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Neural Circuits Mediating Voluntary and Involuntary Attention

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Neural Circuits Mediating Voluntary and Involuntary Attention

by

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University of California, Berkeley

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Neural Circuits Mediating Voluntary and Involuntary Attention

Ayelet N. Landau

Abstract

Neural circuits mediating voluntary and involuntary attention

by Ayelet Nina Landau

Doctor of Philosophy in Psychology

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Chair: Lynn C. Robertson

Spatial attention is the capacity to prioritize part of the environment for processing over other parts. It can be employed in an internally guided manner, advancing current behavioral goals (i.e., voluntary spatial attention), or it can be captured by salient stimuli in the environment (i.e., involuntary attention). This thesis presents a series of studies investigating neural indices of voluntary and involuntary attention as well as aspects of neural circuits related to spatial attention. The first study used electroencephalography (EEG) to provide evidence that sustained spatial attention on a location generates increased coupling between the hemispheres and acceleration of interhemispheric communication. In the second study, EEG was used to measure indices of voluntary and involuntary attention. Using identical stimulus conditions in a spatial cueing paradigm, we found a physiological marker for voluntary attention that is not present for involuntary attention. In the final study we utilized fMRI coherency to measure network dynamics mediating the two types of attention. We found that voluntary attention acts to reduce coupling between regions engaged in spatial attention. In addition we find a hemispheric asymmetry in degrees of coupling such that both types of attention produce greater coupling in the right hemisphere compared to the left hemisphere. Together these studies developed indices of voluntary and involuntary attention and begin to describe the physiological mechanisms that mediate attention.

To my Father Simha F. Landau who sparked my interest in human behavior

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Acknowledgements

In the sciences some would argue that the dissertation as a document is a symbolic milestone rather than a tome of unique content to be cited and read for prosperity. It marks the completion of a considerable project however the content of this project will likely be most referred to in its peer reviewed publication form. Nonetheless the one thing that a dissertation allows its writer to do, which is unique and indispensable, is to pause in appreciation and recognition of the people who supported this project and became important parts of ones life during the years it took to complete it. There are not many venues that allow for this detailed musing and I intend to use this opportunity to its fullest extent; to acknowledge the people who accompanied me in this journey.

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1. Introduction

When whales feed around midday off the northern California coast, the feast commonly attracts many other species hoping that the large mammal may drop some goods off their lunch table. Typically, if you were to seek the sights of the majestic whales, you would be advised to follow the presence of birds hovering over the water as well as seals swimming close to the surface. The birds, if you will, could serve as a spatial cue which, if carefully followed, may allow you to luck out and catch a glimpse of a whales fluke as it traverses the water. Given your heightened state of voluntary attention, you will be able to see that fluke even if it only appears for a very short time and at a considerable distance. Alternatively, some whale watchers simply stumble upon the glorious feast only to notice a whale's presence by its visible spout emerging behind the boat's stern. The latter would certainly be a very salient event (with an extremely salient odor) that would capture involuntary attention. This thesis presents a series of studies investigating neural indices of voluntary and involuntary attention as captured by this example well as aspects of neural circuits related to the two different types of spatial attention.

In the first study (Chapter 2), the case of sustained voluntary spatial attention will be examined, focusing on attentional modulation of interhemispheric coordination. The investigation of attention circuits in the brain has traditionally focused on a "fronto-parietal network" for spatial attention, but only brief reference has been made regarding how these networks share information between the two hemispheres under different attention states (Buschman and Miller, 2007a; Buschman and Miller, 2007b; Corbetta and Shulman, 2002; Esterman et al., 2008; Serences and Yantis, 2007). In this study, electrophysiological evidence is provided demonstrating that spatial attention to a lateralized stimulus integrates neural responses between the two hemispheres through stronger neural coherence and acceleration of callosal transfer time.

In Chapters 3 and 4, I will turn to the distinction between voluntary and involuntary attention. Recently, Prinzmetal, McCool, and Park (Prinzmetal et al., 2005) provided a theoretical framework suggesting that voluntary and involuntary attention are separate systems with unique and dissociated consequences for human performance. Specifically, Prinzmetal and colleagues used the Posner cueing task (Posner, 1978, 1980) to collect evidence supporting this framework. In this cueing paradigm. participants are required to respond to lateralized targets while fixating at the center of a display (attention without eye movements, or covert attention). Before a target appears on the screen, a peripheral cue (e.g. a rectangle on one side of the display) can appear either in the same location as the subsequent target (cued trials) or in a different location as the subsequent target (uncued trials).

Using different versions of this task, Prinzmetal et al. (2005) designed experiments measuring either RT or accuracy effects. In addition, using this paradigm allowed the manipulation of voluntary and involuntary attention. For involuntary attention, the cue location was random with respect to the target location (50% cued trials), while for voluntary attention the cue location was informative with respect to target location (e.g., 80% cued trials). Using this design, they found that while both voluntary and involuntary attention accelerate response speed in trials for which the target appeared in the cued location, only voluntary attention enhanced the accuracy of performance in the cued location compared to the uncued location. From these findings, a theoretical distinction was made between *perceptual enhancement*, which is achieved by voluntary attention, and *response selection*, which is the consequence of involuntary capture of attention. This theoretical framework generates clear predictions in terms of neural manifestations of voluntary and involuntary attention. Conveniently, the use of peripheral cues that are identical for both voluntary and involuntary attention allow for a very clean comparison of the two types of attention when using physiological measures since only the proportion of trial types, which are otherwise identical, governs which type of attention is probed.

One of the predictions that follows the theoretical separation of voluntary and involuntary attention is that the two types of attention will present with different physiological markers, even if the stimulus conditions are identical. Chapter 3 provides confirmation of this prediction (Landau et al., 2007). Electroencephalograms were recorded in a cueing paradigm for cue and target onsets, and a spectral analysis was performed on the data. Responses in the gamma band (30 - 50 Hz) propagating from anterior central to posterior lateral scalp sites were linked to voluntary shifts of attention but not to the involuntary capture of attention. The presence of increased gamma responses for the voluntary allocation of attention, and its absence in cases of involuntary capture, suggest that the neural mechanisms governing these two types of attention are different. Despite the confirmatory evidence provided by EEG for the distinction between voluntary and involuntary attention, these results leave the specific dynamics producing these distinct physiological patterns unknown. A step towards unraveling those dynamics is presented in Chapter 4.

Chapter 4 visits the possibility of characterizing voluntary and involuntary attention networks in the brain. The challenge of brain networks for directing attention was introduced to the field in a seminal review by Marcel Mesulam almost three decades ago (Mesulam, 1981). Mesulam outlined "the network approach" as an intermediary stance between two polar views on the organization of functions in the brain. On the one hand, the equipotentiality view holds that functions are distributed over the entire brain. On the other hand, the centrist view asserts that brain functions are localized in dedicated and segregated centers. While the details of the network approach presented by Mesulam might not be of particular interest here, the fact that such an approach was conceived in the context of the organization of *attention* in the brain is no surprise. One could argue that it is precisely the challenge presented by the curious dissociation of attention from any well-characterized system or modality which gives rise to this idea. In

order to support this view, Mesulam and others (Mesulam, 1981; Posner and Petersen, 1990) relentlessly tried to put the pieces of the "attention network" puzzle together, identifying possible components of the system as well as potential interactions among regions that bear relevance to intact attentional performance. In order to do so, evidence from animal models, human patient work, and human electroencephalography converged on a preliminary notion of the relevant neural substrates and consequences of attention.

The development of new methods to measure and perturb brain activity in humans presents exciting new opportunities to obtain evidence on how the brain mediates allocation of attention. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) allow measurement of the responses of brain regions that are active during an attention task. Neuroimaging studies of attention (Corbetta and Shulman, 2002; Kincade, 2005; Mayer et al., 2004; Posner, 1980; Serences and Yantis, 2006; Serences and Yantis, 2007) adopted the previously coined term "network" in their investigations of attention in the brain. Importantly however, with few exceptions (Bressler et al., 2008; Lauritzen et al., in press, 2009), most of these studies did not examine the circuitry per se or address questions of coupling between regions directly but merely inferred those from patterns of co-activation during attention tasks (Corbetta and Shulman, 2002; Fan et al., 2007; Kincade, 2005; Mayer et al., 2004). It is important to realize that the co-occurrence of neural responses in different parts of the brain during an attention task does not indicate anything about the degree of coupling between the signals measured in different parts of the brain.

Transcranial magnetic stimulation (TMS) is another method that has been utilized in the investigation of spatial attention. When stimulating a brain region with TMS, its role in intact performance can be inferred by virtue of the behaviors disrupted by the stimulation. In addition, this method allows the identification of critical times in the processing stream during which a targeted region in the brain is necessary. Therefore, researchers using this method can reveal which regions and when those regions are indispensable for proper attentional allocation. Recently, several studies have investigated the unique roles of FEF and posterior parietal cortices in visual spatial attention using this approach (Chambers and Mattingley, 2005; Ellison et al., 2007; Grosbras and Paus, 2003; Grosbras and Paus, 2002; Koch et al., 2005; Muggleton et al., 2003; Muggleton et al., 2006; O'Shea and Walsh, 2004; Pourtois et al., 2001; Silvanto et al., 2006). In addition to providing converging evidence about the engagement of these regions in processes of spatial attention, the use of TMS allows causal inferences about their role in the processes under investigation. Additional information regarding network dynamics is provided by studies performing concurrent TMS and fMRI. This novel approach allows a measure of long-range effects of stimulation on a given region (Ruff et al., 2008; Ruff et al., 2006). For instance, using this approach, Ruff et al. (2006, 2008) were able to measure distinct attention effects in extrastriate cortices following FEF stimulation compared to IPS stimulation. While the effects of FEF stimulation on attentional modulation in visual cortex were independent of the visual inputs, the pattern was different when IPS TMS was performed. The effects of IPS

stimulation on attentional modulation in the visual cortex depended on the presence of a visual stimulus. Although TMS has proven to be an important method, it has a number of limitations. First, the spatial extent of the stimulation is coarse, limiting it to the examination of larger regions and regions that are positioned with sufficient distance from other parts of a postulated network. Second, stimulation can only be applied to very few brain regions at a time, limiting the ability to investigate different parts of a network within one study and within one subject. Last, performance on a cognitive task might be the result of multiple regions working together. Some of these regions might be unique in their contribution, while others might be seemingly redundant but nonetheless active. The latter form of contribution to performance would go undetected using TMS and would result in an incomplete depiction of the network (Chambers and Mattingley, 2005).

The recent development of multivariate analysis methods of fMRI data circumvent some of these shortcomings (Friston and Buchel, 2000; Goebel et al., 2003; Kayser et al., 2009; Roebroeck et al., 2005; Sun et al., 2004, 2005). In essence, these methods provide a quantification of coupling between different brain responses and at times temporal information about the nature of inter-regional interactions. The combination of high spatial resolution and whole brain coverage make for extremely rich datasets. Given the appropriate experimental design, and computational power, these methods have the potential to allow a variety of questions on network dynamics to be addressed in a comprehensive way. In the last chapter of this dissertation, I will present such an investigation. Participants performed the cueing task in the fMRI scanner. Functional localizers were used that allowed the identification of regions that have previously been implicated in the research of spatial attention. The study reveals interregional connections whose strength of coupling was altered by the attention type probed. By and large, voluntary attention resulted in a decrease in intrahemispheric coupling compared to involuntary attention. In addition, the right hemisphere was associated with greater coupling for both voluntary and involuntary attention. A post-cue procedure demonstrated that these effects were task selective and not due to differences in display conditions.

2. Spatial Attention Increases Interhemispheric Coupling.

2.1 Introduction

Recent investigations of spatial attention in cognitive neuroscience have focused on networks that control top-down attentional allocation. Specifically, a great deal of research has revealed a "fronto-parietal network" for spatial attention, but only brief reference has been made to how (or when) these networks share information between the two hemispheres under different attention states (Buschman and Miller, 2007a; Buschman and Miller, 2007b; Corbetta and Shulman, 2002; Esterman et al., 2008; Serences and Yantis, 2007). In the present study, we provide electrophysiological evidence that spatial attention to a lateralized stimulus integrates neural responses between the two hemispheres through stronger neural coherence and acceleration of callosal transfer time.

We presented a single face in one visual field or the other and directly investigated transfer from the contralateral stimulated hemisphere to the ipsilateral unstimulated hemisphere under conditions for which the stimulus was either attended or ignored. In the "attend" condition, participants reported whether the lateralized stimulus (a face) was upright or not. In the "ignore" condition, participants reported whether a symbol at fixation was an X or not, and thus could ignore the face. The same stimuli were shown in the two conditions.

Using ERP recordings, we quantified interhemispheric transfer time (IHTT) when the face was attended vs. ignored as well as differences in coupling between the hemispheres under the two attentional conditions (interhemispheric coherence). IHTT was measured by comparing the peak latency of the visual evoked response from contralateral and ipsilateral scalp locations produced by the same lateralized face stimulus (Saron and Davidson, 1989). Most research measuring electrophysiological measures of IHTT has focused on structural callosal differences between different populations (e.g., (Endrass et al., 2002). In the present study, we used this measure to compare interhemispheric coupling and transfer speed in different attentional conditions.

2.2 Methods

Participants: Fourteen undergraduates from the Research Participant Pool at the University of California, Berkeley were recruited to participate in the experiment for class credit. The participants all had normal or corrected to normal vision. All provided written consent as approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley.

Procedure: IHTT was measured for a given lateralized face in two different attention conditions: participants were either instructed to make a judgment about the face (attend-face) or the symbol at fixation (ignore-face) in separate blocks. Stimuli were the same in both attention conditions. Each trial started with the onset of a fixation symbol (e.g. '*', '~', '|','x') at the center of the screen. Following 450-600 msec, a face appeared to the left or right of the symbol (Figure 1a). Participants were instructed to respond at the end of the trial (after the offset of both the lateralized stimulus and fixation) using a button press. The next trial started 950 ms to 1850 ms following the button press.

The symbols used were presented in Arial font 18 point size and subtended approximately 0.3 degrees visual angle. The face stimulus was one of ten grayscale faces subtending 2.17 by 3.8 degrees, centered on the horizontal meridian, presented at 1.45 degrees eccentricity, and viewed at a distance of 100 cm. In addition to explicitly instructing participants to refrain from eye movements, stimulus placement and size were chosen to be easily perceived to ensure that participants could perform the task without the need to move their eyes. In order to motivate participants to allocate spatial attention to the location of the lateralized stimuli throughout a block of trials (in the attend-face condition), the position of the face stimuli was 100% predictable: they appeared in the RVF or in the LVF for entire blocks. Faces were chosen because they produce a clear electrophysiological marker in the ERP over posterior scalp electrodes (N170 component(Carmel and Bentin, 2002) that is distinct from an earlier perceptual marker (P1 component, (Mangun and Hillyard, 1991). Task instructions were blocked: in the attend-face condition, participants reported whether the face was inverted or not on each trial. In the ignore-face condition, participants reported whether the central symbol was an ‘x’ or not. Inverted faces and ‘x’s appeared on only 10% of trials and were excluded from the EEG analyses. Responses were delivered through key presses at the end of a trial. There was a total of twelve blocks consisting of 60 trials each, resulting in 150 trials per condition. Eight of the subjects started with the attend-face blocks, and the remaining participants started with the ignore-face blocks. At the beginning of the experimental session and before switching to the second task, participants performed ten practice trials to familiarize them with the task and to train them on maintaining fixation. Within each task, the visual field of the lateralized face alternated between blocks. Emphasis was placed on accuracy and not on reaction times (responses were prompted by the ending of the trial). All participants performed above 98% correct for both attend-fixation and attend-face trials. Importantly, the onsets of the symbol and

the lateralized face were temporally jittered, allowing clear assignment of the evoked response to the face in order to quantify IHTT in both attend and ignore conditions.

EEG acquisition and analysis: EEG was recorded using a Biosemi Active Two system at a sampling rate of 512 Hz from 64 electrode sites. Additionally, horizontal electrooculographic (EOG) signals were recorded at the left and right external canthi, and vertical EOG signals were recorded below the right eye. Both scalp and EOG electrodes were referenced off line to the tip of the nose. Preprocessing of the data was done in Brain Vision Analyzer. Trials with eye movements or blinks were removed from the data using an amplitude criterion of ±75μV or lower on the EOG channels (the criterion was adjusted for each participant to ensure the exclusion of artifacts). 4.6% of trials were rejected due to horizontal eye movements. The rate of fixation breaks was not significantly different for attend-face compared to ignore-face blocks [$t(13) = 0.144$ $p=0.88$][1]. EEG time series were segmented into epochs from 100 ms before cue onset to 1000 ms after cue onset for correctly performed trials. These segments were then exported to EEGLAB (Delorme and Makeig, 2004) for coherency analysis. In order to quantify effects in the P1 and N170 components, the data were band pass filtered to 1.5 - 17 Hz, and average peak amplitude and latency were extracted for time windows of 80-120 msec (P1) and 150-220 msec (N170), for each participant in each condition. The results of statistical tests for all ERP analyses as well as coherency measures are reported for sites PO7/8 and P7/8 for both P1 and N170 components.

