Large-Scale Gamma-Band Phase Synchronization and Selective Attention

Explaining the emergence of a coherent conscious percept and an intentional agent from the activity of distributed neurons is key to understanding how the brain produces higher cognitive processes. Gamma-band synchronization has been proposed to be a mechanism for the functional integration of neural populations that together form a transitory, large-scale, task- and/or percept-specific network. The operation of this mechanism in the context of attention orienting entails that cortical regions representing attended locations should show more gamma-band synchronization with other cortical areas than would those representing unattended locations. This increased synchronization should be apparent in the same time frame as that of the deployment of attention to a particular location. In order to observe this effect, we made electroencephalogram recordings while subjects attended to one side or the other of the visual field (which we confirmed by event-related potential analysis) and calculated phase-locking statistics between the signals recorded at relevant electrode pairs. We observed increased gamma-band phase synchronization between visual cortex contralateral to the attended location and other, widespread, cortical areas approximately 240–380 ms after the directional cue was presented, confirming the prediction of a large-scale gamma synchronous network oriented to the cued location.

Keywords: alpha, attention, EEG, gamma, neural synchrony

Introduction

Performance of the myriad perceptual and cognitive processes of which the brain is capable requires transient functional coupling, and subsequent decoupling, of specific, task-relevant, neural populations. Gamma-band synchronization is a plausible mechanism for the selection and integration of such neuronal groups (e.g., Varela et al. 2001). Direct brain recordings show that increased gamma-band synchronization within a cortical area occurs most strongly between columns representing information that is being integrated, for example, between columns representing features of a common object (Gray and Singer 1989; Gray et al. 1989; Engel, Kreiter et al. 1991). Stimulus-specific gamma synchronization has been observed between monkey V1 and V2, between V1 and extrastriate motion areas, and between left and right hemisphere V1s of cats (Engel, König, and Singer 1991; Engel, König et al. 1991; Frein et al. 1994). The summation of such gamma synchronous activation yields increased gamma-band power in the electroencephalogram (EEG) and has been experimentally linked to a wide range of cognitive processes including attention, learning, and memory and visual and auditory perception (Ward 2003; Kaiser and Lutzenberger 2005).

Human EEG recordings also reveal increased long-range gamma-band synchrony between task-relevant brain areas during associative learning, mental rotation, conscious recollection, visual working memory, and coherent perception (Tallon-Baudry et al. 1998; Miltner et al. 1999; Rodriguez et al. 1999; Bhattacharya et al. 2001; Burgess and Ali 2002; Gruber et al. 2002). Such results support the hypothesis that gamma-band synchronization enables the selective activation of a functionally coupled ensemble of neuronal groups relevant for the performance of a particular task and for binding the features of an object into a unified percept (Engel and Singer 2001; Varela et al. 2001).

Of more specific relevance to the present experimental paradigm, the deployment of covert attention in humans has been linked to changes in local oscillatory synchronization in the alpha band. Covert deployment of visuospatial attention entails that attended areas in the visual field receive enhanced processing, whereas ignored areas are suppressed (e.g., Posner et al. 1980). Whereas EEG studies have traditionally focused on the enhanced processing of attended targets relative to unattended distractors (for a review, see Gazzaniga et al. 2002), recent research has focused on the anticipatory biasing of the cortex after attention has been deployed to a location but before the appearance of the target. Attending to one visual hemifield yields a sustained increase of alpha-band EEG activity over the ipsilateral visual cortex, a process thought to accomplish the suppression of distractors (Worden et al. 2000; Sauseng et al. 2005; Kelly et al. 2006). Moreover, these lateralized changes in local oscillatory activity have been shown to determine the speed of detection for subsequently appearing targets (Thut et al. 2006).

Cortical gamma-band activity, conversely, appears to be relevant for the enhanced processing of attended information, as studies using implanted electrodes and human EEG have shown that local gamma synchrony is increased by selective attention (Tittinen et al. 1993; Fries et al. 2001; Gobbele et al. 2002). Such evidence, taken together with the data cited above implicating gamma-band synchronization in feature binding and transient functional connectivity between brain areas and the assumption that many of the effects of attention would seem to require transient functional coupling between select populations of cortical neurons, leads to the hypothesis that large-scale gamma-band synchrony might play an important role in selective attention.

As mentioned earlier, the allocation of attention to one location results in certain advantages being given to stimuli appearing at that location, relative to those at unattended locations. Specifically, attended stimuli are promoted for processing in cortical regions responsible for higher cognition and are biased for inclusion in consciousness, a highly integrated yet, apparently, anatomically distributed state (Treisman 1996;
Attention also produces more effective feature binding both within and across sensory modalities. For example, attended stimuli avoid illusory conjunctions and receive feature binding that can be absent for unattended stimuli (for reviews, see Treisman 1996; Wright and Ward 1998). Accordingly, cortical areas representing attended loci must be biased for inclusion in a large-scale functional network to support the enhanced feature binding, higher processing, and propensity for conscious experience that stimuli appearing at such a locus of attention are known to receive. We hypothesized that long-range gamma-band synchronization mediates this transient functional network, enabling the increased communication between cortical areas representing attended loci and other diverse cortical regions and creating a preparatory network for the enhanced processing of attended stimuli.

To test this hypothesis, we recorded EEG while subjects were engaged in a covert attention-orienting task. Our specific a priori hypothesis was that when attention was deployed endogenously to one side of visual space, electrodes over the contralateral visual cortex would show increased gamma-band phase synchronization with other, widespread cortical areas, indexing the establishment of the predicted long-range gamma synchronous attentional network. We also predicted that this would occur in the same time frame as that uncovered in behavioral studies of endogenous orienting that is beginning around 250–300 ms after cue onset (see Wright and Ward 1998). Moreover, we expected that the establishment of this long-range network would occur in coordination with reciprocal changes in local alpha-band and gamma-band activation (see Ward 2003).

