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Predicting and Improving Recognition Memory Using Multiple Electrophysiological Signals in Real Time

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Abstract

Although people are capable of storing a virtually infinite amount of information in memory, their ability to encode new information is far from perfect. The quality of encoding varies from moment to moment and renders some memories more accessible than others. Here, we were able to forecast the likelihood that a given item will be later recognized by monitoring two dissociable fluctuations of the electroencephalogram during encoding. Next, we identified individual items that were poorly encoded, using our electrophysiological measures in real time, and we successfully improved the efficacy of learning by having participants restudy these items. Thus, our memory forecasts using multiple electrophysiological signals demonstrate the feasibility and the effectiveness of using real-time monitoring of the moment-to-moment fluctuations of the quality of memory encoding to improve learning.

Keywords

visual memory, human electrophysiology, event-related potential, memory encoding, alpha oscillations, open data

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Humans are capable of encoding and storing a virtually infinite amount of visual information in long-term memory (Brady, Konkle, Alvarez, & Oliva, 2008; Voss, 2009). Yet the ability to remember this information fluctuates significantly across individuals (Friedman & Trott, 2000; Golby et al., 2005) and from moment to moment within an individual (Fernández et al., 1999; Paller & Wagner, 2002; Wagner et al., 1998). Is there a way to reliably forecast whether someone will remember a particular piece of information by monitoring electrophysiological brain signals during a single, brief encoding event? If so, can one take advantage of these measurements to improve the efficacy of learning by identifying items that require additional study?

Cognitive neuroscientists have found several encoding-related neural signals that differentiate remembered items from items that are later forgotten (Friedman & Johnson, 2000; Paller & Wagner, 2002). Specifically, recordings of the electroencephalogram (EEG) and averaged event-related potentials (ERPs) have provided two excellent candidates. First, a larger sustained positivity is observed at frontal electrodes during encoding for items that are later remembered than for items that are later missed (Friedman & Trott, 2000; Paller, Kutas, & Mayes, 1987; Paller, McCarthy, & Wood, 1988). Second, alpha-band activity is more suppressed during encoding for items that are later remembered than for those that are later missed (Hanslmayr, Spitzer, & Bauml, 2009; Klimesch et al., 1996).

Even though these two neural measures of the quality of memory encoding are well established, it is unclear whether they can be utilized in real time to predict whether a stimulus will be remembered. Indeed, the typical convention is to average hundreds of trials worth of data to derive reliable ERPs because the single-trial EEG has a lower signal-to-noise ratio (Luck, 2005; Woodman, 2010). However, it is unknown whether electrophysiological memory effects are of sufficient magnitude to predict subsequent memory after a single visual stimulus is encoded. If one can establish that these electrophysiological signals reliably forecast later recognition after a single stimulus presentation, then it may be possible to use them to monitor the moment-to-moment fluctuations in memory-encoding ability.

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Currently, it is not known how the frontal positivity and the occipital alpha power are related to each other. These two signals have been studied only independently. Each separate line of work suggests that the electrophysiological signal indexes the depth of encoding of the to-be-remembered stimuli (Hanslmayr et al., 2009; Hanslmayr & Staudigl, 2014; Otten, Henson, & Rugg, 2001). So perhaps they measure the same mechanism. However, because no study has examined these two signals simultaneously, it is unclear whether they index the same or different aspects of memory encoding. If the signals index different mechanisms necessary for successful encoding, then these two signals should account for unique variance, and we should be able to improve predictive power by combining the two independent brain signals.

Experiment 1

In Experiment 1, we determined whether the two electrophysiological measures index the same or separable mechanisms operating at encoding. Experiment 1 also served the broader goal of establishing the feasibility of using these measures to forecast the later recognition of a particular stimulus, the question addressed directly in Experiment 2.

Method

Participants. Using a preliminary data set, we estimated that we needed to collect data from 20 participants across 500 trials. After consenting to procedures approved by the Vanderbilt University Institutional Review Board, 23 individuals (10 males, 13 females; 18–32 years old) participated in exchange for $30. All volunteers self-reported that they were neurologically normal, had normal or corrected-to-normal visual acuity, and were not color-blind. Three participants were excluded from analyses because they did not complete the session.

Stimuli and procedures. The stimuli and tasks are illustrated in Figure 1. The stimuli were adapted from a published set of photographs (Brady et al., 2008). During the encoding task, participants were sequentially presented with 500 pictures of real-world objects with short breaks every 50 pictures. They were instructed to study each item while holding central fixation so that they could later perform a recognition memory test. Participants initiated each trial by pressing a button on a game pad. After a 1,250-ms pre-encoding period, in which the screen was blank except for a central fixation dot, a picture was presented for 250 ms. The picture was followed by a 1,000-ms encoding period, during which the computer screen remained blank. After the encoding task, we measured participants' resting-state EEG activity when their eyes were open and closed for 15 min. Then, we tested participants' memory for the pictures.

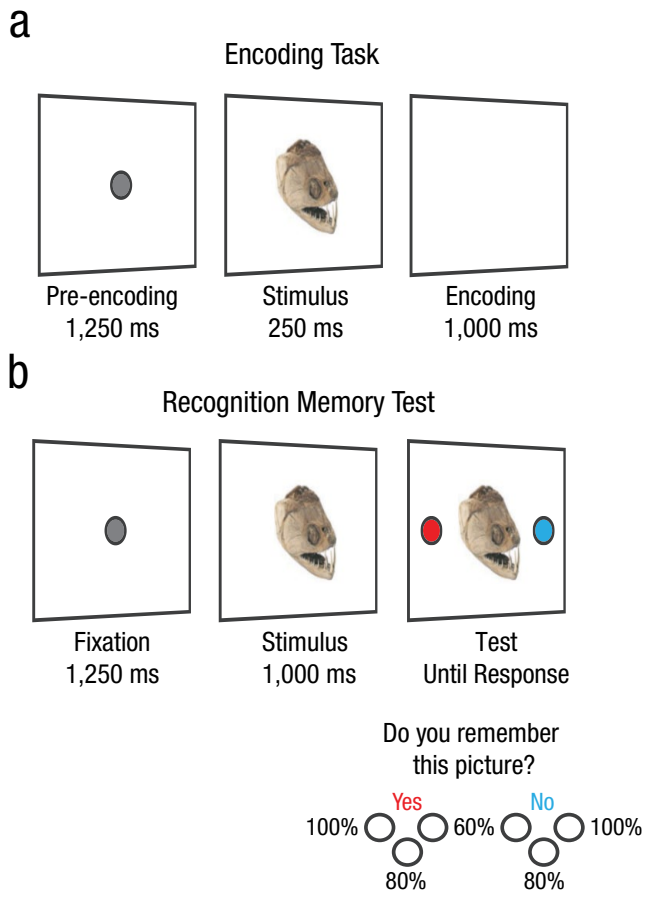

Fig. 1. Sample trial sequence from (a) the encoding task and (b) the recognition memory test in Experiment 1. In the encoding task, a fixation point was followed by a picture of a real-world object and then a blank interval for encoding. After completing all encoding trials, participants performed the recognition memory test, in which they used buttons on a game pad to indicate with 100%, 80%, or 60% confidence whether or not they had seen a picture during encoding. The position of the red and blue dots (to the left or right of the stimulus) indicated which side of the game pad to use in making their response.

