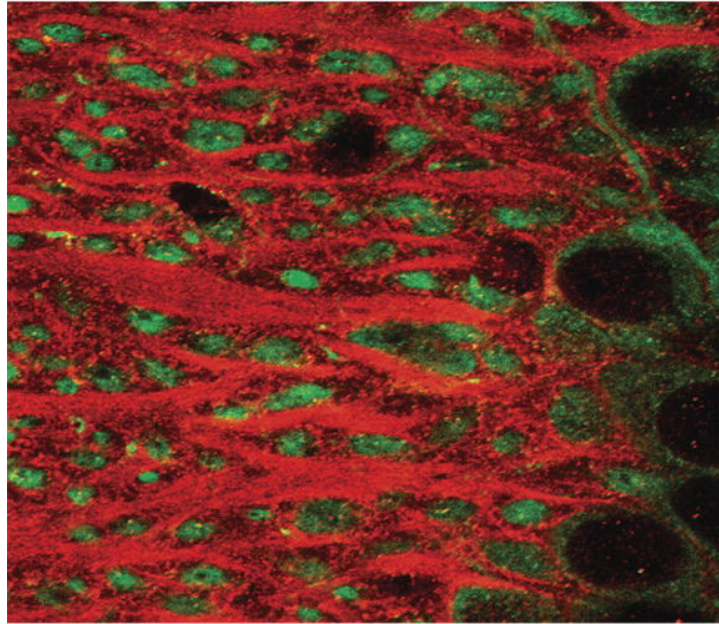


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Research Report

Attentional changes in pre-stimulus oscillatory activity within early visual cortex are predictive of human visual performance

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ABSTRACT

Physiological and neuroimaging studies provide evidence to suggest that attentional mechanisms operating within the fronto-parietal network may exert top-down control on early visual areas, priming them for forthcoming sensory events. The believed consequence of such priming is enhanced task performance. Using the technique of magnetoencephalography (MEG), we investigated this possibility by examining whether attention-driven changes in cortical activity are correlated with performance on a line-orientation judgment task. We observed that, approximately 200 ms after a covert attentional shift towards the impending visual stimulus, the level of phase-resetting (transient neural coherence) within the calcarine significantly increased for 2–10 Hz activity. This was followed by a suppression of alpha activity (near 10 Hz) which persisted until the onset of the stimulus. The levels of phase-resetting, alpha suppression and subsequent behavioral performance varied between subjects in a systematic fashion. The magnitudes of phase-resetting and alpha-band power were negatively correlated, with high levels of coherence associated with high levels of performance. We propose that top-down attentional control mechanisms exert their initial effects within the calcarine through a phase-resetting within the 2–10 Hz band, which in turn triggers a suppression of alpha activity, priming early visual areas for incoming information and enhancing behavioral performance.

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1. Introduction

Efficient visual navigation within a complex environment demands the prioritization of behaviorally relevant stimuli. Attentional mechanisms that exert top-down control are thought to provide one means by which this can be accomplished. Spatially directed attention, for example, is known to modulate activity in the sensory cortex both prior to (Kastner et al., 1999; Worden et al., 2000; Fries et al., 2001; Yamagishi

et al., 2005; Thut et al., 2006) and during a given visual task (Desimone and Duncan, 1995; Watanabe et al., 1998; Somers et al., 1999; Fries et al., 2001; Yamagishi et al., 2003), enhancing neuronal responses to attended stimuli while at the same time suppressing responses to non-attended stimuli (Smith et al., 2000; Huang and Dobkins, 2005; Pestilli and Carrasco, 2005).

There is some evidence to suggest that changes in the amplitude and phase of on-going cortical oscillations may provide the conduit for such top-down influences on perception.

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Consider the following sequence of events. Prior to stimulus onset, attentional control mechanisms operating within the superior frontal, inferior parietal and superior temporal areas (Corbetta et al., 2000; Hopfinger et al., 2000; Friedman-Hill et al., 2003; Giesbrecht et al., 2003) may induce a transient coherence of firing rates within a subpopulation(s) of neurons in early visual areas (Klimesch et al., 2006). This transient neural coherence – or phase resetting – is an example of inter-areal communication (von Stein et al., 2000; Engel et al., 2001; Fries, 2005; Sauseng et al., 2005), and may precede a suppression of alpha activity in early visual cortex (Worden et al., 2000; Fries et al., 2001; Sauseng et al., 2005; Yamagishi et al., 2005). A

decrease in total alpha-band power is to be expected if the subpopulation(s) of alpha generators is phase reset and becomes asynchronous with other subpopulations (Mazaheri and Jensen, 2006). Finally, the decreased alpha-band power may serve to render early visual areas more sensitive to forthcoming information (Pfurtscheller and Lopes da Silva, 1999; Pfurtscheller, 2001; Thut et al., 2006).