[1] In addition, the waveforms at the EOG channels did not significantly differ between the attend-face and ignore-face tasks [$F(1,13) < 1$] nor did the task factor interact with the side of presentation [$F(1,13)<1$].

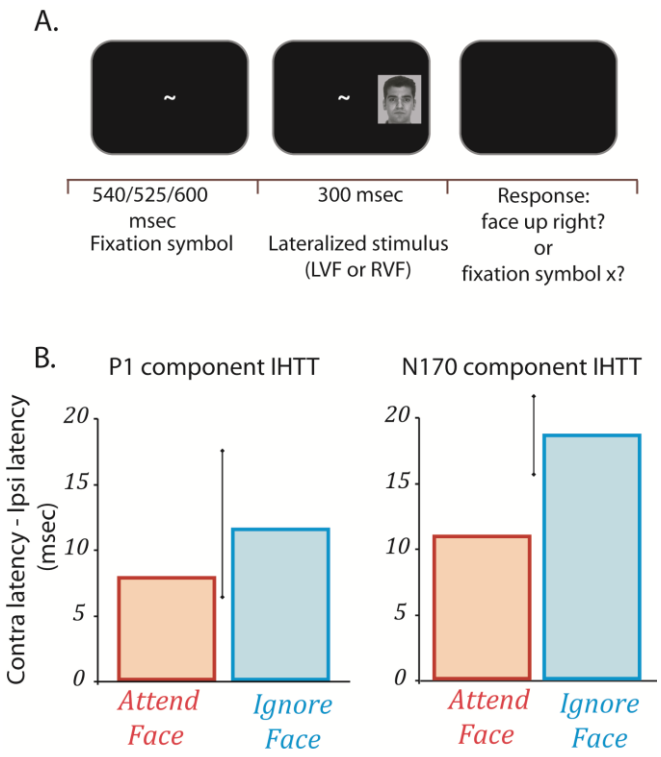


Figure 1: Trial procedure and IHTT measures

(A) On each trial, participants reported whether the face was inverted or not (attend-face) or reported whether the fixation symbol was an 'x' or not (ignore-face). (B) IHTT for P1 and N170 components. Error bars signify the standard error of the difference between the two attention conditions.

2.3 Results

N170 Latency - IHTT: To characterize N170 latency and the interhemispheric transfer time, a three-way, repeated measures ANOVA with Hemisphere (left or right), Visual Field (VF; left or right), and Task (attend-face or ignore-face) as within-subject factors was performed. As predicted, the interaction of Hemisphere and VF was significant [$F(1,13) = 29.47$, $p<0.01$], indicating that the contralateral N170 response preceded the ipsilateral response (Figure 1B). Importantly, there was a three-way interaction among Hemisphere, VF and Task, indicating that the time difference between ipsilateral and contralateral response latency was different for the two task manipulations [$F(1,13) = 6.63$, $p<0.05$]. Specifically, the IHTT of the N170 component was significantly larger when the face stimuli were ignored compared to when they were attended.

N170 Amplitude: To evaluate N170 amplitude, a three-way ANOVA with Hemisphere (left or right), VF (left or right), and Task (attend-face or ignore-face) as within-subject factors was performed. There was a main effect of Task [$F(1,13) = 13.57$, $p <0.01$], indicating that the N170 was more pronounced during the attend-face condition (-8.67μV) than the ignore-face condition (-7.49μV). There was also a significant Hemisphere by VF interaction [$F(1,13) = 18.38$, $p <0.01$] indicating that responses in the hemisphere contralateral to the stimulus (-8.87 μV) were more pronounced than those in the hemisphere ipsilateral to the stimulus (7.26 μV). In addition, there was a significant interaction between Task and VF [$F(1,13) = 6.14$, $p <0.05$]. The effect of task on the N170 was larger when the faces appeared on the left compared to the right side of fixation (2.26 μV difference between the tasks when faces appeared on the left compared to 0.1 μV difference between the tasks when faces appeared on the right). The three-way interaction of Hemisphere by VF by Task [$F(1,13) = 19.77$, $p <0.01$] indicates that the attention effect was largest in the left hemisphere for faces appearing on the left side.

Importantly, a correlation analysis examining the relationship between the attentional IHTT effect and the N170 amplitude modulation demonstrates that the IHTT cannot be accounted for by differences between contralateral and ipsilateral amplitudes for the two conditions ($r=0.01$, $t(55)=0.07$ $p=0.94$; Figure 2).

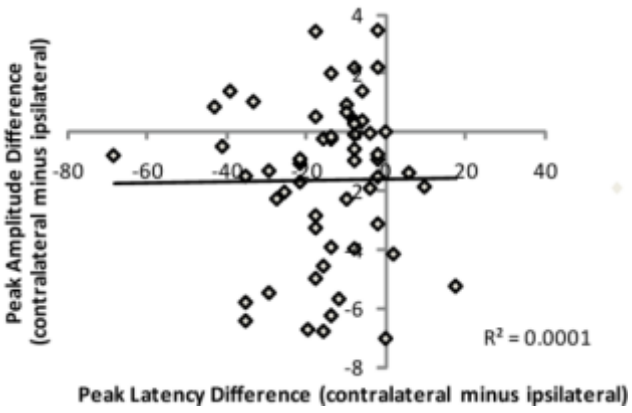


Figure 2: Latency differences between contralateral and ipsilateral response as a function of peak amplitude differences between contralateral and ipsilateral response.

Scatter plot of amplitude interhemispheric difference (computed by the subtraction of ipsilateral amplitude from contralateral amplitude) and peak latency difference (IHTT) for each participant, in each attention condition and each visual field condition (total of 56 points)

P1 Latency - IHTT: An analysis similar to that performed for the N170 was conducted to characterize P1 latency. An ANOVA with Hemisphere (left or right), Task (attend-face or ignore-face), and VF (left or right) as within-subject factors was performed. As expected, for the P1 there was a Hemisphere and VF interaction [$F(1,13) = 8.25$, $p<0.05$], indicating a contralateral bias in the visual response. In addition, there was a significant interaction between Hemisphere and Task [$F(1,13) = 12.15$ $p<0.01$]. Specifically, the response over the right hemisphere was faster in the attend-face condition, while the response over the left hemisphere was faster in the ignore-face condition. This finding is consistent with perceptual biases in the literature (Ivry and Robertson, 1998; i.e., right hemisphere bias for faces and global processing, left hemisphere bias for objects and local processing). While mean transfer time for the P1 response was slightly faster for attend-face (7.7 msec) compared to ignore-face (11.5 msec), in contrast to the N170, this effect was not significant in the broad-band ERP analysis [$F<1$].

P1 Amplitude: To characterize P1 amplitude, an ANOVA with Hemisphere (left or right), Task (attend-face or ignore-face), and VF (left or right) as within-subject factors was performed. There was only a main effect of Task, indicating that the P1 amplitude was modulated by the attention condition [$F(1,13) = 4.88$, $p<0.05$]. Specifically, the P1 response to a face during the attend-face condition was larger than the P1 response during the ignore-face condition. No other effects reached or approached significant levels. The standard depiction of wave–forms for the different conditions can be seen in Figure 3.

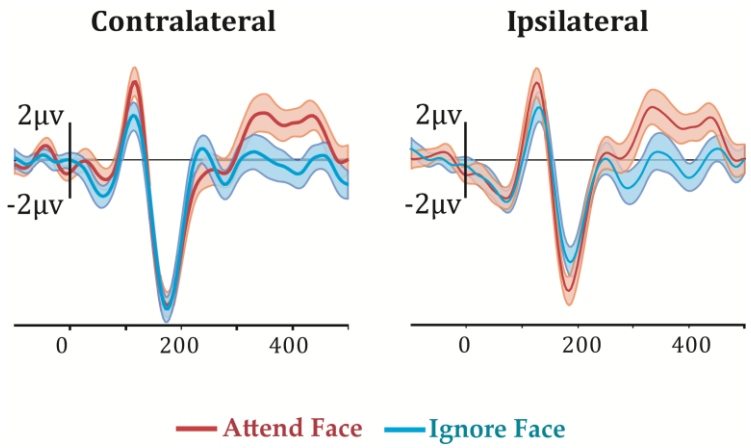


Figure 3: ERPs elicited from contralateral and ipsilateral stimuli in Experiment 1

ERP waveforms for attend-face and ignore-face trials, averaged for ipsilateral and contralateral posterior recording sites. Shaded areas signify the standard error of the difference between the two conditions. Both P1 and N170 amplitude modulation due to attention is measured (as reported in the results).

Frequency analysis of IHTT: In order to further examine attentional modulation of the ERP components, an additional analysis was performed on different frequency bands of the ERP signal. The frequency band analysis was performed as in Nalcaci, Basar-Eroglu, and Stadler (1999). Each epoch of a given segmented trial was bandpass filtered in frequency bands 0.5-4, 4-8, 8-15, 15-20, and 20-32 Hz prior to averaging and computation of peak latency. As seen in Figure 4, most of the interhemispheric transfer time acceleration due to attention was carried by lower frequencies (< 8 Hz). For the N170 component, both frequency ranges 0.5-4 Hz and 4-8 Hz showed a significant acceleration in the attend-face compared to the ignore-face condition [$t(13)=-2.611$, $p<0.05$ and $t(13)= -2.48$, $p<0.05$ respectively]. For the P1 component, the frequency band 4–8 Hz showed a significant acceleration in the attend-face compared to the ignore-face condition [$t(13)=-3.1$, $p<0.01$], and the remaining frequency bands did not show a significant effect of attention [$t(13)<1$ for the statistical tests performed for each remaining frequency band].

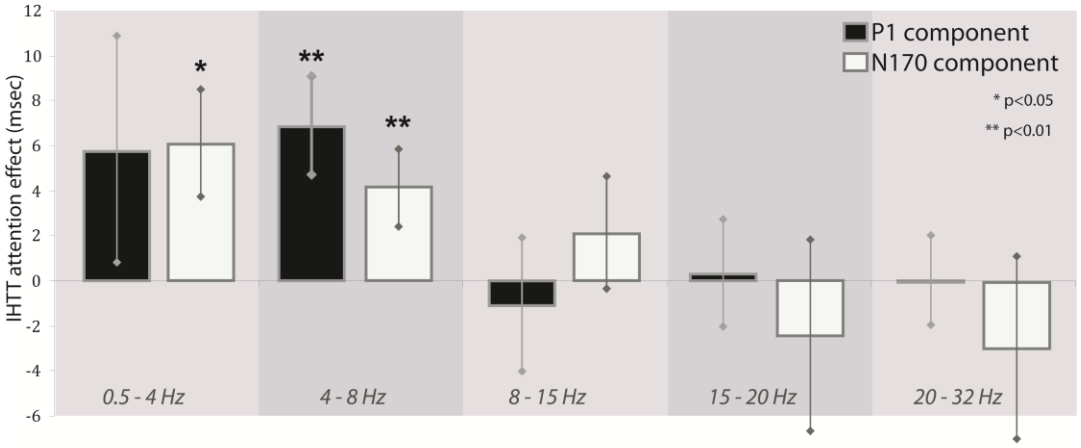


Figure 4: Band pass analysis of the P1 and N1 ERP components in Experiment 1

IHTT attention effects, calculated as the difference in transfer time between the attend-face task and the ignore-face task for each of the displayed frequency bands.

Interhemispheric coherence: To test whether attention increased coupling of the two hemispheres, we analyzed event-related phase coherence between responses over homologous posterior sites (PO7/8 and P7/8). Coherence is a spectral measure assessing coupling between two time series (Brillinger, 2001). In the present study, coherence was computed between time series recorded simultaneously at two homologous scalp sites. Interhemispheric coherence was quantified for single segmented trial epochs, and coherency magnitudes were then averaged over the different trials for each condition. Statistical significance was established using a permutation test (Nichols and Holmes, 2002), and results are presented in Figure 5. A significant increase in interhemispheric coherence occurred 80 – 200 msec after the onset of an attended face compared to coherence associated with an ignored face. The attentional coherence modulation was most marked in lower frequencies up to approximately 15 Hz. The relationship between interhemispheric coupling, as measured with coherence, and interhemispheric amplitude modulations is demonstrated in Figure 6. The attentional modulation of the interhemispheric coupling cannot be explained by the interhemispheric amplitude modulation ($r = 0.24$, $t(27) = 1.26$ $p = 0.2$ and $r = 0.17$, $t(27) = 0.88$, $p=0.4$ for N170 and P1, respectively). In addition, a similar analysis demonstrated that the coherence effects and latency effects are not significantly correlated [$r = 0.12$, $t(13)<1$ and $r=0.1$, $t(13)<1$ for N170 and P1 components, respectively; Figure 7].

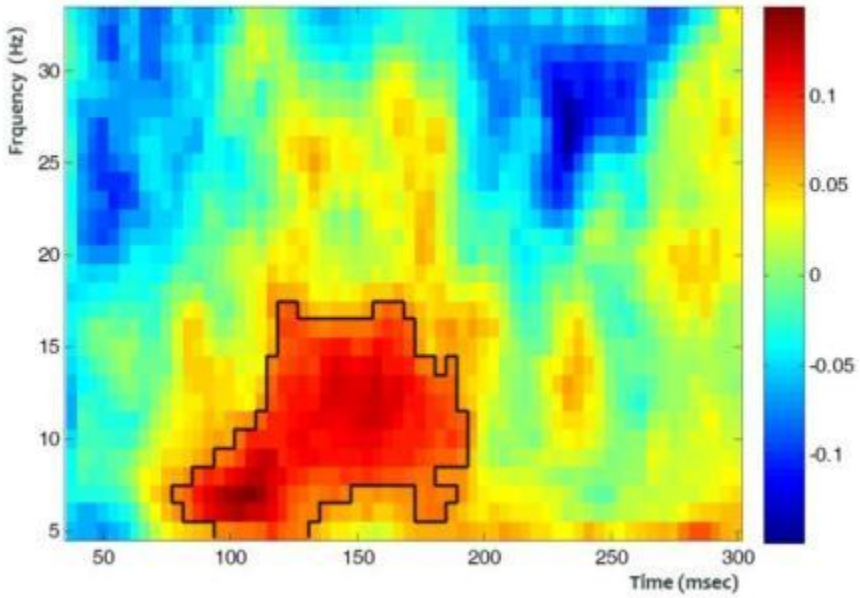
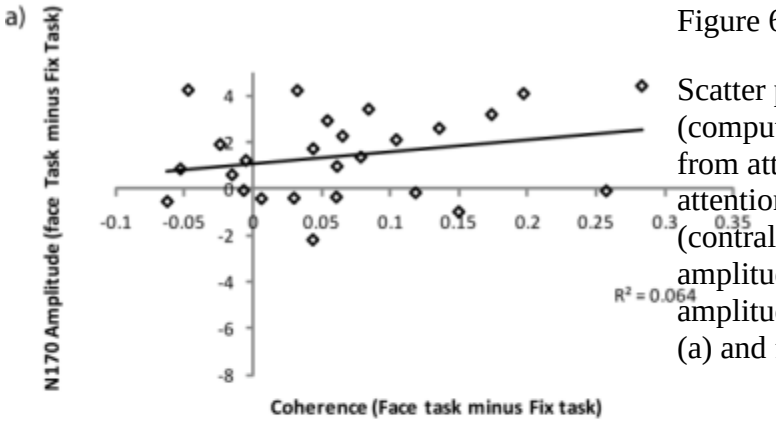


Figure 5: Interhemispheric coherency differences between conditions from Experiment 1

Time frequency plot of coherence magnitudes modulated by attention. Ignore-face coherence values were subtracted from attend-face coherence values. Black outlines mark the times and frequencies for which coherence was significantly greater in the attend-face task ($p<0.0001$).