The recognition memory test started with the onset of a central fixation dot. Participants initiated each test trial by pressing a button on the game pad. They were instructed to maintain central fixation without blinking until each trial was over. Following a 1,250-ms blank period, a picture of a real-world object was presented at the center of the screen (new and old pictures were randomly interleaved across trials). After 1,250 ms, a blue and a red dot appeared, one on each side of the picture. Participants indicated whether they remembered seeing this picture during the study phase by pressing one of three buttons on the side of the game pad indicated by the position of the dot. The red dot indicated which

Table 1. Results of Experiment 1: Mean Proportion of Responses on the Recognition Memory Test

	Response					
Item type	"100% old"	"80% old"	"60% old"	"100% new"	"80% new"	"60% new"
Old	.63 (.03)	.08 (.01)	.06 (.01)	.07 (.02)	.08 (.02)	.07 (.01)
New	.10 (.02)	.07 (.01)	.07 (.01)	.35 (.05)	.24 (.03)	.17 (.04)

Note: Standard errors are given in parentheses. Proportions indicate participants' confidence in their old/new judgment.

buttons to press if they remembered seeing the picture, and the blue dot indicated which buttons to press if they did not. Of the three buttons on each side, the outermost indicated 100% confidence in their judgment, the middle button indicated 80% confidence, and the inner button indicated 60% confidence (see Fig. 1). The sides on which the red and blue dots appeared were randomized from trial to trial.[1] After the response, the trial was over, and participants were provided with a self-determined interval to rest their eyes and blink. Participants were tested on 500 studied pictures and 250 new pictures.

Data acquisition and analysis. EEG data were recorded using a right-mastoid reference and were rereferenced off-line to the average of the left and right mastoids. We used the international 10-20 electrode sites (Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, PO3, PO4, O1, O2, T3, T4, T5, and T6) and a pair of custom sites, OL (halfway between O1 and OL) and OR (halfway between O2 and OR). Eye movements were monitored using electrodes placed 1-cm lateral to the external canthi for horizontal movement and an electrode placed beneath the right eye for blinks and vertical eye movements. The signals were amplified with a gain of 20,000, band-pass filtered from 0.01 to 100 Hz, and digitized at 250 Hz. Trials accompanied by horizontal eye movements (> 30 μV mean threshold across observers) or eye blinks (> 75 μV mean threshold across observers) were rejected before further analyses.

To measure the ERPs preceding memory encoding, we time-locked waveforms to the button-press response that initiated a trial and examined the waveforms recorded from −1,250 ms to 0 ms relative to the onset of the picture. These EEG epochs were baseline-corrected to the mean EEG amplitude measured −400 to 0 ms before the beginning of the measurement epoch of interest.

To examine EEG activity during memory encoding, we time-locked waveforms to the onset of memory stimuli and examined the EEG recording from 0 to 1,250 ms following the onset of each memory stimulus. These EEG epochs were baseline-corrected to the mean EEG amplitude −400 to 0 ms relative to the stimulus onset. For presentation purposes, we needed to concisely summarize the relationship between our electrophysiological measures and behavior. As a result, the pre-encoding and encoding signals for each epoch were binned and averaged based on recognition performance in the memory test. The EEG activity recorded as the participants viewed the items that were later recognized with 100% confidence were binned as high-confidence hit trials, and those recorded as the participants viewed the items that were later recognized at lower confidence levels (80% and 60%) were binned as low-confidence hit trials. The EEG segments recorded as the participants viewed the items that were later missed were binned as miss trials. These binned averages also allowed us to confirm that our findings replicated previous reports of the traditional mean amplitudes across these types of trials.

To examine the oscillatory responses, we measured frequency content during the same pre-encoding and encoding epochs described above on a trial-by-trial basis. Spectral decomposition with a fixed window size of 400 ms and a window overlap of 380 ms was performed using the spectrogram.m function in MATLAB (The MathWorks, Natick, MA) for each single-trial EEG epoch to obtain the time-frequency representation of the signal. Then, the resultant time-frequency representation for each epoch was sorted into the appropriate high confidence, low confidence, or miss bin.

Results

Behavioral results. For studied objects, participants recognized 63% of the stimuli with 100% confidence and 14% of the stimuli at 80% or 60% confidence. Participants failed to recognize the remaining 23% of the stimuli. They successfully rejected 76% of new objects that they had not studied during the encoding phase. Table 1 reports the proportions of trials used to derive the receiver-operating-characteristic (ROC) curves in this experiment. The mean area under the ROC curve (AUC) was .82. These results demonstrate that, on average, participants performed the memory task accurately.

Traditional ERP and EEG analysis. Using traditional ERP and EEG analyses, we found that frontal waveforms exhibited a sustained positivity of larger amplitude