If this putative sequence of events captures the essential elements of attentional processes, we hypothesize that the extent of phase resetting and subsequent alpha-band suppression in early visual areas should be correlated, with the presence of both indicative of good behavioral performance.

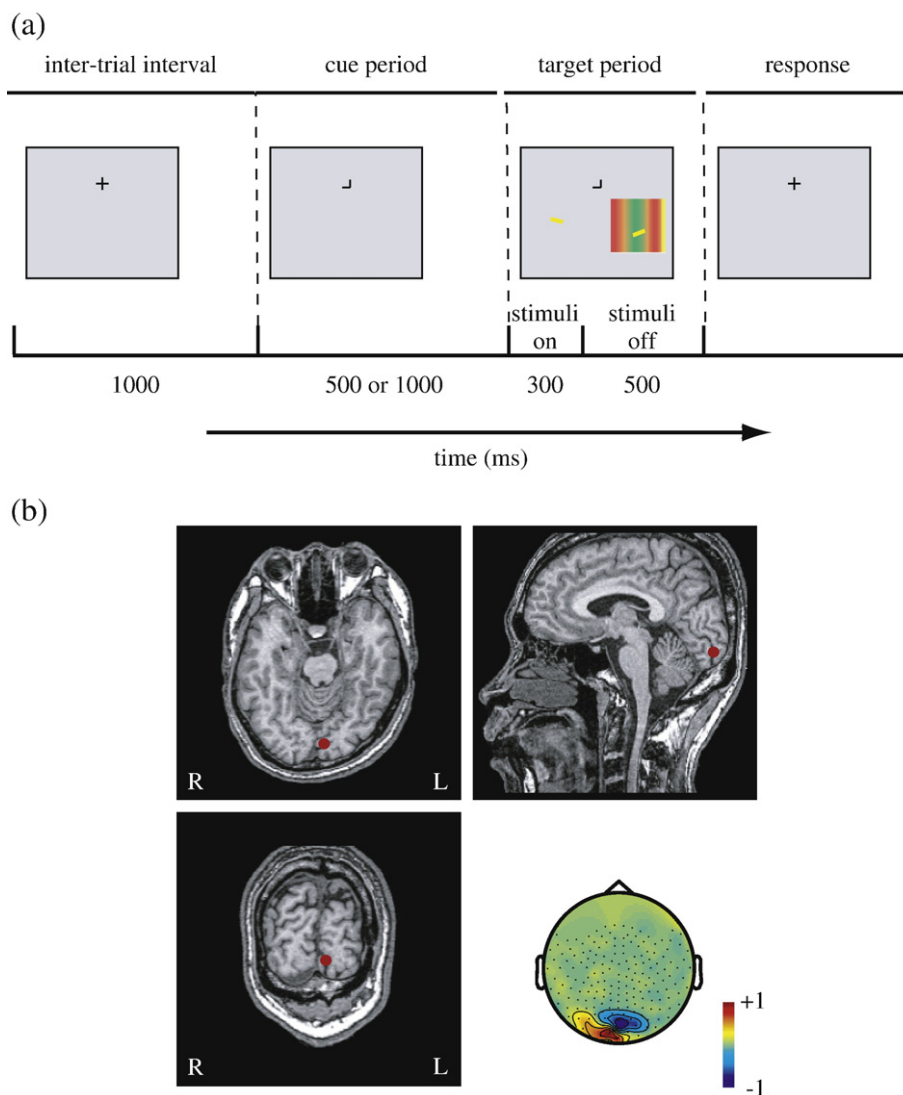


Fig. 1 – Schematic of trial sequence and stimuli within right (grating plus bar) and left (bar only) viewing windows, plus source localization. (a) Trial sequence showing the inter-trial interval (1000 ms), cue period (500 or 1000 ms), stimulus interval (300 ms), post-stimulus interval (500 ms), and observer response period (no deadline imposed). Stimuli were generated using a VSG2/5 graphics board (from CRS Ltd), and projected from outside a magnetically shielded room onto a semi-translucent screen inside the room. The edges of each viewing window were displaced 1° from the principal meridians. Viewing distance to the screen was 170 cm. See text for further explanation. (b) Dipole source solution (red dot) for the IC representing calcarine activity for observer TY, co-registered with sagittal, axial and coronal MR images. The Talairach coordinates of the source location were (-2, -89, -4; GF=98%). The sensor plane projection map W^{-1} is shown in the lower right corner (red shows outgoing field and blue, ingoing field). The Talairach coordinates for all other observers are reported in Table 1 of Yamagishi et al. (2005).

