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Neural Correlates of Visual/Spatial Attention in Electrocorticographic Signals in Humans

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Neural correlates of visual–spatial attention in electrocorticographic signals in humans

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Attention is a cognitive selection mechanism that allocates the limited processing resources of the brain to the sensory streams most relevant to our immediate goals, thereby enhancing responsiveness and behavioral performance. The underlying neural mechanisms of orienting attention are distributed across a widespread cortical network. While aspects of this network have been extensively studied, details about the electrophysiological dynamics of this network are scarce. In this study, we investigated attentional networks using electrocorticographic (ECoG) recordings from the surface of the brain, which combine broad spatial coverage with high temporal resolution, in five human subjects. ECoG was recorded when subjects covertly attended to a spatial location and responded to contrast changes in the presence of distractors in a modified Posner cueing task. ECoG amplitudes in the alpha, beta, and gamma bands identified neural changes associated with covert attention and motor preparation/execution in the different stages of the task. The results show that attentional engagement was primarily associated with ECoG activity in the visual, prefrontal, premotor, and parietal cortices. Motor preparation/execution was associated with ECoG activity in premotor/sensorimotor cortices. In summary, our results illustrate rich and distributed cortical dynamics that are associated with orienting attention and the subsequent motor preparation and execution. These findings are largely consistent with and expand on primate studies using intracortical recordings and human functional neuroimaging studies.

Keywords: visual–spatial attention, covert attention, electrocorticography, intention, motor response

1 INTRODUCTION

Our senses constantly provide the brain with far more information from the surrounding environment than can be processed. Thus, the limited cortical resources need to be selectively allocated to sensory streams that are most relevant to our immediate goals. This cognitive selection mechanism is referred to as *attention*. It improves the processing efficiency of the received information, which in turn allows us to detect changes in a sensory input and guide behavior faster and more accurately (Posner, 1980).

The neural mechanisms supporting orienting of visual attention are distributed across a widespread dynamic network. The rich literature of single-unit recordings in non-human primates has provided substantive insight to the attentional mechanisms of stimulus selection in the visual cortex (Moran and Desimone, 1985; Motter, 1993; Luck et al., 1997; Ghose and Maunsell, 2008; Lee and Maunsell, 2010) and top-down control of visual processing (Awh et al., 2006; Buschman and Miller, 2007; Gregoriou et al., 2009) in the frontal (Moran and Desimone, 1985; Motter, 1993; Luck et al., 1997; Ghose and Maunsell, 2008) and parietal cortices (Colby et al., 1996; Gottlieb et al., 1998; Goldberg et al., 2002; Bisley and Goldberg, 2003). Lesions in only one component

of this fronto-parietal network lead to partial unilateral neglect syndromes (Gainotti et al., 1974; Sperry, 1974; Mesulam, 1981). Functional magnetic resonance imaging (fMRI) studies in humans have repeatedly confirmed the roles of the visual, posterior parietal (PP), and prefrontal cortices in orienting of attention (Corbetta et al., 1998; Kastner et al., 1999; Hopfinger et al., 2000; Corbetta and Shulman, 2002; Yantis et al., 2002; Strotzer, 2009; Mantini et al., 2010; Szczepanski et al., 2010). Neural correlates of visual attention were also studied in humans using electroencephalography (EEG; Ray and Cole, 1985; Worden et al., 2000; Fan et al., 2007).

Despite this body of work, the relative contributions of these areas to guiding spatial selection and visuomotor behavior are still poorly understood. This is due mainly to the limitations of traditional imaging methods. In particular, while microelectrode recordings shed light on the specialized functions of highly localized cortical regions, they typically do not capture activity across spatially distributed networks simultaneously. Thus, they cannot characterize activity in distributed networks or their interactions. fMRI, on the other hand, cannot capture the dynamics of attentional mechanisms with high temporal resolution. This limitation is due in part to technical factors (e.g., scanning durations), but

more fundamentally to the temporal characteristics of the hemodynamic response, which limits the temporal resolution of fMRI to several seconds (Aine, 1995; Shibasaki, 2008). In addition, the hemodynamic response is a metabolic, and thus indirect, measurement, which is influenced not only by local cortical processing (Logothetis et al., 2001), but also by larger-scale brain dynamics (Hermes et al., 2011). Finally, scalp-recorded EEG has high temporal resolution, but also has low signal-to-noise ratio (SNR) and low spatial resolution (Nunez and Srinivasan, 2005), which limits the degree to which activity from specific brain regions can be resolved.

In contrast to these signal modalities, recordings from electrodes placed subdurally on the surface of the brain (electrocorticography, ECoG) offer a unique opportunity to study electrophysiological mechanisms of orienting attention in humans with broad spatial coverage, high temporal resolution, and high signal fidelity. In this paper, we report on the spatial distribution of goal-directed visual processing and motor planning/execution in a modified Posner cueing task (Posner et al., 1980) in five subjects and show examples of its temporal evolution. This is the first comprehensive human ECoG study that provides a detailed spatiotemporal characterization of distributed cortical areas engaged across different phases of the task (i.e., sensory selection/detection, motor preparation/execution). These task-related ECoG modulations are studied and compared across alpha (8–12 Hz), beta (18–26 Hz), and high gamma bands (70–170 Hz). The spatiotemporal evolution of the attentional networks at a temporal resolution of 100 ms yields the order of engaged cortical regions and suggests different functional mechanisms across the spectral bands of interest.

2 MATERIALS AND METHODS

2.1 HUMAN SUBJECTS

Four subjects at Albany Medical Center (AMC) and one subject at Washington University at St. Louis (WashU) participated in this study. The study was approved by the Institutional Review Boards

of both hospitals, as well as by the Human Research Protections Office of the U.S. Army Medical Research and Materiel Command. All subjects gave informed consent. Subjects were patients with intractable epilepsy who underwent temporary placement of subdural electrode arrays to localize seizure foci prior to surgical resection. Neuropsychological evaluations revealed low average to superior motor performance (25th–99th percentile, Wechsler, 1997) as well as average to superior visuomotor scanning performance and visual search capacity (37th–91st percentile, Reitan, 1958) across patients.