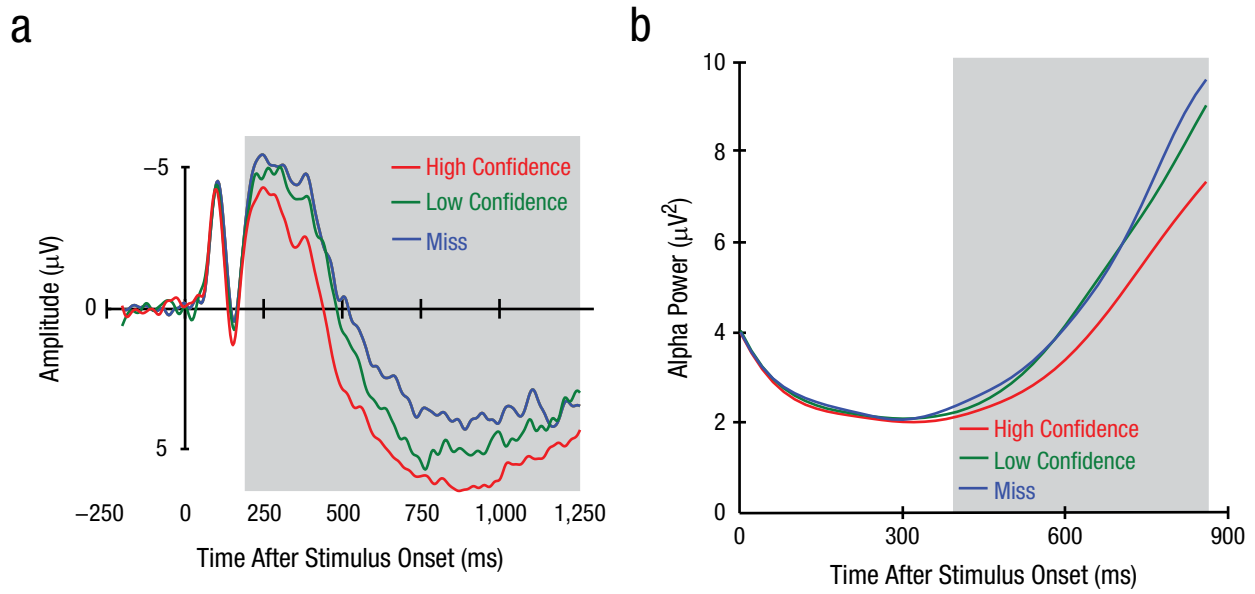

Fig. 2. Electroencephalogram results of Experiment 1: mean amplitude at the Fz site (a) and mean alpha power at the O2 site (b) during the encoding task. Gray shading indicates the time window over which data were averaged to quantify the amplitude of each event-related potential. The data points used to plot the curves in (b) represent the alpha power observed within a 400-ms sliding window that had a 20-ms step size. The values on the *x*-axis represent the front ends of these time windows.

for high-confidence items than for low-confidence and miss items (Fig. 2a; see also Fig. S2 in the Supplemental Material available online). We quantified the sustained frontal positivity as the mean amplitude in the time window 200 ms to 1,000 ms after the onset of each studied item at the midfrontal channel (i.e., channel Fz) where the effect was maximal. An analysis of variance (ANOVA) confirmed that this subsequent memory effect was highly significant, $F(2, 38) = 15.34$, $p < .001$, $\eta_p^2 = .45$, and was driven by more positive amplitudes in response to the high-confidence items than to both low-confidence items, $t(19) = 3.30$, $p < .01$ (95% confidence interval, or CI, for the difference = [0.45, 1.99 μV], Bayes factor = 15.5), and miss items, $t(19) = 5.75$, $p < .001$ (95% CI for the difference = [1.30, 2.78 μV], Bayes factor = 2,349.0). These observations are supported by other work that has examined such differences using conventional mean ERP analyses (Friedman & Johnson, 2000).

We worried that the mean amplitude differences might be driven by the more jittered onset times across participants because of the smaller number of trials for the low-confidence (14% of trials) and miss items (23% of trials) than for the high-confidence items (63% of trials). If this were the case, the amplitude of the frontal positivity measured with the fewest trials (i.e., low-confidence items) should be the lowest because of the largest variability of onset times. However, the fact that the mean amplitude for low-confidence items was significantly higher than the mean amplitude for miss items, $t(19) = 2.11$, $p < .05$ (95% CI for the difference = [0.01, 1.63 μV], Bayes factor = 1.6) rules out this simple explanation.

Next, we examined the oscillatory activity during the encoding period. As shown in Figure 2b (see also Fig. S4 in the Supplemental Material), the EEG during the encoding period showed a clear suppression of occipital alpha power following the onset of the to-be-remembered items (Hanslmayr & Staudigl, 2014). Occipital alpha power was quantified as the mean power between 8 and 12 Hz in the time window 400 to 1,250 ms after the onset of the study items at a right occipital channel (i.e., channel O2; but this was similar across occipital channels; see the Supplemental Material). An ANOVA confirmed that the occipital alpha power varied as a function of participants' later recognition, $F(2, 28) = 4.88$, $p = .01$, $\eta_p^2 = .20$. High-confidence items exhibited lower occipital alpha power than low-confidence items, $t(19) = 2.12$, $p < .05$ (95% CI for the difference = [0.01, 1.55 μV^2], Bayes factor = 1.6) or miss items, $t(19) = 2.80$, $p = .01$ (95% CI for the difference = [0.24, 1.69 μV^2], Bayes factor = 5.7). The only other oscillation that was related to participants' later recognition was a low-frequency frontal effect underlying the aforementioned frontal positivity (see Fig. S5 in the Supplemental Material).

No pre-encoding ERPs or oscillations were predictive of successful memory encoding in our paradigm (see the analyses, Fig. S1, and Fig. S3 in the Supplemental Material). This demonstrates that the memory effects were not simply due to tonic changes in brain activity

that were present prior to the presentation of the pictures. Instead, these signals reflect the ability of the brain to encode accurate representations of the items immediately following their presentation.

Forecasting later recognition of an object. How would one forecast the later recognition of an item based on the electrophysiological signals of memory encoding? Our approach in this experiment was to compute measures of successful memory encoding given the magnitude of the frontal positivity and the strength of occipital-alpha-power suppression for each trial. We calculated the AUC and the proportion of high-confidence responses to provide diverse measures of successful memory encoding (also see the Supplemental Material, where we show the same pattern using the d_a metric of performance). We first sorted the stimuli based on the magnitude of each memory-encoding signal. Then, we computed the memory metrics in each quintile bin (i.e., each bin contained 20% of the trials). These measures estimated the strength of encoded memory given the magnitude of the electrophysiological signals.

When we sorted trials by the amplitude of the frontal positivity, there was a monotonic increase in the strength of encoded memory as a function of its magnitude (Fig. 3a). We observed a significant increase in the AUC from the first quintile (M = .79) to the fifth quintile (M = .84), $F(4, 76) = 9.63$, $p < .001$, $\eta_p^2 = .34$; Fig. 3b), and the likelihood of a high-confidence response showed a similar increase, from 58% in the first quintile to 68% in the fifth, $F(4, 76) = 14.15$, $p < .001$, $\eta_p^2 = .43$ (Fig. 3c). When we sorted trials by the magnitude of the occipital alpha power, there was a highly significant monotonic decline in the memory strength as a function of the alpha power (Fig. 3d). We observed a significant decrease in the AUC from the first quintile (M = .84) to the fifth quintile (M = .79), $F(4, 76) = 8.97$, $p < .001$, $\eta_p^2 = .32$ (Fig. 3e), and the likelihood of a high-confidence response showed a similar decrease, from 68% in the first to 58% in the fifth quintile, $F(4, 76) = 6.38$, $p < .001$, $\eta_p^2 = .26$ (Fig. 3f). These results demonstrate the reliability of both the frontal positivity and the occipital alpha power as predictors of subsequent recognition memory when measured on each trial.

To test for independence between the frontal positivity and the occipital alpha power, we examined the correlation between the two signals across trials within each participant. Although the correlation coefficient was reliably different from zero (M = −0.06), $t(19) = -4.33$, $p < .001$ (95% CI = [−0.08, −0.03], Bayes factor = 132.1), the relationship accounted for less than 0.3% of the variance (see Fig. S6 in the Supplemental Material for the scatter plots).[2] This negligible correlation between the two electrophysiological signals suggests that they index dissociable aspects of memory encoding.

