25% of trials), or 2,950 ms (25% of trials). This truncated geometric distribution of ISIs was used to avoid the possibility that strong effects of temporal expectation might influence our results. Target arrays were presented for 67 ms, followed by a 67-ms bilateral backwards-mask array. Target arrays consisted of a horizontally or vertically oriented target Gabor patch (Gaussian-vignetted sinusoidal grating) and a ±45°-tilted distractor Gabor patch. Presentation of a bilateral array including similar target and distractor stimuli avoided any automatic attentional capture by the target stimulus. The short array duration and bilateral mask further prevented reorienting to the target after it was presented. This ensured that performance levels were determined by participants’ attentional state when the target array was presented and encouraged them to orient their attention in a graded fashion based on spatial certainties provided by cues. Target, distractor, and backward mask stimuli were presented 4.8° below the horizontal meridian and ±3.2° from the vertical meridian. Gabor patch stimuli were presented in greyscale at 90% contrast and with a spatial frequency of 2.5 cycles per degree. The Gaussian envelope had a space constant of 0.457°. The locations of the target and distractor were determined probabilistically by the cue. The orientations of the target and distractor were randomly selected on each trial. Backward-mask stimuli were constructed by applying a Gaussian-vignette to the convolution of 90%
contrast square-wave gratings at the four target and distracter orientations. Target, distracter, and mask stimuli were presented atop 10% contrast luminance pedestals, which were present throughout the experiment to aid target localization and the allocation of visual attention (see Fig. 1A).

Participants discriminated the target orientation (horizontal or vertical) by making a right-handed index or middle finger button-press during a response period of up to 1,500 ms. Response mappings were counterbalanced between participants. Feedback was provided for 250 ms after the response period by coloring the fixation cross green for correct responses or red for incorrect responses or misses. The subsequent inter-trial interval was 1,500 ms.

All participants completed two testing sessions within 1 wk. In the first session, participants completed 540 training trials, practicing first with single cues and then with pairs of cues at each cue validity level. The number of cues within each block was then increased to 4 and then to 6 for the last 290 trials. In the experimental session, participants completed 30 practice trials with all 6 cues and then 450 trials during which EEG was recorded. Rest breaks were provided every 30 trials. Statistical analysis was performed using Matlab and SPSS. Where appropriate, the Greenhouse-Geisser correction for nonsphericity was applied. All post hoc pairwise comparisons were Bonferroni corrected.

EEG recording and preprocessing. EEG was recorded continuously (1,000-Hz sampling rate; left mastoid reference; NuAmps digital amplifiers; Neuroscan, El Paso, TX) from 36 scalp sites using Ag/AgCl electrodes mounted on an elastic cap (Easy Caps) according to the 10–20 international system. The montage included 7 midline sites (OZ, POZ, PZ, CPZ, FCZ, FZ, and CZ), 12 sites over each hemisphere (O1/O2, PO3/PO4, P7/P8, P3/P4, P7/P8, CP3/CP4, C3/C4, FC3/FC4, FT7/FT8, F3/F4, F7/F8, and FP1/FP2), left and right mastoids, horizontal electrooculogram (EOG) and vertical EOG electrodes to monitor the EOG bipolarly, and an additional electrode (AFZ) used as ground. Vertical EOG was calculated as the bipolar derivation between FP2 and the lower vertical EOG electrode. Recordings were re-referenced offline to the average of the mastoids. Continuous epochs from 100 ms before fixation onset to the end of the response period were included in analyses except when showing recording artifacts, if saccades or blinks occurred in the EOG, or if participants made early (<300 ms) or late (>1,500 ms) responses (80 ± 14% SE trials accepted). Epochs were defined using digital codes sent to the EEG recording computer to mark the presentation of the cue and target in each trial type. A low-pass filter (40 Hz, 24 dB/octave) was applied to data used in ERP analyses before epoching.