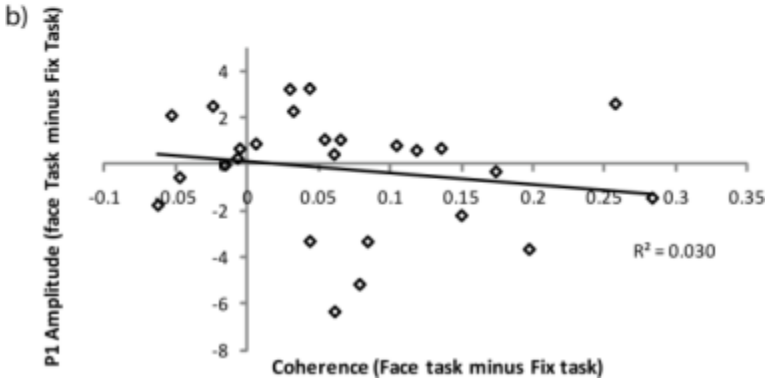
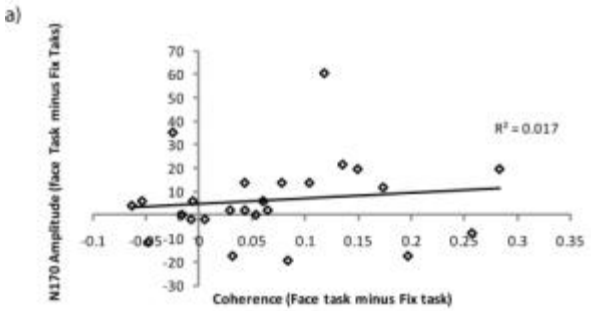


Figure 6

Scatter plot of the Coherence attention effect (computed by the subtraction of ignore-face from attend-face coherence) and Amplitude attention effects (computed as: [attend-face (contralateral amplitude - ipsilateral amplitude)] - [ignore-face (contralateral amplitude - ipsilateral amplitude)]) for N170 (a) and for P1 (b) components.



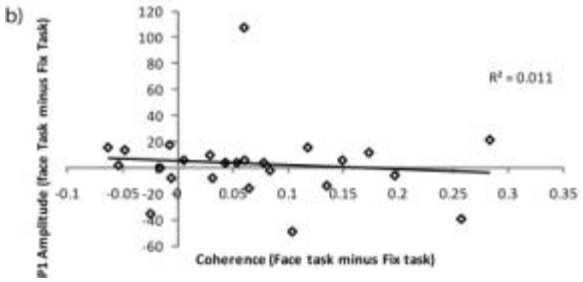


Figure 7

Scatter plot of the Coherence attention effect (computed as the subtraction of ignore-face from attend-face coherence) and Latency attention effects (computed as: [Attend face (contralateral latency - ipsilateral latency)] - [Ignore face (contralateral latency - ipsilateral latency)]) for N170 (a) and for P1 (b) components.

2.4 Discussion

The present study reveals converging evidence for greater interhemispheric cooperation when voluntary sustained spatial attention is directed to a lateralized stimulus. Temporal differences between contralateral and ipsilateral evoked responses to a lateralized face are smaller when the lateralized face is attended compared to when it is ignored. In line with previous work on attentional modulation of ERPs (Hillyard et al., 1998), attention does not affect the initial latency of the contralateral response, indicating that the speed of the geniculostriate transmission is not affected by deployment of attention to the lateralized stimulus. These results constrain the interpretation of our findings to attentional accelereation of cortico-cortical cross talk between the hemispheres.

Previous ERP studies reporting P1 and N1 attentional modulation have typically been limited to amplitude measures and reported no marked latency effects (Di Russo et al., 2003; Wijers et al., 1997). There is an important difference between these studies and the present one. Namely, in previous studies, participants reported lateralized targets only if they appeared on the attended side. When a lateralized stimulus appeared on the ignored side, participants were not required to do anything. It is possible that IHTT modulations were not found due to the fact that while participants were not required to report the unattended stimuli, they defaulted to processing it and even attending to it in the absence of a defined task during those trials. In the present study, attention was controlled in both attend-face and ignore-face (attend-fixation) conditions. In the attend-face condition, attention was allocated to the face stimulus that evoked a response, while in the ignore-face condition, attention was directed away from the face stimulus and to the central fixation point. This task design facilitated comparison of the ignored and attended visual onset, a comparison not present in previous studies.

In addition, our findings demonstrate that the effects of spatial attention on interhemispheric interactions go beyond the mere acceleration of callosal transfer. Attending to a lateralized face is also accompanied by an increase in the coupling between responses in the two hemispheres. The results also indicate that the hemisphere receiving no direct sensory input shares information processing with the stimulated hemisphere more rapidly and interactively when attention is directed to the location of the stimulus. While ample data support fronto-parietal circuits for spatial attention (Buschman and Miller, 2007a; Buschman and Miller, 2007b; Corbetta and Shulman, 2002; Esterman et al., 2008; Serences and Yantis, 2007), the present findings demonstrate that spatial attention also modulates the functional connectivity between these circuits.

Finally, these findings address a question that has been debated in the hemispheric lateralization literature for decades, namely, how attention influences hemispheric communication (Banich, 1998). Here we used physiological measures to demonstrate that hemispheric coherence and transfer time are indeed modulated depending on whether a single, lateralized stimulus is attended or not.

3. Different Effects of Voluntary and Involuntary Attention on EEG Activity in the Gamma-band.

3.1 Introduction

Behavioral evidence suggests that spatial attention can be summoned in at least two ways. One is goal directed and engages top down control mechanisms, while the other is automatic and independent of the task. The former is often referred to as endogenous or voluntary attention (Posner 1978) and the latter as exogenous or involuntary attention (Jonides 1981).

Ample evidence, using the spatial-cueing paradigm (Posner 1978), Figure 8a), indicates that for both voluntary and involuntary attention, targets are detected and discriminated faster at a validly-cued location compared to invalidly-cued locations (the "validity effect"). It is often assumed that both forms of attention enhance perceptual processing similarly and are controlled by the same neural mechanisms (Gazzaniga et al. 1998). However, behavioral evidence indicates that voluntary and involuntary attention might have different time courses and consequences (Müller and Rabbitt 1989; Berger et al. 2005).

In the present study a cueing task was combined with electrophysiological measures, to compare voluntary and involuntary attention in identical stimulus-conditions. Previous work coupling electrophysiology with cueing paradigms mostly focused on Event-Related Potentials (ERPs). The most consistent finding is an increase in early sensory potentials (P1 component) elicited by a cued target compared to an uncued target (Mangun and Hillyard 1991; Hopfinger and Ries 2005). Later components may also be modulated, but the results are less consistent. While some authors reported greater N1 on valid trials (Luck et al. 1994) others found the reverse (greater N1 on invalid trials, (Hopfinger and Ries 2005). Hopfinger and West (2006) measured interactions between voluntary and involuntary attention manipulating the two types of attention concurrently. They found that although mutually affecting each other, voluntary and involuntary attention act on different stages of processing. However, in the procedure they used, the voluntary and involuntary cues were visually different, and were presented at different times in a given trial. Voluntary and involuntary attention effects have seldom been directly compared under equal stimulus conditions within the same ERP study. Studies that attempted this comparison, revealed no marked differences in the amplitudes of either P1 or N1 (Doallo et al. 2005).

Recent work in both animals and humans examined the spectral content of the EEG signal (Gruber et al. 1999; Fries et al. 2001; Vidal et al. 2006; Fan et al. 2007) suggesting that activity in the gamma range (>30Hz, Tallon-Baudry, and Bertrand, 1999) is modulated by

attention. We therefore focused on the gamma-band response as it relates to voluntary and involuntary attention. Whereas ERPs did not distinguish voluntary from involuntary attention, we report clear differences between these two attention systems in the gamma-band.

3.2 Materials and Methods:

Task and Procedures – Participants performed an easy face-discrimination task under conditions of voluntary and involuntary attention conditions. As shown in Figure 8a, one of two faces was presented immediately after a cue-offset, either to the left or to the right of fixation, and the participants reported which face had been presented by pressing one of two keys. A peripheral cue preceded the target face in both voluntary and involuntary conditions. Voluntary attention was measured in the predictive-cue-condition. In this condition the face appeared more often in the cued location (70% valid) than the uncued location. Involuntary attention was measured in the nonpredictive-cue-condition. In this condition the cue location was unrelated to target location. Both conditions included target-absent trials, which allowed evaluation of cue-related activity in isolation of a target face. A third key was used to report the absence of a target. The only difference between the attention conditions was the proportion of valid, invalid, and cue-only trials. This design enabled examination of the physiological time course of cue and target processing for voluntary and involuntary attention without confounding physical stimulus parameters. The predictive-cue-condition consisted of six 100-trial blocks separated by breaks. The nonpredictive-cue-condition consisted of five 112-trial blocks (see figure 8a). Each participant completed one cue-condition before starting the other cue-condition, and cue-conditions were counterbalanced between subjects. Each cue-condition began with a short practice block (20 trials).

Note that in the predictive cue-condition the participant was encouraged to utilize the cue when it appeared, and anticipate the probable location of the target. In the nonpredictive cue-condition participants were instructed to ignore the cues as they are independent of target location. Here, predictive and nonpredictive cue-conditions were used as operational variables for voluntary and involuntary attention. With a predictive cue voluntary attention would be allocated when the cue appears. With a nonpredictive cue voluntary attention will not be allocated until the target appears.

Stimuli - Stimuli were presented on a 20” monitor. Seen from 155 cm, the visual angle of each cueing square was 2.2°, and they were centered 2.7° from a 0.4° fixation cross. Faces appeared centered in one of the squares and were 2.4° wide.

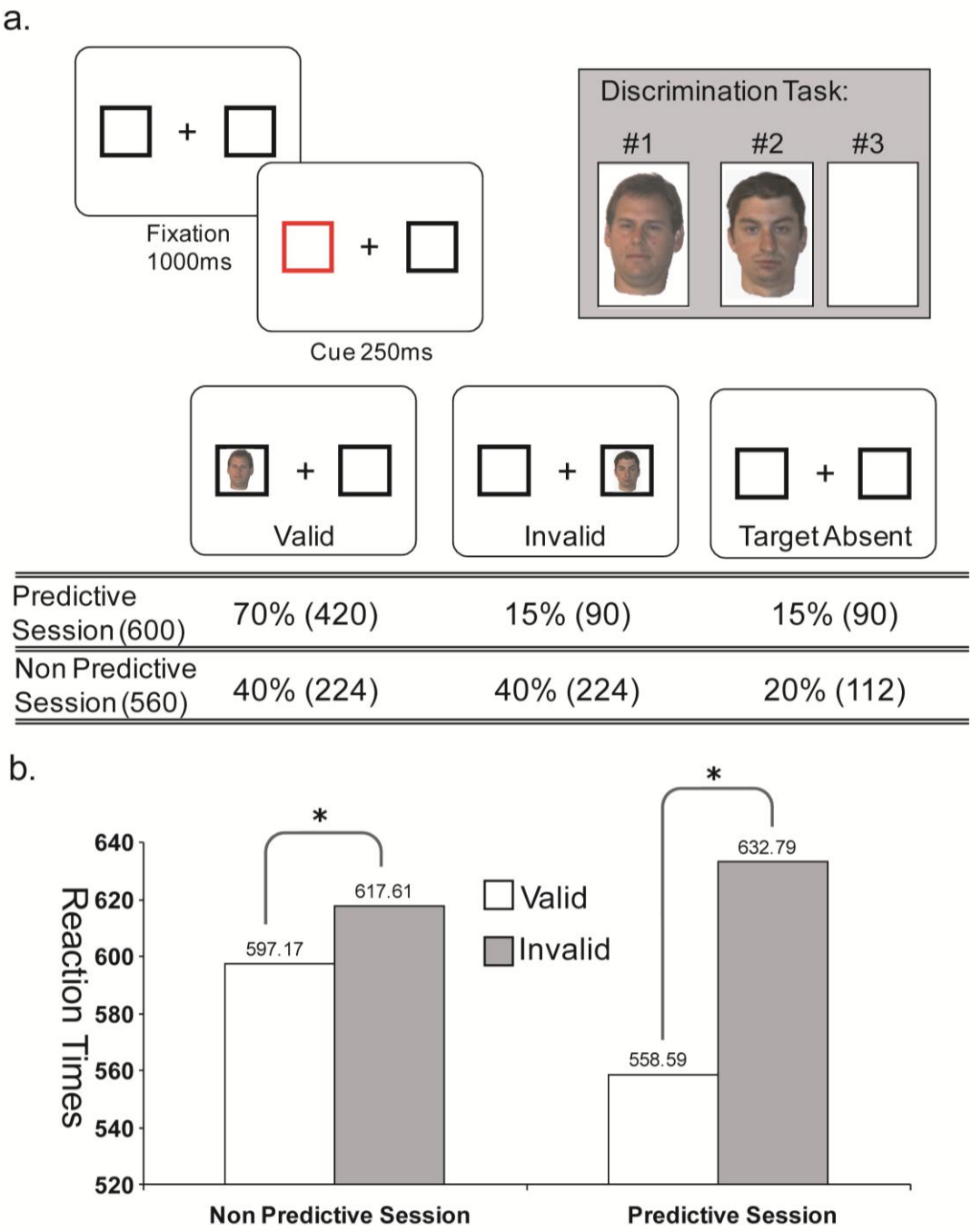


Figure 8: Trial procedure from and RT data from Experiment 2

a) After 1s of fixation a cue (one rectangle changed to red, denoted by the dotted rectangle) was displayed for 250 ms, followed by one of two face targets displayed for 300 ms or a blank screen. Bellow the illustration are the probabilities (and trial numbers) of each trial-type (valid, invalid, cue-only) in the different cue-conditions (predictive and nonpredictive). Participants indicated by a key press which face appeared or whether no face appeared. b) Reaction time performance.

Participants - Sixteen undergraduates participated in the experiment for class credit. All participants had normal or corrected-to-normal visual acuity. Participants gave informed consent as approved by the UC-Berkeley IRB.

EEG acquisition and processing - EEG was recorded using a Biosemi Active-Two system at a sampling rate of 256 Hz from 64 sites of a modified 10-20 system montage. Horizontal electrooculographic (EOG) signals were recorded at the left and right external canthi, and vertical EOGs were recorded below the right eye. All electrodes were referenced off line to the tip of the nose. Preprocessing of the data was done in Brain Vision Analyzer. Trials with eye-movement or blinks were removed from the data using an amplitude criterion of ±150μv or lower. Ongoing EEG was segmented into epochs from 200 ms before cue onset to 1000 ms after cue onset of correctly performed trials. These data were then exported to EEGLAB (Matlab Toolbox; Delorme and Makeig 2004) for spectral analysis.

EEG spectral analysis - To measure the power at each frequency band and time point, the data were processed using the "timef" function of EEGLAB (Delorme and Makeig 2004). For each experimental condition, approximately 60 randomly-selected EEG epochs were convolved with Gaussian-windowed sinusoidal wavelets of two-cycle duration. At each frequency band, the mean spectral energy of the pre-stimulus baseline (from -200 to -50 ms, excluding the last 50ms of fixation in which fixation changed color) was subtracted from the pre- and post-stimulus time-frequency energy. The absolute power measure was converted to decibels (dB; 10 * log (μV^2). Baseline levels in the two attention conditions were equivalent as revealed by a planned paired t-test [$t(15)=1.05$, $p=0.92$]. The resulting time-frequency maps were averaged across trials for each subject to form the event-related spectral perturbation (Makeig, 1993). The individual subject maps were averaged to create grand average ERSP maps (figure 10).

For statistical analysis an unbiased time by frequency range of maximal gamma-band response was selected from the averaged data for cue-related responses and target-related responses separately (Yuval-Greenberg 2007). The average power within these regions for each condition was then used as the dependent variable in an ANOVA with repeated factors. Due to the wide scalp distribution the data were collapsed for analysis into three groups (anterior, central and posterior) in each hemisphere (Gruber et al. 1999; see Figure 9).

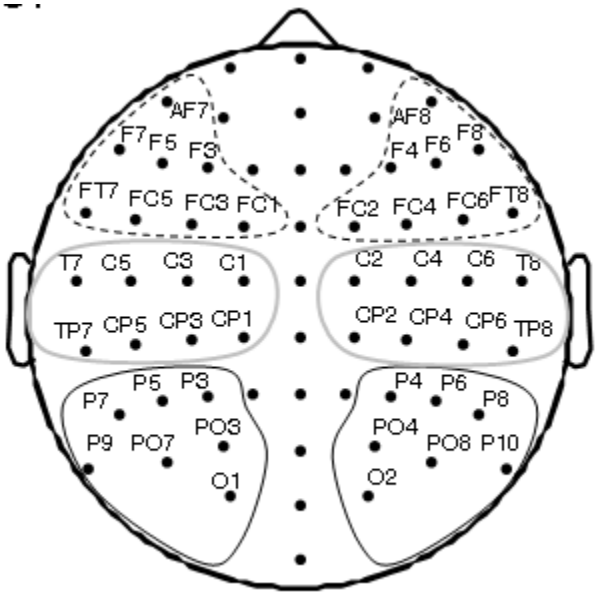


Figure 9: A schematic of the cap used for Experiment 2

A schematic of the sites grouped for the spectral analysis statistics. Anterior, central and posterior groups outlined in dashed, gray and black lines respectively.