A summary of the subjects’ clinical profiles is given in **Table 1**. Subjects A, B, D, E had grids implanted over the left hemisphere, whereas Subject C’s grid was placed on the right hemisphere. We established three-dimensional cortical models of individual subjects using pre-operative structural magnetic resonance imaging (MRI). We then co-registered these MRI images with post-operative computer tomography (CT) images using Curry software (Compumedics, Charlotte, NC, USA), transformed the result into the Talairach coordinate system (Talairach and Tournoux, 1988), and identified electrode locations from the CT images (see **Figure 1**). We also assigned these electrode locations to Brodmann areas using the Talairach Daemon¹ (Lancaster et al., 2000). We generated cortical activation maps using custom Matlab software. To generate these activation maps for individual subjects, we used the cortical model derived from the respective subject. For activation maps that were computed across subjects, we used the three-dimensional cortical template provided by the Montreal Neurological Institute² (MNI). Note that for visualization

¹<http://www.talairach.org>
²<http://www.bic.mni.mcgill.ca>

Table 1 | Clinical profiles of participants.

Subject	Age	Sex	Handedness	Full scale-IQ Performance-IQ	Seizure focus	Grid locations (number of contacts)
A	29	F	R	122	Left temporal	Left fronto-parietal (64)
				136		Left temporal (23)
						Left temporal pole (4)
						Left occipital (6)
						Left frontal (48)
B	30	M	R	74	Left temporal	Left temporal (35)
				90		Left temporal pole (4)
						Left occipital (4)
C	28	F	R	109 N/A	Right frontal	Right frontal (64) Left frontal (64)
D	26	F	R	112	Left temporal	Left temporal (35)
				117		Left temporal pole (4)
						Left occipital (6)
						Left frontal (56)
E	56	M	R	84	Left temporal	Left temporal (35)
				87		Left occipital (6)

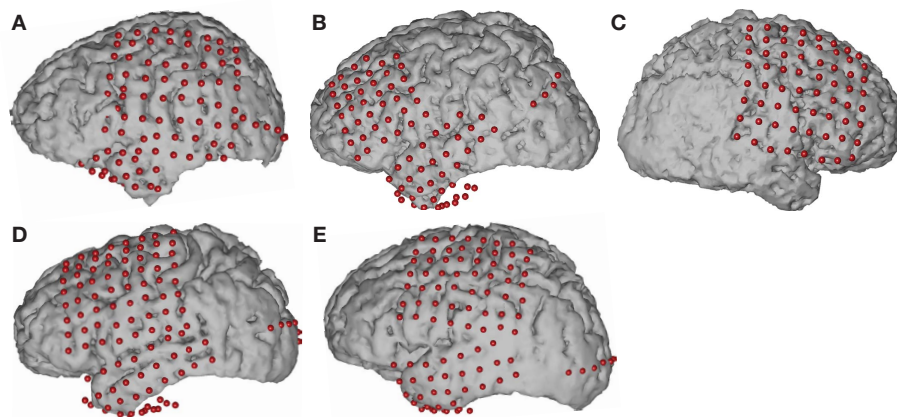


FIGURE 1 | Projected locations of implanted grids on individual subject cortical models reconstructed by pre-op MRI and post-op CT co-registration.

purposes, we projected the grid implants of Subject C (whose electrodes were implanted on the right hemisphere) to the left hemisphere.

2.2 DATA COLLECTION

The experimental setup is depicted in **Figure 2**. We recorded ECoG signals at the bedside using eight 16-channel g.USBamp biosignal acquisition devices (g.tec, Graz, Austria) at a sampling rate of 1200 Hz. The implanted electrode grids (Ad-Tech Medical Corp., Racine, WI, USA) consisted of platinum-iridium electrodes that were 4 mm in diameter (2.3 mm exposed), spaced at an inter-electrode distance of 1 cm, and were embedded in silicone. Electrode contacts distant from epileptic foci and areas of interest were used for reference and ground. The number of implanted electrodes varied between 64 and 109 contacts across subjects (**Table 1**).

In addition to recording brain activity, we also recorded the subjects' eye gaze using a monitor with a built-in eye tracking system (Tobii Tech., Stockholm, Sweden) positioned 54–60 cm in front of the subjects, and the activity from a push button. The built-in sampling rate of the eye tracker was 60 Hz and it was upsampled to 1200 Hz by sample-and-hold (i.e., no interpolations between two samples from the eye tracker). The eye tracker was calibrated to each subject at the beginning of the experimental session using custom software. Data collection from the biosignal acquisition devices, stimulus presentation, and behavioral variables (i.e., eye tracker, push button), as well as control of the experimental paradigm, were accomplished simultaneously using BCI2000 software (Schalk et al., 2004; Schalk and Mellinger, 2010).