Determination of individual alpha-frequency bands. Time-frequency analysis of alpha-band EEG data was performed with respect to each participant’s individual alpha frequency (IAF) to allow for individual variations in alpha bands (Doppelmayr et al. 1998; Klimesch et al. 1998). IAF frequencies were defined from the fast Fourier transform over occipital and parieto-occipital electrodes (O1/O2, PO3/PO4, PO7/8, and P3/4) across all short-trial epochs (4,000 ms), giving a frequency resolution of 0.25 Hz. Each participant’s IAF was defined as the frequency with the largest power in the 8- to 12-Hz range. The frequency band subsequently analyzed was defined as the participant’s IAF ± 2 Hz, as modulation of this frequency band has been demonstrated in previous attentional orienting studies (e.g., Thut et al. 2006). The mean IAF was 9.9 Hz (± 0.25 SE). Time-frequency analysis. Time-frequency analysis was performed on all epochs using a multitaper approach (2–30 Hz, 0.5-Hz steps, 500-ms temporal smoothing window, 2-Hz frequency resolution) using Fieldtrip (Donders Institute for Brain; http://www.ru.nl/neuroimaging/fieldtrip) under Matlab (The Mathworks). Raw power data at each time-frequency sample were log transformed, yielding approximately normally distributed data suitable for standard parametric statistical tests (Kiebel et al. 2005). Log-transformed data were linearly baseline related to the 200 ms preceding cue onset.

Time-frequency analysis of alpha power data was conducted in three bilateral regions of interest (ROI) within which electrodes showed similar effects. The “parieto-occipital” ROI included O1/O2 and PO7/PO8, electrodes commonly reported as showing lateralized alpha modulation in attentional tasks (Kelly et al. 2006; Thut et al. 2006). The “parietal” ROI included PO3/PO4 and P3/P4, and the “parieto-central” ROI included CP3/CP4 and C3/C4, electrodes commonly reported as showing mu (8–12 Hz) and beta desynchronization in motor planning and imagery studies (McFarland et al. 2000; van Wijk et al. 2009).

Repeated-measures ANOVAs were performed on alpha (IAF ± 2 Hz) frequency data 1,050–1,250 ms after onset of the cue stimulus. This time window corresponds to the 200 ms before the first possible time at which a target could be presented, when attention should have been strongly engaged (Rihs et al. 2009; Sauseng et al. 2005). To investigate motor preparation, beta-band (15–25 Hz) data from the parieto-central ROI were also analyzed over the same time window (Donner et al. 2009; Doyle et al. 2005; McFarland et al. 2000; van Wijk et al. 2009). As participants did not know when the target would appear at this stage in the trial, data were pooled across all cue-target ISIs to maximize statistical power in our analyses.

ERP analysis. To test for the consequences of spatial attention on visual processing of the target, we also analyzed target-evoked visual ERPs at electrodes O1/2 and PO7/8 (epochs: −50 to 600 ms; baseline: −50 to 0 ms). As enhancement of both the P1 and N1 potentials is a common consequence of spatial attention and is likely to reflect the operation of gain control mechanisms (Hillyard and Anllo-Vento 1998; Hillyard et al. 1998), we used the peak-to-peak P1-N1 complex amplitude to characterize the overall effects of gain control by attention on visual ERPs. The amplitude of the P1-N1 complex evoked by validly cued targets was calculated by subtracting the mean voltage around the peak N1 latency (192–222 ms) from that around the peak P1 latency (104–124 ms). These P1 and N1 time windows correspond to ±10 ms from the peak P1 and N1 latencies, the values of which were determined from group averages using Scan 4.4 (Neuroscan). Data from invalidly cued targets (i.e., trials with a spatial predictability of 20 or 40%) were not analyzed due to there being relatively few trials in these conditions (∼24 trials when spatial predictability was 20%, after artifact rejection).

RESULTS

Behavioral results. Repeated-measures ANOVAs were carried out on accuracy, reaction times from correct trials, and inverse efficiency (calculated as reaction time divided by accuracy) data with factors of “spatial predictability” (the cued probability of the target Gabor patch appearing in the visual field it was presented; 20, 40, 60, 80, and 100%) and ISI (short, medium, and long).