Using of magnetoencephalography (MEG) in combination with magnetic resonance imaging (MRI), we recently showed that attentional shifts towards an expected visual stimulus alter the level of ongoing alpha-band activity within the calcarine prior to stimulus onset (Yamagishi et al., 2005). Here, we use data from our previous study in a new analysis to test our hypothesis that attention-driven changes in *pre-stimulus* activity are correlated with visual performance. Performance was assessed using a line-orientation judgement task (Yamagishi et al., 2005) (see Fig. 1a in this paper). The line targets were superimposed upon chromatic gratings because the latter evoke strong responses in the human calcarine cortex (Engel et al., 1997; Fylan et al., 1997; Anderson et al., 1999), allowing independent components (ICs) with dipole sources

localized to Brodmann's area 17 to be determined and used for correlational analyses. Our results provide evidence that the combined presence and sequential order of attention-driven transient neural coherence and alpha suppression within the calcarine may be used to predict human visual performance. We suggest that these sequential neural changes may be fundamental to attentional processes, serving to prime early visual areas for incoming information.

2. Results

All results shown below represent activity generated in the left calcarine cortex. Except where indicated, the brain imaging and behavioral results are based on the viewing condition in which attention was directed towards the right stimulus window (yellow bar plus grating) following a post-cue delay period of 1000 ms.

2.1. Relationship between inter-trial coherence and task performance

Fig. 2 shows group-mean, time-frequency plots of ITC (inter-trial coherence) for the independent components representing calcarine activity. For these plots, observers were divided into high and low performance groups based on their psychophysical performance for the bar-orientation judgment task. A performance measure of $\geq 90\%$ correct was defined as high (Fig. 2b, $n=6$), while a measure of $< 90\%$ was defined as low (Fig. 2a, $n=7$). Note that a pre-stimulus increase in ITC was evident for the high performance group, manifest at low frequencies (< 10 Hz) shortly after cue onset (Fig. 2b). For the low performance group, however, the ITC values remained close to zero during the entire cue period (Fig. 2a).

Using the data for all observers, we tested for correlations between task performance and ITC values in the 1.9–13.7 Hz range across the entire time period from cue onset to stimulus

