Spontaneous Neural Fluctuations Predict Decisions to Attend

Jesse J. Bengson, Todd A. Kelley, Xiaoke Zhang, Jane-Ling Wang, and George R. Mangun

Abstract

■ Ongoing variability in neural signaling is an intrinsic property of the brain. Often this variability is considered to be noise and ignored. However, an alternative view is that this variability is fundamental to perception and cognition and may be particularly important in decision-making. Here, we show that a momentary measure of occipital alpha-band power (8–13 Hz) predicts choices about where human participants will focus spatial attention on a trial-by-trial basis. This finding provides evidence for a mechanistic account of decision-making by demonstrating that ongoing neural activity biases voluntary decisions about where to attend within a given moment. ■

INTRODUCTION

A fundamental property of a neural system is the presence of ongoing spontaneous variability (Cohen & Maunsell, 2011; Nir et al., 2008; Romei et al., 2008; Goldstein, King, & West, 2003; Tsodyks, Kenet, Grinvald, & Arieli, 1999; Arieli, Sterkin, Grinvald, & Aertsen, 1996). As a consequence of this property, a neural system may generate time-varying outputs (e.g., percepts) though the input does not change (Keil, Muller, Ihssen, & Weisz, 2012). Neural variability may also influence cognitive functions such as memory retrieval success (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011) and the efficacy of control functions (Bengson, Mangun, & Mazaheri, 2012; Kelly, Gomez-Ramirez, & Foxe, 2009; O'Connell et al., 2009) and may play a role in the normal neural development (McIntosh, Kovacevic, & Itier, 2008). A recent theoretical model describes how variability in the activity of sensory systems may play a role in decision-making (Brunton, Botvinick, & Brody, 2013). Here, we test the hypothesis that ongoing variability in visual cortex activity might bias decisions about where to focus visual-spatial attention.

The study of selective attention provides the ideal proving ground for understanding decision-making because models of attention include theoretical constructs for voluntary orienting. The neural mechanisms associated with the deployment of attention are often studied using cuing paradigms (Posner, Snyder, & Davidson, 1980), which have helped to establish that spatially focused visual attention in humans is under the top–down control of a frontal-parietal attention network (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000). Under real-world conditions, however, it is not clear what antecedent neural conditions result in the voluntary deployment of attention to one location versus another in the absence of compelling sensory information (Hopfinger, Camblin, & Parks, 2010; Nobre, 2001). To explore this issue, we permitted participants to choose where to attend on a trial-by-trial basis. This enabled us to investigate the relationship between momentary patterns of ongoing brain activity and subsequent attention decisions. Given that the sensitivity of the visual cortex varies over time in a stochastic fashion that can be indexed by the alpha-band power (8–13 Hz) of the EEG (Romei et al., 2008) and that the hemispheric lateralization of the alpha-band power indexes the allocation of spatial attention (Worden, Foxe, Wang, & Simpson, 2000), we hypothesized that the momentary state of visual alpha-band lateralization might predict decisions about where to attend.

EEG measures were obtained from healthy volunteers while they engaged in a variant of a classic voluntary spatial attention paradigm. On a trial-by-trial basis, participants were presented with "choose" cues that signaled the participants to spontaneously choose where to attend on that trial (Figure 1), whereas in other randomly interleaved trials, spatial cues at fixation instructed them to covertly attend to right or left hemifield locations. The task was to selectively deploy spatial attention and then to discriminate the spatial frequency of the target (a vertical grating) at only the chosen or cued (attended) location, ignoring the unattended location targets. Targets appeared with equal probability on the right or left. After every trial, participants reported the side to which they had been attending. Importantly, we used a highly variable intertrial interval (ITI) that varied from 2 to 8 sec. The variable ITI ensured