**Methods**

Thirteen healthy adults (8 males) with normal or corrected-to-normal vision participated in the experiment after giving written informed consent (approved by University of British Columbia Behavioral Research Ethics Board; mean age, 19.4 years; standard deviation [SD], 1.2 years). Subjects were seated with eyes approximately 35 cm from a computer monitor and were instructed to maintain fixation on a plus sign in the center of the screen. An arrow cue appeared at the center of the screen, replacing the fixation plus, to instruct subjects to covertly attend to a box either to the left or to the right (18.5° visual angle laterally) of fixation on a given trial (see Fig. 1). Arrow cues (1.64° by 1.64° visual angle) were presented for 100 ms, after which the fixation point (1.31° by 1.31° visual angle) reappeared. Targets were presented in boxes (1.97° by 1.97° visual angle), which were positioned 6.2° below the plane of fixation (Fig. 1). Either a “+” or an “x” (50/50 probability) would appear in one of the 2 boxes (50/50 probability) 1000–1200 ms after the cue onset (rectangular distribution to produce random jitter, both to reduce the overlap of event-related potentials [ERPs] from the cue on those to the target and to reduce the effects of evoked neural sources on phase synchrony measures). Target stimuli were presented for 100 ms and subtended a visual angle of 1.64° by 1.64°. Subjects were instructed to make a button-press response if they detected a “+” but not if they detected an “x” in the cued location and to make no response if either stimulus appeared at the uncued location. This paradigm was adapted from that of an earlier study (Worden et al. 2000) and was chosen because it successfully produced lateralized changes in ongoing local power following the deployment of spatial selective attention.

The EEG was recorded from 59 electrodes positioned at standard 10-20 locations plus 3 electrodes at nonstandard sites near the inion. The electro-oculogram (EOG) was recorded bipolarly with electrodes positioned 1 cm from the outer canthi of both eyes and above and below the right eye. Electrode impedances were kept below 15 kΩ (sufficient because of amplifier input impedance >2 GΩ). EEG and EOG were amplified with a gain of 20,000, band-pass filtered between 0.1 and 100 Hz, digitized at 500 Hz, and stored on disk for analysis. Scalp voltages were referenced to the right mastoid.

**Synchrony Analysis**

Four subjects were excluded for the synchrony analysis due to particularly noisy data in the postcue period and/or in the high frequency domain (both of which are irrelevant for the ERP analysis; mean age of the 9 analyzed subjects, 19.6 years; SD, 1.3 years; 6 males). Epochs for the synchrony analysis were extracted from -400 ms before the cue until 1200 ms after its onset. After deleting any epochs containing ocular or nonocular artifacts (identified by the automatic rejection algorithm in EEGLAB; Delorme and Makeig 2004), 3530 epochs for the left cue and 3584 epochs for the right cue remained for all 9 subjects combined ranging from 130 to 598 epochs per subject per cue condition. The data in the retained epochs were band-pass filtered digitally at 1 Hz intervals between 6 and 60 Hz [passband = f ± 0.05f, where f represents the filter frequency; e.g., at 40 Hz the passband was from 40 - (0.05 × 40) = 38 to 40 + (0.05 × 40) = 42 Hz]. Then, using algorithms in the MATLAB Signal Processing Toolbox, we calculated the analytic signal

\[ z(t) = f(t) + j\tilde{f}(t) = A(t)e^{i\phi(t)} \]

of the filtered waveform for each epoch, \( f(t) \), to obtain the instantaneous phase, \( \phi(t) \), and amplitude, \( A(t) \), at each sample point (800 points per epoch), where \( \tilde{f}(t) \) is the Hilbert transform of \( f(t) \) and \( e^{i\phi(t)} \) of Pikovski et al. 2001). Instantaneous amplitudes from this analysis represent the envelope of the filtered waveform and are roughly equivalent to Fourier amplitudes except that they are estimated for each instant in time rather than as an average over a sliding window. We interpreted these amplitudes as reflecting variations in local neural synchrony in the various frequency bands, much as do power spectral densities (Fourier amplitude squared) from a Fourier analysis.

We measured long-range neural phase synchrony by calculating phase-locking values (PLVs) both for individual data and for the

---

**Figure 1.** Stimulus display and its time course (not drawn to scale for clarity). See text for measurement intervals for synchrony and ERP analyses.
combined data. PLVs were obtained by comparing the instantaneous phases of the signals recorded by various pairs of electrodes, for example, electrodes \(j\) and \(k\), at each point in time, \(t\), across the \(N\) epochs available (Lachaux et al. 1999):

\[
\text{PLV}_{j,k} = N^{-1} \sum_{n=1}^{N} |\langle e^{ij(t-f(t)}\rangle|.
\]

PLV is a real value between 0 (random phase difference, no phase locking) and 1 (constant phase difference, maximum phase locking). Because of distortions involved in calculating the Hilbert transform at the edges of the analyzed epochs (e.g., Freeman 2004), we do not display the first or the last 200 ms (100 sample points) of the synchrony analyses of our epochs (note that the last 200 ms also would be contaminated by the target presentation at a random time within that interval). Thus, we report amplitude and phase-locking measures only for reduced epochs from 200 ms before until 1000 ms after cue onset.

To remove the record of ongoing synchrony unrelated to the task, we standardized PLVs and amplitudes relative to the precise interval from 200 ms before cue onset until cue onset (0 ms). This was done by subtracting the mean PLV for the baseline interval at a given frequency from the PLV for every data point at that frequency and dividing the difference by the SD of PLV for the baseline interval at that frequency. The resulting index, \(\text{PLV}_\text{norm}\), indicates standardized changes from the average baseline PLV at a given frequency in the direction of increased synchronization (positive values) or decreased synchronizati(nega-

tive values). The same standardization was applied to the amplitude values. To reduce the effects of volume conduction (see Appendix for a more detailed discussion of the problem of volume conduction in the analysis of phase locking using these techniques) and to remove spurious synchrony arising from using a right mastoid reference electrode, the same calculations were performed for the scalp current density (SCD) or more properly the scalp divergence of the current density, a reference-free measure that sharpens the borders of synchronous regions and reduces spurious synchronies (Lachaux et al. 1999). Classically, SCD = Laplacian of scalp potential, where the Laplacian is the local second spatial derivative. Perrin et al. (1987) showed that SCD, in a spherical coordinate system, could be approximated for any point on the scalp surface using a 3-concentric sphere head model, Legendre polynomials, and spline interpolation. To compute SCD, we used a MATLAB script supplied by Carsten Allefeld (http://www.agnld.uni-potsdam.de/~allefeld/index.html) that implements the algorithm of Perrin et al. (1987) (see their eqs 3 and 5). Allefeld’s script computes a spherical Laplacian operator using Legendre polynomials, the supplied spherical coordinates of a set of electrodes, and splines of order 4. In a separate script, we then applied the Laplacian operator to the potentials recorded at our electrodes to compute SCD. This procedure has been shown to be superior to other methods used previously to approximate SCD from recorded potentials and to give a close approximation to the “true” SCD (Perrin et al. 1987, 1989).