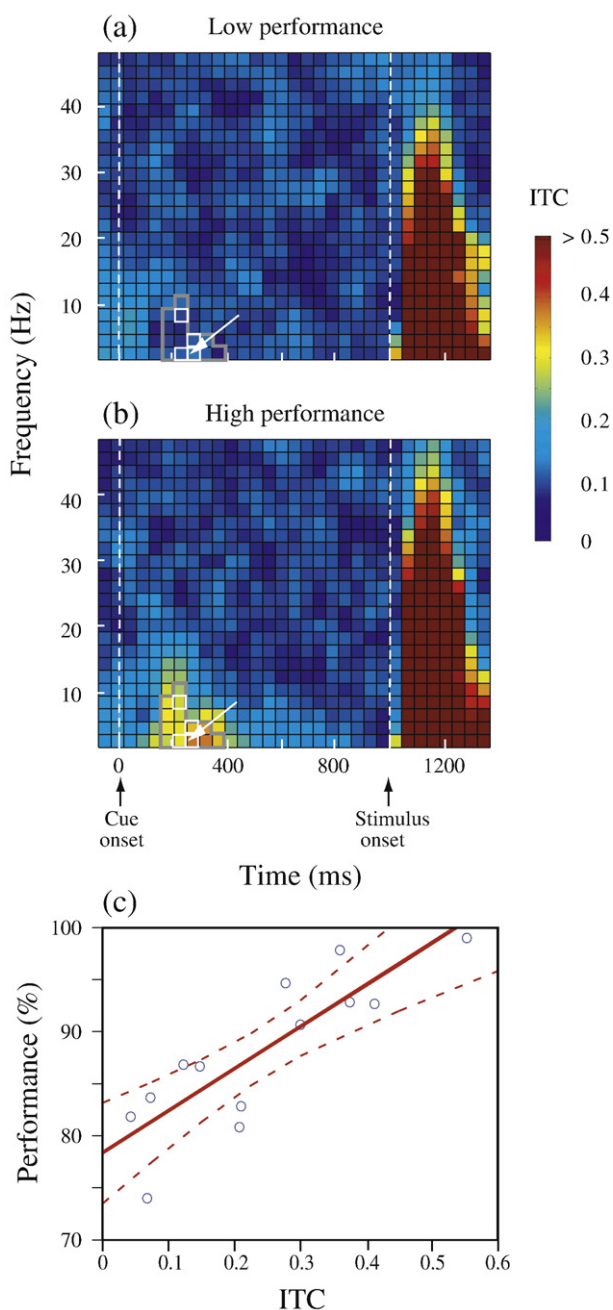


Fig. 2 – Inter-trial coherence (ITC) and performance. (a–b) Group-mean ITC of the ICs representing calcarine activity, showing the strength of phase locking across trials for attention directed towards the right viewing window (grating plus bar). The ITC values vary from 0 (blue) to > 0.5 (red). The onset times of the cue (0 ms) and grating (1000 ms) are indicated by vertical broken lines. Data are shown for both (a) low and (b) high performance observers. The overall performance group ($n=13$) mean = 88.03% (range 74.0–99.0%). The low performance group ($n=7$) mean = 82.4% (range 74.0–86.9%), and high performance group ($n=6$) mean = 94.6% (range 90.6–99.0%). White squares in panels (a) and (b) indicate time/frequency points where, averaged across observers, significant correlations between performance and ITC were evident (range: $t=161$ – 347 ms, $f=1.9$ – 9.8 Hz). (c) Example of correlation between ITC and task performance for the time/frequency point indicated by white arrows in panels (a) and (b) ($t=254$ ms, $f=1.9$ Hz). The solid red lines show linear regression fits to the data, and the broken lines show the 95% confidence intervals.

onset (0–1000 msec). Significant correlations ($p < 0.005$, uncorrected) were found within a limited time-frequency region ($t = 161\text{--}347$ ms, $f = 1.9\text{--}9.8$ Hz, area enclosed by solid grey lines in Fig. 2a,b). Correcting for multiple comparisons within $f = 1.9\text{--}13.7$ Hz from $t = 0\text{--}1000$ ms, significant positive correlations ($p < 0.05$) between task performance and ITC were evident at four points within this region, indicated by the four white squares in Figs. 2a,b. By way of example the correlation ($r = 0.84$) for one such point (at $t = 254$ ms and $f = 1.9$ Hz, indicated by white arrows in Fig. 2a,b) is shown in Fig. 2c, where the broken lines are the 95% confidence interval. Note, however, that no significant correlation was found at this same time/frequency point for the condition in which attention was directed towards the left viewing window, away from the grating stimulus ($r = -0.12$, $p > 0.6$, Fig. 3a).

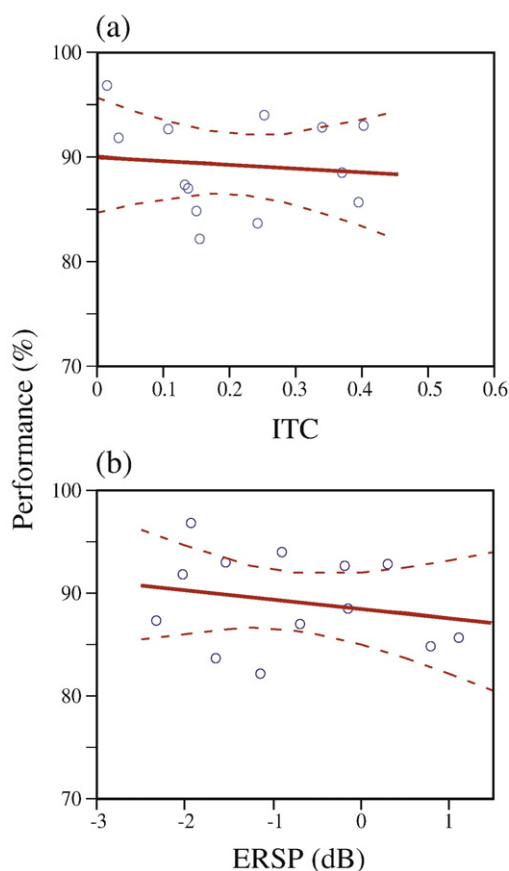


Fig. 3 – (a) Correlation between ITC and performance for the condition in which attention was directed towards the left viewing window, away from the forthcoming grating stimulus: calculations are based on the time/frequency point indicated by white arrows in Fig. 2a–b ($t = 254$ ms, $f = 1.9$ Hz). (b) Correlation between ERSP and performance when attention was directed towards the left viewing window, away from the forthcoming grating: calculations are based on the time/frequency point indicated by white arrows in Fig. 4a–b ($t = 673$ ms, $f = 9.8$ Hz). In each panel, the solid red lines show linear regression fits to the data and the broken lines show the 95% confidence intervals. For attention directed leftwards, the overall performance group ($n = 13$) mean = 89.26% (range 82.2–96.8%).