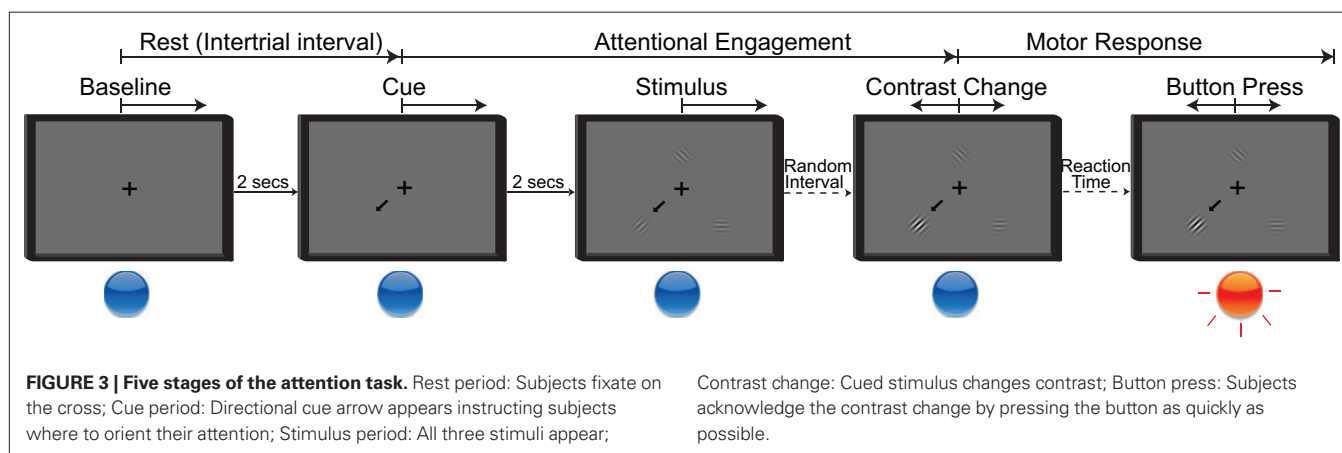
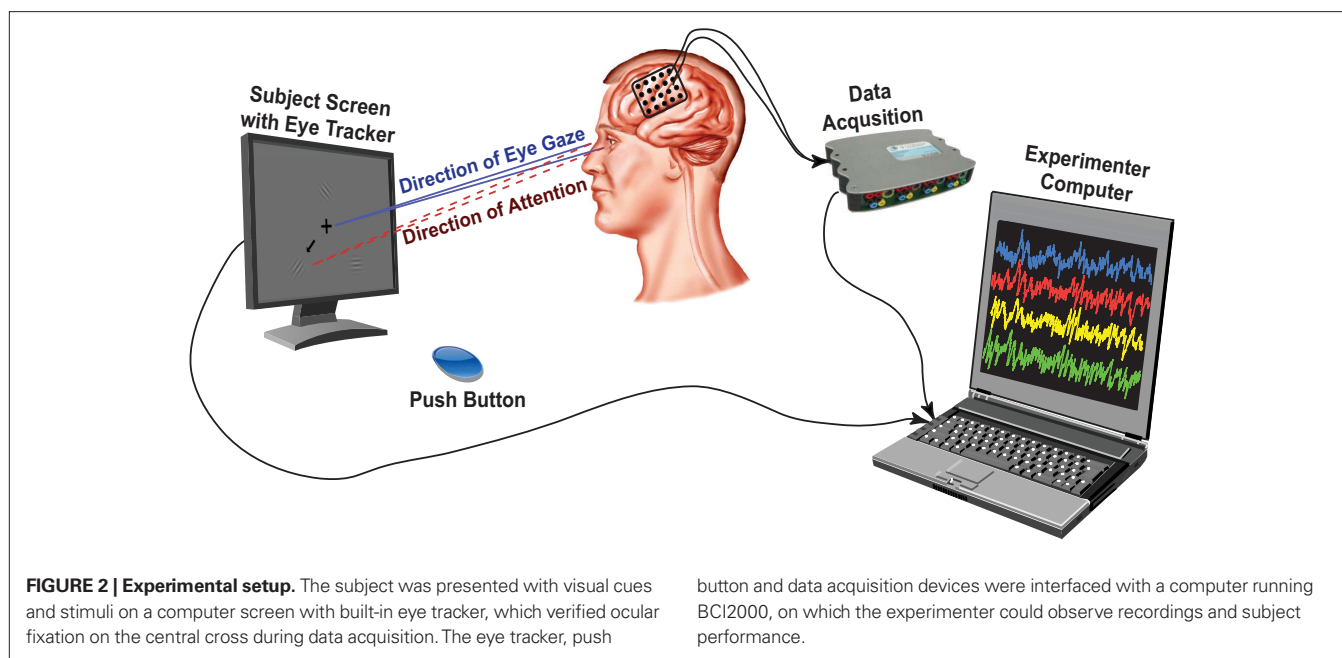
2.3 EXPERIMENTAL PARADIGM

The behavioral paradigm used in this study was a modified Posner cueing task (Posner et al., 1980; Posner and Petersen, 1990). Throughout the session, subjects maintained fixation on a cross presented at the center of the screen. A trial aborted if the subjects directed gaze away from the fixation cross beyond a defined radius (20% of the screen height) for more than 500 ms. The

experimental stages are summarized in **Figure 3**. A trial started with the presentation of a cue arrow that pointed away from the center to one of three possible directions (up, down left, or down right). The subjects' task was to orient covert attention to the cued portion of the screen. Two seconds later, three cosine gratings (i.e., the visual stimuli) appeared around the fixation cross. On valid cue trials, the cue arrow pointed to one of the three stimuli that would subsequently change. After a random short interval (uniformly distributed between 1.5 and 2.5 s), the cued grating changed contrast. Once the subject detected this contrast change, he/she responded by pressing the push button with the hand contralateral to the implant (regardless of their handedness), which ended the trial. The level of contrast change was adaptively estimated for each subject through a parameter estimation through sequential testing (PEST) procedure (Taylor and Creelman, 1967; Hammett and Snowden, 1995) that was run at the beginning of the session. The PEST procedure selected the amount of contrast change such that the performance in detecting the contrast change was approximately 75%.

To ensure that subjects were attending to the stimulus change before responding, we interleaved trials in which the cued stimulus did not change (i.e., a “no change” trial); the subjects were instructed not to respond in such trials. We also incorporated “neutral” cue trials in which three arrows appeared on the screen. This discouraged subjects from attending to any particular location on the screen. In neutral cue trials, when one of the stimuli changed contrast, the subjects again had to respond by pressing the button. Consistent with the literature (Posner, 1980; LaBerge, 1995), the subjects' reaction time was longer for “neutral” trials compared to valid cue trials.