ERP analysis: Segmented data was averaged separately for each condition. Averaged waveforms were band pass filtered (0.8 Hz-17 Hz 24db/oct as in Zion-Golumbic and Bentin 2006) and baseline corrected from 100 ms pre-cue-onset. For each participant the P1 peak was determined as local maximum between 80-150 ms post target onset and the peak of the N170 face selective component (Bentin et al. 1996) was determined as local minimum between 130-220 ms. Amplitudes of these components at sites P8, PO8 and P10 over the right hemisphere and the homologue sites over the left were included in the analysis. ANOVA with repeated measures with factors cue-condition (predictive, nonpredictive), hemisphere (left, right), site (P7/8, PO7/8, P9/10), target-side (Left, Right) and Validity (Valid, Invalid) were manipulated as within subject variables and were performed on P1 and N170 amplitudes separately.

3.3 Results:

3.3.1 Performance:

Overall, discrimination of targets was faster for valid than invalid trials (Figure 8b). The validity effect was greater in the predictive than nonpredictive cue-condition. These results were supported by a two-way ANOVA conducted for target-present trials. Overall, responses were slightly faster in the predictive than the nonpredictive cue-condition. However this difference was not significant [$F(1,15)=3.32$, $p=0.09$]. The validity effect was significant [$F(1,15)=30.29$, $p<0.001$], and interacted with cue-condition [$F(1,15)=15.91$, $p<0.01$]. This interaction indicated

that validity effects were larger in the predictive-cues-condition than in the nonpredictive-cue-condition. Planned paired comparisons indicated that in both cue-conditions the validity effect was significant [$t(15)= 5.14$, $p<0.001$) for predictive and $t(15)= 3.4$, $p<0.01$ for nonpredictive]. For target absent trials, performance was identical for the two cue-conditions (636 ms in both).

The percent correct for valid and invalid trials following predictive cues were 94.7% and 92.4% respectively. The corresponding accuracy rates following nonpredictive cues were 95.2% and 93%. ANOVA showed a main effect of validity in error rates [difference=2.25%, $F(1,15)=17.3$, $p<0.01$] and no interaction with cue-condition [$F<1$].

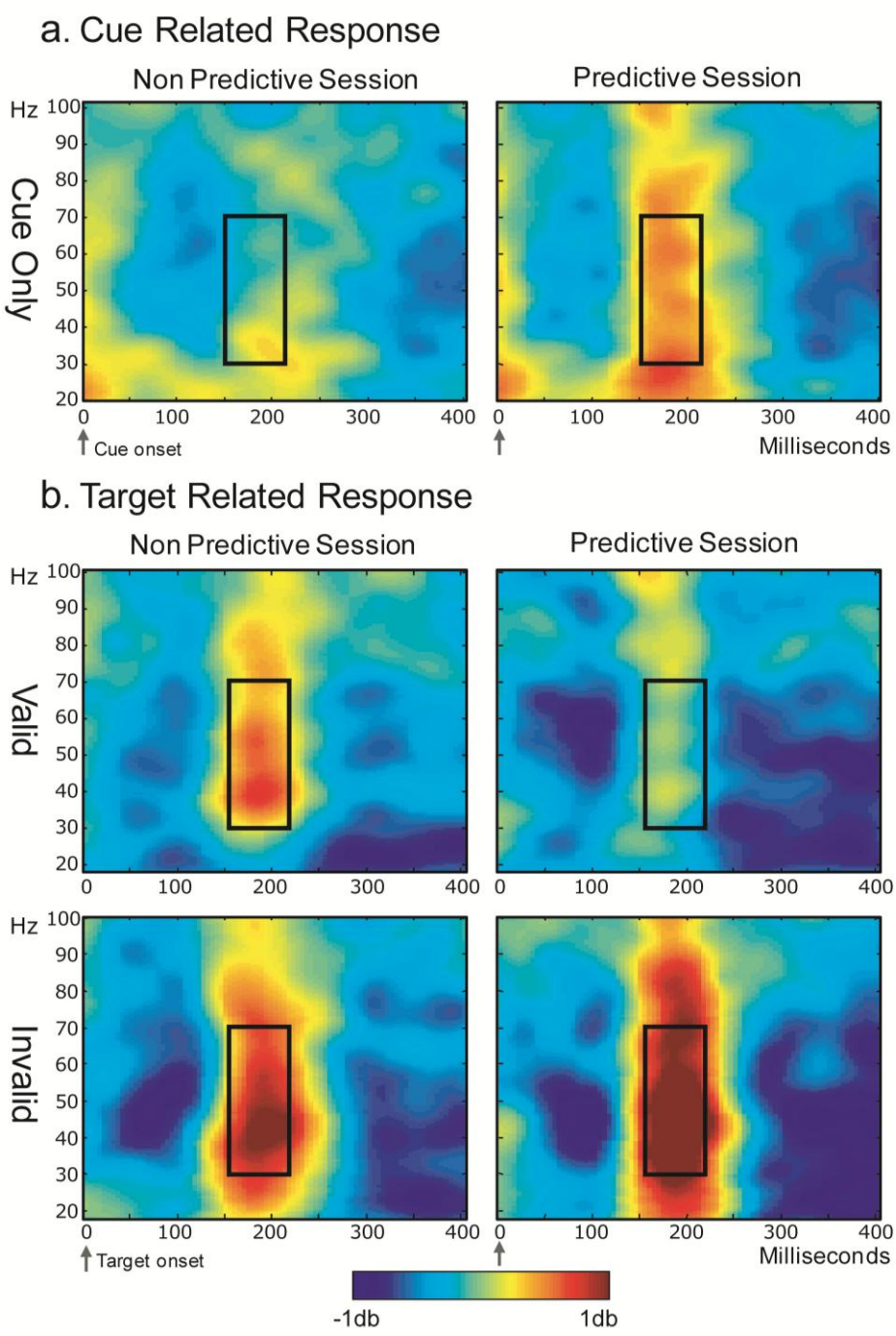


Figure 10: Spectral analysis data from Experiment 2

Time (x-axis)/frequency (y-axis) plots for nonpredictive (left column) and predictive (right column) conditions. (a) Data from cue-only trials. Cue onsets at zero -- marked by an arrow. (b) Data from target-present trials (valid and invalid in the first and second rows respectively). Target onsets at zero -- marked by an arrow. Dark rectangles mark the time/frequency window used in the statistical analysis.

3.3.2 Spectral analysis:

Activity in the gamma range (defined here as 30-70 Hz) was averaged for the temporal window from 150 to 225 ms post-cue-onset to measure cue-related activity and from 150 to 225 ms post-target-onset to measure target related-activity (figure 10, time-frequency window selection process as described in the methods section).

Cue-Related Activity: Analysis of target-absent trials showed that gamma-band power to cues was higher in the predictive than in the nonpredictive cue-condition (Figure 10a). This observation was supported by an ANOVA with cue-condition (predictive, nonpredictive), cue-side (left, right), hemisphere (left, right), and site (posterior, central, anterior). The main effect of cue-condition was significant [$F(1,15)=4.63$, $p<0.05$] while the effects of all other factors were not (for the complete statistical analysis, see Table 1).

Target-Related Activity: The gamma activity elicited in the predictive-cue-condition by invalid targets was higher than that elicited by valid targets. In the nonpredictive cue-condition, the gamma elicited by both target types (valid and invalid) was similar (Figure 10b). An ANOVA with cue-condition (predictive, nonpredictive), validity (valid, invalid), target-side (left, right), hemisphere (left, right), and site (posterior, central, anterior) as within subject factors showed a main effect of validity [$F(1,15)=5.12$, $p<0.05$], which interacted with cue-condition [$F(1,15)=4.7$, $p<0.05$]. Paired planned comparisons showed that in the predictive-cue-condition gamma-band response was significantly greater on invalid then valid trials [$F(1,15)=5.20$, $p<0.05$]. In the nonpredictive-cue-condition this was not the case [$F(1,15)=3.51$, $p=0.08$]. The trend in the non predictive case could be due to a number of factors[2]. Importantly, the significant interaction reflects the reliable differences in gamma activity between valid and invalid conditions for predictive and nonpredictive conditions.

In addition, the analysis revealed evidence for laterality in the gamma-band response in the predictive cue-condition. Both the hemisphere by target-side interaction and the hemisphere by target-side by site interaction were significant [$F(1,15)=6.20$, $p<0.05$ and $F(2,30)=7.04$, $p<0.01$, respectively]. Gamma power was higher over the hemisphere contralateral to the target location than over the ipsilateral hemisphere. The difference between the contralateral and ipsilateral response was significant for posterior and anterior sites [$F(1,15)=7.16$ $p<0.05$ and $F(1,15)=0.33$, $p<0.01$ respectively]. Figure 11a-c presents scalp distributions of the gamma-band response at three time points after target onset demonstrating the differences in the propagation of gamma over different scalp sites. For the central sites the statistical test did not reveal significant laterality effects. (target-side by hemisphere effect [$F(1,15)=2.086$, $p=0.169$, ns]).

[2] It is possible that this trend reflects an indirect influence of involuntary capture on the distribution of attention. While nonpredictive cues do not elicit gamma-band activity, the RTs suggest that they indeed affect the locus of visual attention in space (fig 1b significant validity effect in the nonpredictive cue-condition). Hence, attentional capture, while having different temporal dynamics and seemingly different neural signatures, might determine the starting point from which a voluntary attentional shift is initiated upon target display. This account is post hoc and would require further experimental investigation.

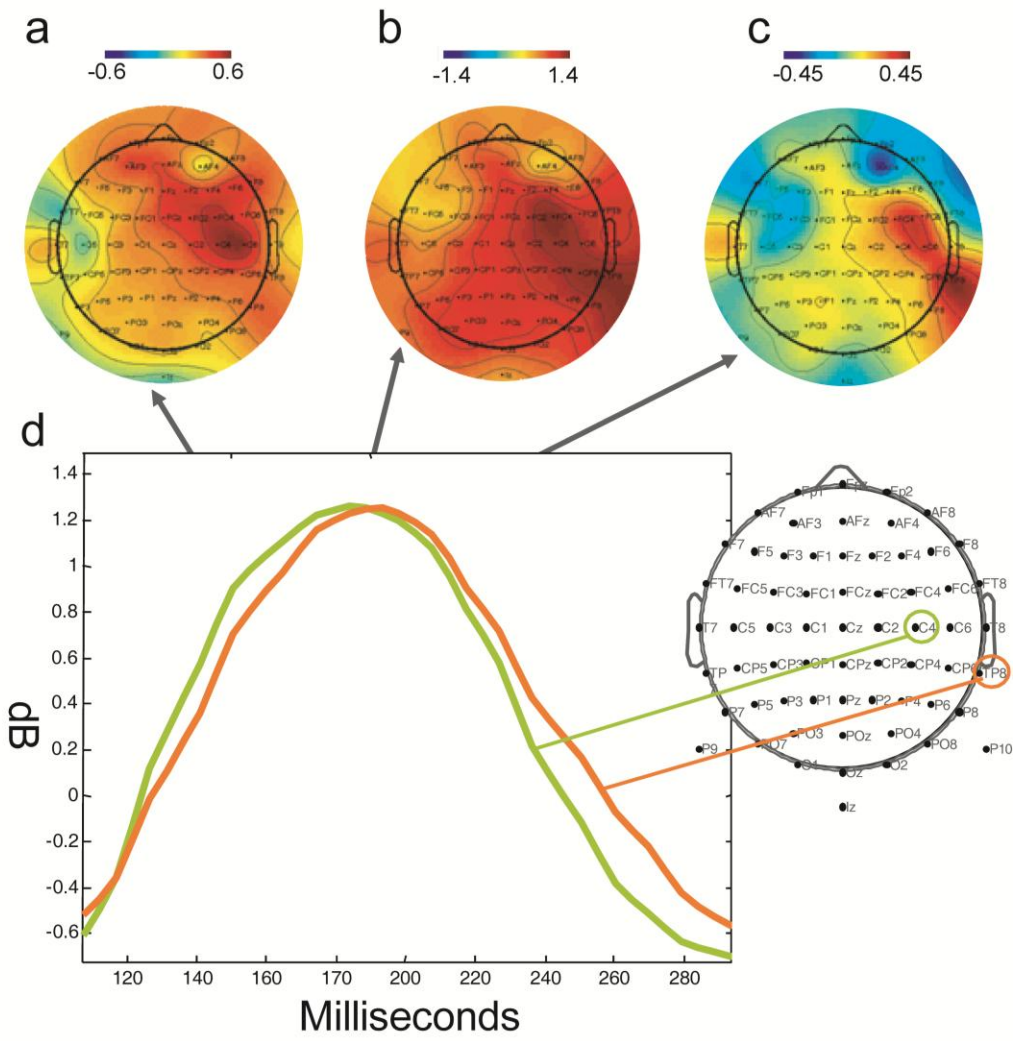


Figure 11: The scalp distribution of the gamma-band activity from Experiment 2

(a-c) The scalp distributions of gamma-band activity at 141ms, 198ms and 236ms on invalid trials in the predictive cue-condition. Frequencies 30-70 Hz were collapsed, and scales changed in order to emphasize differences in activity between different sites.

3.3.3 ERPs:

P1 and N170 components did not differ between predictive and nonpredictive cue-conditions ($F<1$ for all relevant comparisons for both P1 and N170 components). Both components showed maximal response for sites located contralateral to the target side (hemisphere by target-side significant interaction: $F(1,15)=8.16$, $P<0.05$ for P1 and $F(1,15)=8.67$, $p<0.05$ for N170). Consistent with previous reports in the literature (Mangun and Hillyard 1991; Hopfinger and Ries 2005), for both attention conditions the P1 component was larger for valid conditions compared to invalid conditions when the target was presented in the contralateral visual field (Figure 12). This effect was supported by a significant hemisphere by

target side by validity interaction [F(1,15)=17.142, p<0.01]. For the N170 no such validity effect was found (hemisphere by target-side by validity: F(1,15)=1.23, ns p=0.28, ns).

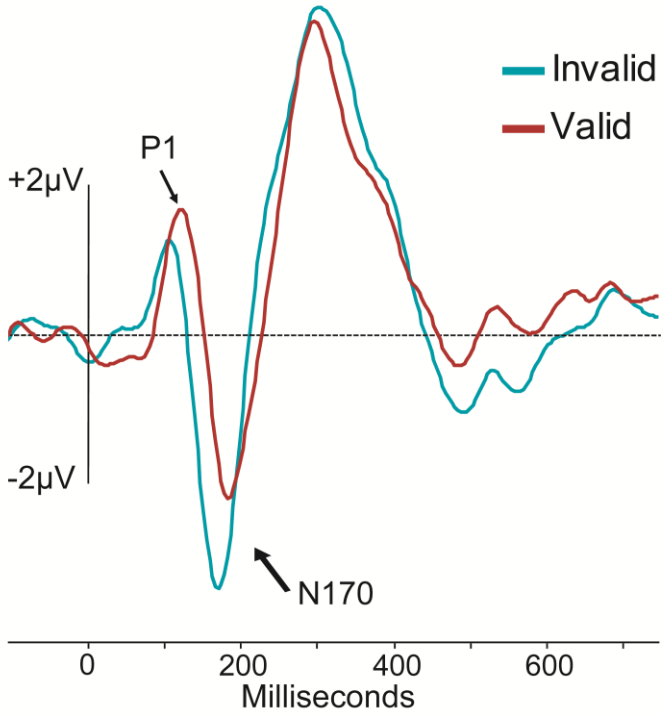


Figure 12: ERPs elicited for the different conditions from Experiment 2

ERP waveforms to voluntary and involuntary cue-conditions (a and b respectively) at contralateral-to-target channels (P7/8, PO7/8, P9/10 collapsed over side). Cue only trials were subtracted from target present trials and wave forms were baseline corrected from 100 ms pre target onset to produce this figure.