If these signals index different encoding mechanisms, then combining these measures on each trial should result in an increase in our ability to forecast later memory performance. To test this, we sorted each trial into a two-dimensional array using the frontal positivity and the occipital alpha power as two orthogonal axes. As Figure 4 shows, for the trials with the highest frontal positivity and the lowest occipital alpha power, the AUC and the likelihood of a high-confidence response were .85 and 74%, respectively. In contrast, for the trials with the lowest frontal positivity and the highest occipital alpha power, the AUC and the likelihood of high-confidence response were .78 and 56%, respectively. Thus, our ability to predict later memory improved substantially when we combined the two electrophysiological signals.

Discussion

In Experiment 1, we showed that the frontal positivity and the occipital alpha power indexed dissociable mechanisms of memory encoding that could predict whether a given stimulus would be remembered. Next, we asked the following two questions. First, what encoding mechanisms do our electrophysiological measures of memory encoding reflect? One hypothesis is that they index the difficulty of encoding determined by the physical properties of a stimulus (e.g., a bright object might be easier to remember than a dim object). Alternatively, they might reflect the variance in the quality of endogenous memory-encoding processes. Second, can we select individual items that were poorly studied using our neural measures, target such items for remedial study, and improve the efficacy of the learning period?

Experiment 2

In Experiment 2, participants studied 800 pictures while we recorded their EEG. Immediately following the initial study phase, we used the amplitudes of the two neural signals to categorize the pictures as either poorly studied or well-studied. Participants then restudied half of the poorly studied and well-studied items. If the frontal positivity and the occipital alpha power are stimulus-driven measures, then the restudy EEG signals should continue to reflect the poorly studied and well-studied categories to the same degree. However, if the two signals reflect the endogenous variance of memory encoding, then the amplitudes of restudy EEG signals should track later recognition memory performance, instead of the categories defined during the initial study phase. Additionally, if our EEG-based memory forecasting is useful in identifying objects that are poorly studied, and thus need additional studying, then we should expect that the benefit of

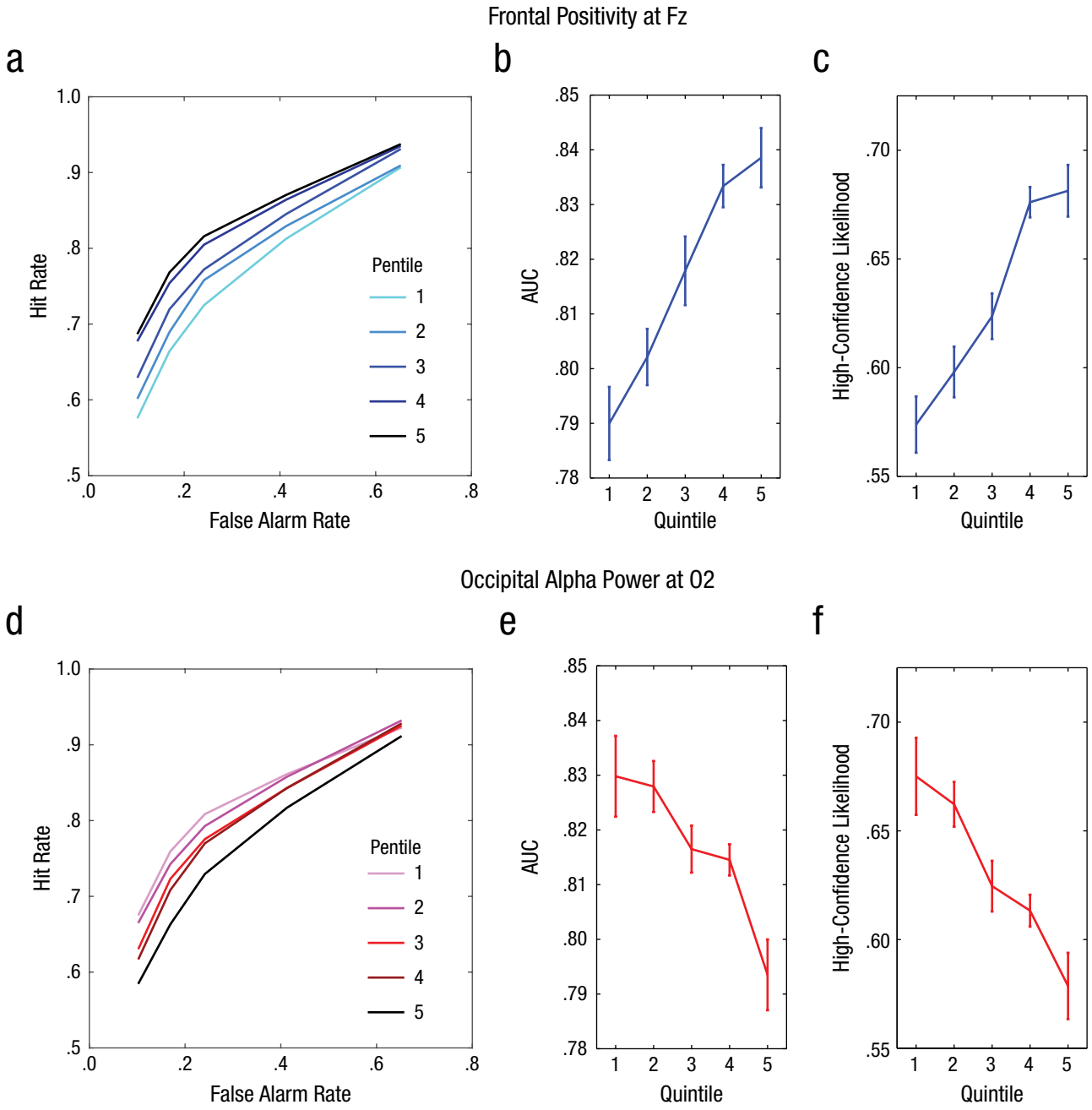

Fig. 3. Results of Experiment 1: receiver-operating-characteristic (ROC) curves and performance on the recognition memory test for the frontal positivity at the Fz site (top row) and the occipital alpha power at the O2 site (bottom row). For each signal, graphs show the ROC curve (a, d), the area under the ROC curve (AUC; b, e), and the likelihood of a high-confidence response (c, f), separately for each quintile. Quintile 1 contained the trials associated with the lowest 20% of the signals, and Quintile 5 contained those associated with the highest 20% of the signals. Error bars show standard errors of the mean.

restudying is greater for poorly studied items than for well-studied items.

Method

Participants. A new group of 20 participants (12 males, 8 females; 18–32 years old) volunteered. They met the same criteria and were compensated as in Experiment 1.