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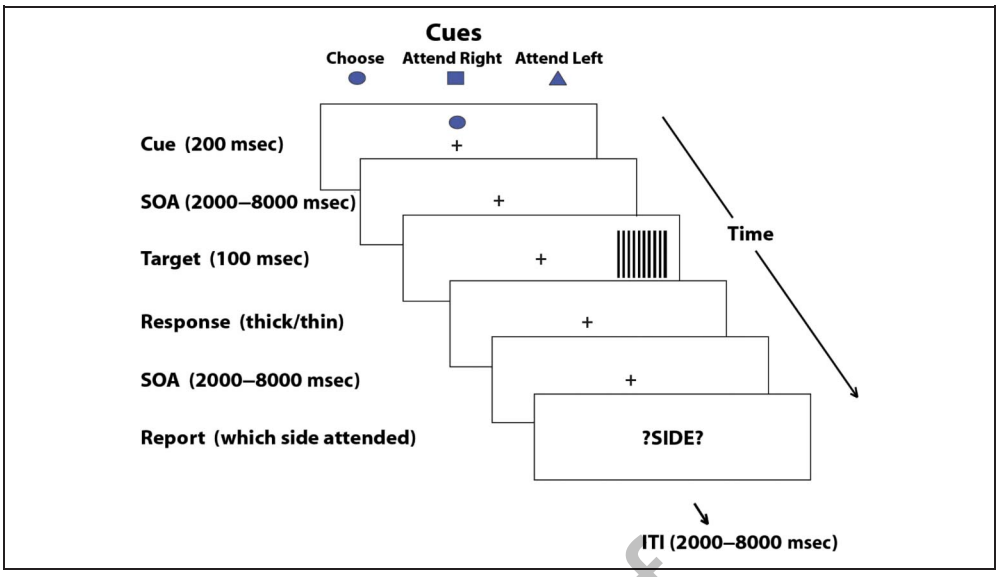

Figure 1. An example trial sequence for the attention task.

that the participants could not predict the precise moment in time that the next cue would appear. As a result, it was possible to determine whether any momentary EEG patterns that predicted the participants' choices were the result of spontaneous fluctuations in neural activity as opposed to strategic advance decisions about where to attend when the choice cue arrived.

METHODS

Participants

EEG data were recorded from 19 undergraduate students at the University of California, Davis. All participants had normal or corrected-to-normal vision, gave informed consent, and were paid for participation. All artifact-free trials with correct behavioral performance were entered into statistical analysis of the EEG data.

Apparatus and Stimuli

Each trial began with the pseudorandomly selected presentation of one of the three possible cue types for 200 msec (1° × 1° diamond, cross, or circle) that instructed participants to attend to the left or right or to freely choose to attend left or right. Following a pseudorandomly (determined by a Mersenne-twister algorithm) selected SOA of 2000–8000 msec from cue presentation, target stimuli (5° × 5° square target gratings) were presented at location markers 11.5° to the left or right of a white dot placed at fixation and 3.5° below the horizontal midline in the left and right hemifields. Targets were presented at a proportion of .50 for each hemifield for each participant. To hold validity constant across both choose-cue trials and cued trials, the target appeared at the attended location on 50% of trials. The spatial frequency of each grating varied pseudorandomly within each condition and hemifield at a ratio of 0.50 between high (0.53° per cycle) and low (0.59° per cycle) spatial frequencies of alternating black and white square waves. After target presentation, following a pseudorandomly distributed ISI varying between 2000 and 8000 msec, the text "?SIDE?" (2° × 8°) was presented at fixation to cue participants to report which side they had attended to for that trial.

Procedure

Participants were informed that this was a study of covert spatial attention and were instructed to deploy attention in the direction of the cue on a trial-by-trial basis while maintaining fixation at the center of the screen. If a choose cue appeared, participants were instructed to make a spontaneous decision to attend left or right and were explicitly instructed not to invoke any type of decisional strategy (such as always attending to the side the target appeared on the last trial). Participants were instructed to maintain attention to the cued hemifield until target presentation. Upon target presentation, participants were required to make a 2-Alternative Forced Choice discrimination on the spatial frequency of the gratings (low vs. high spatial frequency, described to the participants as "thick" or "thin" lines) by pressing their index or middle finger (response finger counterbalanced across participants). Participants were instructed to only respond to the target if it appeared on the attended side (if it appeared on the unattended side, they were instructed to ignore it). Grating spatial frequency (low and high), hemifield of presentation (left and right), and validity of the cue (valid vs. invalid, when a spatial cue) were varied randomly. Participants were instructed to respond as quickly and as accurately as possible to the targets. Upon the presentation of the text "?SIDE?," participants were instructed to accurately respond with where they had been attending for