Each session consisted of one PEST run with 25 trials to estimate the subject-specific level of contrast change. This PEST run was followed by 10 runs of 30 trials each. Twenty percentage of the trials were “no change” trials and 20% were “neutral” cue trials. The remaining trials were valid cue trials. We recorded one experimental session in Subjects A, C, D, and E, and two sessions on two different days in Subject B.



2.4 FEATURE EXTRACTION AND SIGNIFICANCE ANALYSIS

Our data analyses began by first high-pass filtering all raw ECoG signals at 0.01 Hz and re-referencing signals from each electrode to a common average reference (CAR; Schalk et al., 2007). The CAR was computed separately for each 16-channel amplifier by spatially averaging its input channels. For each 300 ms time period (66% overlap) and each location, we computed the power spectral density using an autoregressive model (Stoica and Moses, 2005) of order 25 between 0.01 and 170 Hz in 1 Hz bins. We then averaged the spectral amplitudes in alpha, beta, and gamma ranges (i.e., 8–12, 18–26, and 70–170 Hz, respectively).

To study the ECoG correlates of visual-spatial attention, we divided the task into rest (inter-trial interval), attentional engagement, and motor response periods. **Figure 3** highlights these time periods and the reference time points for feature extraction. We first labeled the baseline period as “−1” and the attention period as “+1,” and computed the correlation (Pearson’s r) between a particular spectral feature (e.g., high gamma amplitudes at a particular location) with these behavioral labels [i.e., baseline (−1)

or attention (+1)]. Thus, a high positive r -value suggests that the amplitude of the examined spectral band (e.g., high gamma) at the location of interest increases relative to rest when the subject attends to a spatial location. Conversely, a high negative value suggests decreased amplitude compared to rest. We repeated this analysis for baseline versus motor response. In addition, we determined the significance (i.e., p -value) that corresponded to a particular r -value. In summary, this analysis, for a particular subject, location, and ECoG feature, yielded the statistical difference between the ECoG features during behavioral engagement and rest. We then projected, for all locations with significant statistical differences ($p < 0.05$), the negative natural logarithm of the p -values (i.e., activations or *significance indices*) onto the template brain (see **Figure 5**).

3 RESULTS

In this study, we set out to identify the distributed brain network that is recruited during attention and the subsequent visuomotor task using human ECoG at high temporal and spectral resolution.

For this, we examined the spatiotemporal dynamics of cortical regions during the four stages of the task. The main results of the study are given in **Figure 5** which samples the temporally evolving topographical distribution of significant ECoG activity across all patients. **Figures 7 and 8** provide a quantitative comparison of the significant activations across different subjects, different spectral bands (i.e., alpha, beta, gamma), and different stages of the task. We describe these results in more detail below.