Behavioral data are presented in Fig. 1, C–E. Significant main effects of spatial predictability were observed on both accuracy [F(4,42) = 3.84; \( P = 0.04 \)] and reaction time [F(4,42) = 4.27; \( P = 0.045 \)]. The effects of spatial predictability were related to an increase in accuracy with spatial predictability [linear contrast: F(1,13) = 9.59; \( P = 0.008 \)] and a decrease in reaction time with spatial predictability [linear contrast: F(1,13) = 7.54; \( P = 0.017 \)]. To investigate whether speed-accuracy tradeoffs affected the reaction-time and accuracy data, we performed an ANOVA on inverse efficiency measures. This revealed a main effect of spatial predictability [F(4,42) = 8.39; \( P = 0.005 \)] due to inverse efficiency decreasing with spatial predictability [linear contrast: F(1,13) = 14.6; \( P = 0.002 \)], confirming that task performance improved with spatial predictability. No other significant main effects or
interactions were observed, including all effects involving the ISI factor.

Alpha power. The topography of changes in alpha-band power relative to the precue baseline is presented in Fig. 2. A four-way ANOVA of alpha-band power was performed with factors of ROI (parietooccipital, parietal, and centroparietal), hemisphere (ipsilateral or contralateral relative to the cued direction), cue direction (left, right), and the cued spatial certainty (60, 80, and 100%). This analysis revealed a significant main effect of hemisphere \([F(1,13) = 12.83; \ P = 0.003]\) and spatial certainty \([F(2,26) = 6.0; \ P = 0.007]\) and a cue direction X hemisphere interaction \([F(1,13) = 7.6; \ P = 0.017]\). Most importantly, the analysis revealed a ROI X cue direction X hemisphere interaction \([F(2,26) = 4.35; \ P = 0.043]\) and a ROI X hemisphere X spatial certainty interaction \([F(4,52) = 3.27, \ P = 0.044]\). To clarify the nature of these interactions, subsidiary three-way ANOVAs and pairwise comparisons were carried out within each ROI.

Results from the occipitoparietal ROI are presented in Fig. 2, C and D. A significant main effect of hemisphere \([F(1,13) = 21.58; \ P < 0.001]\) was observed, reflecting greater alpha-band desynchronization at contralateral electrodes relative to ipsilateral electrodes (pairwise comparisons: \(P < 0.001\)). A main effect of spatial certainty \([F(2,26) = 4.30, \ P = 0.024]\) was also observed, reflecting greater desynchronization when spatial certainty was higher [linear contrast: \(F(1,13) = 6.61; \ P = 0.023\)]. Critically, a hemisphere X spatial certainty interaction \([F(2,26) = 4.12; \ P = 0.028]\) was also observed, indicating that the degree with which alpha-band desynchronization was lateralized increased linearly with spatial certainty [linear contrast: \(F(1,13) = 6.42; \ P = 0.025\)]. This effect was primarily driven by a significant effect of spatial certainty at contralateral electrodes [linear contrast: \(F(1,13) = 10.96; \ P = 0.006\)], where alpha power decreased progressively as spatial certainty increased. At ipsilateral electrodes, a similar trend was observed (see Fig. 2C); however, this effect was not significant [linear contrast: \(F(1,13) = 2.13; \ P > 0.16\)].

For the parietocentral ROI, there was a main effect of spatial certainty \([F(2,26) = 5.35; \ P = 0.011]\), due to a bilateral desynchronization that increased linearly with spatial certainty [linear contrast: \(F(1,13) = 6.80; \ P = 0.022\)]. A significant cue direction X hemisphere interaction was also observed \([F(1,13) = 19.96; \ P = 0.001]\). Consistent with the right-handed responses made in the task, this reflected greater desynchronization in the left vs. right hemisphere; following left cues contralateral alpha was greater than ipsilateral alpha (pairwise comparisons: \(P = 0.046\)) and following right cues ipsilateral alpha was greater than contralateral alpha (pairwise comparisons: \(P < 0.001\)).