2.2. Relationship between alpha activity and task performance

Fig. 4 shows, for the independent components reflecting calcarine activity, group-mean ERSP (event-related spectral perturbation) plots of the postcue spectral power differences (in decibels) referenced to a 200 ms precue baseline recording. As in Fig. 2, observers were divided into high (Fig. 4b) and low performance groups (Fig. 4a). All observers showed a pre-stimulus decrease in alpha (near 10 Hz), beginning approximately 400 ms after the attentional cue onset — the decrease was most evident for the high performance group (Fig. 4b). At the point of maximal alpha-band power suppression averaged across all observers (at $t = 673$ ms and $f = 9.8$ Hz, depicted by the white squares in Figs. 4a,b), there was a significant negative correlation ($r = -0.56$, $p < 0.05$) between task performance and ERSP (Fig. 4c — no correction for multiple comparisons was necessary as only one pixel was assessed). However, no significant correlation between task performance and ERSP values was found at this same time/frequency point when attention was directed towards the left viewing window, away from the grating ($r = -0.22$, $p > 0.5$, Fig. 3b).

2.3. Relationship between ITC and ERSP measures

We also observed that there was a significant negative correlation between ITC and ERSP values ($r = -0.6304$, $p < 0.05$, Fig. 5): observers with high ITC values (at $t = 254$ ms and $f = 1.9$ Hz) demonstrated the greatest suppression of alpha-band activity (at $t = 673$ ms and $f = 9.8$ Hz). Note that the ITC time-frequency co-ordinate chosen for this calculation was maximally correlated with visual performance.

3. Discussion

Based on previous experimental work and theoretical arguments on the nature of brain rhythms, we hypothesized that attention-driven changes in neural coherence and alpha-band power may be predictive of behavioral performance. Experimentally, we showed that attentional shifts towards an impending visual target are associated with a sequence of neural changes, beginning with a short-lived increase in ITC within the 2–10 Hz range (Fig. 2), followed by a suppression of alpha-band activity (Fig. 4). We further showed that the magnitude of ITC (Fig. 2c) and the magnitude of alpha activity (Fig. 4c) are predictive of behavioral performance, and that the two measures of cortical function are negatively correlated (Fig. 5). Importantly, our use of MEG in combination with ICA enabled us to establish that the neural changes in question were located within the early visual cortex.

We assume these changes in calcarine activity reflect the influence of top-down attentional control mechanisms, as opposed to more general anticipatory mechanisms, because the changes observed were only evident when subjects directed their attention towards the forthcoming grating. When attention was shifted away from the grating we did not find any significant correlation between ITC and task performance (Fig. 3a), or between ERSP and performance (Fig. 3b). Given this, we suggest the variability in performance with directed attention

(Figs. 2c, 4c) reflects differing degrees of attentional change between subjects, rather than differing degrees of subject arousal or task comprehension.

The increased coherence level observed shortly after the attentional cue onset (Fig. 2) is indicative of a partial phase resetting of on-going oscillatory activity (Makeig et al., 2004). We assume that the phase resetting was a consequence of the attentional demands imposed on the subject, and reflected a top-down neuronal communication with the calcarine (Engel et al., 2001). While the functional significance of neuronal coherence (phase resetting) continues to be debated, one possibility is that it controls the timing of cortical excitability

within task-relevant cortical areas (Klimesch et al., 2006). Biologically, phase resetting may place neurons in a similar state of activation, enabling those most salient for the task at hand to fire synchronously. The increased ITC values observed were in the frequency range 2–10 Hz, which spans the frequency range purported to mediate inter-areal communications (von Stein et al., 2000). We suggest, therefore, that the phase resetting observed within the calcarine may reflect the first neural change in response to top-down control mechanisms, preparing the early visual cortex for forthcoming sensory information.