Stimuli and procedures. The initial study phase was similar to the encoding phase of Experiment 1, except that participants studied 800 pictures instead of 500. Approximately 5 min after the initial study phase, the participants completed a restudy phase, in which they restudied half of the poorly studied and half of the well-studied items, as defined by the EEG signals recorded during the initial study phase. We defined the well-studied items as

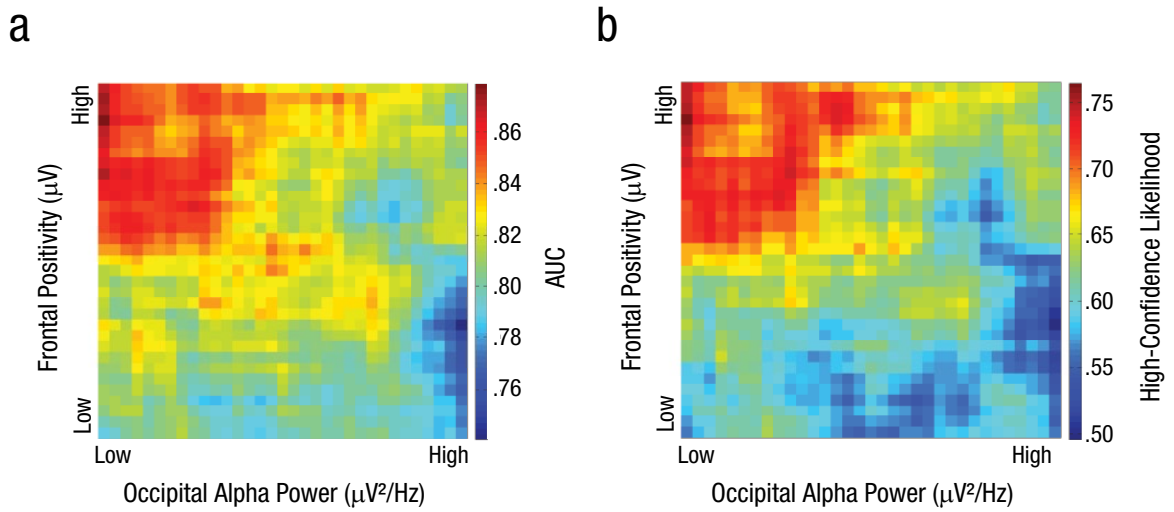

Fig. 4. Results of Experiment 1: heat map depicting the combined predictive power of the frontal positivity and the occipital alpha power. In (a), the color of each pixel indicates the area under the curve (AUC) for the corresponding values of the occipital alpha power and the frontal positivity. In (b), the color of each pixel indicates the likelihood of a high-confidence judgment for each combination. For instance, in (b), the very top left pixel depicts the likelihood of high-confidence responses for trials with the highest frontal positivity and the lowest occipital alpha power. As the pixel moves to the bottom, the criterion window for the frontal positivity slides lower by 2.5%. As the pixel moves to the right, the criterion window for the occipital alpha power slides higher by 2.5%.

those that elicited the largest 40% of all frontal positivities and the lowest 40% of occipital-alpha-power measurements. The poorly studied items were defined as those that elicited the smallest 40% of all frontal positivities and the highest 40% of occipital-alpha-power measurements. The pictures were presented in the same format as in the initial study phase. On average, participants restudied 58 poorly studied pictures and 56 well-studied pictures during restudy. After the restudy phase, participants' resting-state EEG with eyes open and eyes closed was recorded for 15 min. Then, they performed the recognition memory test, which was identical to that in Experiment 1 except that participants were tested on five categories of pictures: poorly studied baseline pictures (58 pictures on average), well-studied baseline pictures (56 pictures on average), poorly studied restudy pictures (58 pictures on average), well-studied restudy pictures (56 pictures on average), and 160 new pictures.

Results

Participants recognized 80% of the well-studied restudy items, 80% of the poorly studied restudy items, 52% of the well-studied baseline items, and 44% of the poorly studied baseline items with 100% confidence. Of the remaining items, they recognized 9% of the well-studied restudy items, 10% of the poorly studied restudy items, 18% of the well-studied baseline items, and 21% of the poorly studied baseline items with moderate confidence (60% or 80%). Participants successfully rejected 73% of new items. Table 2 reports the proportion of trials used to derive the ROC curves. The AUC values were .76 for well-studied baseline items, .73 for poorly studied baseline items, .88 for well-studied restudy items, and .88 for poorly studied restudy items. These results demonstrate that participants learned the pictures reasonably well and benefitted from restudy.

Figure 5 shows the amplitude of the frontal positivity and the occipital alpha power during the initial study phase (Figs. 5a and 5b) and during the restudy phase (Figs. 5c and 5d) elicited by poorly studied, well-studied, and new items. The difference in the sustained frontal positivity between well-studied and poorly studied items was significant, $t(19) = 2.59$, $p < .05$ (95% CI for the difference = [0.20, 2.00 μV], Bayes factor = 3.8), but much reduced during the restudy phase. The difference in the occipital alpha power was much reduced and not significant in the restudy phase, $t(19) = 1.57$, $p > .1$ (Bayes factor in favor of the null hypothesis = 1.44). These findings are inconsistent with what we should have observed if the neural signals were due to the physical characteristics of the stimuli and consistent with the signals tracking the endogenous state of the participant during encoding.

Table 2 and Figure 6 show performance from the final recognition test. First, we replicated the results from Experiment 1. That is, we found that for baseline (i.e., not restudied) items, memory strength was significantly weaker for the items that elicited a low frontal positivity and high occipital alpha power (i.e., poorly studied items) than those that elicited a high frontal positivity and low occipital alpha power (i.e., well-studied items)—for

Table 2. Results of Experiment 2: Mean Proportion of Responses on the Recognition Memory Test

	Response					
Item type	"100% old"	"80% old"	"60% old"	"100% new"	"80% new"	"60% new"
Well-studied baseline	.52 (.05)	.13 (.01)	.05 (.01)	.08 (.01)	.15 (.02)	.07 (.02)
Poorly studied baseline	.44 (.05)	.15 (.02)	.06 (.01)	.11 (.02)	.17 (.03)	.07 (.02)
Well-studied restudy	.80 (.05)	.07 (.01)	.02 (.01)	.03 (.01)	.05 (.02)	.03 (.02)
Poorly studied restudy	.80 (.04)	.08 (.02)	.02 (.01)	.03 (.01)	.05 (.02)	.02 (.01)
New	.09 (.03)	.11 (.02)	.06 (.01)	.29 (.04)	.33 (.03)	.12 (.02)

Note: Standard errors are given in parentheses. Proportions indicate participants' confidence in their old/new judgment.

the AUC: $t(19) = 2.63$, $p < .02$ (95% CI for the difference = [0.01, 0.06 μV], Bayes factor = 4.1); for the likelihood of high-confidence responses: $t(19) = 4.22$, $p < .0001$ (95% CI for the difference = [4, 13%], Bayes factor = 105.0). More critically, recognition performance was essentially identical across the two types of restudied items—for the AUC: $t(19) = 0.24$, $p > .8$ (Bayes factor in favor of the null hypothesis = 4.5); for the likelihood of high-confidence responses: $t(19) = 0.23$, $p > .8$ (Bayes factor in favor of the null hypothesis = 4.5); there was a significant interaction between item category (poorly studied vs. well-studied) and study condition (baseline vs. restudy), $F(1, 19) = 8.8$, $p < .01$, $\eta_p^2 = .32$, for the AUC and $F(1, 19) = 13.48$, $p < .01$, $\eta_p^2 = .42$, for the likelihood of high-confidence responses. In fact, the restudy effect in terms of the likelihood of high-confidence responses was 1.3 times larger for poorly studied items than for well-studied items (27% vs. 35% change, respectively).