All reported results pertain to the PLV \(_j\) values based on SCD unless otherwise specified, although analyses of scalp potentials and SCDs gave highly similar results. For this reason and because the SCD derived from the scalp potential at a given electrode should reflect primarily neural sources in cortical regions close to that electrode (see Appendix), we often refer to synchrony changes between the cortical regions underlying the relevant electrodes interchangeably with the recording electrodes themselves. In addition, we measured long-range synchrony only for a sparse array of 19 electrodes distributed uniformly across the scalp; the distance between the closest electrode pairs was approximately 4 cm. At this distance, the effects of volume conduction on phase synchrony is much reduced, both for intracranial electrodes (Lachaux et al. 1999) and for scalp electrodes (Nunez et al. 1999; see Appendix). This array was chosen before any analyses were conducted and was used in previous studies as well (e.g., Doesburg et al. 2005).

Finally, to characterize the statistical reliability of changes in synchronization and desynchronization in the time courses of recorded potentials and inferred SCD between pairs of electrodes, relevant sets of epochs were shuffled 200 times for each frequency and data point combination, measuring PLV \(_j\) in the same way for each shuffled data set, to create surrogate distributions of PLV \(_j\) values (Lachaux et al. 1999).

This procedure produces distributions of PLV \(_j\), that very closely approximate a normal distribution. We considered a measured PLV \(_j\) above the 97.5th percentile of the relevant surrogate distribution to be a significant increase in synchronization and one below the 2.5th percentile to be a significant decrease in synchronization. Only changes in synchronization that met or exceeded this criterion are discussed. This still results in a large number of possible tests, and the surrogate method by itself does not protect against the accumulation of experimentwise Type I error from making many such tests. To deal with this problem, we rely upon demonstrations that 1) the changes we observed were predicted \(a\) \(p\)riori\(i\) in the regions of interest (ROIs) in which they were found and 2) the patterns of changes we observed persist across several nearby frequencies and time points, the surrogate distributions of which are derived from independent shufflings, rendering it highly unlikely that the observed patterns resulted from a random set of false positives.

ERP Analysis

Epochs for analysis of ERPs were extracted from 100 ms before until 600 ms after target onset. After deleting any of these epochs contaminated by ocular or nonocular artifacts (in this case using the automatic rejection algorithm of ERPS from the University of California San Diego ERP Lab), ERPs to targets were computed by averaging the EEG signal across artifact-free epochs for each subject. For these ERP analyses, the EEG records were digitally rereferenced to averaged mastoids and, after averaging, digitally low-pass filtered using a half-amplitude Gaussian filter to view ERPs \(<13\) Hz. Three of the 13 subjects were excluded from the ERP analysis because their EEG signals contained too many artifacts, in particular eye movements or blinks after presentation of the target, resulting in a large number of trials being rejected from their data. Thus, the subject groups used in the ERP analysis differed slightly from that used in the synchronization analysis. Although the subgroup used for ERP analysis is the optimum one for that analysis, ERPs were also analyzed using data only from the 9 subjects included in the PLV analysis in order to ensure that any observed ERP effects were also present in that data set.

Multitrial analyses of variance (ANOVA)s were performed on averaged ERPs. ERPs at electrodes P7 and P8, the electrodes of interest in the phase synchronization analysis, were analyzed, as were electrodes PO7, POz, and PO8, which are electrodes typically of interest when examining ERPs in visual attention tasks. These particular electrodes are known to reflect attentional modulation of activity over parietal and occipital cortices reflected by shifts of attention at the electrode contralateral to visual field presentation (see Results for a more extensive rationale). Because our interest in the ERP analyses was solely to confirm that attention had been directed to the cued location by the arrow cue and maintained there until target onset, our analyses focused on the P1 component, the first positive component, within a window of 75–150 ms after target onset and the N1 component, or first negative component, within a window of 100–200 ms after target onset.

Results

Phase Synchronization

Our main \(a\) \(p\)riori\(i\) prediction was confirmed, as increased gamma-band (36–43 Hz) phase synchronization was observed between posterior visual cortical areas contralateral to the cued location and other, widespread, cortical areas occurring from about 240 ms until about 380 ms after the cue appeared (Fig. 2). The most prominent increases were observed between electrode P7 and electrodes over widespread cortical areas, and electrode P8 and electrodes over widespread cortical areas, following right and left cues, respectively (Fig. 2A,B). Although present following the onset of either directional cue, the effect is more pronounced and more prolonged following the left cue. We interpret this burst of increased, lateralized, phase synchronization as an indicator of the establishment of the hypothesized gamma synchronous attentional network. This effect was
 maximal around 39 Hz (because the data were filtered using a bandwidth of 0.1f, this signal contains energy from nearby frequencies) but was also visible at other frequencies in the gamma band (see Supplementary Material A). A second burst of lateralized large-scale gamma-band phase synchronization, again maximal at 39 Hz, was also observed approximately 520–580 ms postcue onset (Fig. 2C,D). As was the case for the first burst of increased gamma-band synchrony, this lateralization was anchored at electrodes P7 and P8 following the right and left cues, respectively, and was more pronounced and more prolonged following the left cue. No such bursts of long-range synchronization lateralized as a function of cue direction were present in other frequency bands; they occurred only in the gamma frequency band, although nonlateralized increases and decreases in synchronization did occur in other frequency bands around the time of the first gamma burst (see Supplementary Material A). No reliable patterns of coordinated synchronization or desynchronization in other frequency bands were observed in conjunction with the second gamma burst. Analysis of individual subject data revealed similar, although less striking, patterns of lateralized gamma-band synchronization (because of poorer signal-to-noise ratio, which is a function of the number of epochs analyzed). For some subjects, reliable effects closely resembled those in the group data, whereas for some others, the pattern took the form of decreases in synchronization between visual cortical areas ipsilateral to the cued hemifield and widespread electrodes as well as, or in place of, the increases contralateral to the cued hemifield observed in the main effect for our group data (Supplementary Material B).