3.4 Discussion:

The present findings demonstrate that voluntary and involuntary attention have different effects on gamma-band response whereas both affect RT similarly. These effects were manifested in two stages. The first was in response to the cue: only voluntary attention induced gamma-band increases to the cue alone (predictive-cue-condition). The second was in response to targets: gamma-band increased whenever a voluntary shift of attention was required to a target or not. These patterns of gamma-response and the way they relate to voluntary and involuntary attention are detailed bellow.

Replicating many past studies, valid targets were detected faster than invalid targets regardless of the cue's predictive value. This is evidence that abrupt onsets of peripheral stimuli captured the observer's attention reflexively. When the cue was predictive, however, participants also oriented voluntarily to the cued location, which led to enhanced validity effects. Since the

addition of voluntary attention was the only difference between the two conditions, the higher the gamma power elicited by the predictive relative to nonpredictive cues reflects EEG activity associated with voluntary attention[3].

Responses to the targets differed depending on whether the cue was predictive or nonpredictive. In the nonpredictive condition, when the target appeared, a voluntary attention shift to the target was required to carry out the discrimination task (for both valid and invalid trials). EEG response in those trials revealed that after a target appears in the nonpredictive condition, there was an increase in the gamma-band response (Figure 10b). Hence for the nonpredictive cue-condition, response to the targets was supporting the correspondence between gamma-band response and voluntary shifts of attention.

In the predictive cue-condition, on valid trials, the cue summoned voluntary attention and there was no additional shift required to the target. In these trials, there was less gamma-band response because participants had already shifted their attention to the cued location. In contrast, in invalid trials, while a shift of attention has occurred to the predictive cue, attention has shifted to the wrong location and an additional shift of attention was required when the target appears. Examining the EEG response in these trials revealed a marked increase in gamma-band response on invalid trials. Once again, EEG response in the gamma-band seems to mirror the voluntary shift of spatial attention.

Previous investigations in the spectral domain of the EEG signals have suggested diverse roles for gamma activity which include perception, higher cognitive functions such as memory and object representation (Herrmann et al. 2004; Zion-Golumbic and Bentin 2006). Tallon-Baudry et al. (1999) have extensively examined the role of gamma-band activity in perceptual binding. In initial studies gamma activity was measured to stimuli requiring perceptual integration to form a visible object. However, since the object requiring binding was also the object of attention, it was unclear whether the factor eliciting the increases in induced gamma in these studies was perceptual binding, attentional selection or some combination of the two (Tallon-Baudry et al. 2005).

Recent work has shown that gamma-band response can be related to selective attention. Gruber et al. (1999) have reported increases in gamma-band activity at parieto-occipital sites contralateral to attended movement, and recently Vidal et al. (2006) have dissociated between the response to visual grouping and focused attention. In this study however participants were requested to selectively attend to a subset of the stimuli in a display for later report of the items orientation, a task involving a memory component in addition to the selective attention components. Fan et al. (2007) have recently reported increases in gamma-band response to a peripheral predictive cue, as we found here. The authors term this effect a spatial-orienting effect. However in their study it is unclear whether these increases are due to the peripheral

[3] The time course of the voluntary attention EEG modulation found here is consistent with previous work measuring SSVEPs in response to an attentional cue in a sustained attention paradigm (Müller et al, 1998).

sensory stimulation, the exogenous capture of attention by the peripheral cue or the voluntary deployment of attention to the cued location (cues were 100% predictive).

Our data ruled out a sensory interpretation for these findings and suggested that increases in gamma-band response were related to voluntary rather than involuntary deployment of attention. Because mechanisms of selection and perceptual organization are thought to be highly interactive, perceptual binding and attention are difficult to tease apart. In the present study we circumvented this problem by observing the effects of voluntary and involuntary attention on gamma-band activity in the absence of sensory differences between these two attention conditions. It might be the case that the neural mechanisms that support voluntary shifts of attention are also involved in perceptual binding (Treisman and Gelade 1980), however these questions await further investigation.

In contrast to gamma, ERPs did not discriminate between voluntary and involuntary attention. Similar to previous studies (Mangun and Hillyard 1991; Hopfinger and Ries 2005) we found evidence for early sensory processing for validly cued compared to invalidly cued locations (indicated by a larger P1-component on valid trials). However, this difference was largely unaffected by cue predictability (Doallo et al. 2005). This dissociation between higher frequency responses in the gamma-band range and the low frequency responses in ERPs suggest that high- and low-frequency EEG activity reflect different cognitive mechanisms.

Our findings in the gamma-band response relate to previous findings from single unit recordings. In monkey V4, gamma activity correlates with attentional selection (Fries et al. 2001). Recordings in this study were limited to the extra-striate regions. Our data are complementary to the animal work, as they reveal contralateral responses to predictive cues and attended targets that initially appear in anterior regions and then propagate to posterior regions (figure 11). Such contralateral fronto-parietal distribution is consistent with evidence from both fMRI studies in humans and investigations in animals showing the relevance of cortical regions such as the frontal eye fields (FEF) in selective voluntary attention (Corbetta 1998; Buschman and Miller 2007).

EEG Activity in the alpha-band has been shown to be modulated by sustained voluntary attention (Worden et al. 2000, Thut et al, 2006). These modulations typically take 400ms to develop after the onset of a spatial cue. It is possible that alpha-band and gamma-band-responses interact, and future studies could address this issue using longer cue target intervals than those used here. The present study was designed to allow a direct comparison between voluntary and involuntary attention requiring relatively short cue-to-target intervals.

The differences in neural response between voluntary and involuntary attention conditions fit well with the hypothesis that they involve different mechanisms and suggest how these two types of attention may affect performance and perceptual processing. Previous support for this hypothesis can be found in both behavioral and imaging work. RT studies showed that

involuntary attention effects dissipate rapidly and reverse at long cue-target SOAs while the effects of voluntary attention on performance are sustained (Berger et al. 2005). Prinzmetal et al. (2005) suggest that there are several cases where voluntary attention affects accuracy while involuntary attention does not within identical stimulus conditions. fMRI studies also report differences between voluntary and involuntary attention, mostly in dorsal regions (Kincade et al. 2005). A recent study by Esterman and colleagues (Esterman et al., 2008) demonstrated that BOLD response to faces in the fusiform face area (Kanwisher et al. 1997) increased when a target face was presented at a cued location compared to an uncued location, but only if the cues were predictive of target location. The current EEG study provides insight to the temporal dynamics of voluntary and involuntary attention and reveals that gamma-band response reflects voluntary shifts of attention. The discovery of a unique marker of voluntary attention that is absent for involuntary attention contributes to the theoretical distinction between these two attention systems and suggests that there are distinct neural mechanisms mediating the two types of attention.

Table 1: Complete statistical analysis of the gamma band response

Main effects and Interactions (levels)	F-value	P-value
Cue Related Gamma Band Response		
Cue Condition (Predictive/Nonpredictive	4.63	0.04
Cue Side (Left/Right)	0.13	0.72
Hemisphere (Left/Right)	1.03	0.33
Site (Frontal/Central/Posterior)	0.03	0.95
Cue Condition X Cue Side	0.001	0.98
Cue Condition X Hemisphere	0.38	0.54
Cue Side X Hemisphere	1.39	0.25
Cue Condition X Cue Side X Hemisphere	0.08	0.77
Cue Condition X Site	2.14	0.15
Cue Side X Site	2.13	0.14
Cue Condition X Cue Side X Site	1.2	0.31
Hemisphere X Site	1.18	0.31
Cue Condition X Hemisphere X Site	1.76	0.18
Cue Side X Hemisphere X Site	0.28	0.65
Cue Condition X Cue Side X Hemisphere X Site	0.16	0.75
Target Related Gamma Band Response		
Cue Condition (Predictive/Nonpredictive)	0.5	0.48
Validity (Valid/Invalid)	5.12	0.03
Target Side	0.98	0.33
Hemisphere	2.45	0.13
Site	3.6	0.04
Cue Condition X Validity	4.7	0.04
Cue Condition X Target Side	0.72	0.4
Validity X Target Side	061	0.44
Cue Condition X Validity X Target Side	0.13	0.71
Cue Condition X Hemisphere	0.03	0.85
Validity X Hemisphere	0.09	0.76
Cue Condition X Validity X Hemisphere	0.00	0.99
Target Side X Hemisphere	0.84	0.37
Cue Condition X Target Side X Hemisphere	0.001	0.98
Validity X Target Side X Hemisphere	0.65	0.43
Cue Condition X Validity X Target Side X Hemi	0.34	0.61
Validity X Site	2.57	0.1
Cue Condition X Validity X Site	1.57	0.22
Target Side X Site	1.31	0.28
Cue Condition X Target Side X Site	0.08	0.92
Validity X Target Side X Site	0.6	0.55
Cue Condition X Validity X Target Side X Site	0.02	0.97
Hemisphere X Site	3.17	0.08
Cue Condition X Hemisphere X Site	0.18	0.79
Validity X Hemisphere X Site	2.66	0.09
Cue Condition X Validity X Hemisphere X Site	2.29	0.14
Target Side X Hemisphere X Site	3.54	0.04
Cue Condition X Target Side X Hemisphere X Site	0.72	0.49
Validity X Target Side X Hemisphere X Site	1.67	0.2
Cue Condition X Validity X Target Side X Hemisphere X Site	0.73	0.48

4. Effects of Voluntary and Involuntary attention on intrahemispheric functional connectivity

4.1 Introduction

The question of the functional organization of spatial attention is an old problem in the field of psychology (Helmholtz, 1925; Wundt, 1912/1973, 1902). Spatial attention is the capacity to prioritize part of the environment for processing over other parts of the environment. It is a crucial capacity for dealing with the massive influx of sensory information. Perhaps the complexity of this problem can be captured by the pattern of deficits of spatial attention in patients with unilateral neglect. Patients suffering from this syndrome, as its name implies, will neglect events occurring on the side contralateral to their brain injury. Importantly, these patients may not have any lateralized sensory loss. However, their fully intact sensory systems can hardly support daily functioning, since they suffer from an inability to deploy spatial attention to half of their sensory inputs. This apparent dissociation between sensory capacities and the ability to select certain portions of the environment for processing poses a challenge in the attempt to localize the functions supporting spatial attention. This challenge created the need for a new way of thinking about functional organization in the brain as well as new methods for probing brain functions.

The conceptual leap in the attempt to characterize attention in the brain arrived about three decades ago. In a seminal review (Mesulam, 1981), Marcel Mesulam introduced the idea of "cortical networks for directed attention". Mesulam outlined "the network approach", a novel approach at that time, to the study of attention, and presented it as an intermediary stance between two polar views on the organization of functions in the brain. It can be argued that it is precisely the challenge presented by the curious dissociation of attention from any well-characterized system or modality which gave rise to this idea.

The development of new methods to measure brain activity presented a plethora of new opportunities to investigate how the human brain mediates the allocation of attention. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) allowed measurement of responses of brain regions that are active during an attention task. Neuroimaging studies of attention (Corbetta and Shulman, 2002; Kincade, 2005; Posner, 1980; Serences and Yantis, 2006; Serences and Yantis, 2007) adopted the previously coined term "network" in investigations of attention in the brain. However, most of these studies did not examine the circuitry per se or address questions of coupling between regions directly but merely inferred those by virtue of co-activations during attention tasks (Corbetta and Shulman, 2002; Fan et al., 2007; Kincade, 2005; Mayer et al., 2004).

A primary goal of the present study is to directly address the coupling between different brain regions that have been previously implicated in voluntary and involuntary attention

(Esterman et al., 2008; Kincade, 2005; Mayer et al., 2004). While many candidate regions have been identified in previous work, most of this work did not assess the network dynamics or the degree of coupling between regions for voluntary and involuntary attention.

As a first step, the present study focuses on previously identified regions that are engaged in attention tasks and provides measures of the degree of coupling among these regions for voluntary and involuntary attention. The regions explored in this study and their purported role in spatial attention are: (1) IPS1 and IPS2 are regions in the intraparietal sulcus that contain topographic representations of space (Silver et al., 2005). However, unlike the topographic representations in early visual cortex, IPS regions have topographic maps that are maximally responsive to the location of attention rather than the location of a visual stimulus (for a review see (Silver and Kastner, 2009). (2) The human homologue of the frontal eye fields (FEF) is a region that traditionally has been thought to control the generation of voluntary eye movements in monkey (Bruce and Goldberg, 1985) and humans (Connolly et al., 2005). Recently, there is accumulating evidence that the FEF also contain a neural representation of the current locus of attention (Connolly et al., 2002; Juan et al., 2004) and that this region is engaged when participants are performing attentionally demanding tasks (e.g., (Serences and Yantis, 2007). (3) Areas that may be on the receiving end of attentional modulation, i.e., areas where the consequences of attentional control can be measured. These regions are the topographically-organized visual areas (V1, V2, V3, V4, V3AB and V7) as well as the fusiform face area (FFA; (Kanwisher et al., 1997), an object-selective region that maximally responds to faces,. Both monkey and fMRI studies have suggested that modulation of this class of regions can be seen with spatial attention (Esterman, 2008; Gandhi, 1999; Martinez, 1999; Motter, 1993; Tootell, 1998).

To measure functional connectivity we used fMRI coherency analysis (Kayser et al., 2009; Lauritzen et al., 2009; Sun et al., 2004, 2005). Coherency corresponds to covariation in the frequency domain. Since the dynamic range of the blood oxygenation level-dependent (BOLD) signal measured with fMRI is in the lower temporal frequencies, coherency was measured for these low frequencies (here 0.6-0.14 Hz). Measuring fMRI coherency allows an estimation of the degree of coupling between regions (coherency magnitude) as well as the temporal order of activation among regions (derived from coherency phase relationships). The current paper will focus on the magnitude of coupling among the independently defined regions mentioned above.

4.2 Materials and methods:

Participants: Eight neurologically intact subjects (four female) participated in this study. All had normal or corrected to normal vision. All provided informed consent as approved by the UC Berkeley Committee for the Protection of Human Subjects.

Behavioral Procedure: There were two scanner sessions each consisting of two independent localizer scans and twelve experimental scans during performance of the cueing task. Importantly, for both the cueing task and the localizer scans, the placement and identity of the stimuli were identical.

Stimuli and Cueing Task: The target stimuli were pictures of a male and a female face. To increase stimulus similarity and consequently task difficulty, the images were processed to equate skin tone and hairline. The trial sequence can be seen in Figure 13. The fixation point was present throughout the trial. Following a display containing only the fixation point, a horizontal red bar (4.12° visual angle wide; the cue) appeared above the horizontal meridian (HM) for 250 msec. Immediately after the cue offset, a face (4.12° X 5.36° visual angle) appeared below the HM (for both cue and target, the boundary of the stimulus that was closest to the HM was 0.85° visual angle from the HM), and participants were required to indicate with a button press whether the face was male or female. The cues and targets were presented at 5.5° visual angle eccentricity (measured as the distance from the center of the display to the closer edge of the cue and target). In addition, on some trials no face appeared, and these trials required a separate button press (total of three response categories: male/female/no-face). The face could either appear on the cued side or on the uncued side. The cue and target separation in the displays was chosen to allow separate measurement of cue and target related activity in topographically-organized visual cortical areas (Liu et al., 2005).

Block of trials were either predictive or nonpredictive. In the predictive block, the onset of the cue was 70% predictive of the side in which the target face would appear. In these blocks, 70% of trials were cued, 15% were uncued, and 15% were cue-only trials. In the nonpredictive blocks, cue side was random with regard to target location. Forty percent of trials in these blocks were valid, 40% were invalid, and 20% were cue-only trials.

The experiment consisted of two fMRI sessions, each preceded by a short practice session the day before the fMRI session. In the first fMRI session, the stimulus configuration was as described above (cue above HM and target below HM), and in the second fMRI session, the stimulus configuration was reversed (cue below HM and target above HM, all other display parameters were identical in the two sessions). Each session consisted of three predictive cue blocks (96 trials per block) and three nonpredictive cue blocks (100 trials per block). Practice

sessions consisted of a short version of the entire experiment to be performed in the scanner the following day with the goal of familiarizing the participant with the appropriate configuration, training participants to avoid moving their eyes during the trials, and allowing them to reach the desired performance level (above 90% correct). During the practice sessions, auditory feedback was given for incorrect responses as well as for breaks of fixation. Eye movements were monitored manually using a direct video display of the participants eye as in (Prinzmetal et al., 2005). The experimenter entered their eye movement observation usind a key press on every trial which in turn triggered feedback when an eye movement occurred.