that trial (left or right). For both cued and choose trials, cue direction and target validity were determined using both the participant's end of trial report, and their response to the targets for those trials in which both participant's report and response to targets were consistent (i.e., if the target appeared on the right and the participant responded to the target and reported attending to the right). For over 96% of trials, the participants' reports and responses to target gratings were consistent. For each participant, at least six blocks of 60 trials each were presented. For the choice-cued condition, attend left was chosen on 1036 trials and attend right was chosen on 1078 trials across all participants.

EEG Recording and Analysis

The EEG was recorded from 64 tin electrodes embedded in an Electro-cap (Electro-Cap International, Inc., Eaton, OH) from the following sites: FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T3, T4, T5, T6, FZ, Pz, CZA, PZA, C3P, C4P, CZ, C3A, C4A, T3L, T4L, FPZ, OZ, FT7, FT8, F3A, F4A, F1, F2, F5, F6, C1A, C2A, C1, C2, C5, C6, C1P, C2P, TCP1, TCP2, P1, P2, P5, P6, P1P, P2P, P3P, P4P, CB1, CB2, PZP, LM (left mastoid), RM (right mastoid). Scalp channels were referenced to the right mastoid during online recording, and electrode impedances were kept below 5 kΩ. Data were recorded using a bandpass of DC-100 Hz, at a sampling rate of 1000 Hz using a Synamps II amplifier under the control of Scan 4.2 software. To monitor eye position and blinks, bipolar recordings were made from pairs of electrodes placed on the outer left and right ocular canthi and above and below the left eye. Before artifact rejection, an IRR Butterworth filter between 0.1 and 30 Hz was applied to all channels for all participants, and independent component analysis was used to remove EEG components related to eye blinks. Channels (F8, F3A, P1, T3L, C3) for which signal was lost (four participants) during data collection were recovered and replaced by interpolation from the electrode array, and artifacts were detected and eliminated using ERPLAB (erpinfo.org/erplab) software's moving window peak to peak artifact rejection function with a 100-μV voltage threshold, within any given trial using a moving window of 100 msec in steps of 50 msec. In addition, for each participant, each epoch was inspected, and artifacts were also manually rejected before averaging. For the analysis of the alpha-band activity in the pre-cue interval, trial-by-trial time–frequency representations of power were calculated over the −2000 msec pre-cue to 2000 msec post-cue interval using short sliding Hanning tapers having an adaptive time window of three cycles for each frequency ($\Delta T = 3/f$). The oscillatory analysis was performed using the Fieldtrip toolbox (www.ru.nl/neuroimaging/fieldtrip) plugin for EEGLAB (sccn.ucsd.edu/eeglab/). The Alpha Metric (AM) in Figure 5 was calculated by subtracting the mean (−800 to 0 msec) Choose Right alpha power from the Choose Left alpha power for the 16 occipital electrodes (Choose Left − Choose Right) and then subtracting the mean of the eight right occipital electrodes from the mean of the eight left occipital electrodes (Left Electrode Average − Right Electrode Average). A positive metric indicates that participants were influenced by pre choose cue alpha lateralization.