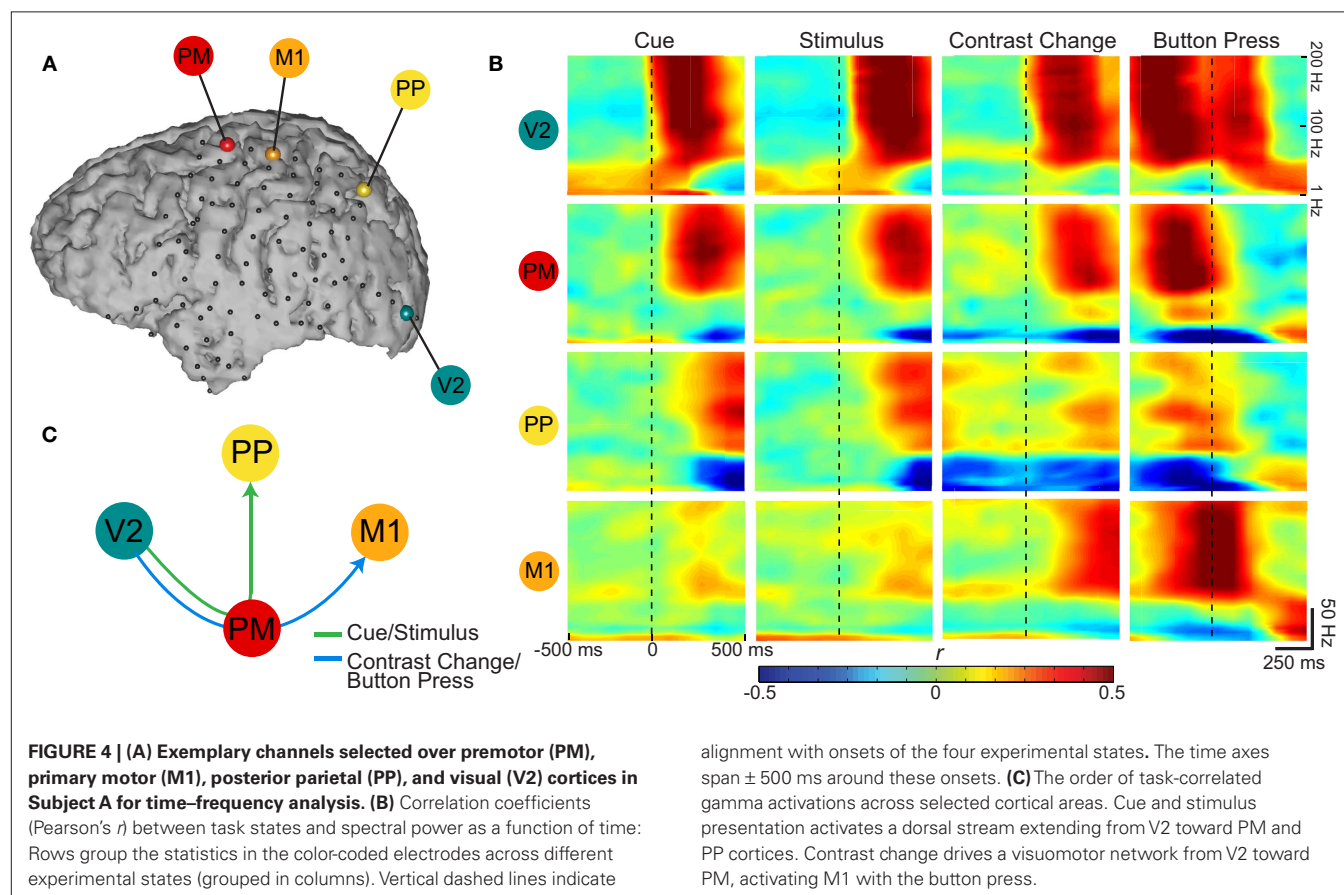
3.1 SPATIOTEMPORAL CORRELATES OF ATTENTION AND MOTOR RESPONSE

Figure 4 shows time–frequency plots of four exemplary locations for Subject A. The four electrodes were selected based on primate electrophysiology and human imaging literature, and were over premotor (PM; shown in red), primary motor (M1; orange), PP (yellow), and visual (V2; teal) cortices, respectively. These areas cover areas of sensory, attentional, and intentional processing. Electrode locations were identified using MRI–CT co-registration and Talairach Daemon mapping (see Section 2); motor areas were verified by clinical electrocortical stimulation. Each row in **Figure 4B**, color coded for its corresponding electrode, shows the time-varying correlation coefficients calculated between ECoG spectral amplitudes (1–200 Hz) and the task, 500 ms before and after the onsets of the four stages of the task. This figure captures the temporal evolution of the task-related activations: After onset of the visual cue (first column), responses are first present over V2 (top row) in the gamma band indicating visual processing. These

activations are followed by responses in PM, and then PP, respectively. Over PM and PP, alpha and beta amplitudes show negative correlations, which is consistent with event-related desynchronizations that are often detected in those areas. These transient activations (which disappear ~600 ms after cue onset) are reinforced after stimulus presentation (see second column). As a button press does not follow, there are no activations over M1 (second row). This dorsal stream extending from visual cortex toward premotor and PP cortices (illustrated in **Figure 4C**; green arrow), has been implicated in spatial attention studies in primates (Desimone and Duncan, 1995; Rao et al., 1997).

In a similar fashion to the presentation of the cue or the stimulus, the contrast change in the stimulus (third column) first elicits activations in visual areas. In marked contrast to cue or stimulus presentation, this visual activation is followed by not only PM but also M1 activations as button press soon follows (**Figure 4C**; blue arrow). In fact, activations over the M1 contact are time aligned with the button press (rightmost column). The gamma activations over PP are reduced (**Figure 4**; third and fourth columns) as motor preparation and execution (i.e., output-oriented processes) take precedence over attentional (i.e., sensory-oriented) processes. The final visual activations are in response to the visual feedback on the screen prompting the end of the trial.

Since it is not practical to present these time–frequency activations on the cortical models for all electrodes, we restricted subsequent spectral analyses to the gamma, beta, and alpha bands. We topographically distributed the behavioral significance of



activations across the channels for each spectral band at every 100 ms time shift for each subject. We then accumulated the electrode locations across all subjects and superimposed these findings on the template cortical model. **Figure 5** shows the topographic distribution of the superimposed significance indices at the indicated times during the four stages of the task (i.e., 400 ms after cue and stimulus presentation, and at the onset of contrast change and button press). Activations at these representative time points capture the involvement of all cortical areas significant for that stage of the task. The temporal evolution of these activations are not presented here, but follow a similar trend to the example in **Figure 4** (i.e., visual activations followed by prefrontal and parietal activations, which lead to primary motor activation).

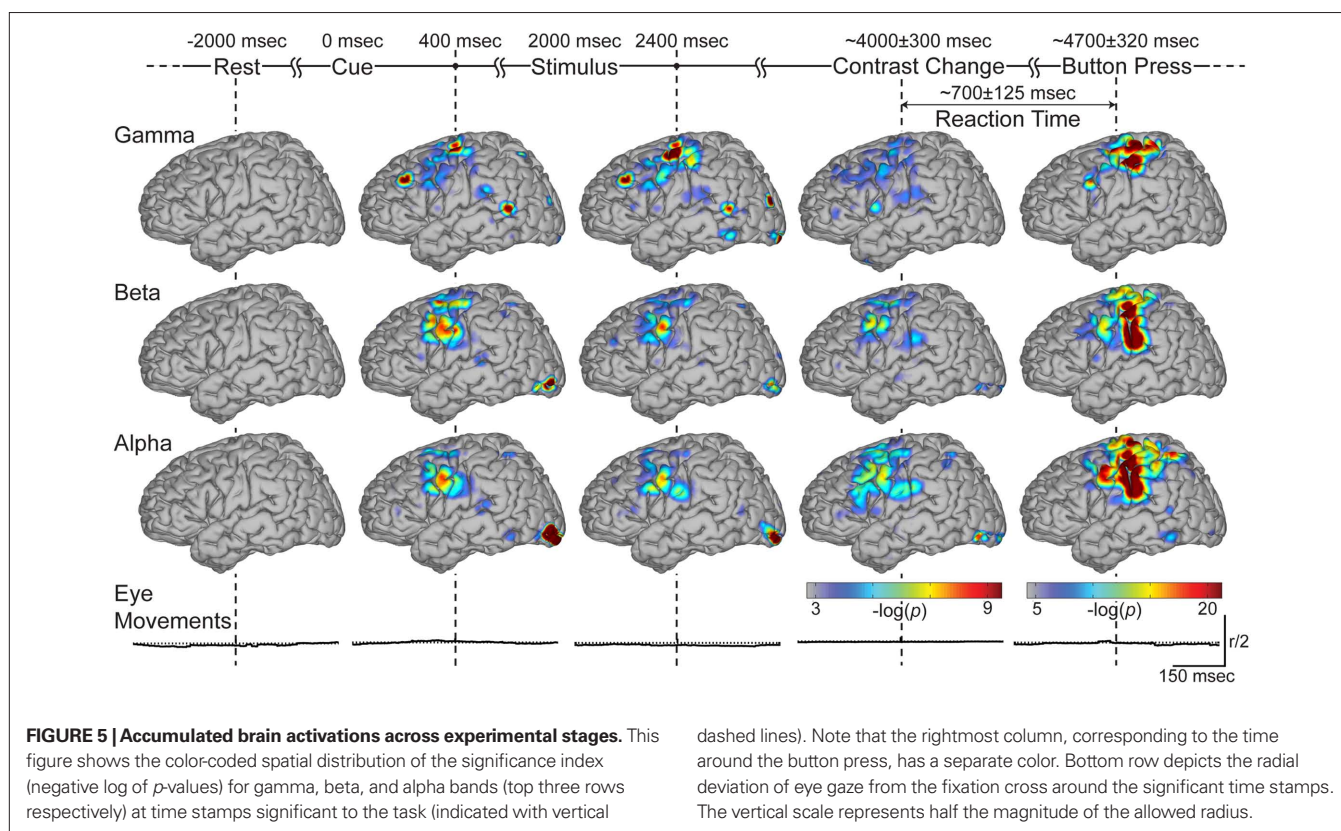
Significant activations are present over visual areas following the presentation of the cue, stimulus, and contrast change. Activations over premotor areas are common in these experimental stages across all frequency bands, with more localized activity in the gamma features. During the periods of covert attention (**Figure 5**; columns two and three), isolated activations are observed in PP cortex in all three bands. Gamma activations are also present in dorsolateral prefrontal cortex (on the border of Brodmann areas 8 and 9), superior temporal cortex (Brodmann area 39) and around the temporo-parietal junction. We see that these gamma activations are more transient compared to the lower frequency bands (**Figure 5**; column four). Finally, primary sensorimotor cortex is activated during the button press (**Figure 5**; column five). Once again, gamma activations over sensorimotor cortex during the button press are more localized. It is of note that significance indices