Some 200 ms subsequent to the observed phase resetting, there was a reduction in alpha-band power (Fig. 4a–b), the extent of which was significantly correlated with task performance (Fig. 4c). The reduction in alpha is unlikely to reflect changes in eye movements or status (open/closed), as trials in which the EOG exceeded $\pm 50 \mu\text{V}$ were rejected (see section Experimental procedure). The suppression of alpha activity following an attentional shift has been reported in previous MEG and EEG studies, all of which suggest that this neuronal change might reflect an active neural area (Worden et al., 2000; Sauseng et al., 2005; Yamagishi et al., 2005; Thut et al., 2006). Attention-related modulation of gamma has also been reported (Fries et al., 2001), though we did not find any with our experimental protocol. Using a plausible neuronal model to investigate how responses at each level of cortical hierarchy depended on the strength of neuronal connections, David et al. (2005) demonstrated that increasing the strength of top-down (backward) connections may act to decrease the power of low frequency oscillations within early cortical areas. This finding is consistent with the suggestion that the decreased alpha activity we observed within the calcarine follows the actions of top-down control processes. It remains an open question as to whether or not top-down control is sustained during the entire cue–target interval (influencing both the phase and amplitude of cortical oscillations), or is present only during the early post-cue period (driving the 2–10 Hz phase resetting). Although speculative, the latter is suggestive that the 2–10 Hz phase resetting may in turn trigger the suppression of alpha activity.

There was a significant negative correlation between the levels of phase resetting and alpha activity (Fig. 5), with phase

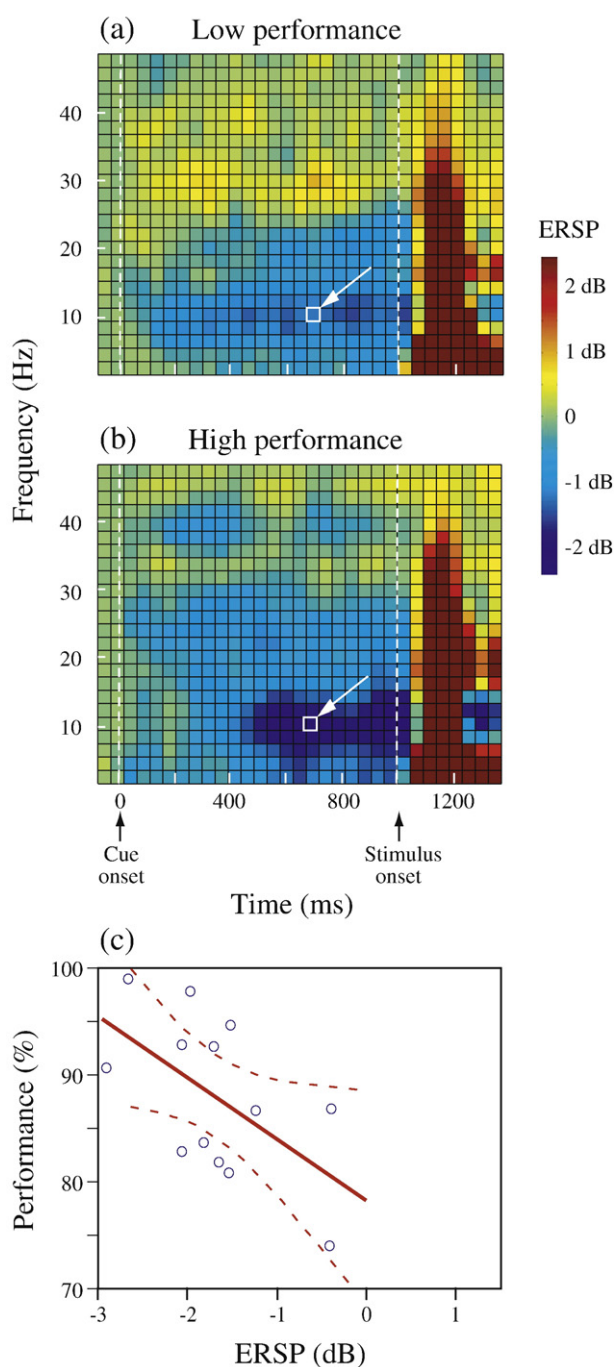


Fig. 4 – Event-related spectral perturbation (ERSP) and performance. (a–b) Group-mean ERSP plots derived from the activation waveform of the ICs representing calcarine activity for attention directed towards the right viewing window (grating plus bar). Both spectral power increases (red) and decreases (blue) are evident. The onset times of the cue (0 ms) and grating (1000 ms) are indicated by vertical broken lines. Data are shown for (a) low and (b) high performance observers. White squares in panels (a) and (b) indicate the time/frequency point ($t=673 \text{ ms}$, $f=9.8 \text{ Hz}$) where, averaged across all observers, the greatest alpha-band power suppression was observed. (c) Correlation between ERSP values and task performance are shown at this time/frequency point. The solid red lines show linear regression fits to the data, and the broken lines show the 95% confidence intervals.