In addition to the changes in long-range gamma-band synchrony just described, we observed a reduction in the local (standardized) amplitude of the signal in the alpha frequency band (8–12 Hz) occurring from about 200 to 650 ms after cue onset over the left visual cortex and from cue onset until about 500 ms after it over the right visual cortex (Fig. 3). This reduction of alpha-band amplitude coincided with an increase in gamma-band amplitude (Fig. 3) and with the lateralized gamma-band synchronization patterns described earlier. The decrement in alpha amplitude was, surprisingly, larger at visual electrodes ipsilateral to the cued location than at contralateral electrodes. A subsequent reversal was then observed as greater alpha-band amplitude was seen at electrodes ipsilateral to the cued location relative to that at contralateral electrodes. This latter effect endured from about 650 ms until about 1000 ms after cue onset over the left visual cortex and from about 500 ms after cue onset until beyond the end of the displayed epoch over the right visual cortex (Fig. 3) and replicates the pattern reported by Worden et al. (2000). Although also visible in the scalp, plotted data for this result are taken from the scalp potentials because they pertain only to local EEG amplitude (comparable SCD amplitude data can be seen in Supplementary Material A).

The possibility should be considered whether the bursts of lateralized gamma-band synchrony we observed could have arisen from a single oscillating source whose activity could have been volume conducted to several electrodes, for example, a strong local gamma-band activation located in visual cortex contralateral to the cued location. Such a scenario, however, would entail a much greater gamma amplitude increase over contralateral visual cortex than over ipsilateral visual cortex. This was not observed; in fact, gamma amplitude increased more over ipsilateral visual cortex than over contralateral visual cortex (see Figs 2 and 3 and Appendix). For these reasons, we can confidently reject the notion that our lateralized long-range phase synchrony results arose from this kind of volume conduction scenario. Other possibilities are discussed in the Appendix.

An increase in beta-band phase synchronization also was observed from about 220 ms until about 400 ms after the cue onset (see Supplementary Material A). This increased synchronization was strongly anchored at the right occipitoparietal and left frontal electrodes, with strong connectivity linking these 2 regions and increased phase synchrony between these
electrodes and other cortical areas. Corresponding local amplitude changes were also evident, with prominent increases in left frontal, right occipitoparietal electrodes, and those over the right frontal areas. The topology of this beta oscillatory network emerged following both the left and the right cue but did not appear to be affected by the direction of attentional deployment.

**Event-Related Potentials**

The current paradigm was chosen due to its success in a previous study in illuminating changes in local EEG power during selective visual attention (Worden et al. 2000). In that study, electrophysiological measures were used to confirm that attention had been effectively deployed, as no behavioral measures are available in this paradigm, and it is important to any arguments about the mechanism of attention deployment to confirm that attention was indeed deployed as specified to subjects. Worden et al. (2000) did confirm appropriate attention deployment in their study although they based their conclusion only on attentional modulation of the N1 amplitude. They failed to find P1 modulations although some other studies with similar endogenous orienting paradigms have found modulations of both components (e.g., Mangun and Hillyard 1991; Sauseng et al. 2005).

We also confirmed that attention indeed was shifted to the cued location by analyzing ERPs to the targets. Figure 4 presents the results of our analyses (see also Supplementary Material C). For trials where the stimulus presented was a target, we performed 2 sets of 3-way ANOVAs on the P1 and N1 amplitudes separately: Electrode (P7, P8) × Stimulus side (Left, Right) × Validity (Valid, Invalid) and Electrode (PO7, POz, PO8) × Stimulus side (Left, Right) × Validity (Valid, Invalid).

Analysis of the N1 component revealed a significant attention modulation, replicating the results of Worden et al. (2000). At electrodes P7 and P8, a significant main effect of validity was found ($F_{1,9} = 5.47, P < 0.05$), showing that N1 amplitude was larger on trials where the stimulus appeared in a validly cued location. The interaction of Electrode × Side was also significant ($F_{1,9} = 19.89, P < 0.01$), revealing that N1 amplitude was greatest when the stimulus was presented contralateral to the recording electrode. The 3-way interaction between Electrode, Side, and Validity was also significant ($F_{1,9} = 7.49, P < 0.05$), indicating that the effect of attention on the N1 was larger on the side contralateral to the cued location.

![Figure 3](https://academic.oup.com/cercor/article-abstract/18/2/386/337916/386)

**Figure 3.** Standardized amplitude from filtered (alpha, 11 Hz and gamma, 39 Hz) electrode (P7 and P8) potentials (vertical axes) as a function of time after cue onset (at 0 ms) for the various cue conditions.

![Figure 4](https://academic.oup.com/cercor/article-abstract/18/2/386/337916/387)

**Figure 4.** ERP waveforms to targets at electrodes P7, P8, PO7, POz, and PO8. Waveforms to targets presented in the right visual field are at the top of the figure; waveforms to targets presented in the left visual field are presented at the bottom of the figure. Note that N1 amplitude to validly cued targets is largest contralateral to target presentation.
Analysis of N1 amplitude at electrodes PO7, POz, and PO8 showed the same pattern with a significant main effect of Validity ($F_{2,9} = 6.51, P < 0.05$). Also as for electrodes P7 and P8, an interaction between Electrode and Side was found ($F_{2,9} = 24.37, P < 0.01$), with larger amplitude to targets presented contralateral to electrodes PO7 and PO8 and larger amplitude at electrode POz to targets presented to the left of fixation. Finally, there was also a significant 3-way interaction between Electrode, Side, and Validity ($F_{2,9} = 5.28, P < 0.05$). Analysis of ERPs using only data from the 9 subjects included in the synchrony analysis showed the same patterns of results, confirming that results from the main ERP analysis generalize to the subject group for whom the synchrony results are presented (see Supplementary Material C).