during the button press are larger in magnitude than those during the preceding periods (of covert attention) and thus use a different amplitude scale.

In summary, **Figure 5** shows the cortical networks involved in the different stages of the behavioral task, as well as the distribution of activations across different spectral bands. It demonstrates that ECoG activity can capture neural responses not only during sensorimotor tasks, but it can also characterize the distributed neural networks during covert visual attention.

3.2 CONTROL FOR EYE MOVEMENTS

We performed additional analyses to verify the potentially confounding influence of eye movements. Although we controlled for eye movements online using an eye tracker, it was still possible that the subjects made small and/or brief eye movements that were related to the cued direction. To determine whether such small or brief eye movements existed, and how they related to the cued direction, we computed, at each point in time and for each trial, the inner product of the eye gaze vector (calculated between the fixation cross and the current eye position) and the cue vector (calculated between the fixation cross and the cue arrow), and normalized the result to the allowed radius. We then averaged the results across trials and subjects. A high value of the resulting “gaze amplitude” would imply that the subjects tended to shift their gaze consistently toward the cued stimulus at a given time. The results are shown in the bottom row of **Figure 5**. The vertical scale (shown on the right) represents half the magnitude of the allowed radius. These figures demonstrate that, on average, eye movements had only a

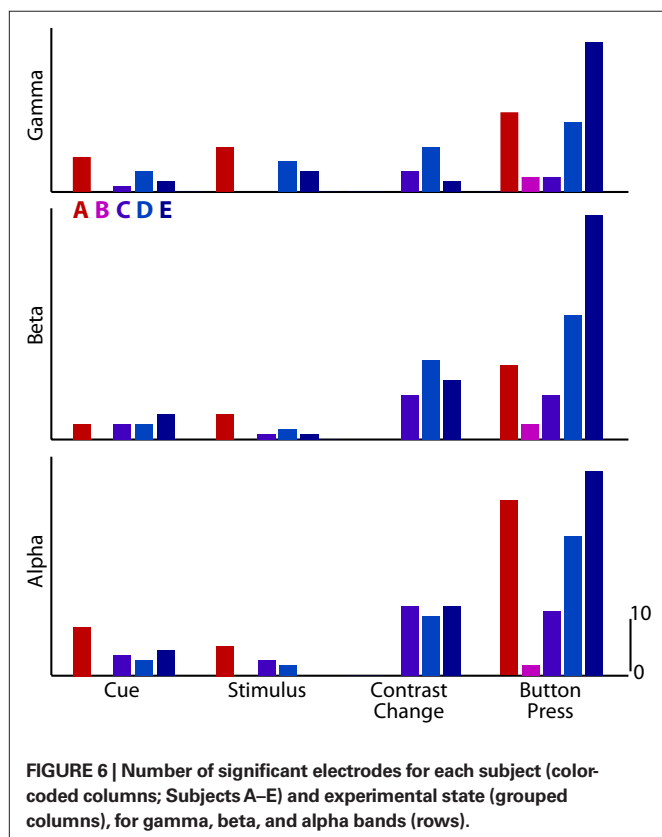


very negligible relationship with the cued direction. In sum, this offline analysis demonstrates that our results are not related to consistent shifts of gaze toward the attended stimulus.

3.3 COMPARISON OF CORTICAL ACTIVATIONS ACROSS BEHAVIORAL STAGES AND SPECTRAL BANDS

Figure 5 demonstrated the spatial distribution of significant ECoG activations. To quantify different aspects of these results, we tabulated the number of electrodes with significant activations, separately for different subjects, frequency bands, and task periods. These results are shown in **Figure 6**. Because one electrode, on average, covers an area of one square centimeter, the results allow for an estimate of the size of the cortical area involved in a particular task. We observe the largest number of significant activations during motor execution across all subjects and frequency bands. Their significance values were also higher than during the covert stages of the task (**Figure 5**).