RESULTS

Target Response Results

To verify that participants were orienting attention in response to the choose and spatial cues, we examined the mean amplitude for the target-evoked ERPs in the P1 (100–140 msec) and N1 time ranges (160–210 msec) for the average of the eight occipital electrode sites contralateral to side of target presentation (collapsed across hemifield). We found a larger N1 component for targets appearing at the attended location compared with unattended targets (Figure 2). The results of a 2 (Attention Type: choose vs. cued) × 2 (Validity: valid vs. invalid) repeated-measures ANOVA on the N1 component reveal a significant main effect of Validity, $F(1, 18) = 17.524$, $p = .001$, $\eta^2 = .493$, with no significant effect of Attention Type and no interaction, both $p > .05$. Furthermore, RTs and accuracy to targets were similar whether appearing in the cued attended location or chosen location. For targets appearing at the chosen location, the mean RT was 961 msec and mean accuracy was 82%. For cued location targets, mean RT was 951 msec and mean accuracy was 81%. No

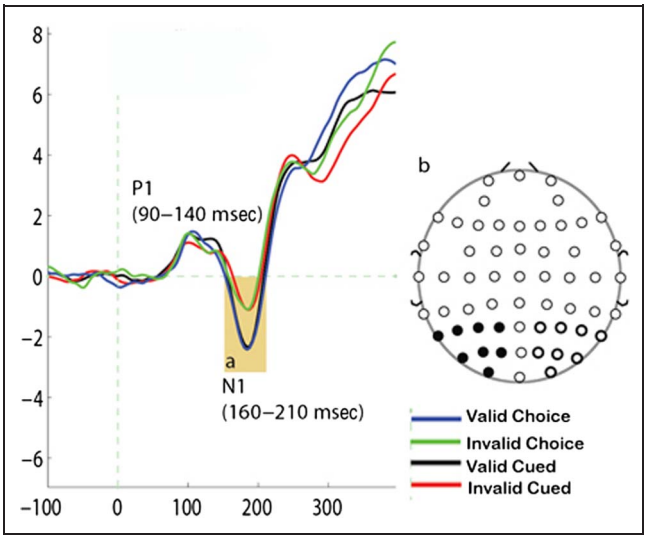

Figure 2. Illustration of the target-evoked sensory ERPs averaged over the eight occipital electrode pairs contralateral to the hemifield of the target as a function of validity and cue type (cued vs. choice). The waveforms are collapsed over left and right visual field targets for the contralateral sites. (A) N1 component difference is shown in shaded yellow between 160 and 210 msec after target onset. (B) Electrode sites of interest (filled black dots and open thick circles) shown in a dorsal view (nose at top of image).

differences in RT or accuracy were observed between cued and choice attention target responses across participants (both ps $> .5$). No significant main effects or interactions were observed in the P1 time window (100–140 msec).

We also conducted a separate behavioral validation study in which participants responded to both attended and unattended targets instead of only responding to attended targets. We did this to behaviorally verify that typical behavioral cuing effects are observed when participants voluntarily chose where to orient spatial attention. All other experimental parameters were the same as outlined in the main experiment. For the cued attention condition, mean RTs were 53 msec faster (715 vs. 768 msec) when the target appeared in the cued hemifield compared with the uncued/unattended hemifield. For the choose condition, we observed a similar pattern. RTs were 42 msec faster (731 vs. 773 msec) when a target appeared within the chosen hemifield versus the unchosen/unattended hemifield. We entered RTs as the dependent variable in a 2 (Cue Type: willed vs. cued) × 2 (Validity: valid vs. invalid) ANOVA and observed no significant interaction between Cue Type and Validity, $F(1, 11) = 1.592$, $p = .223$, $\eta^2 = .126$, but we did observe a significant main effect of Validity, $F(1, 11) = 11.063$, $p = .007$, $\eta^2 = .501$. Thus, typical behavioral cueing effects can be observed in this paradigm, and these cuing effects do not differ as a function of attention type (chosen vs. cued). In summary, these results confirm that participants were orienting attention in this paradigm and orienting attention equally whether locations were cued explicitly or chosen voluntarily on each trial by the participant.