Pre- and Post-Cue Conditions: Predictive and nonpredictive runs contained identical stimulation conditions at the level of individual trials and hence provided a useful way of manipulating voluntary and involuntary attention when comparisons of trial responses are planned (as will be presented here for the behavioral data). However, when comparing overall activity for an entire run, these two types of runs differed dramatically in the consistency of bilateral stimulation compared to unilateral stimulation. In a predictive block, there were more unilateral stimulation trials (cue and target in the same visual field) compared to a nonpredictive block. In order to control for this difference, another type of cue was utilized in the design. In addition to trials in which the cue preceded the target, post cue trials were used (Liu et al., 2005; Prinzmetal et al., 2008). For each pre-cue run, an identically composed run of post cues was performed in which the temporal order of target and cue was reversed. This temporal manipulation created runs that contain the sensory stimulation provided by the pre cues but in the absence of the attentional component (as confirmed by the behavioral results, see results). The terminology "cued" and "uncued" trials as well as "predictive" and "nonpredictive" runs were used with quotation marks to signify that the post cues do not provide the information implied by those terms. However, this terminology allowed for a clear correspondence with the trial types and block types in the pre-cue procedure.

FEF and cue response localizer: Participants started the scanner session with a localizer task designed to activate the Frontal eye fields (FEF) as well as portions of retinotopic areas responding to the cue stimulus used in the cueing task. For the first scanner session, the cue stimulus was presented 0.85° above the HM, and for the second session 0.85° below the HM (as they were in the cueing task for a given session). This localizer consisted of one of five types of blocks: (1) saccade to stimulus presented on the left, (2) saccade to stimulus presented on the right, (3) fixate while stimulus was presented on the right, (4) fixate while stimulus was presented on the left, (5) fixation only. Each block lasted 14.4 seconds (9 TRs) and was repeated five times in a run. Within each stimulus block, a cue identical to that in the cueing task was flashed (400 msec on / 860 msec off). During saccade blocks, participants were instructed to initiate a saccade to the stimulus upon its onset and then immediately saccade back to the fixation point. During non-saccade blocks (stimulus or fixation only), participants were instructed to maintain fixation at the center of the display. A fixation cross was present throughout the run. Between blocks, the fixation symbol was used to indicate whether the next

block would be a saccade or a fixate block (black '+' sign indicated fixate, gray 'x' sign indicated saccade). FEF ROIs were defined by contrasting saccade blocks and fixation blocks. Retinotopic regions of maximal response to the cue were defined using stimulus blocks (for right and left separately) contrasted with fixation blocks.

FFA and target response localizer: After the FEF localizer run, participants performed a localizer run designed to define the fusiform face area (Kanwisher et al., 1997) as well as retinotopic regions in visual cortex maximally responding to the face targets subsequently used in the cueing part of the experiment. Faces in the localizer task were the same faces used for the cueing task and were presented at the same eccentricity (5.5° visual angle). For the first session, the faces were presented 0.85° below the HM, and for the second session they were presented 0.85° below the HM (as they were in the cueing task for a given session). The localizer run was a blocked design consisting of five types of blocks: (1) left presented face, (2) right presented face, (3) left presented house, (4) right presented house, and (5) fixation. House pictures subtended the same size as the faces (4.12° by 5.36° visual angle). Each block lasted 16 seconds (10 TRs) and was repeated five times. Within each stimulus block, the stimulus was flashing (300 msec on, 519 msec off). Participants were instructed to fixate and continuously allocate covert attention to the stimulus throughout the run.

fMRI Data Acquisition: Participants were scanned with a 3T Siemens Trio Scanner at the UC Berkeley Brain Imaging Center. Functional images were acquired using a gradient echo-planar imaging sequence sensitive to BOLD contrast (TR = 1600 msec, TE = 24 msec, matrix size = 96 X 96, FOV = 22.4 X 22.4 cm (resulting in an inplane resolution of 2.3 mm X 2.3 mm X 4 mm voxel size), flip angle = 80°). Each functional volume consisted of 26 4-mm thick slices in an axial orientation parallel to the anterior commissure - posterior commissure line with a 0.6 mm gap between each pair of slices, providing full coverage of the cerebral hemispheres. The experimental display was back projected onto a custom screen behind the radiofrequency (RF) head coil inside the scanner bore and viewed via an angled mirror placed on top of the RF coil. Responses were made with the right hand using a button box.

fMRI data preprocessing: Each fMRI run began with 4 dummy images which were discarded to remove artifacts due to incomplete magnetic saturation and to allow the hemodynamics to attain a steady-state baseline. Head motion was corrected using a 3-D image registration algorithms (MCFLIRT; (Jenkinson et al., 2002). The time series of each voxel was then high-pass filtered to remove low-frequency noise and slow drift (Smith et al., 1999; Zarahn et al., 1997). Finally, each voxel's time series was divided by its mean intensity to convert the data from arbitrary image intensity units to percentage signal modulation and to compensate for the decrease in mean image intensity as a function of distance from the RF coil.

Definition of Regions of Interest (ROIs): The boundaries of areas V1, V2, V3, V4, V3AB, V7, IPS1 and IPS2 were predefined for the participants in this study using well established retinotopic mapping procedures (Engel et al., 1994) as well as attention mapping

procedures described elsewhere (Silver et al., 2005). Those boundaries were imported into the current study by aligning all sessions to a high-resolution volume anatomy for each subject and were then restricted to include the relevant portions of the visual areas responsive to the cue and target stimuli used in this study. Cue-related areas were defined using the contrast of cue stimulus presentation vs. fixation for each side of the visual field. Target-related areas were defined using the contrast of target stimulus presentation (both faces and houses from the FFA localizer) vs. fixation for each side of the visual field. Frontal eye fields were defined by contrasting both saccade blocks (left and right side) with fixation, and the FFA was defined by collapsing all face stimuli (left and right side) and contrasting them with all house stimuli (combined left and right side).

FEF and FFA were selected based on a conjunction of functional and anatomical criteria. The anatomical criteria were within the fusiform gyrus for FFA and in the vicinity of the junction of the frontal sulcus and the precentral sulcus for FEF, and the functional criteria were a significantly greater response to the relevant contrast that remained centered at the same brain location for a range of different statistical thresholds.

Coherency Analysis: For each experimental run, the average time series from independently defined ROIs was computed. This resulted in 18 averaged time series for each run (V1, V2, V3, V4, V7, V3AB, IPS1 IPS2 for cue and for target ROIs and regions FEF and FFA that do not have cue and target separation). Coherency is defined as:

$$R_{xy}(\lambda) = \frac{\langle f_{xy}(\lambda) \rangle}{\sqrt{\langle f_{xx}(\lambda) \rangle \langle f_{yy}(\lambda) \rangle}}$$

where $<f_x(\lambda)>$ and $<f_y(\lambda)>$ are the means of the power spectra of segments of time series x and y at frequency λ, and $<f_{xy}(\lambda)>$ is the mean of the cross spectrum of segments of x and y (Sun et al., 2004). $R_{xy}(\lambda)$ is a complex quantity. For a given frequency, the absolute value of coherency corresponds to the magnitude of coupling between x and y. Coherency magnitude takes a value ranging between 0 and 1, with zero indicating no coupling and 1 indicating perfect coupling between two time series. The complex argument, or polar angle, of $R_{xy}(\lambda)$ defines the phase relationship between the time series. Dividing these phase values by a given temporal frequency yields the delay between x and y in units of time (taking positive or negative values, depending on the direction of the delay between the areas). Thus, coherency analysis allows the measurement of both the strength of functional coupling between two time series (magnitude) as well as the direction of signal transmission (phase relations). Compared to correlation-type analyses of functional connectivity, coherency analysis possesses several advantages that allow for clearer interpretation of functional connectivity data. The implementation of the coherency analysis was as in Lauritzen et al. (Lauritzen et al., 2009). Briefly, condition-specific coherency

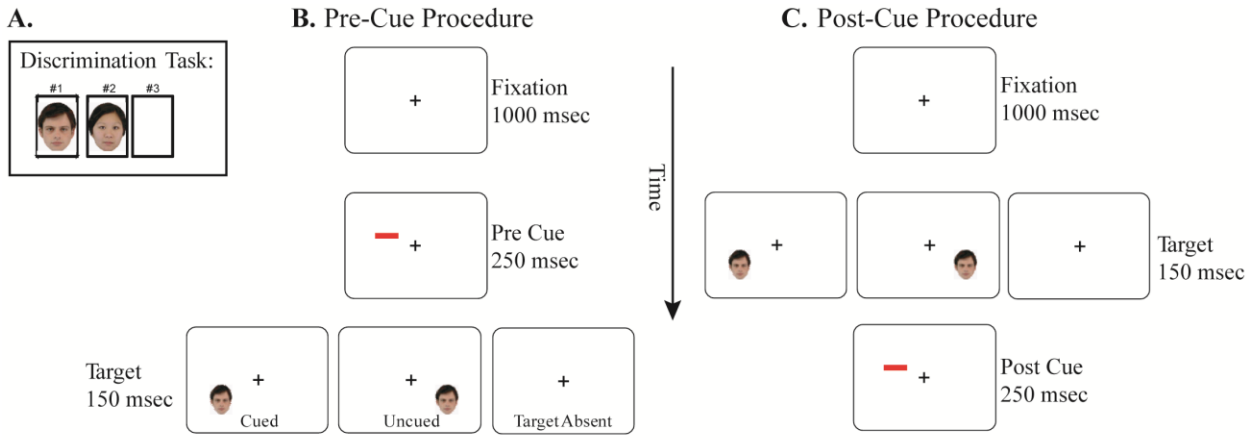
was computed using Welch's periodogram-averaging method with a 64-point discrete Fourier transform (DFT) Hanning window (Sun et al., 2004) and 32-point overlap between windows. Coherency was analyzed for frequency bands 0.06 – 0.15 Hz. The upper bound on this band was chosen based on the known properties of the frequency content of fMRI BOLD signals (Cordes et al., 2001; Sun et al., 2004). Coherency was computed for nine frequency bands centered about 0.068, 0.078, 0.087, 0.097, 0.10, 0.117, 0.127, 0.136, and 0.146 Hz.

4.3 Results

Behavioral Results

Reaction times (RTs) for correct trials, for each condition and each participant, were analyzed by ANOVA with factors of configuration (cue above the HM or target above the HM), trial type (target appearing on cued or uncued side), attention type (predictive or nonpredictive runs), and cue order (pre-cue or post-cue) as within-subject factors. As expected, performance on the cued side was faster than performance on the uncued side (main effect of trial type: $F(1,7) = 16.95$, $p < 0.01$). In addition, there was a significant interaction of attention type and trial type [$F(1,7) = 8.79$, $p < 0.05$], indicating that the difference between cued and uncued reaction times (cueing effect) was larger when cues were predictive of target location (25 msec) compared to when cues were nonpredictive of target location (5 msec). The interaction of cue order and trial type was also significant [$F(1,7) = 17.22$, $p < 0.01$], indicating that the cueing effect was larger in the pre-cue condition (32 msec; $t(7) = 19.16$, $p < 0.01$) compared to the post-cue condition (-2 msec; $t(7) = 1.05$). In addition, there was a significant three-way interaction of attention type, trial type and cue order [$F(1,7) = 9.44$, $p < 0.05$]. This interaction was qualified by a separate ANOVA for post-cue and pre-cue performance separately.

In the pre-cue procedure there was a significant interaction of trial type and attention type [$F(1,7) = 10.24$, $p < 0.05$]. In the post-cue procedure there was no interaction of trial type and attention type [$F<1$ ns] indicating that the temporal manipulation introduced by post cueing was a valid control for sensory stimulation that has minimal attentional impact on target performance. None of the remaining factors or interactions was significant. Figure 13E presents the RT data in the form of cueing effects (RT difference between cued and uncued trials for the different conditions).



D.

	Pre Cue: Trial-Type Proportions			Post Cue:Trial-Type Proportions		
	Cued	**Uncued**	**Target Absent**	**"Cued"**	**"Uncued"**	**"Target Absent"**
Nonpredictive (involuntary)	40%	40%	20%	40%	40%	20%
Predictive (+voluntary)	70%	15%	15%	70%	15%	15%

E.

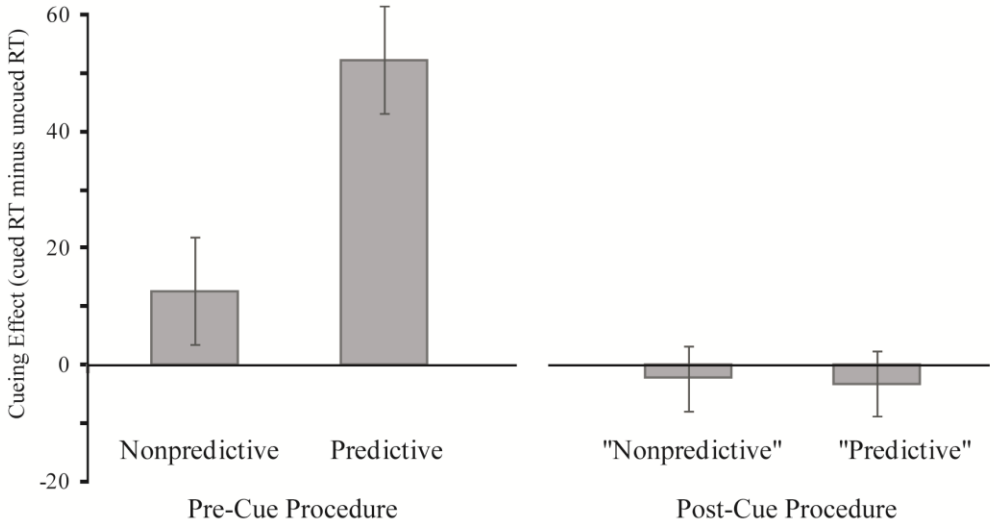


Figure 13: Experimental procedure and RT data from Experiment 3

(a) Stimuli used for the face discrimination task and the corresponding response categories. In addition to the two faces for discrimination, a third response category was used for target-absent trials. Trial procedure for (b) pre-cue and (c) post-cue conditions. (d) Trial type proportion table. Note that trial proportions were the same for pre-and post-cue conditions. However, as denoted by the used of quotation marks in the post-cue condition, a target is not literally cued or uncued, given that the cues appear after the targets. (e) Behavioral data: Cueing effects calculated as cued RT minus uncued RT in msec. Error bars represent the standard error of the difference between predictive and nonpredictive performance for pre-cue (9 msec) and post-cue (5 msec) conditions.

An additional analysis was performed to establish that both cues in the predictive and in the nonpredictive runs generated an attention effect that was significant. While voluntary attention, engaged in the predictive run, produced large behavioral effects, it was important to confirm that the cue to target spatial separation did not diminish the ability to capture involuntary attention in the nonpredictive runs. Data from both configurations were combined, and cueing effects were computed by subtracting cued trial types from uncued trial types. A one sample t-test was performed for each attention condition separately. Cueing effects for both predictive (mean 52 msec; $t(7) = 4.08$ $p < 0.01$) and nonpredictive blocks (mean 13 msec; $t(7) = 2.65$ $p < 0.05$) were significantly different from zero, indicating that the cue-target separation in this experiment probed both voluntary (predictive runs) and involuntary (nonpredictive runs) attention.

Imaging data

Coherency magnitudes

Coherency magnitudes for all pairwise combinations of ROIs within hemisphere (V1, V2, V3, V4, V3A, V7, IPS1, IPS2, FEF, FFA) were calculated for each run separately. This calculation was performed separately for cue related ROIs and for target related ROIs. For each of forty-five pairs of ROIs (i.e. connections), an ANOVA with attention type (predictive or nonpredictive), display configuration (cue above the HM or target above the HM) and hemisphere (left or right) was performed. A full report of the main effects is presented in Tables 2-4.

Attention Type Effects

Figure 14 displays functional connectivity that was significantly affected by attention type (voluntary or involuntary). The main finding revealed from this comparison is that involuntary attention is associated with greater coherency magnitudes relative to voluntary attention. That is, voluntary attention acts to reduce coupling among different regions within a hemisphere. The pattern of effects for cue-related and target-related ROIs is similar. However, there is a quantitative difference in the proportion of connections significantly altered by the attention type manipulation for cue- and target-related ROIs. For target-related ROIs, there was only a moderate number of connections affected by attention type (three) compared to cue-related ROIs (ten). Given that the two attention types primarily differed in the spatial information carried by the cue (rather than in target processing), this pattern is predicted.