Results for the parietal ROI showed a combination of the effects observed at the parietooccipital and parietocentral
ROIs. Main effects of hemisphere \( [F(1,13) = 8.31; P = 0.013] \) and spatial certainty \( [F(2,26) = 6.53; P = 0.005] \) were observed, reflecting greater contralateral than ipsilateral desynchronization (pairwise comparisons: \( P = 0.013 \)) and desynchronization that increased linearly with spatial certainty [linear contrast: \( F(1,13) = 8.27; P = 0.013 \)]. A cue direction \( X \) hemisphere interaction was also observed \( [F(1,13) = 5.59; P = 0.034] \). Pairwise comparisons revealed that for rightward cues ipsilateral hemisphere alpha was greater than contralateral alpha (pairwise comparisons: \( P = 0.003 \)); however, there was no significant hemisphere difference for leftwards cues \( (P > 0.4) \). Unlike the occipitoparietal ROI, the hemisphere \( X \) spatial certainty interaction was only of marginal significance \( [F(2,26) = 2.65; P = 0.089] \), due to a trend towards increasingly lateralized alpha-band activity as spatial certainty increased [linear contrast: \( F(1,13) = 4.46; P = 0.055 \)].

**Beta power.** Beta-band effects were predominant at electrodes over left hemisphere motor areas (Fig. 3A). To investigate how beta-band activity linked to motor preparation was modulated in the task, we performed a repeated-measures ANOVA on beta-band power at the parietotemporal ROI with factors of cue direction (left, right), hemisphere (ipsilateral, contralateral), and spatial certainty (60, 80, and 100%). This revealed a significant main effect of spatial certainty \( [F(2,26) = 4.1; P = 0.029] \), with greater beta desynchronization when spatial certainty was high [Fig. 3B; linear contrast: \( F(1,13) = 8.7; P = 0.011 \)]. A significant cue direction \( X \) hemisphere interaction \( [F(1,13) = 9.6; P = 0.008] \) was also observed. As for this ROI in the alpha-band frequency range, this reflected greater desynchronization over left vs. right hemisphere following both leftwards (pairwise comparisons: \( P = 0.024 \)) and rightwards (pairwise comparisons: \( P = 0.006 \)) cues.

**Visual potentials.** To investigate how spatial certainty affected the amplitude of early sensory ERPs elicited by the target array at electrodes showing graded alpha-band lateralization (Fig. 4), a repeated-measures ANOVA was performed on P1-N1 amplitude data from the parietocentral ROI, with factors of hemisphere (contralateral or ipsilateral relative to the cued direction) and spatial predictability (60, 80, and 100%). The ANOVA revealed a spatial predictability \( X \) hemisphere interaction \( [F(2,26) = 7.6; P = 0.002] \). Post hoc analyses revealed that as spatial predictability increased, the P1-N1 potential amplitude was larger in the contralateral hemisphere relative to the ipsilateral hemisphere [linear contrast: \( F(1,13) = 11.1; P = 0.005 \)]. Consistent with this effect, pairwise comparisons revealed an increase in the contralateral relative to ipsilateral P1-N1 amplitude that was significant when spatial predictability was 100% \( (P = 0.006) \) and 80% \( (P = 0.01) \) but not 60% \( (P = 0.10) \).

**Correlation between behavioral and neural results.** To investigate the relationship between individual subjects’ behavioral and neural effects, we regressed the behavioral and neural measures described above against the spatial certainty indicated by the cues (for alpha and beta power) or against the spatial predictability of the target location (for behavioral measures and target-evoked ERPs). The resulting regression slope coefficients were then compared across subjects using two-tailed Pearson correlations.

For the P1-N1 complex, the slopes were calculated as the average contralateral-ipsilateral difference at electrodes O1/2 and PO7/8. Supporting a tight link between ERP measures of target processing and behavior, P1-N1 complex slopes were positively correlated with the slopes of individuals’ accuracy measures \( (r = 0.63; P = 0.016) \) and negatively correlated with their reaction-time slope \( (r = -0.82; P < 0.001; \) Fig. 5, A and B).