The same analyses showed no attentional modulation of P1 amplitudes, again, as found by Worden et al. (2000). For electrodes P7 and P8, there was no main effect of, nor significant interactions involving, Validity. There was an interaction between Side and Electrode, with larger P1 amplitude for targets presented contralateral to the electrode ($F_{1,9} = 6.93, P < 0.05$). For electrodes PO7, POz, and PO8, as for P7 and P8, the analysis revealed no main effect, nor any interactions involving, Validity. There was, however, an interaction between Side and Electrode ($F_{2,9} = 7.65, P < 0.01$), with larger amplitude contralateral to target presentation for electrodes PO7 and PO8 and larger amplitude to targets to the left of fixation at electrode POz.

Although they reveal nothing new about attention orienting in this paradigm, these ERP results do provide convincing evidence that attention was indeed directed to the cued location by the arrow cue and maintained there until target onset. First, as mentioned earlier, previous experiments with similar endogenous attention-orienting paradigms have found that the N1 ERP component is larger when targets are presented in an attended (cued) location than when presented in an unattended location and in particular that the ERP modulation is closely tied to faster responding to the target at the cued location, a more traditional behavioral measure of attention orienting (e.g., Mangun and Hillyard 1991). Our finding of a significantly larger N1 component to targets presented at the cued location is a strong indicator that subjects were reliably shifting their attention to that location when directed to do so by the arrow cue. The fact that we, and Worden et al. (2000), found no significant cue effect on the P1 component in this paradigm does not contradict this interpretation. Modulations of P1 and N1 components are known to be dissociable from one another depending upon the task (e.g., Luck et al. 1990). In endogenous cueing tasks involving stimulus discrimination like the one used in this experiment, Luck et al. (1990) found that whereas the N1 was significantly larger on validly cued trials, this effect was not found for the P1 component. Further, Vogel and Luck (2000) found evidence that the N1 component is a reflection of the discrimination of visual stimuli; as our task was a visual discrimination task, it is reasonable to understand the modulation of the N1 component to be a reliable indicator of the subjects’ successful shift of attention to the cued location.

**Discussion**

Cue-directed deployment of attention to one side of the visual field, confirmed by the modulation of the N1 component of the ERP to the subsequent target, coincides with an increase in gamma-band phase synchronization between the contralateral visual cortex and other, widespread cortical areas. Our results support the view that gamma-band synchronization is the mechanism that implements 1) the selective properties of attention (certain neuronal groups are biased for inclusion into the network and others are not), 2) its integrative properties (when neurons corresponding to attended objects’ features are included in a long-range network they are more integrated with other perceptual and cognitive representations), and 3) the special relationship between attention and conscious executive processes (inclusion in the network is equivalent to inclusion in a global conscious workspace allowing cognitive and behavioral operations on this information that are informed by other considerations such as goal and context; e.g., Dehaene and Naccache 2001). Synchronously oscillating neurons can perform such integration because they communicate more effectively than do nonsynchronous neurons. Bursts of action potentials from a sending neuron must be consistently received during the depolarized phase of a target neuron’s membrane potential fluctuation in order for those action potentials to be efficacious, and this happens when the sending and receiving neurons are phase locked (Fries 2005). What is still mysterious is how and why synchronization in the various frequency bands plays the role it does. Our results on the relationship between local and long-range synchronization in alpha, beta, and gamma bands begin to address this question.

**Gamma-Band Phase Synchronization**

The selection and integration of information into a large-scale complex that extends across brain areas has been posited to be consciousness (Tononi 2004). We propose that the selection of certain neuronal groups for integration into a large-scale gamma synchronous network accounts for how selective attention enables the increased integration of attended information, relative to unattended information, within and across sensory modalities and biases attended information for higher processing and entry into consciousness (cf., Lamme 2003; Koch and Tsuchiya 2006). In this view, the emergence of a dynamic executive consciousness within the brain may result from a large-scale gamma-synchronous network of task-relevant neural populations. This implements functional integration and serves to activate a specific network from a large repertoire of possible networks. The representational contents of neural groups included in this coherently oscillating network define the content of consciousness and are dynamically assigned according to task demands, perceptual input, and motor output (Varela et al. 2001).

Local brain recordings have demonstrated that synchronously gamma oscillatory cortical columns code figure-ground segregation and the binding of features for the encoding of global stimulus properties, leading to the proposal that gamma-band synchrony underlies sensory awareness (Gray et al. 1989; Engel, König and Singer 1991; Engel and Singer 2001). Long-range complexes of gamma synchronous brain regions correspond to the emergence of a coherent conscious percept and the binding of local features into a global visual percept (Rodriguez et al. 1999; Doesburg et al. 2005; Rose et al. 2006). Such results show frequency specificity similar to the results reported here, suggesting a common neural mechanism of large-scale integration. Conscious recollection, moreover, is associated with greater gamma-band EEG connectivity than is familiarity (Burgess and Ali 2002). Gamma oscillations are generally restricted to brain states associated with consciousness (waking and rapid eye movement
sleep) and are more spatially segregated than low-frequency oscillations present during nonconscious central nervous system states, thereby allowing the increased specificity of information selection required for consciousness (Nunez 1995).