We also quantified the percentage of overlapping activations shown in **Figure 5** across the different frequency bands and for each experimental stage. The color coded results are shown in **Figure 7**. They demonstrate that the spatial pattern of gamma activations is quite different compared to that of alpha and beta activations during cue presentation, stimulus presentation, and contrast change. They also show that alpha and beta activations are much more co-localized with gamma activations during the button press. This is consistent with a recent study (Miller et al., 2010) that also found co-localization during motor performance.



Finally, we quantified the percentage of overlap within each band, but across the four experiment stages (see **Figure 8**). The results show that the activations during the button press are significantly different in their spatial distribution from those of the three previous experimental stages for all three frequency bands. The activations for the cue and stimulus periods overlap significantly in the gamma and alpha bands, whereas cue presentation and contrast change have higher overlap in the beta band.

In summary, these analyses provide a quantitative assessment of the qualitative results shown in **Figure 5** across attentional and motor preparation/execution networks, and across the gamma, beta, and alpha bands.

4 DISCUSSION

In the first comprehensive study of its kind, we investigated attentional networks using ECoG recordings from human subjects. The experimental paradigm used in our study specifically taxes goal-directed attention, which is engaged following the display of the instructional cue and goal-relevant stimuli. Our results illustrate rich and distributed cortical dynamics that are associated with visual attention, visuomotor preparation, and execution.

These findings are largely consistent with and expand on animal electrophysiology studies using intracortical recordings and human studies using fMRI that have identified cortical areas involved in visual attention. For instance, activations over the PP cortex shown in our study (**Figure 5**; columns one and two) have been related to orienting attention in a previous study (Fan et al., 2007), and are also in line with primate and human studies on attentional networks that pinpoint dorsal PP cortex along the intraparietal sulcus (Posner and Dehaene, 1994; Corbetta and Shulman, 2002; Simon et al., 2002; Bisley and Goldberg, 2003; Ganguli et al., 2008; Posner, 2008; Sestieri et al., 2010). Activations in premotor cortex may be attributable to both executive attention (i.e., the anticipation of the contrast change and movement initiation) and orienting attention (Lebedev and Wise, 2001; Simon et al., 2002; Brovelli et al., 2005; Fan et al., 2007). Gamma activations over the dorsolateral prefrontal cortex (superior frontal sulcus) have been associated with sustaining attention (Dias et al., 1996; Lloyd, 2007), executive attention (Posner, 2008), and higher cognitive processing (Strotzer, 2009) in previous studies. These gamma activations are also close to frontal eye fields, which have been linked to orienting attention (Rizzolatti et al., 1983; Shelliga et al., 1994; Corbetta and Shulman, 2002; Monosov et al., 2008; Capotosto et al., 2009). In addition, gamma activations are present also over superior temporal cortex (Brodmann area 39) and close to the temporo-parietal junction. The former region is involved in spatial orientation, imagery (Strotzer, 2009) and attention (Lloyd, 2007), whereas the latter has been associated with stimulus-driven (i.e., alerting) attention (Corbetta and Shulman, 2002; Shulman et al., 2009; Doricchi et al., 2010).

Our results are also in line with previous studies that used scalp-recorded EEG. For instance, Ray and Cole (1985) showed that attention involves a fronto-parietal network. Fan et al. (2007) demonstrated that the orienting network shows increased gamma-band activity at approximately 200 ms after a spatial cue over superior and inferior frontal gyri. A more recent study Capotosto et al. (2009) showed that spatial attention is controlled by desynchronization

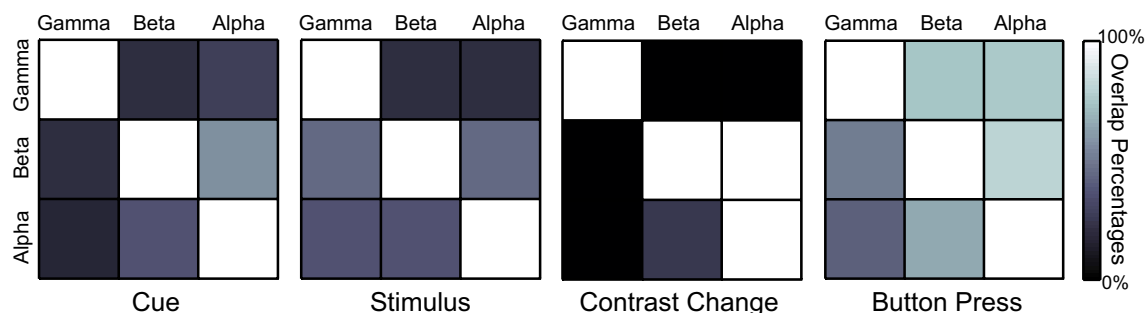


FIGURE 7 | Overlap percentages of accumulated activations across three spectral bands at four task stages. A color-coded element at row i and column j represents the percentage of the activations in band i that are present in activations of band j at a particular stage of the task.

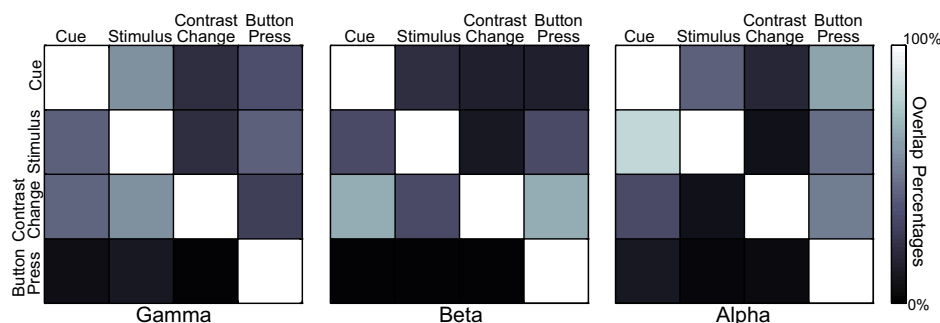


FIGURE 8 | Overlap percentages of accumulated activations across four task states in each spectral band. A color-coded element at row i and column j represents the percentage of the activations at state i that are present in activations at state j for a particular spectral band.

of alpha rhythms in frontal and parietal regions prior to the onset of visual stimulation. This effect is similar to the suppression of power we observe in lower frequencies during visual stimulation (Figure 4; columns one and two), and is most pronounced in PP and premotor cortices.