Pre-choice Alpha Power Results

To examine the effect of momentary patterns of neural variation on decision-making, we modeled the trial-by-trial lateralization of occipital alpha power in narrow time windows in the pre-decision period as a function of subsequent decision direction. We first averaged the power of EEG activity in the alpha-band for the 16 occipital electrode sites in the −800 to 0 msec time interval just before choose-cue presentation. To obtain a trial-by-trial estimate of alpha lateralization, we subtracted the alpha-band power for the eight right occipital electrodes from the mean alpha power for the eight left occipital electrodes for each trial. The alpha lateralization index ($\text{hem}_{\text{left}} - \text{hem}_{\text{right}}$) for the −800 to 0 msec interval was entered as a predictor on a trial-by-trial basis in a generalized estimating equation (Zeger & Liang, 1986) using a logistic link function with decision outcome (left = 0, right = 1) as the dependent variable (see Equation 1).

$$\beta_0 + \beta_1 * (\text{hem}_{\text{left}}\text{hem}_{\text{right}}) = \log\left[\frac{\Pr(\text{chooseright})}{\Pr(\text{chooseleft})}\right] = \log\left[\frac{\Pr(\text{Reportnum} = 1)}{\Pr(\text{Reportnum} = 0)}\right] \quad (1)$$

This analysis revealed a significant parameter estimate for alpha lateralization ($B = -.00560$, $\chi^2 = 7.30$, $p = .0069$) in the −800 to 0 msec interval, suggesting that, for any given trial, a decision to attend was influenced by the direction of alpha lateralization immediately before decision onset. Figure 3A displays the topographic map of the subtraction of alpha power in the −800 to 0 msec pre-decision interval between subsequent choose-left and choose-right decisions.

Figure 4 shows the raw spectrograms for left and right hemisphere recordings in the pre-choose cue interval from which the topographic maps in Figure 3 were derived. As can be seen in the topographic maps (Figure 3) and spectrograms (Figure 4), decisions to attend left showed greater alpha power over the left hemisphere relative to decisions to attend right. Figure 5 displays the degree to which each participant's decisions were influenced by alpha power in the −800 to 0 msec interval before choice cue presentation.

To test whether the pre-choice cue alpha lateralization from −800 to 0 msec reflected a momentary state of ongoing neural variability and was not because of strategic anticipatory decisions made by the participants about where to attend, we conducted the same analysis for the −1700 to −900 msec pre-cue interval. We found no significant effect on subsequent decisions ($B = .000306$, $\chi^2 = .01$, $p = .963$) in this earlier −1700 to −900 msec interval (Figure 3B). The absence of a significant effect of alpha laterality on subsequent choices in this earlier time interval, coupled with the fact that participants did not know when the next cue would appear (because of the highly variable ITI) or what type of cue (choose or cued) would be presented, indicates that decisions to attend left or right were influenced by the momentary state of ongoing occipital alpha-band variability and not prior-trial contingencies or strategic factors. In line with this interpretation, we found no evidence that either prior target location ($r = -.24$, $p = .32$) or prior cue

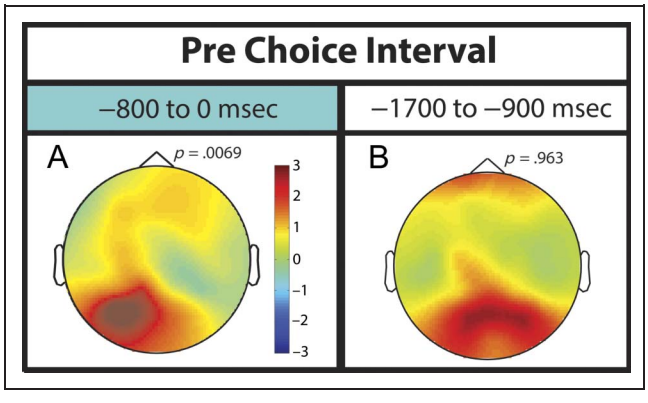

Figure 3. Topographic maps of alpha lateralization. (A) Depicts (Choice Left–Choice Right) alpha (8–13 Hz) difference map across all electrode sites in the −800 to 0 msec interval. (B) Depicts (Choice Left–Choice Right) alpha (8–13 Hz) difference map across all electrode sites in the −1700 to −900 msec interval.