Next, we addressed the possibility that the lack of difference between recognition accuracy for well-studied and poorly studied items following restudy was simply due to a ceiling effect that eliminated the true difference that would otherwise be observed. In other words, maybe the restudy benefit was larger for poorly studied items than for the well-studied items because every restudied stimulus was relearned maximally. If so, there should be no variability left in recognition performance to be explained by the electrophysiological signatures measured during the restudy phase. To address this possibility, we classified the restudied items as poorly restudied and well-restudied on the basis of the signals recorded during the restudy phase. Again, we found that well-restudied items had a significantly higher memory strength ($M = .92$) than poorly restudied items ($M = .89$) for the AUC, $t(19) = 2.3$, $p < .05$ (95% CI for the difference = [0.02, 0.52], Bayes factor = 2.2) and that this was also the case for the likelihood of high-confidence responses (well-restudied items: $M = .85$, poorly restudied items: $M = .78$), $t(19) = 2.9$, $p = .01$ (95% CI for the difference = [2, 12%], Bayes factor = 6.9). This indicated that not all the restudied items were encoded to ceiling. Instead, the variability in the encoding quality for restudied items was still distinguishable using the frontal positivity and the occipital alpha power. Therefore, the significant interaction between study condition and item category does not appear to be due to a ceiling effect for restudied items obscuring a potential difference.

Discussion

In Experiment 2, we discriminated between exogenous and endogenous explanations of the variability in our electrophysiological indices of memory encoding. Our results indicate that both the frontal positivity and the occipital alpha power heavily reflect endogenous variability in memory-encoding processes. There appears to be only a hint of exogenous contribution to the difficulty of encoding on these electrophysiological signals, evidenced by a small but preserved difference in the frontal positivity for poorly studied and well-studied items during the restudy phase. Furthermore, by having participants restudy the items that were classified as poorly studied by our electrophysiological signals, we were able to dramatically enhance the efficacy of learning. Thus, these results provide theoretical insight as to the nature of the frontal positivity and the occipital alpha signals of memory encoding, and they provide a clear demonstration of the practicality of our EEG-based learning intervention.

General Discussion

People's ability to encode new information fluctuates from moment to moment. It would be extremely valuable if it could be identified in real time when people are not encoding information into memory to the best of their ability. Numerous studies have successfully identified neural signals sensitive to success in later recognition memory tests. However, no study so far had examined the usefulness of such signals in forecasting the later recognition of each studied stimulus and used this forecast to improve learning as people study.

In Experiment 1, we simultaneously measured two electrophysiological signals that differentiated later recognized items from later missed items, the sustained frontal positivity and the occipital alpha power. We found

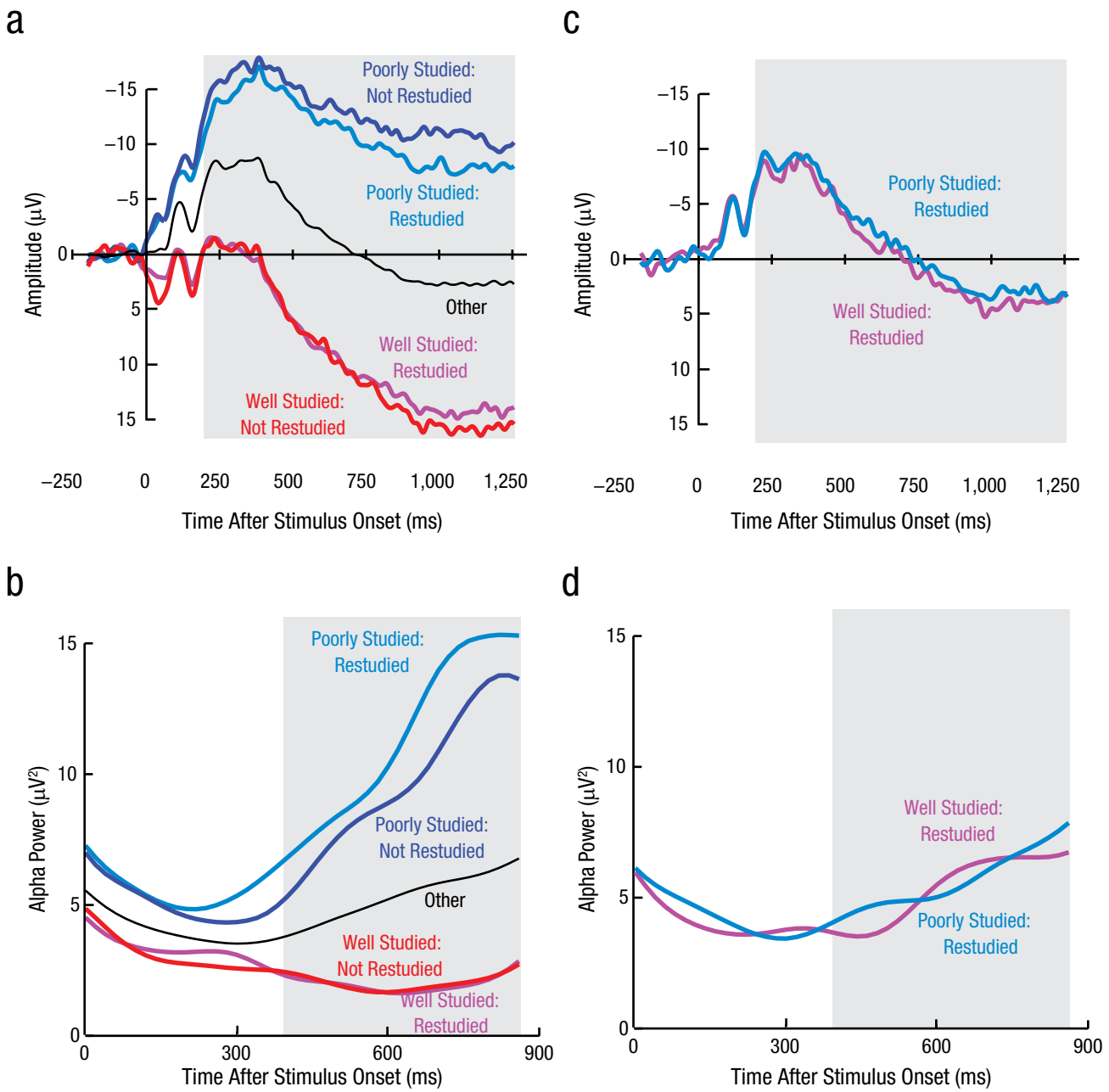

Fig. 5. Electroencephalogram results of Experiment 2: mean amplitude at the Fz site (a, c) and mean occipital alpha power at the O2 site (b, d) during the initial study phase (left column) and the restudy phase (right column). Results are shown separately for all five item types in the initial study phase and for the two restudied item types in the restudy phase. Gray shading indicates the time window over which data were averaged to quantify the amplitude of each event-related potential. The data points used to plot the curves in the bottom row represent the alpha power observed within a 400-ms sliding window that had a 20-ms step size. The values on the *x*-axis represent the front ends of these time windows.