Neural modulations during the course of a goal-directed attentional task may not be attributed to attention alone, in particular when the task requires a motor response. Increases in neural activity can indicate a role for motor preparation in the premotor cortex (Riehle and Requin, 1989; Boussaoud and Wise, 1993a; Wise et al., 1997) and directional intention in the PP cortex (Assad and Maunsell, 1995; Mazzoni et al., 1996; Quiroga et al., 2006). Still, non-motor attentional involvement of the premotor cortex has been suggested by results from primate neurophysiology and human neuroimaging (Boussaoud and Wise, 1993b; Boussaoud, 2001; Lebedev and Wise, 2001; Simon et al., 2002). The premotor theory of attention (Rizzolatti et al., 1982) also suggests that spatial attention derives from a weaker activation of the same frontal-parietal circuits that determine motor behavior toward specific spatial locations. In addition, the alpha and beta activations over premotor cortical regions are consistent with reports that human beta-band local field potential (LFP) modulations can reflect goal-directed attentional processing prior to motor planning and execution (Saleh et al., 2010). Moreover, using high gamma ECoG activity in a single patient, Brovelli et al. (2005) showed attentional involvement

in the premotor cortex that could be dissociated from motor planning. Thus, the premotor and parietal activations during the cue and stimulus presentation epochs can be associated to attentional processing and differentiated from a preparation network. Still, our results point to clear differences between attentional processing and movement execution. Around the button press, activations across all three frequency bands overlapped significantly in the classic sensory-motor cortex comprising the precentral and post-central gyri (Donoghue et al., 1998; Baker et al., 1999), consistent with recent findings (Miller et al., 2010). These results mirror an overall increase of activation with motor initiation compared to stimulus processing.

We demonstrate that cue and stimulus responses are segregated across different frequency bands into largely non-overlapping areas (typical percentages of overlap ~30%). During these epochs, the gamma band reveals more focal and distributed activations, while alpha and beta bands are more broadly activated, overlaying premotor cortices (Figure 5). These results indicate that different frequency bands in ECoG represent different physiological phenomena with differential, although not yet fully defined, functional significance. Studies comparing gamma LFP activity with hemodynamic responses have repeatedly found that fMRI BOLD activations correlate with high gamma activations as opposed to slower rhythms Logothetis et al. (2001), Brovelli et al. (2005), Mukamel et al. (2005), Niessing et al. (2005), and Lachaux et al. (2007). The

gamma activations we observe over lateral frontal, premotor, and PP cortices following the presentation of the cue and stimulus (**Figure 5**) in fact highly co-localize with fMRI findings that implicate a dorsal attention network during orienting cues (Gitelman et al., 1999; Corbetta and Shulman, 2002). Gamma activations over the sensorimotor cortex during the button press are also more localized compared to the lower frequency bands, which is consistent with previous motor mapping studies in ECoG Crone et al. (1998), Miller et al. (2007) and fMRI Hermes et al. (2011). Taken together, our findings suggest that it is possible to decompose ECoG signals into different constituent physiological processes.

While our study adds to the understanding of the neural mechanisms of visual attention, there are some noteworthy limitations that mainly relate to difficulties and complexities of ECoG recordings in patient populations. First, the coverage of the grids is based on clinical needs and thus is variable and/or incomplete across subjects. In fact, the highly localized activity in the parietal region during attentional states in **Figure 5** is mainly due to signals from Subject A, as the other subjects had no or minimal coverage of this area. Also, the difference between activations across behavioral states of the individual subjects (**Figure 6**) may in part be attributable to non-uniform electrode coverage. Moreover, the lateralized electrode coverage does not allow for differential analysis across the two hemispheres within subjects. This is unfortunate, as spatial attention has been considered to be right hemisphere dominant based on lesional studies (Gainotti et al., 1974; Sperry, 1974; Mesulam, 1981). On the other hand, recent neuroimaging studies suggest a larger population with bilateral attentional fronto-parietal networks than previously thought (de Schotten et al., 2011), and report symmetrical activations over the dorsal fronto-parietal network during attentional control (i.e., suggest that asymmetrical activations that are distinct from this network; Shulman et al., 2010). Furthermore, current methods to study ECoG limit analyses and interpretation to activations on the surface of the cortex, and thereby ignore the likely involvement of subcortical structures in attentional control,

such as the superior colliculus and lateral pulvinar (Desimone et al., 1990; Robinson and Kertzman, 1995; Kustov and Robinson, 1996). Recordings with electrode grids with higher density may eventually allow for functional interpretation of subcortical structures using source localization techniques, similar to the techniques currently applied to scalp-recorded EEG. Finally, conduction of relatively complex experimental paradigms (such as the one used here) in the hospital faces many practical difficulties. These difficulties limit the amount of data that can be acquired and increase its variability. Nevertheless, ECoG provides an exciting opportunity for recording brain activity in humans that allows for detailed spatiotemporal characterization of electrophysiological phenomena.

Overall, in this paper we focused on identifying the neural correlates of visual attention in ECoG signals. Such attentional correlates may eventually prove useful for brain-based augmentation systems that allow people to respond to and control their surroundings more rapidly and accurately (van Gerven and Jensen, 2009; Bahramisharif et al., 2010; Treder et al., 2011). For instance, detection of the locus of visual attention may assist in alerting during vehicle operation, or targeting during a tactical scenario. As a clinical application, it could allow people with motor impairments to select items or characters on a screen simply by paying attention to them. This would be of most immediate benefit to people who are completely paralyzed and cannot fixate gaze. Ongoing work is therefore aimed at determining the general level of attention, as well as decoding the spatial locus of attention from ECoG signals, in single trials.

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