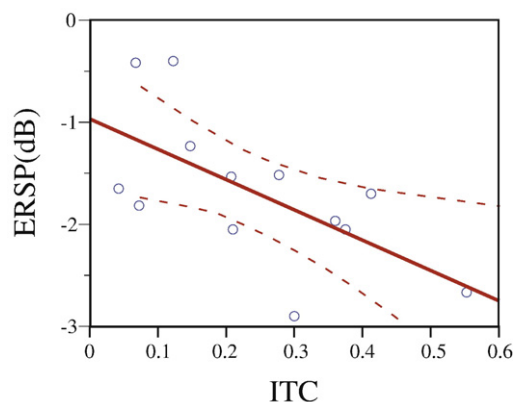


Fig. 5 – Correlation between ITC and ERSP values. The correlation is shown based on time/frequency points of $t=254$ ms and $f=1.9$ Hz for ITC values, and $t=673$ ms and $f=9.8$ Hz for ERSP values ($n=13$). The solid red line shows a linear regression fit to the data, and the broken lines show the 95% confidence intervals.

resetting preceding alpha suppression by about 200 ms. Although we have no direct evidence for a causal relationship between these two neural attributes, it is possible that one exists. Mazaheri and Jensen (2006) provide one possible theoretical framework for just such a relationship. If one subpopulation of alpha generators within the calcarine was phase reset, following the influences of top-down control mechanisms for example, the total power within the alpha band (range 7–13 Hz) may decrease because the phases of the reset subpopulation and remaining subpopulations become asynchronous. Given that a spatially localized reduction in alpha activity reflects an area of heightened neural activity (Pfurtscheller and Lopes da Silva, 1999), rendering it potentially more sensitive to incoming stimuli (Sauseng et al., 2005), we suggest that the sequential neural changes of phase resetting and alpha-band suppression may be fundamental to attentional processes.

Our results are consistent with several EEG and MEG studies which provide evidence that the levels of pre-stimulus oscillatory activity may co-vary with human behavioral performance in visual (Ergenoglu et al., 2004; Hanslmayr et al., 2005), memory (Otten et al., 2006) and somatosensory tasks (Linkenkaer-Hansen et al., 2004). Although the attentional status of observers was not manipulated directly in these studies, each noted it may spontaneously vary from trial to trial. Our results provide confirmatory evidence that the variability of oscillatory activity observed in previous EEG/MEG studies reflects the variability of attentional status between observers (or trials). Accepting this to be the case, we conclude that attention-related changes in pre-stimulus oscillatory activity are predictive of behavioral performance on a wide variety of tasks.

To summarize, we examined the relationship between attentional modulation, activity within early sensory cortex and visual discrimination performance by asking subjects to complete a line-orientation judgment task while undergoing a magnetoencephalographic assessment of their brain function.

We showed that high performance measures on this task are associated with a particular sequence of pre-task neuronal changes within the calcarine; namely, an increase in ITC within the 2–10 Hz ranges followed by a suppression of alpha activity. We suggest that these attention-driven neuronal changes will act to prime early visual areas for incoming sensory information, resulting in enhanced behavioral performance.

4. Experimental procedure

Stimulus and procedural details are reported in full in (Yamagishi et al., 2005). Here, we reiterate essential experimental details for the convenience of the reader, and give a complete description of the re-analyses conducted.

4.1. Stimuli and procedure

On each trial, a small yellow bar was presented within a 9° square viewing window in each quadrant of the inferior field: the bar on the right was superimposed upon an isoluminant chromatic (red/green) grating that occupied the full extent of the right viewing window (Fig. 1a). The yellow bars were randomly positioned within each window, independently presented either clockwise or anti-clockwise oriented (with equal probability) by about 10° from the horizontal meridian. For each observer ($n=14$), the rotation angle of the bar was set equal to that which gave approximately 85% correct performance for judging its orientation, as determined prior to the MEG experiments using forced-choice procedures. Note that the data for one observer (NK) from our previous study (Yamagishi et al., 2005) was excluded from the new analyses because their performance measure during the MEG recording was near chance (53%), despite the bar-orientation angle being set at that which yielded a measure of 85% correct during pre-MEG measures. Between trials, the display screen was blank except for a small, centrally-viewed fixation target.