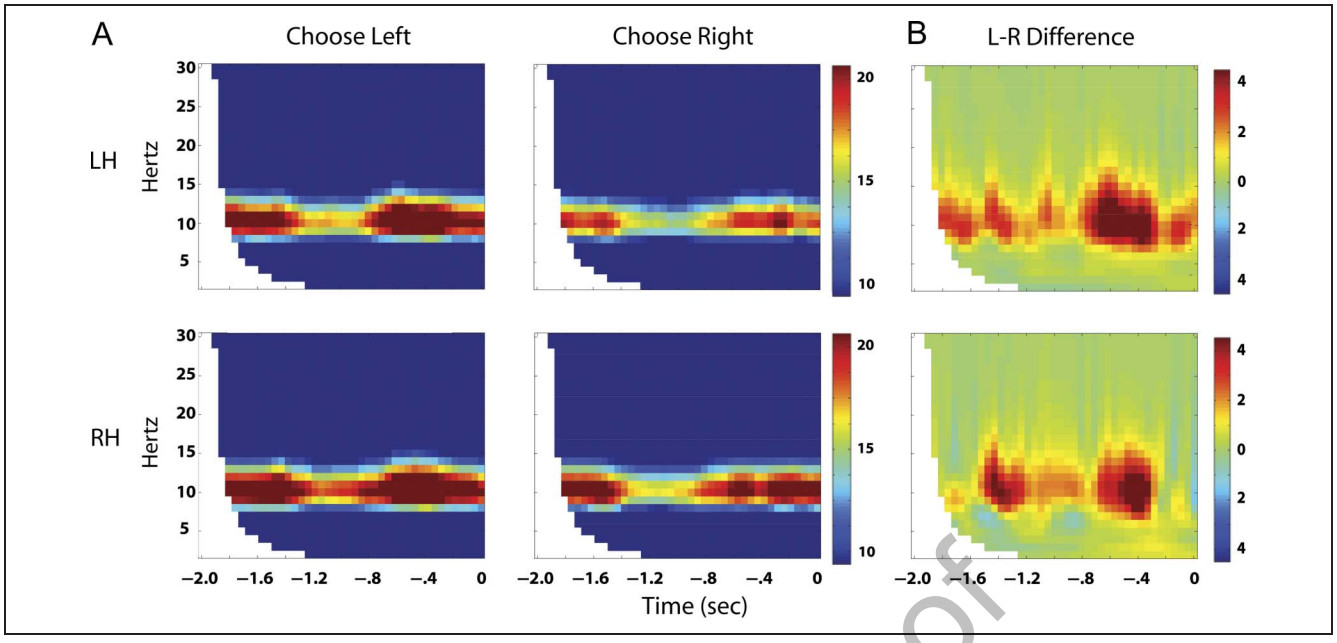

Figure 4. Time–frequency representations for occipital electrodes. (A) Depicts time–frequency representations in the 2-sec interval before choose cue onset for left and right occipital electrode averages for the Choose Left and Choose Right conditions. (B) Depicts the time–frequency representations for Choose Left–Choose Right subtraction for left and right occipital electrode averages.

direction ($r = -.20$, $p = .40$) were significantly correlated with the effect of alpha lateralization on decisions. Finally, analysis of the horizontal EOG showed that eye position in the −800 to 0 msec pre-cue interval was not significantly different between subsequent decisions to attend left or right, $t(18) = .583$, $p = .567$. Thus, the transient variability in alpha power predicts attention decisions on a trial-by-trial basis, even before participants have knowledge (from the appearance of the choose cue) that a decision must be made.