A variety of previous findings support the notion that gamma-band synchrony is relevant for attention and that it is a mechanism for functional integration across brain areas. These include: lateralization of induced gamma-band responses to somatosensory stimulation and visual stimuli can be modulated by selective attention (Gruber et al. 1999; Gobbele et al. 2002); the auditory 40-Hz transient response is larger for attended stimuli than it is for those that are ignored (Tittinen et al. 1993); intracranial recordings of area V4 in monkeys show greater gamma-band synchronization between neurons activated by an attended stimulus relative to those activated by an unattended stimulus (Fries et al. 2001); intracranial EEG recordings in humans have shown that successful memory formation is associated with greater gamma-band synchronization between the rhinal cortex and the hippocampus (Fell et al. 2001); increased EEG gamma-band coherence between somatosensory and primary visual areas occurs when subjects learn an association between a finger shock and a visual stimulus (Miltner et al. 1999); gamma-band phase synchronization across posterior electrodes is greater when a stimulus is identified in a fragmented pattern, relative to when a stimulus is not identified (Gruber et al. 2002); EEG phase synchronization between posterior and frontal cortical regions is increased during mental rotation (Bhattacharya et al. 2001); gamma-band activity is increased at frontal and occipitotemporal electrodes during the delay phase of a short-term memory task (Tallon-Baudry et al. 1998); and perceptual grouping is associated with increased gamma-band oscillations in the high gamma band (70–120 Hz) at central occipital locations, whereas the requirement to focus attention on the perceptual groups activates additional low gamma-band (44–66 Hz) oscillations in parietal locations (Vidal et al. 2006).

The prominence of increased long-range gamma-band synchronization at right parietal electrodes in our data strengthens the attentional interpretation of the effect, as the right parietal lobe is particularly relevant for visual attention (Egly et al. 1994), and this area shows increased gamma activity when attentional focusing is required (Vidal et al. 2006). This introduces a theoretical bridge between gamma-band phase synchronization and current knowledge about the functional neuroanatomy of attention. Moreover, coordinated changes in gamma and alpha oscillations are maximal ∼280 ms after the onset of the cue, at the time where previous work has shown that behavioral enhancement as a function of attention reaches its zenith (Wright and Ward 1998). Prior to the increase in gamma-band phase synchronization, a period of desynchronization is also observed in our data beginning when the cue is presented and lasting until about 175 ms after cue onset (Fig. 2B; see Supplemental Material A for detailed time course). This may reflect phase scattering, a process thought to disrupt existing gamma synchronous neural assemblies in order to enable the emergence of new transient assemblies. Similar patterns have been found preceding transient bursts of increased gamma-band synchronization in coherent perception (Rodriguez et al. 1999; Doesburg et al. 2005). Moreover, stimulus processing can produce either local synchronization or desynchronization in the gamma band depending on task relevance (Mazeheri and Picton 2005). Our analysis of individual subjects’ data revealed some instances of global gamma-band desynchronization between visual cortex ipsilateral to the cued hemifield and widespread electrodes (Supplementary Material B). We interpret this as a functional decoupling between cortical regions representing the to-be-ignored location, thus indicating a suppression of unattended information.

Our results indicate that bursts of lateralized gamma-band phase synchronization are transient, occurring about 240–380 ms after cue. Although this is within the predicted time frame for the initiation of endogenous orienting (e.g., Wright and Ward 1998), our subjects were required to maintain their attention at the cued location far beyond the termination of this gamma burst. This suggests that the observed synchronization is related to the deployment of attention to a location but is not required for the maintenance of attention at that location. Bursts of gamma-band phase synchronization related to the onset of a coherent percept have also been found to be short lived relative to the duration of the percept itself (Rodriguez et al. 1999; Doesburg et al. 2005). Large-scale gamma-band synchronization must therefore be regarded as a mechanism for integrating a functional network rather than one that is responsible for maintaining that integration.

Our analysis revealed a second burst of lateralized long-range gamma synchrony at 520–580 ms after cue onset. This finding echoes earlier findings from coherent perception where a second burst of long-distance gamma-phase synchrony has also been recorded (Rodriguez et al. 1999; Doesburg et al. 2005). The temporal relationship between the first and second burst of gamma synchrony in this, as well as in previous studies, is consistent with a theta frequency (4–7 Hz) cycle. Phase coupling between theta and gamma activity has been observed across brain regions during cognitive processing in studies employing scalp or intracranial EEG and has been interpreted as a mechanism mediating neural communication across long distances (Schack et al. 2002; Canolty et al. 2006). In light of this, it seems likely that the second burst of lateralized long-range gamma synchrony reported here may be related to the maintenance or refinement of the attentional network established by the first burst.

**Alpha-Band Amplitude Reduction**

Previously it has been shown that shifts of visuospatial attention to locations in one hemifield yield a sustained increase in alpha activation over ipsilateral visual cortical areas beginning around 500 ms after cue onset (Worden et al. 2000; Thut et al. 2006). Our study replicated this result. We also replicated an earlier reduction of alpha activity over both contralateral and ipsilateral visual areas reported by Worden et al. (2000). Our results, however, also indicated that this early reduction was much more pronounced over visual cortex ipsilateral to the attended location. One possible explanation for this discrepancy between our results and those of Worden et al. (2000) is the several differences in the analysis techniques used. Here we report local activity changes in instantaneous amplitude that are standardized relative to the mean of a precise baseline, whereas studies using temporal spectral evolution, which report lateralization only for the later-occurring alpha-band evolution, plotted the nonstandardized amplitude of the filtered, rectified, and smoothed signal as a function of time (Worden et al. 2000; Thut et al. 2006).

A striking temporal correspondence is evident between the early, bilateral but unequal, decrease of local alpha amplitude,
the similar bilateral but unequal increase of local gamma amplitude, and the first burst of lateralized long-distance gamma-band phase synchronization: all these effects were maximal ~300 ms after cue onset. This suggests that the activities of oscillatory mechanisms in multiple frequency bands interact across local and long-distance scales to enable selective visuo-spatial attention. Specifically, we propose that local alpha-band activity reflects suppression of a cortical area, local gamma-band activity reflects active processing in a cortical area, and long-range gamma synchronization serves to establish a transient network promoting the transfer of information appearing at attended locations from the relevant modality-specific cortical areas (in this case contralateral occipital and posterior temporal cortices) to other cortical regions (cf., Ward 2003). The lateralization effects in local amplitude discussed earlier, however, suggest that the relationship between neural oscillations and attentional processing is more complex, given that gamma-band amplitude is slightly lower in the hemisphere contralateral to the attended location during this period. A possible explanation for this is that when cortical tissue is engaged in a long-range gamma-band synchronous assembly, increased columnar selection and segregation occur locally, leading to relatively lower gamma-band and relatively higher alpha-band amplitude as a comparatively restricted set of columns are engaged in active processing. In support of this notion, it has been found that cortical stimulation at 40 Hz produces increasingly focal responses (intercolumnar inhibition), whereas 10 Hz stimulation propagates to other cortical areas (Llina's et al. 1998).