There were two viewing conditions, executed in pseudo-random order: (1) observers made a covert shift of attention towards the right viewing window, which contained the chromatic grating plus a yellow bar ($n=200$ trials); and (2) observers shifted their attention towards the left viewing window, which contained a yellow bar only ($n=200$ trials). Assuming attentional effects within primary visual areas do not differ between right and left cortex, the grating stimulus was confined to a single quadrant in order to minimize the extent of calcarine activity and simplify Independent Component Analysis. The observer's task was to judge the orientation of the yellow bar on the side to which they had attended. On each trial, the cue indicating which side to attend was a change in the fixation target from a cross to an arrowhead. Following a delay of either 1000 ms ($n=200$) or 500 ms ($n=200$) (presented in pseudo-random order), the stimuli (yellow bars plus grating) were presented for 300 ms. Although two post-cue delay periods were used to help maximize attention, we treated trials containing a post-cue delay of 1000 ms as the main condition with which assess neural changes associated with attentional shifts (Yamagishi et al., 2005). The attentional cue reverted back to a cross 500 ms after stimulus offset. This was the signal for observers to record (using an optical switch)

whether the yellow bar on the side to which they had attended was clockwise or anti-clockwise rotated. To avoid recording preparatory motor activity (Deecke et al., 1969), the task was not speeded and no response deadline was imposed.

Magnetic responses were recorded using a 201-channel (axial gradiometer), whole-head biomagnetic imaging system (Shimadzu Corp., Japan), with simultaneous recording of the electro-oculogram (EOG) being used to monitor eye movements. Trials were rejected if the EOG exceeded $\pm 50 \mu\text{V}$. Most trials (>95%) for each observer were $< \pm 30 \mu\text{V}$, and no systematic eye movement bias occurred for any observer.

4.2. Data analysis

Independent component analysis (ICA) was conducted using EEGLAB (Delorme and Makeig, 2004) over the normalized single-sweep data using procedures described in detail elsewhere (Yamagishi et al., 2005). Independent components (ICs) were determined using an unsupervised neural network to train a weight matrix that maximizes the joint entropy between the nonlinearly transformed channel data (Makeig et al., 1997). Multiplying the original input data by the rows of the trained weight matrix gives the activation waveform for each IC. To determine an IC originating from early visual cortex, all sensor projection maps were examined, and the ICs showing large weights over the occipital regions were projected onto the sensors by multiplication with the inverse weight matrix, and were subjected to a single-equivalent current dipole (ECD) analysis to determine source location. Best-fit solutions were obtained using a least-squares error fit between the observed magnetic signals and those predicted by the ECD model. The solution yielding the best goodness of fit (GF) was determined as:

$$\text{GF} = 1 - \sqrt{\frac{\sum_{i=1}^N (S_i - D_i)^2}{\sum_{i=1}^N S_i^2}}$$

where N is a number of channels, and S_i and D_i are the observed and predicted magnetic signals in channel i , respectively. ICs with dipole sources localized to Brodmann's area 17, as determined using Talairach coordinates (Talairach and Tournoux, 1988), were assumed to reflect early visual activity (Yamagishi et al., 2005) and used for correlational analyses. Note that, for each observer, we found only one IC (GF > 93%) with a dipole source located adjacent to the calcarine sulcus in the left hemisphere (i.e. contralateral to the grating stimuli; see Fig. 1b).

We applied event-related spectral perturbation (ERSP) methods to assess attention-driven changes in cortical oscillatory power, and inter-trial coherence (ITC) measures to assess phase coherence across trials (Delorme and Makeig, 2004; Makeig et al., 2004). The latter is often termed a phase locking factor (Tallon-Baudry et al., 1996), and ranges from 0 (non phase-locked) to 1 (strictly phase-locked). For each observer, ERSP and ITC were calculated using the single-sweep activation waveforms of the IC reflecting calcarine activity. For the ERSP calculation, the power spectrum was determined using a short-time Fourier transform with a sliding latency window of 11.6 samples (46.7 ms) over the 425

samples, ranging from -200 ms to 1500 ms (cue onset time set to zero). The sliding latency window was applied 32 times with a window size of 64 samples wide. The resultant ERSP plot consisted of 25×32 pixels (frequency \times time); the time range consisted of 32 sub-windows with central times ranging from -72 ms to 1372 ms, and the frequency range consisted of 25 equally spaced bins with central frequencies ranging from 1.95 Hz to 48.8 Hz. For the ITC calculation, the same frequency-by-time window size (25×32 pixels) was used.

Because attentional shifts are known to suppress the amplitude of spontaneous alpha rhythms (Fries et al., 2001; Sauseng et al., 2005; Yamagishi et al., 2005; Thut et al., 2006), the correlation between ERSP and behavioral performance was determined at the point of maximal alpha-band suppression. In the absence of any *a priori* knowledge about attention-related ITC modulations, we tested for correlations between performance and ITC over the entire time period from cue onset to stimulus onset. The frequency range for these calculations was restricted to 1.9–13.7 Hz, which incorporates those frequencies thought to be crucial for inter-areal communications (von Stein et al., 2000). We also assessed the extent to which ITC and ERSP were correlated.

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