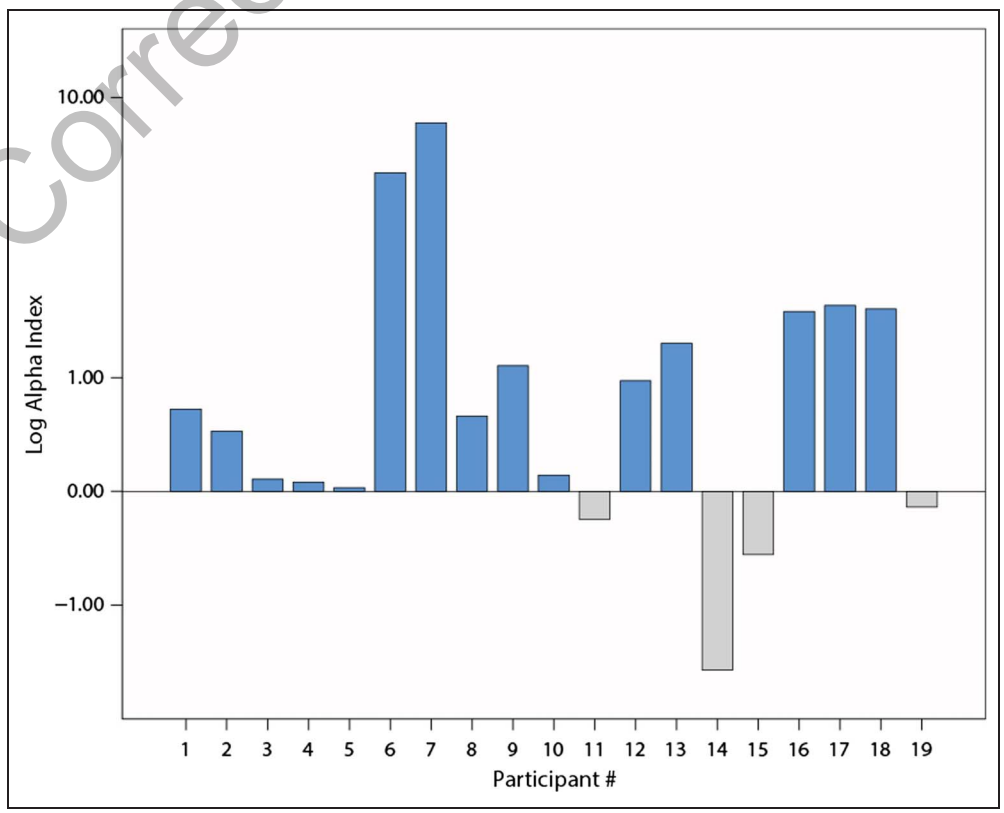

Figure 5. AM for each individual participant ($n = 19$). This AM indexes the degree to which baseline alpha lateralization influenced decisions for each participant. Note that the individual participant averaged ($df = 18$) alpha lateralization values also significantly predict decision outcome using a standard repeated-measures 2 (Decision Direction) × 2 (Hemisphere) ANOVA, $F(1, 18) = 5.144$, $p = .036$, $\eta^2 = .574$.

Hemispheric Specificity of Alpha Results

Upon viewing Figure 3, it appears that the effect of alpha power on subsequent decisions is left hemisphere specific. To explore this possibility, we conducted a follow-up test using alpha power from the left and right hemispheres (−800 to 0 msec) as independent trial-by-trial predictors. Results of this analysis reveal that the left hemisphere significantly influences decisional outcomes ($B = -.00788$, $\chi^2 = 6.33, p = .012$) and that right hemisphere alpha does not significantly predict decisions ($B = .00404$, $\chi^2 = 2.79$, $p = .095$). Furthermore, the predictive utility of the left hemisphere is significantly different than that of the right hemisphere ($p = .026$), suggesting a unique role for left hemisphere alpha power in influencing the willful allocation of attention. Furthermore, as can be seen in Figure 6, the topography of predictive alpha lateralization appears to be distinct from the topography of attention-induced alpha lateralization during the 1000 to 1800 msec post-cue interval. Although we did not hypothesize such a pattern of left-hemispheric specificity for predictive alpha power, this pattern of results suggests the intriguing possibility that left hemisphere alpha power may play a special role in influencing decision-making. This perspective is consistent with research that has shown left-hemisphere dominance of alpha lateralization under conditions of uncertainty (Haegens, Handel, & Jensen, 2011). However, only further research can explore this pattern of results and determine the reason for the left-hemispheric specificity observed here. In summary, although the exact mechanism by which alpha lateralization influences decision-making remains to be explored, the role of ongoing alpha power in decision-making is clear from the present results.