Previous studies have specifically linked facilitation of attended stimulus processing to contralateral alpha desynchronization (Kelly et al. 2009; Sauseng et al. 2005; Thut et al. 2006; Yamagishi et al. 2008) and/or suppression of distracter stimuli processing to increased ipsilateral alpha synchronization (Kelly et al. 2006; Ries et al. 2009; Worden et al. 2000). We therefore calculated the slopes of alpha modulation separately for the contralateral and ipsilateral hemispheres in the occipitoparietal

---

**Fig. 3.** Beta-band desynchronization was predominant over left hemisphere (hemi) motor areas 1,050–1250 ms after cue onset and increased in magnitude with spatial certainty. Note that the left hemisphere is contralateral to motor responses, which were always made with the right hand. A: topography of beta desynchronization at 60, 80, and 100% spatial certainty levels. B: mean beta power at parietocentral electrodes CP3/4 and C3/4 at each spatial certainty level (error bars are SE).
ROI. Contralateral alpha was positively correlated with reaction time ($r = 0.70; P < 0.005$; Fig. 5C), whereas ipsilateral alpha was only marginally associated with reaction times ($r = 0.53; P = 0.053$). Given that there was high multicollinearity between ipsilateral and contralateral alpha-slope measures ($r = 0.73; P = 0.003$), we calculated one-tailed partial correlations to investigate whether significant reaction-time variance was uniquely accounted for by ipsilateral and/or contralateral alpha. Alpha desynchronization over the contralateral hemisphere explained a significant amount of reaction time variance after controlling for ipsilateral alpha (partial $r = 0.54; P = 0.027$); however, a nonsignificant relationship was observed between ipsilateral alpha and reaction times after controlling for contralateral alpha (partial $r = 0.034; P > 0.45$).

Further supporting a tight link between contralateral alpha and target processing, there was also a significant correlation between P1-N1 slopes and contralateral ($r = -0.565; P = 0.035$; Fig. 5D) but not ipsilateral ($P > 0.2$) alpha slopes.

Finally, we correlated beta-power slopes from parieto-central electrodes with behavioral performance slopes and with alpha-modulation slopes. Significant positive correlations were found between left-hemisphere beta slopes and reaction-time slopes ($r = 0.56; P = 0.039$) and between left-hemisphere beta slopes and contralateral alpha slopes ($r = 0.62; P = 0.018$). The correlation between beta slopes and ipsilateral alpha slopes was of marginal significance ($r = 0.48; P = 0.084$).