If long-distance synchronization between neural groups underlies transient functional integration, as we and others have proposed, then increased long-distance synchronization should be exhibited throughout the period during which the neural populations in question are coupled. In the case of selective attention, this entails synchrony between cortical areas representing attended information and other brain regions throughout the period of attention maintenance. In support of this notion, 2 studies have found evidence for long-duration, long-range coupling of attention-related brain regions in an attention-orienting paradigm. First, in a cued target-discrimination paradigm, increased high-alpha-band phase coupling in the EEG between frontomedial electrodes and parietal electrodes contralateral to the attended hemisphere was found to occur during the 200 ms just preceding target onset (Sauseng et al. 2005). Second, our own magnetoencephalographic results using a paradigm identical to the experiment reported here showed increased long-distance high-alpha-band phase synchronization between sensors over occipital cortex contralateral to the cued location and sensors over other, widespread cortical regions beginning ~500 ms after cue onset and lasting throughout the period of attentional maintenance (Doesburg and Ward forthcoming). Moreover, we also observed an initial, bilateral, long-range desynchronization in the alpha-band peaking around 280 ms after cue onset. The tight correspondence of these effects with the amplitude changes in the alpha band described here suggests that an alpha oscillatory mechanism involving local desynchronization and long-range synchronization is responsible for the maintenance of selective attention.

**Beta-Band Attention Network**

Previous magnetoencephalographic results from an attention blink paradigm have shown that when subjects were able to successfully report perceiving the second of 2 successive targets in a rapid-serial-visual-presentation stream, compared with trials on which perception of the second target was not reported, synchronization of a beta-band oscillatory network was observed between the right cingulum, right posterior parietal lobe, and left frontal areas shortly after the second target was presented (Gross et al. 2004). A long-range beta oscillatory network bearing a similar topography and time course was also present in our data (see Supplementary Material A). This effect was maximal at about 18 Hz, did not vary according to the direction of attentional deployment, and reached its maximum during the peak of the lateralized gamma-band synchronization. This suggests that this beta synchronous network is of general relevance for attentional deployment and that this mechanism operates in tandem with gamma-band oscillations. The pattern of interactions between the gamma-band and beta-band networks is still to be explored.

On the basis of these results, however, we postulate that the beta-band network is a general mechanism that implements attentional preparation, or readiness, whereas the gamma-band network selects task-relevant neural populations and integrates them into a transient functional network.

**Supplementary Material**

Supplementary materials can be found at: http://www.cercor.oxfordjournals.org/

**Notes**

This research was supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada to L.M.W. We thank Stephanie Thai, Vivian Pan, and Lauren Emberson for help in collecting the data. We thank Carsten Allefeld for supplying the MATLAB algorithm for the SCD analysis. We also thank Dr Kentaro Yamanaka, Graduate School of Education, University of Tokyo, for help in developing the phase synchrony analysis program. *Conflict of Interest* None declared.

Address correspondence to Sam M. Doesburg, Department of Psychology, University of British Columbia, 2136 West Mall, Vancouver BC V6T 1Z4, Email: sam@psych.ubc.ca.

**Appendix**

In the context of EEG and MEG recordings of brain activity, volume conduction refers to the propensity for electric or magnetic fields to be transmitted from an electrical source through the tissues of the brain, skull, and scalp to sensors distributed over a wide area on or near the scalp. The problem has been considered extensively in the context of source analysis in EEG and MEG. Here the well-characterized inverse problem is to reconstruct the primary current distribution within the brain from the electric or magnetic fields measured on or near the scalp. Extensive modeling and sophisticated algorithms have made this problem less of an issue in recent times. In the context of the analysis of neural phase synchrony, however, much less work has been done and the possibility of volume conduction creating spurious synchronies remains a serious consideration.

The most extensive research relevant to this problem was done by Lachaux et al. (1999). They defined and investigated, in the context of intracranial EEG recordings, the measure of PLV used here. They also specifically addressed the possibility of spurious synchrony indicated by this measure arising from volume conduction and concluded that long-range synchronies were unlikely to arise because of this effect. This conclusion was based on both direct measurements of PLV at intracranial electrodes spaced at 1 cm intervals, over which
volume-conduction-induced spurious synchrony did not extend further than 2 cm in normal tissue, and on simulations using local field potential recordings from a subject as dipole sources and forward calculating the resulting scalp potential using a 3-layer spherical head model. In the simulation, they calculated PLV for scalp potential, SCD (the local second spatial derivative of the scalp potential), and electrocorticogram (ECoG, obtained from a deblurring technique introduced by Le and Gevins 1993) for scalp electrodes at various positions relative to the 2 radial dipole sources, which were located in separate hemispheres around the midline. Both the SCD and the deblurred ECoG sharpened synchronous regions in the simulations and reduced spurious synchronies relative to those calculated for the scalp potential. They had this effect because both reduce the overlap of the volumes recorded by different scalp electrodes, in particular eliminating the contributions of deep sources and shrinking the surface areas of the scalp affected by shallow sources. In addition, another study by Nunez et al. (1997) also found that SCD or ECoG reduced the effects of volume conduction on coherence between scalp electrodes at various distances (which includes but is not the same as phase synchrony because coherence is also influenced by amplitude correlation), with spurious coherence dropping to near zero when scalp electrodes were separated by 4 cm or more.