DISCUSSION

Prior work has shown that alpha-band power may reflect the functional inhibition of a brain area not relevant for a task (Jokisch & Jensen, 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Foxe, Simpson, & Ahlfors, 1998). Moreover, it has been shown that alpha lateralization over the occipital cortex is associated with the deployment of spatial attention and that post-cue/pre-target occipital alpha-band power can predict subsequent performance on visual discrimination and response inhibition tasks (Bengson et al., 2012; Thut et al., 2006). The present findings expand this understanding of the functional role of alpha activity to show that ongoing, pre-cue fluctuations in alpha power (Romei et al., 2008) over the occipital cortex predict which hemifield a participant will decide to attend. This result provides a fundamental new insight into the mechanisms of voluntary attentional control (Hopfinger et al., 2010; Taylor, Rushworth, & Nobre, 2008) by showing that the momentary pattern of ongoing neural activity in the visual system can influence decisions about where to attend when the participant freely orients attention.

The idea that voluntary attention decisions can be biased by the pattern of ongoing brain activity also has implications for contemporary models of decision-making. The literature on decision-making consistently points to the frontal or motor cortex as the neural locus of decisions to act (Euston, Gruber, & McNaughton, 2012; Nachev, Rees, Parton, Kennard, & Husain, 2005). Studies have shown that the outcome of a decision to act can be predicted by indexing neural activity within these brain regions before overt behavior (Fried, Mukamel, & Kreiman, 2011; Soon, Brass, Heinze, & Haynes, 2008; Haggard & Eimer, 1999; Libet, Gleason, Wright, & Pearl, 1983). Such findings suggest that overt motor decisions are made within modular neural systems before conscious intention and have been used to argue that the experience of volition is an illusion constructed after behavioral output (Bargh, 2008). Decisions related to perception have also been studied extensively, revealing that neurons in parietal cortex index decision-making about sensory events, accumulating evidence over time before the instant of the decision (Churchland, Kiani, & Shadlen, 2008; Shadlen & Newsome, 2001). Decisions about actions and perceptions contain variability (Churchland et al., 2011), and recent models predict that variability in sensory systems can contribute to errors in decision-making (Brunton et al., 2013). Our findings provide empirical support for a model whereby voluntary decisions are influenced by interactions between stochastic variability in perceptual systems and cognitive control systems. A broader implication of this finding is that the appearance of free will, as manifested through seemingly arbitrary cognitive decisions, may be a consequence of the role that inherent variability in brain activity plays in biasing momentary behavior.

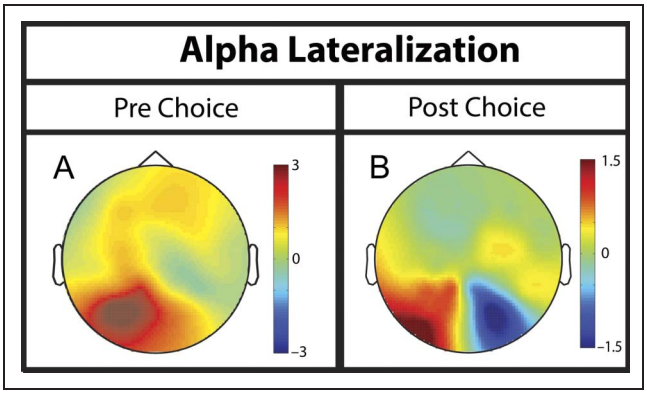

Figure 6. Alpha lateralization (Choice Left–Choice Right) for (A) predictive pre-choice alpha in the −800 to 0 msec interval. (B) Post-choice attention induced alpha lateralization for the 1000–1800 msec interval.

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