Post cue control: This control was included to determine whether the effect of attention type could be influenced by differences in display conditions over the course of a run. While the stimuli for each trial type (cued compared to uncued) are identical, a predictive block contains more unilateral stimulation (70% cued trials) compared to the nonpredictive block (equal

probability of unilateral and bilateral stimulation). The use of the post-cueing procedure serves as a control for this alternative account. Post-cue data was subjected to the same analysis as pre-cue data in order to examine whether any of the significant attention type modulations observed in the pre-cue conditions were also present in the post-cue trials. Significant main effects in the post-cue procedure would suggest that some of the effects observed in the pre-cue condition were due to differences in display rather than attention type. As can be seen in Table 2, connections that showed significant effects of attention type in the pre-cue condition generally did not have corresponding effects in the post-cue condition.

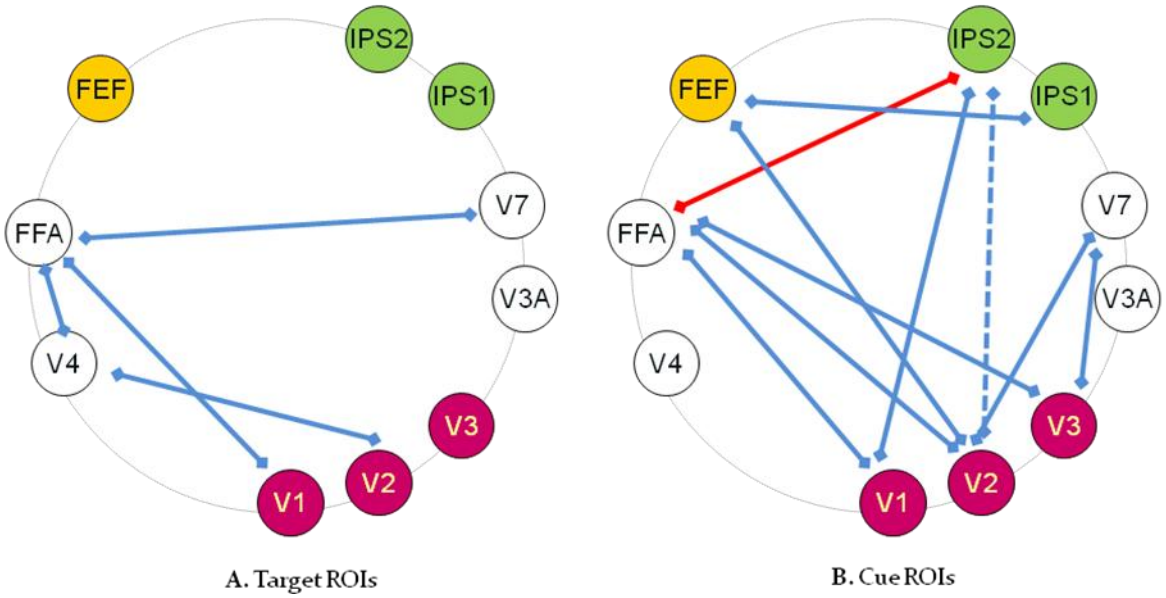


Figure 14: Circuit diagram comparing coherency magnitudes for voluntary and involuntary attention

Circuit diagram comparing coherency magnitudes for voluntary and involuntary attention (as measured in predictive and nonpredictive pre-cue trials). Only coupling modulations that reached significance are displayed. Blue, connections for which the coupling for involuntary attention is greater than that of voluntary attention. Red, connections for which coupling for voluntary attention was greater than that of involuntary attention. Solid lines denote modulations in coupling that were unique to pre-cue procedure. Dashed line denotes a modulation in coupling that was present for both pre- and post-cue procedures (i.e,. is not a attention-related modulation per se). For a complete statistical report of this main effect, see Table 2.

Hemisphere Effects

A comparison of connectivity in the left and right hemispheres revealed that, there was generally greater coupling in the right hemisphere compared to the left hemisphere (Figure 15; Table 3).

Post-cue control: In order to examine whether this lateralization is related to attention, the significant effects for the pre-cue condition were compared to those in the post-cue condition. Here, the post-cue condition determines whether the hemispheric asymmetry is specific to pre cueing of a spatial location or whether it is a global property of the measured connections. For target-related ROIs, all but one connection showed right hemisphere dominance in the pre-cue but not the post-cue condition. For cue-related ROIs, a mixed picture is seen, where part of the hemispheric asymmetry was present in the post-cue procedure and part of the asymmetry was unique to the pre-cue procedure.

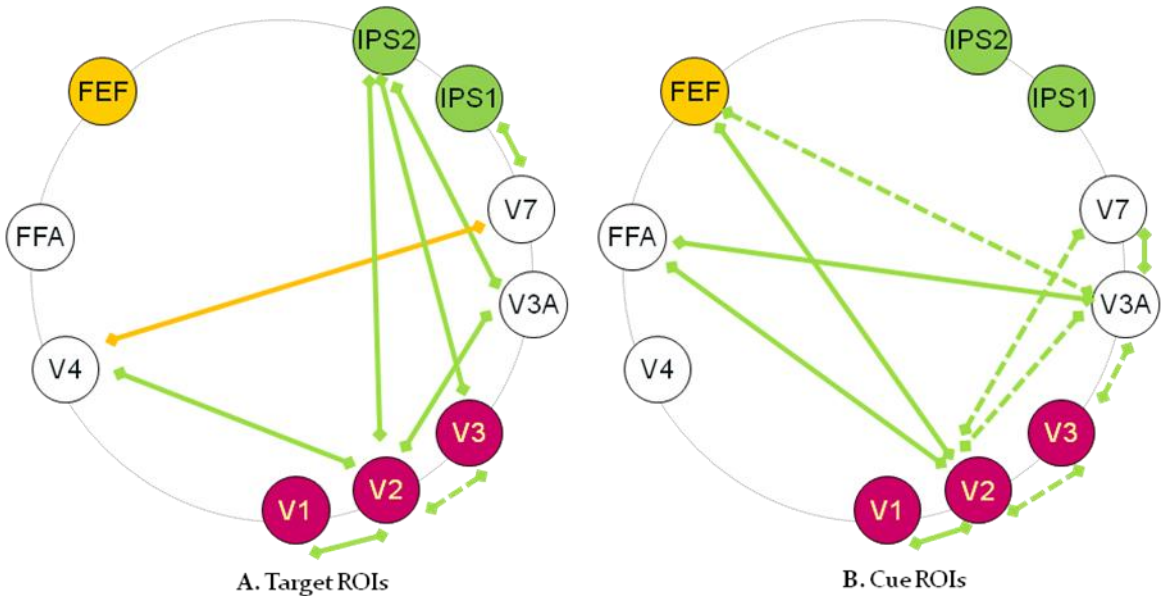


Figure 15: Circuit diagram comparing coherency magnitudes for the left and right hemisphere

Circuit diagram of the comparison of coherency magnitudes for the right and left hemispheres. Only significant hemispheric differences in coupling are plotted. Green, connections for which the coupling in the right hemisphere is greater than that in the left hemisphere. Yellow, connections for which coupling in the left hemisphere is greater than that in the right hemisphere. Solid lines denote modulations in coupling that were unique to the pre-cue condition. Dashed lines denote modulations in coupling that were present for both pre- and post-cue procedures (i.e., might reflect global differences in coupling between the two hemispheres). For a complete statistical report of this main effect see Table 3.

Table 2: Full statistical report for the main effect of attention type (predictive or nonpredictive condition).

	Target ROIs						Cue ROIs					
	Pre Cue Procedure			Post Cue Procedure			Pre Cue Procedure			Post Cue Procedure		
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**		**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	
FEF-FFA	2.1164	0.162		1.024	0.358		2.731	0.117		1.024	0.358	
FEF-IPS1	0.1797	0.676		0.034	0.860		5.099	0.037	*	0.080	0.789	
FEF-IPS2	1.8185	0.193		0.005	0.945		2.676	0.120		0.239	0.646	
FEF-V1	0.8934	0.356		0.170	0.697		0.300	0.591		0.001	0.981	
FEF-V2	1.1701	0.293		1.978	0.219		3.278	0.088	.	0.949	0.375	
FEF-V3A	0.2225	0.643		0.779	0.418		0.927	0.349		7.281	0.043	*
FEF-V3	0.395	0.537		0.513	0.506		0.045	0.834		0.187	0.683	
FEF-V4	1.4544	0.243		0.871	0.394		0.856	0.368		0.147	0.717	
FEF-V7	0.0082	0.929		0.448	0.533		1.177	0.293		1.332	0.301	
FFA-IPS1	1.4796	0.239		0.013	0.913		0.015	0.904		0.059	0.817	
FFA-IPS2	1.6931	0.209		0.878	0.392		4.715	0.044	*	1.669	0.253	
FFA-V1	6.1435	0.023	*	0.551	0.491		12.864	0.002	**	0.064	0.810	
FFA-V2	2.6038	0.123		1.589	0.263		5.512	0.031	*	0.042	0.846	
FFA-V3A	1.6572	0.213		3.440	0.123		0.836	0.374		3.293	0.129	
FFA-V3	2.578	0.125		3.607	0.116		7.505	0.014	*	2.205	0.198	
FFA-V4	3.3294	0.084		0.242	0.644		0.404	0.534		4.201	0.096	
FFA-V7	4.7055	0.043	*	0.382	0.564		0.003	0.957		3.481	0.121	
IPS1-IPS2	1.8471	0.190		1.942	0.222		2.570	0.127		9.997	0.025	*
IPS1-V1	0.2239	0.642		0.210	0.666		4.104	0.059	.	1.173	0.328	
IPS1-V2	0.0025	0.961		0.013	0.913		2.650	0.122		0.019	0.897	
IPS1-V3A	0.9315	0.347		0.014	0.910		3.949	0.063	.	0.002	0.969	
IPS1-V3	0.7598	0.394		0.360	0.575		2.633	0.123		0.161	0.705	
IPS1-V4	1.1112	0.305		0.087	0.780		0.454	0.510		0.001	0.981	
IPS1-V7	2.2605	0.149		1.159	0.331		1.690	0.211		0.044	0.843	
IPS2-V1	1.6769	0.211		4.731	0.082		6.014	0.025	*	0.121	0.743	
IPS2-V2	1.8943	0.185		0.043	0.844		14.722	0.001	**	8.474	0.033	*
IPS2-V3A	2.774	0.112		0.061	0.815		0.000	0.986		0.206	0.669	
IPS2-V3	3.7566	0.068		1.028	0.357		2.665	0.121		0.209	0.667	
IPS2-V4	1.19E-05	0.997		2.158	0.202		0.096	0.761		0.421	0.545	

Table 2 (continued)

	Target ROIs					Cue ROIs				
	Pre Cue Procedure			Post Cue Procedure		Pre Cue Procedure			Post Cue Procedure	
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**
IPS2-V7	0.2783	0.604		0.154	0.711	1.457	0.244		0.097	0.768
V1-V2	0.0137	0.908		0.032	0.864	0.000	1.000		2.195	0.199
V1-V3A	1.4057	0.250		0.160	0.706	0.031	0.863		0.019	0.896
V1-V3	0.2139	0.649		3.374	0.126	0.089	0.770		5.081	0.074
V1-V4	0.1199	0.733		0.062	0.813	0.024	0.878		0.007	0.935
V1-V7	0.0001	0.993		0.609	0.471	0.739	0.402		0.182	0.688
V2-V3A	0.0051	0.944		0.025	0.880	0.037	0.850		0.696	0.442
V2-V3	1.0647	0.315		0.044	0.842	0.763	0.395		1.388	0.292
V2-V4	4.3754	0.050	*	0.103	0.761	0.000	0.993		0.931	0.379
V2-V7	0.9398	0.345		0.020	0.894	5.409	0.033	*	2.235	0.195
V3A-V3	1.1756	0.292		1.261	0.313	0.000	0.995		0.056	0.823
V3A-V4	1.6332	0.217		0.122	0.741	0.009	0.925		0.000	0.995
V3A-V7	0.0882	0.770		0.128	0.735	3.905	0.065	.	5.053	0.074
V3-V4	1.4997	0.236		0.364	0.573	0.003	0.959		0.045	0.841
V3-V7	1.1612	0.295		0.008	0.931	4.424	0.051	.	0.709	0.438
V4-V7	3.1616	0.091		0.044	0.842	0.111	0.743		1.133	0.336

Table 3: Full statistical report for the main effect of hemisphere (Left or Right).

	Target ROIs						Cue ROIs					
	Pre Cue Procedure			Post Cue Procedure			Pre Cue Procedure			Post Cue Procedure		
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**		**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	
FEF-FFA	0.145	0.708		1.485	0.277		0.145	0.708		1.485	0.277	
FEF-IPS1	2.630	0.121		0.670	0.450		0.273	0.608		0.008	0.930	
FEF-IPS2	3.929	0.062	.	1.443	0.283		0.715	0.410		0.531	0.499	
FEF-V1	1.560	0.227		0.009	0.929		1.116	0.306		0.000	0.987	
FEF-V2	2.464	0.133		3.231	0.132		10.305	0.005	**	2.441	0.179	
FEF-V3A	4.210	0.054	.	0.076	0.794		8.904	0.008	**	13.419	0.015	**
FEF-V3	1.542	0.229		1.270	0.311		0.248	0.625		1.859	0.231	
FEF-V4	0.252	0.622		0.315	0.599		0.171	0.684		0.000	0.987	
FEF-V7	0.011	0.919		0.082	0.786		1.723	0.207		2.443	0.179	
FFA-IPS1	0.391	0.539		1.072	0.348		1.083	0.313		1.060	0.350	
FFA-IPS2	2.530	0.128		0.180	0.689		0.344	0.565		0.000	0.986	
FFA-V1	1.687	0.210		0.173	0.695		3.499	0.079	.	0.075	0.796	
FFA-V2	3.091	0.095	.	0.633	0.462		10.012	0.006	**	0.069	0.803	
FFA-V3A	1.235	0.280		2.286	0.191		10.884	0.004	**	0.068	0.804	
FFA-V3	3.240	0.088	.	0.489	0.516		0.019	0.891		0.041	0.848	
FFA-V4	2.023	0.171		0.129	0.734		0.968	0.339		1.698	0.249	
FFA-V7	1.568	0.226		2.140	0.203		0.800	0.384		0.141	0.723	
IPS1-IPS2	1.484	0.238		0.665	0.452		0.687	0.419		0.006	0.940	
IPS1-V1	2.486	0.131		1.086	0.345		0.269	0.611		0.033	0.864	
IPS1-V2	2.000	0.174		2.580	0.169		0.035	0.854		1.346	0.298	
IPS1-V3A	2.323	0.144		1.576	0.265		3.564	0.076	.	0.055	0.824	
IPS1-V3	0.002	0.964		0.000	0.996		1.078	0.314		0.294	0.611	
IPS1-V4	0.076	0.786		0.022	0.889		0.734	0.404		1.149	0.333	
IPS1-V7	9.574	0.006	**	4.258	0.094	.	1.463	0.243		0.033	0.863	
IPS2-V1	2.491	0.131		1.446	0.283		0.000	0.989		0.764	0.422	
IPS2-V2	17.305	0.001	***	4.908	0.078	.	0.570	0.461		1.496	0.276	
IPS2-V3A	5.213	0.034	*	2.576	0.169		1.865	0.190		3.366	0.126	
IPS2-V3	5.106	0.036	*	5.451	0.067	.	0.610	0.446		0.540	0.496	
IPS2-V4	1.914	0.183		0.914	0.383		0.011	0.919		0.0016	0.97	
IPS2-V7	2.329	0.143		0.912	0.383		0.389	0.541		0.2003	0.6732	
V1-V2	4.737	0.042	*	1.019	0.359		8.202	0.011	*	0.729	0.4322	
V1-V3A	0.000	0.988		2.559	0.171		4.094	0.059	.	0.5776	0.4815	
V1-V3	0.630	0.437		0.468	0.525		1.878	0.188		0.2805	0.619	

Table 3 (continued)

	Target ROIs						Cue ROIs					
	Pre Cue Procedure			Post Cue Procedure			Pre Cue Procedure			Post Cue Procedure		
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**		**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	
V1-V4	0.447	0.512		0.076	0.794		0.175	0.681		0.241	0.645	
V1-V7	0.624	0.439		0.362	0.574		2.611	0.125		2.157	0.202	
V2-V3A	13.667	0.002	**	1.659	0.254		9.875	0.006	**	10.974	0.021	
V2-V3	72.537	0.000	***	11.279	0.020	*	23.183	0.000	***	18.580	0.008	
V2-V4	4.638	0.044	*	0.896	0.387		1.691	0.211		1.721	0.247	
V2-V7	0.805	0.381		1.703	0.249		15.970	0.001	***	9.421	0.028	*
V3A-V3	0.001	0.974		0.035	0.859		5.116	0.037	*	9.616	0.027	*
V3A-V4	0.586	0.453		1.740	0.244		0.036	0.852		0.838	0.402	
V3A-V7	0.120	0.732		0.096	0.769		6.649	0.020	*	2.538	0.172	
V3-V4	0.820	0.377		0.205	0.670		2.486	0.133		0.080	0.788	
V3-V7	0.030	0.865		0.387	0.561		2.195	0.157		4.349	0.091	
V4-V7	10.942	0.004	**	0.012	0.916		3.409	0.082	.	0.031	0.866	

Table 4: Full statistical report for the main effect of configuration (cue above HM or target above HM).