The studies of Lachaux et al. (1999) were based on instantaneous phase and instantaneous amplitude obtained from convolving a Morlet wavelet of appropriate frequency interval with the EEG signals. An alternative approach, and the one we use here, is to obtain these quantities from the analytic signal, based on the Hilbert transform, for the filtered EEG signals (Tass et al. 1998). Le Van Quyen et al. (2001) directly compared the 2 methods for analysis of neural synchrony for data from neuronal models, intracranial EEG, and scalp EEG and found that they were essentially equivalent. We have also analyzed some of our other data using both methods, but we found the areas of synchrony to be more sharply delineated with the Hilbert transform-based technique, so we used that technique here.

To set the problem of volume conduction effects on neural synchrony measured by sensors more sharply, consider the simple case simulated by Lachaux et al. (1999). We have 2 radial dipoles oscillating at some frequency, call them $x_1$ and $x_2$, located at some distance from one another, recorded by 2 electrodes, each near to one of the sources. The dipoles generate signals

$$x_1 = a_1 \exp \left[ j (\omega t + \phi_1) \right],$$

$$x_2 = a_2 \exp \left[ j (\omega t + \phi_2) \right],$$

(A1)

where $j = \sqrt{-1}$, $a_1$ and $a_2$ are the amplitudes of the signals, $\phi_1$ and $\phi_2$ are the respective phase angles, and $\omega$ is the common frequency (for clarity, we are assuming noiseless signals with constant phase offset; however, the results apply to the averages of noisy signals). The signals actually recorded by the electrodes are affected by the conductivity of the brain, skull, and scalp (here assumed to be one constant, average value, $c$) and the distance of electrode $j$ from source $k$ ($d_{jk}$), so that the recordings can be written as

$$e_1 = \frac{c}{d_{11}^2} x_1 + \frac{c}{d_{12}^2} x_2,$$

$$e_2 = \frac{c}{d_{21}^2} x_1 + \frac{c}{d_{22}^2} x_2.$$  

(A2)

Because the conductivity and distance are constants and substituting for $x_1$ and $x_2$ from equations A1, we can write

$$e_1 = a_1' \exp \left[ j (\omega t + \phi_1) \right] + a_2' \exp \left[ j (\omega t + \phi_2) \right],$$

$$e_2 = a_1' \exp \left[ j (\omega t + \phi_1) \right] + a_2' \exp \left[ j (\omega t + \phi_2) \right],$$

(A3)

and summing the signals for each electrode using the rules of vector addition, we obtain

$$e_1 = a_1' \exp \left[ j (\omega t + \phi_1) \right],$$

$$e_2 = a_2' \exp \left[ j (\omega t + \phi_2) \right],$$

(A4)

where the dots (e.g., $a_1'$) indicate the sums across sources and where

$$a_1' = \left[ (a_1' \cos \phi_1 + a_1' \cos \phi_2)^2 + (a_1' \sin \phi_1 + a_1' \sin \phi_2)^2 \right]^{1/2},$$

$$a_2' = \left[ (a_2' \cos \phi_1 + a_2' \cos \phi_2)^2 + (a_2' \sin \phi_1 + a_2' \sin \phi_2)^2 \right]^{1/2},$$

(A5)

and

$$\phi_a = \arctan \left[ \frac{a_1' \sin \phi_1 + a_1' \sin \phi_2}{a_1' \cos \phi_1 + a_1' \cos \phi_2} \right]$$

$$\phi_b = \arctan \left[ \frac{a_2' \sin \phi_1 + a_2' \sin \phi_2}{a_2' \cos \phi_1 + a_2' \cos \phi_2} \right].$$

(A6)

These expressions (A1–A6) readily generalize to any number of sources. When we add these electrode recordings to $i$ times their Hilbert transforms to obtain the analytic signal (see Methods), we obtain

$$\zeta_i = e_1 + i e_2 = A_1 \exp i \phi_a,$$

$$\zeta_i = e_2 + i e_2 = A_2 \exp i \phi_b,$$

(A6)

where $A_1 = a_1'$ and $A_2 = a_2'$. Recall that

$$PLV_{i,j} = N^{-1} \sum_{n=1}^{N} (\tilde{e}_n(t), \tilde{e}_{i+n}(t)),$$

(A7)

so that the above development (i.e., especially eq. A6) and $\phi_j(t) = \phi_i + \phi_0$ for any specific time $t$.

$$PLV_{i,j} = f(a_1, a_2, \phi_i, \phi_0).$$

(A7)

This means that raw PLV depends on the relative amplitudes of the 2 sources as well as the constancy of their relative phases across trials. For this reason, we use the standardized PLV, to eliminate the volume conduction effects of sources whose amplitudes do not change from those in the baseline period (see Methods). For PLV to be different from zero, one (or possibly both) of 2 things must happen: 1) $\phi_1 - \phi_2$ must become more (or less) constant across trials, making $\phi_1 - \phi_2$ also more (or less) constant across trials (true synchronization or desynchronization) or 2) the amplitude of one source must increase (or decrease) reliably across trials and by enough that both $\phi_1 - \phi_2$ now contain significantly more (or less) contribution from that particular source, thus making $\phi_1 - \phi_2$ more (or less) constant across trials (spurious synchrony caused by volume conduction). The latter could happen either because a source that is already active becomes more (or less) active reliably across trials or because a source that is inactive during the baseline is reliably activated by the task during part of the analyzed epoch. This means that spurious, volume-conducted synchrony does not appear in the absence of changes in local amplitude. For this reason, we emphasize inspection of both PLVs and local amplitude in our interpretation of synchrony changes. In particular, the lateralized changes we found in 39 Hz PLV, anchored at P7 and P8 occurring at approximately 300 ms after cue onset were not accompanied by corresponding changes in local amplitude, so we can be confident that these changes are not spurious (Figs 2 and 4).

References


Koch C, Tsuchiya N. 2006. Attention and consciousness: two distinct
Kelly SP, Lalor EC, Reilly RB, Foxe JJ. 2006. Increases in alpha oscillatory
Gruber T, Müller MM, Keil A. 2002. Modulation of induced gamma band
Gray CM, Singer W. 1989. Stimulus-specific neuronal oscillations in
cognitive dynamics: neuronal communication through neuronal coherence. Trends Cogn Sci. 5:474–479.