**DISCUSSION**

The primary aim of this study was to investigate whether graded changes in alpha lateralization are associated with graded changes in the spatial allocation of voluntary attention. Presenting participants with central symbolic cues of varying validity levels resulted in a graded lateralization of alpha-band activity over occipitoparietal electrodes. To our knowledge, these results provide the first demonstration that parametric changes in top-down attentional goals can modulate the anticipatory lateralization of alpha rhythms in a graded manner. The consistency of the relationship supports the hypothesis that lateralization of alpha rhythms contributes to the neural mechanisms underlying the allocation of selective attention (Foxe et al. 1998; Worden et al. 2000). We also characterized the relationship between spatial certainty provided by cues and individual subjects’ anticipatory modulation of alpha-band activity and the relationship between spatial predictability and subjects’ behavioral and neural measures of target processing. We found that alpha modulation contralateral to attention during a preparatory period significantly predicted three subsequent measures: lateralization of the early sensory P1-N1 complex, reaction times, and a beta-band measure of motor preparation. Together, these results suggest that greater modulation of alpha-band activity may reflect larger attentional shifts, resulting in greater attentional effects on behavioral performance. This finding complements previous studies that...
did not distinguish whether variations in lateralization of alpha-band activity reflected variations in the top-down control of attention or simply spontaneous variations in cortical excitability (Kelly et al. 2009; Thut et al. 2006), as well as studies emphasizing a link between visual detection performance and tonic differences in individuals’ alpha-band activity (Dockree et al. 2007; Romei et al. 2008b). For this task, behavior was more closely linked with the slope of contralateral than ipsilateral hemisphere alpha modulation. Although our results highlight the relationship between contralateral alpha activity and behavioral performance, such effects may depend on precise aspects of task configuration. For example, in a steady-state visual evoked potential study by Kelly et al. (2006), a continuous stream of bilateral stimuli was presented while participants attended to one side of the display. Increased alpha synchronization was observed ipsilateral to the attended side; however, attention did not affect contralateral alpha activity. Although the authors did not directly link the increases in ipsilateral alpha power to behavior, and acknowledge that the lack of contralateral alpha modulation may have resulted from the continuous bilateral visual stimulation in their task, their data provide compelling evidence that allocation of attention can also result in ipsilateral alpha enhancement. Given the high contrast stimuli used in our task, a recent functional MRI study is also of note. Sylvester et al. (2008) demonstrated that when participants expected either low or high contrast targets, spatial attention led to anticipatory increases in prestimulus BOLD activity contralateral to the attended side. However, a greater BOLD signal reduction was observed ipsilateral to the attended side, and this predicted behavior, when low-contrast vs. high-contrast targets were expected. More generally, a range of studies have suggested that attentional selection affects behavioral performance via the operation of different mechanisms as a function of task difficulty (Boudreaux et al. 2006; Prinzmetal et al. 2009; Rees et al. 1997), stimulus contrast (Martinez-Trujillo and Treue 2002; Reynolds et al. 2000; Sylvester et al. 2008), individual differences in behavioral strategies (Abbey and Eckstein 2006; Boudreaux et al. 2006), the presence and location of distracters (Shiu and Pashler 1994), spatial certainty (Gould et al. 2007; Palmer et al. 1993; Pelli 1985), external noise levels (Lu et al. 2002), the nature of the visual judgment being made about targets (Abbey and Eckstein 2006; Smith 2000), and the nature of attentional cues (Prinzmetal et al. 2005). Additional research is necessary to clarify whether such differences influence whether behavioral performance is associated with modulation of alpha activity contralateral and/or ipsilateral to attention.

At parietal and parietocentral electrodes, we observed bilateral modulation of alpha power with changes in spatial certainty, regardless of the cued direction. Given that alpha sources are widely distributed across occipitoparietal cortex (Basar et al. 1997; Hari and Salmelin 1997) and that modulation of alpha-band activity results from a wide range of task manipulations (Hari and Salmelin 1997; Palva and Palva 2007; Rihs et al. 2009; Salenius et al. 1995; Salmelin et al. 1994; Snyder and Foxe 2010; Tuladhar et al. 2007; Vanni et al. 1997), this bilateral effect may reflect additional cortical activity that scales with spatial certainty. Speculatively, the bilateral effect we report here may be related to the extent with which attention was shifted or maintained (Kelley et al. 2008; Vandenberghe et al. 2001; Yantis et al. 2002).

Given that participants made right-handed button responses in our task, our observation of greater beta desynchronization over left hemispheric motor regions is consistent with the well-established role of beta desynchronization in motor preparation (Donner et al. 2009; Doyle et al. 2005; McFarland et al. 2000; Tzagarakis et al. 2010; van Wijk et al. 2009). In addition, we found that beta desynchronization scaled with the spatial certainty provided by cues, and the slope of this effect correlated with participants’ alpha modulation at occipitoparietal electrodes contralateral to attention, and with their reaction times. As the spatial cues in this study did not provide information about the target orientation, they did not allow participants to prepare a specific motor response. However, when spatial certainty was higher participants may have been able to anticipate being able to respond more quickly to the target array when it appeared, resulting in greater generalized motor preparation at the end of the cue-target interval. This finding is consistent with the suggestion that the role of beta-band desynchronization in response preparation may be similar to the role of alpha-band desynchronization in visual attention (van Wijk et al. 2009).

**GRANTS**

This work was supported by a Wellcome Trust Studentship to I. Gould.

**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**REFERENCES**


Dockree PM, Kelly SP, Foxe JJ, Reilly RB, Robertson IH. Optimal sustained attention is linked to the spectral content of background EEG activity: Greater ongoing tonic alpha (~10 Hz) power supports successful phasic goal activation. *Eur J Neurosci* 25: 900–907, 2007.