that these signals revealed a reliable and dissociable ability to predict subsequent memory, and combining them improved their predictive power. These findings support the hypothesis that dissociable cognitive subprocesses underlie the frontal positivity and the occipital alpha power and that these subprocesses conjunctively determine the efficacy of memory encoding.

In Experiment 2, we used the two brain signals to identify items that needed restudying during the learning episode, which allowed us to intervene and improve our participants' recognition memory. Here, we hypothesized that restudying items that were initially poorly studied (i.e., forecasted to be recognized at a low rate) would lead to a greater enhancement of overall recognition

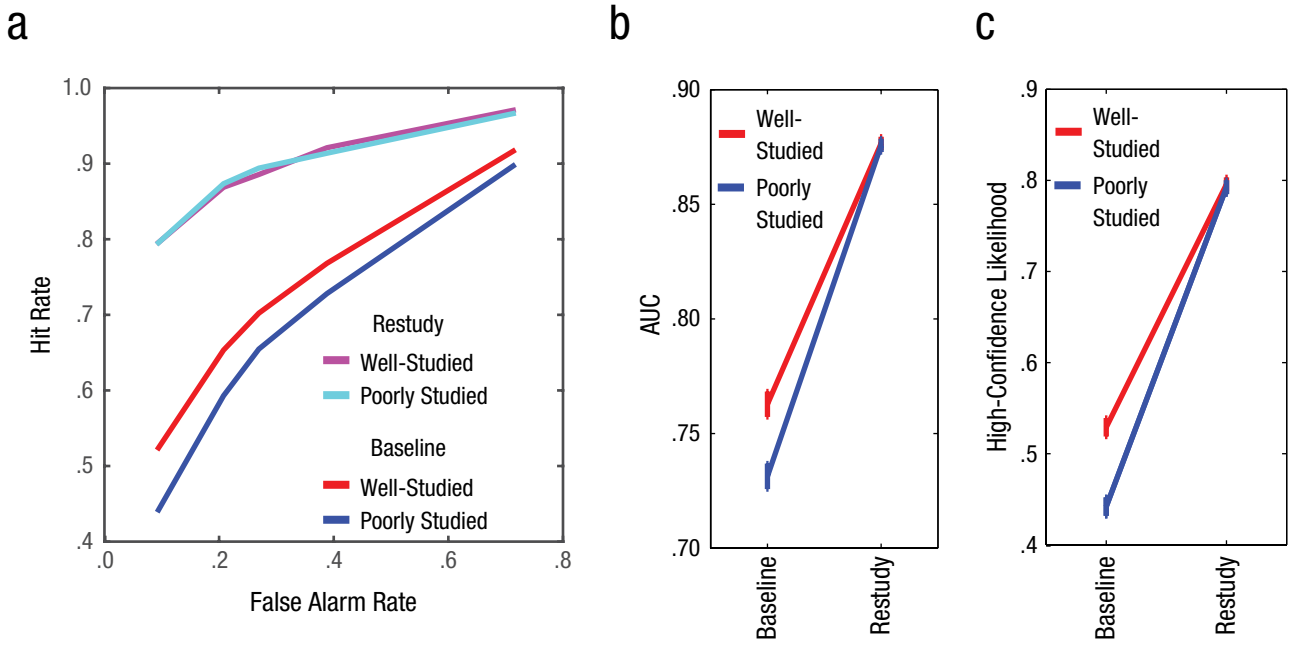

Fig. 6. Results of Experiment 2: performance on the recognition memory test. The graphs show the receiver-operating-characteristic (ROC) curve (a), the area under the ROC curve (AUC; b), and the likelihood of a high-confidence response (c), separately for the restudy and baseline items. Error bars show standard errors of the mean.

memory than restudying initially well-studied items (i.e., forecasted to be recognized at a high rate). We indeed found that restudying the poorly studied items led to a benefit of restudying that was 30% larger than the benefit for restudying initially well-studied items. This restudy effect, along with the much-reduced difference in the brain signals in the restudy phase between poorly studied and well-studied items, suggests that the encoding quality read out by the two brain signals is due to internal fluctuations in the ability of participants to store information in memory, rather than to low-level variability of the stimuli themselves.

Our findings have broad theoretical and practical implications. Our evidence that the modulations of both the frontal positivity and the occipital alpha power reflect endogenous variability in memory encoding is in line with previous studies suggesting that both signals are sensitive to the depth of processes brought to bear on to-be-remembered information (Hanslmayr et al., 2009; Hanslmayr & Staudigl, 2014; Otten et al., 2001). Notably, our correlational analysis revealed that the two measures account for dissociable variance in memory performance. What might each neural correlate represent? Fernández and colleagues (1999) showed that the characteristics of the frontal positivity closely resembled the local-field potentials recorded at the hippocampus but not at the rhinal cortex. This observation suggests that the frontal positivity reflects the hippocampus-dependent encoding processes, such as formation of source memories for later recollection (see Diana, Yonelinas, & Ranganath, 2007, for a review). As for the suppression of the occipital alpha power, one might hypothesize that it reflects a higher level of arousal. However, if that were the case, one would expect alpha suppression to be evident even before the stimuli appeared. The fact that the alpha power suppression was stimulus-locked, not preceding the stimulus, suggests that this effect was specific to the memory encoding itself. One potential explanation offered by Klimesch (2012) is that the sustained alpha-band suppression indicates successful access to information already stored in long-term memory, thus indicating better associative learning. To better characterize the functional differences of the two neural signals, it is critical to experimentally dissociate these two signals in future studies.

Note that we are not claiming that the two electrophysiological measures we used are the only signals that predict successful memory encoding. Previous studies that utilized different experimental procedures have shown that other electrophysiological signals differentiated later-recognized items from later-forgotten items (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Dube, Payne, Sekuler, & Rotello, 2013; Karis, Fabiani, & Donchin, 1982; Osipova et al., 2006; Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Otten, Quayle, & Puvaneswaran, 2010). Therefore, it will also be important for future studies to systematically examine what determines the usefulness of each signal in

predicting successful memory encoding. This will be critical for using these signals in the real world to improve learning.