	Target ROIs						Cue ROIs					
	Pre Cue Procedure			Post Cue Procedure			Pre Cue Procedure			Post Cue Procedure		
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**		**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	
FEF-FFA	7.926	0.012	*	0.002	0.967		7.926	0.012		0.002	0.967	
FEF-IPS1	0.029	0.868		0.390	0.560		2.663	0.121		0.149	0.715	
FEF-IPS2	0.917	0.355		6.483	0.052	.	0.134	0.719		0.022	0.889	
FEF-V1	11.623	0.004	**	0.514	0.505		1.264	0.277		0.112	0.752	
FEF-V2	2.151	0.165		0.003	0.959		0.986	0.335		0.125	0.738	
FEF-V3A	0.559	0.467		4.067	0.100	.	0.819	0.378		0.365	0.572	
FEF-V3	17.242	0.001	***	1.023	0.358		0.035	0.854		1.978	0.219	
FEF-V4	4.929	0.043	*	0.013	0.915		6.446	0.021		1.057	0.351	
FEF-V7	0.098	0.759		2.197	0.198		4.949	0.040		0.313	0.600	
FFA-IPS1	0.011	0.919		0.276	0.622		0.148	0.705		0.096	0.769	
FFA-IPS2	3.176	0.096	.	0.092	0.774		0.063	0.804		0.062	0.813	
FFA-V1	5.127	0.040	*	0.280	0.619		2.125	0.163		0.000	0.999	
FFA-V2	2.140	0.166		0.016	0.905		0.190	0.668		0.078	0.791	
FFA-V3A	0.021	0.886		0.578	0.482		0.015	0.905		0.643	0.459	
FFA-V3	12.894	0.003	**	0.783	0.417		0.017	0.899		4.387	0.090	
FFA-V4	0.027	0.872		0.050	0.833		0.000	0.984		0.005	0.949	
FFA-V7	1.856	0.195		0.175	0.693		0.077	0.785		0.002	0.964	
IPS1-IPS2	1.135	0.305		1.568	0.266		2.381	0.141		0.088	0.779	
IPS1-V1	0.345	0.566		0.468	0.524		0.017	0.898		0.233	0.650	
IPS1-V2	0.124	0.730		0.381	0.564		0.645	0.433		0.464	0.526	
IPS1-V3A	0.005	0.945		0.018	0.899		0.811	0.380		0.082	0.786	
IPS1-V3	0.570	0.463		0.060	0.816		0.644	0.433		0.059	0.818	
IPS1-V4	1.764	0.205		1.538	0.270		1.889	0.187		0.010	0.924	
IPS1-V7	3.497	0.083	.	0.865	0.395		0.112	0.742		0.391	0.559	
IPS2-V1	8.096	0.013	*	1.017	0.360		1.089	0.311		0.148	0.716	
IPS2-V2	7.394	0.017	*	3.560	0.118		0.007	0.933		0.024	0.883	
IPS2-V3A	4.193	0.060	.	0.811	0.409		0.396	0.537		0.102	0.762	
IPS2-V3	2.958	0.108		0.142	0.722		1.833	0.194		5.955	0.059	
IPS2-V4	5.415	0.035	*	7.451	0.041	*	0.542	0.472		0.001	0.982	
IPS2-V7	6.353	0.024	*	2.885	0.150		4.490	0.049		0.742	0.428	
V1-V2	0.119	0.735		0.029	0.872		0.749	0.399		0.006	0.941	
V1-V3A	0.247	0.627		0.578	0.481		0.070	0.795		0.015	0.907	

Table 4 (continued)

	Target ROIs						Cue ROIs					
	Pre Cue Procedure			Post Cue Procedure			Pre Cue Procedure			Post Cue Procedure		
ROI pair	**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**		**$F_{(1,17)}$**	**p**	**sig**	**$F_{(1,17)}$**	**p**	
V1-V3	7.067	0.019	*	2.884	0.150		4.071	0.060		4.574	0.085	
V1-V4	0.279	0.605		2.213	0.197		0.493	0.492		0.457	0.529	
V1-V7	2.000	0.179		0.354	0.578		0.000	0.997		0.704	0.440	
V2-V3A	0.117	0.737		0.070	0.802		0.262	0.615		0.210	0.666	
V2-V3	4.244	0.058	.	0.637	0.461		0.683	0.420		0.325	0.593	
V2-V4	3.620	0.078	.	0.005	0.946		0.946	0.344		0.235	0.649	
V2-V7	0.063	0.806		0.466	0.525		1.187	0.291		0.266	0.628	
V3A-V3	2.737	0.120		0.002	0.966		1.078	0.314		0.079	0.790	
V3A-V4	0.204	0.658		2.296	0.190		0.145	0.708		0.001	0.979	
V3A-V7	0.032	0.861		0.004	0.954		0.292	0.596		0.382	0.563	
V3-V4	73.893	0.000	***	4.502	0.087	.	8.301	0.010		5.679	0.063	
V3-V7	0.413	0.531		0.684	0.446		0.087	0.772		0.022	0.888	
V4-V7	0.187	0.672		1.363	0.296		0.138	0.715		0.002	0.964	

4.4 Discussion

The studies described here represent a first step towards characterizing network dynamics mediating voluntary and involuntary attention. The current investigation focused on previously identified regions in the brain shown to be engaged in attention tasks (Corbetta and Shulman, 2002; Serences and Yantis, 2006). One main finding was that, compared to involuntary attention, voluntary attention reduced coupling between many pairs of regions within the previously postulated attention network. Cue and target separation on either side of the horizontal meridian in the stimulus display allowed separate examination of target and cue regions. This approach revealed that the differences between voluntary and involuntary attention are more pronounced for cue-related ROIs than target-related ROIs. Voluntary and involuntary attention showed similar degrees of coupling within target-related ROIs. This result was consistent with the nature of the attention manipulation. The voluntary and involuntary conditions differed primarily in the information carried by the cue. Hence, the cue, and not the target, was the aspect of the task that either captured involuntary attention (when the cue location was random with respect to target location) or which also summoned voluntary attention (when the cue was informative). This pattern of coupling for the two types of attention was not evident in a post-cue procedure, supporting the conclusion that it can be attributed to differences in attention type rather than display conditions (i.e. proportion of bilateral compared to unilateral trials).

An important difference between the current investigation and previous studies probing networks of attention is the temporal scale at which inferences are made. While many studies investigated spatial attention (mostly voluntary) at the single trial level, the data reported here provided a comparison of coupling under two continuous states (since the measurement of coherency is over an entire six minute run). In one state, the system was biased to use the information carried by the cues and voluntarily summoned visual attention to the cued side. In the other state, participants did not employ voluntary attention, and the cues only captured involuntary attention. Despite differences in the temporal scale of analysis, I will cautiously discuss the present findings in light of previous work.

The finding of reduced coupling in voluntary relative to involuntary attention stands in contrast to the common intuition about the way voluntary attention operates. For example, a popular model for brain attention networks suggested by Corbetta and Shulman (Corbetta and Shulman, 2002) has two main parts that map onto the distinction between top-down attention and stimulus-driven attention (similar to the current use of the terms voluntary and involuntary spatial attention). The dorsal network is thought to govern "top-down" attentional control and the ventral network is thought to be related to stimulus-driven attention. The dorsal network includes regions such as the FEF and the IPS, while the ventral network is lateralized to the right hemisphere, including ventral frontal cortex as well as temporal parietal junction areas. In the right hemisphere, the model postulates an interaction between the ventral and dorsal networks for attention. In the present study we chose to only examine regions that can be functionally

localized, therefore our investigation was focused on the "dorsal" component of the network. Given that the ventral loci of the postulated attention network are not readily defined functionally, these regions would require a different approach for investigation (i.e. a seed analysis where coherency is computed for a time series from a functionally defined region and individual voxels in other portions of the brain).

Focusing on the "dorsal" component of the model, other researchers have suggested that spatially selective responses in parietal and occipital as well as frontal attention regions give rise to a distributed representation of attention maps that are the results of the joint influence of voluntary and stimulus-driven attention on neural activity (Kastner and Ungerleider, 2003; Serences and Yantis, 2006; Serences and Yantis, 2007). As previously discussed in the Introduction, these inferences lack direct evidence and are typically based on the aggregation of disparate BOLD responses in attention tasks.

While the current approach allowed quantification of relative engagement of the network in the two attention conditions, we did not present a baseline condition to which we could compare degrees of voluntary and involuntary attention separately. As a result, we did not make claims regarding exclusiveness of the network for one system or the other. However, we can conclude that while this network might be engaged in both types of attention, involuntary (stimulus-driven) attention is associated with increased levels of coupling in the network. One could postulate that involuntary capture of attention is a heightened state of stimulus sensitivity, and that the greater degrees of coupling with involuntary attention are in fact indicating that the network is cohering with the external stimulus events. In contrast, voluntary attention can be thought of as a state in which this coupling with external events is reduced by internal goals directing attention to parts of the external environment and away from other parts of it.

Another possible interpretation of these findings is that a heightened state of coupling within the dorsal attention network during involuntary attention is the result of an active effort to ignore the uninformative cues. This account has a clear behavioral prediction. If indeed ignoring the cues is an active and effortful process, behavioral attention effects (the differences in reaction times between the cued and uncued trials) should reflect this effort and result in longer RTs in the cued location. However this was not the case. Significant cueing effects were measured in the involuntary attention condition albeit smaller than those in the voluntary attention condition.

In a study by Liu and colleagues (Liu et al., 2005), cue and target separation as well as temporal order manipulation were used in the cueing paradigm to measure involuntary attention effects in early visual cortical areas. Using an uninformative cue with a short SOA, they found greater responses in target ROIs of retinotopic cortices when (pre) cue and target were on the same side compared to the rest of the conditions (uncued pre and post cues and cued post cue). Liu et al. (2005) report results only from target-related ROIs. In the current study, we found that the portions of retinotopic cortical areas representing the cue play an important role in differences in coupling between involuntary and voluntary attention. It is possible that had they

measured the cue ROIs as well, those would complete the picture and converge with the findings reported here.

A few previous studies investigated both voluntary and involuntary attention within the same event related design (Kincade et al., 2005; Mayer et al., 2004). A common limitation of these studies is the use of different stimulus displays for voluntary and involuntary attention. For example, Kincade et al. investigated voluntary attention with a central cue and involuntary attention using a color singleton appearing prior to target onset. While an effort was made to keep the two display types similar, they were not visually identical, resulting in a stimulus confound when comparing neural correlates of voluntary and involuntary attention. In addition, the temporal lag between the cue and the target in the fMRI session was over two seconds, a temporal interval that is probably too long for the investigation of involuntary attention (for a similar approach see (Mayer et al., 2004). At the event level, Kincade et al. found greater responses in FEF and IPS when voluntary attention was employed compared to involuntary attention. In addition they found that these dorsal regions were also engaged when involuntary attention was captured (compared to a neutral cue). As previously discussed, the occurrence of activity in these regions were merely suggestive of the presence of a network, and differences in magnitude of univariate response did not provide a clear prediction regarding the amount of coupling between the regions. However, the excessively long cue-target interval and differences in the display condition for the two attention types limited interpretation of the magnitude differences in univariate response.

Bressler et al. (Bressler et al., 2008) recently examined effective connectivity among dorsal attention regions in a voluntary attention cueing paradigm. Participants had to discriminate orientation of a grating following an auditory cue that was 75% predictive of grating location. The use of Granger causality examined the amount of improvement of the prediction of a given time series when taking into account the information from another time series (Goebel et al., 2003; Kayser et al., 2009; Roebroeck et al., 2005). Granger causality analysis was performed at the event level, revealing that including time series from FEF and IPS[4] regions improved the prediction of the time series for early visual areas. This study provided support for the existence of significant coupling among frontal, parietal and visual areas during voluntary attention. Our data extend this finding and reveal that involuntary attention produced even greater coupling between the investigated regions than voluntary attention.

In a recent paper (Lauritzen et al., 2009), fMRI coherency was employed to measure functional connectivity associated with sustained visual spatial attention. In this study, trained participants were required to detect the presence of a pre-learned stimulus (attention condition). fMRI coherency in this condition was contrasted with coherency obtained from a passive fixation condition, revealing several significant differences in the degree of coupling in visual cortical areas as well as IPS regions. While it is tempting to compare the current connectivity

[4] Importantly Bressler et al did not utilize topographic mapping of parietal attention regions.

diagrams to Lauritzen et al.'s data it is important to recognize that the two studies were designed to investigate different types of attention, under very different trial conditions. First, the type of attention investigated in Lauritzen et al. and here operate on a different time scales. The sustained attention task examined in Lauritzen et al. spanned several seconds, while here we measured attention effects that occur on a time scale of hundreds of milliseconds. Moreover, The sustained spatial attention examined in Lauritzen et al. isolated attention at a set location while in the present study both voluntary and involuntary attention include the shift of attention to different locations. Lauritzen et al. also measured the maintenance of attention in the absence of visual stimulation, while the present study had both cue and target onsets throughout trials probing both voluntary and involuntary attention. Last, Lauritzen et al. investigated sustained spatial attention compared to a passive viewing condition while the present study contrasted two different types of attention, voluntary compared to involuntary attention. These fundamental differences make it difficult to compare the two studies.

The present study also provides insights into task-specific hemispheric asymmetries. For both voluntary and involuntary conditions, there was greater right- compared to left-hemisphere coupling. For target-related ROIs, this effect was specific to the pre-cueing procedure in which attention (voluntary and involuntary) was directed prior to target onset. When cues were presented after the target (post-cue procedure), degrees of coupling within the two hemispheres were mostly equivalent for target-related ROIs. Interestingly, the conditions for which laterality effects in the degree of coupling occurred are the conditions exhibiting the greatest behavioral advantages of spatial attention (cueing effects in both voluntary and involuntary pre-cueing). Further, the minimal differences in coupling between the hemispheres in the post-cue procedure suggests that the differences found in the pre-cue procedure cannot be attributed to differences due to right hemisphere dominance in face processing (Kanwisher et al., 1997). Rather, the hemispheric difference in target-related ROI coupling is specific to attentional orienting. For cue-related ROIs, a more mixed set of effects is found. Half of the significant connections showing hemispheric asymmetry were unique to the pre-cue condition, and half were shared by both pre- and post-cue conditions, suggesting the existence of global asymmetries between the hemispheres. These data are consistent with theories suggesting that the right hemisphere plays a key role in the orienting of spatial attention (Mesulam, 1999) and with studies reporting left visual field (LVF) advantages in IPS regions (Siman-Tov et al., 2007). In fact, Siman-Tov et al. hypothesize that LVF advantages might be due to enhanced connectivity within the right hemisphere (Barnett and Corballis, 2005; de Schotten et al., 2005). The authors imply that anatomical asymmetries might support this hypothesis. Our data provide evidence supporting this hypothesis in the form of greater right hemisphere coupling. However, these results also suggest that the differences in coupling between the hemispheres are at least partly task-related and not entirely structural. Hemispheric asymmetries in coupling between brain regions provides a mechanistic account for the fact that right hemisphere lesions more often result in persistent deficits of spatial attention than left hemisphere lesions (Mesulam, 1999).

In conclusion, the present study provides evidence for increased coupling among visual cortices, IPS regions and FEF regions for involuntary attention compared to voluntary attention. These findings suggest a new way of thinking about the dynamic interactions of voluntary and involuntary states of spatial attention. In addition, these results provide evidence that voluntary attention acts to disrupt a state of heightened synchronization with external events capturing involuntary attention. Both the voluntary and involuntary orienting measured here were associated with right hemisphere dominance in coupling of fMRI signals. Since both conditions share the salient onsets that capture involuntary attention, it is likely that the right hemisphere dominance is associated with the consequences of involuntary attention capture on target processing.

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