From a practical perspective, our findings demonstrate the feasibility of monitoring the moment-to-moment fluctuations of encoding in real time using noninvasive electrophysiology. The relative ease and cost effectiveness of acquiring EEG data compared with other neural signals (e.g., blood-oxygen-level-dependent responses in functional MRI) means that the present measurements and procedure could quickly translate into real-world applications. The fact that our analysis required only two recording electrodes to successfully forecast subsequent memory performance is an additional advantage. The results from Experiment 2 demonstrate one way to utilize this electrophysiology-based forecasting to efficiently improve an individual's subsequent memory by measuring activity in real time as people learn new information.

Similar approaches of monitoring the quality of encoding have been attempted by assessing learners' subjective judgments about the quality of learning (i.e., judgments of learning; Metcalfe, 2009). Although some studies showed that judgments of learning can be a reliable measure of successful learning in certain situations (Nelson & Dunlosky, 1991; Underwood, 1966), other studies showed that the reliability of such meta-memory judgments varied wildly depending on the specific task or the subject population (Daniels, Toth, & Hertzog, 2009; Kornell & Bjork, 2007; Maki, 1998; Serra & Metcalfe, 2009; Townsend & Heit, 2011). Using neural signals as predictors of encoding quality could potentially bypass such problems. The methods developed here could be particularly advantageous for individuals who exhibit conditions that impair learning (e.g., dyslexia or attention-deficit hyperactivity disorder).

Author Contributions

K. Fukuda designed and conducted the research and analyzed the data. K. Fukuda and G. F. Woodman wrote the manuscript.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at http://pss.sagepub.com/content/by/supplemental-data

Open Practices

All data have been made publicly available via Open Science Framework and can be accessed at https://osf.io/8bqaj/. The complete Open Practices Disclosure for this article can be found at http://pss.sagepub.com/content/by/supplemental-data. This article has received a badge for Open Data. More information about the Open Practices badges can be found at https://osf.io/tvyxz/wiki/1.%20View%20the%20Badges/ and http://pss.sagepub.com/content/25/1/3.full.

Notes

1. This procedure was followed to remove the potential confound of lateralized response-related potentials (e.g., the lateralized-readiness potential) from the recognition effect (i.e., the old/new effect).
2. To achieve a normal distribution for the occipital alpha power, we log-transformed the alpha power before examining its correlation with the frontal positivity. The correlational analysis using the raw alpha power revealed the same result.

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Predicting and improving recognition memory using single-trial electrophysiology

Keisuke Fukuda & Geoffrey F. Woodman

SUPPLEMENTAL INFORMATION

Traditional ERP analysis of the pre-encoding period. The ERP data recorded during pre-encoding period were binned in the same manner described in the Method section, forming High Confidence (HC), Low Confidence (LC), and Miss (Miss) bins. Figure S1 shows the ERP responses for each bin across the entire set of 19 channels. As can be seen in Figure S1, the ERP responses for all the bins were overlapping across all the channels. These plots show that pre-encoding ERPs did not differentiate the quality of memory encoding for the upcoming study item at any channel, not just the channels that were the focus in the main text.

Traditional ERP analysis of the encoding period. In contrast to the pre-encoding ERPs, Figure S2 shows the ERP responses during encoding period did discriminate between the High Confidence (HC), Low Confidence (LC), and Miss (Miss) bins. Specifically, there was a larger sustained positivity in the HC bin (from approximately 200ms-1000ms after the onset of the stimulus) than for the other bins. This effect was observed across frontal and central channels (i.e., a broad frontocentral distribution). The effect was statistically significant at channels F3, F4, Fz, C3, C4, and Cz ($ps < .001$).

Time-frequency analysis of the pre-encoding period. To determine if oscillations prior to stimulus onset could predict if subjects would remember it, we performed a time-frequency analysis of the pre-encoding EEG signals in the same manner as described in the Method section. Here, we focused on the contrast between HC items and Miss items. Figure S2 shows the results of paired t-tests at each time-frequency data point at each scalp channel. As can be seen, there is no frequency band that showed a consistent statistical pattern at nearby electrodes. This suggests that either the pre-encoding EEG does not exhibit the quality of memory encoding for the upcoming study item in our paradigm, or that such an effect is extremely focused in time and frequency band.

Time-frequency analysis of the encoding period. Here we show the scalp distribution of time-frequency effects measured during encoding. As Figure S4 shows, the analysis revealed two distinctive time-frequency signals across the scalp channels. First, there was a sustained increase in the power across the lowest frequencies (0-3hz) that was maximally observed at frontal channels. To statistically evaluate this effect, we calculated the mean power from 0-3hz at Fz channel in the time window of 260ms to

1250ms for High Confidence, Low Confidence, and Miss bins. An ANOVA revealed a highly significant main effect of confidence bin (*ps* < .001, see Figure S5 for an example). This effect was observed at electrode F3, F4, Fz, C3, C4, and Cz. This was consistent with the sustained frontal positivity of the averaged ERPs described in the main text.

We sought to verify that this low-frequency signal was, in fact, the frontal positivity measured in the ERP analysis. We examined the correlation between the activity measured on High Confidence and Miss trials using the amplitude of the frontal positivity and the power of the frontal low-frequency oscillations. As expected, we observed a strong positive correlation (r = .55, p =.01), buttressing the observation that these two signals had identical scalp distributions. Second, there was a sustained decrease in the power of alpha power that was maximally observed at occipital channels as discussed in the main manuscript. This effect was significant across channels P3, P4, Pz, PO3, PO4, O1, O2, OL, OR, T5, and T6 (*ps* < .001).

Individual-subject correlations between the frontal positivity and occipital alpha. In Figure S6, we show the correlations between the amplitude of the frontal positivity and the log of the occipital alpha power for each of the individual subjects in Experiments 1, with each point representing an individual study event. These plots demonstrate that the mean correlation (r = -0.06) was not due to a mixture of strongly positive and negative correlations from individual subjects.

Analyzing behavioral results using the d_a metric. We further confirmed our behavioral results using the sensitivity measure *da.* This metric has the advantage that it allows standard deviations for true memory and false memory distributions to vary independently (Dube, Rotello, & Pazzaglia, 2013; Wixted & Mickes, 2010). In Experiment 1, we first sorted trials by the amplitude of the frontal positivity. We observed a significant increase in d_a, from 1.40 to 1.75 ($F(4,76)=11.74$, $p < .001$, η_p^2 = .38) from the first pentile to the fifth pentile. When we sorted trials by the magnitude of the occipital alpha power, we observed a significant decrease in d_a, from 1.74 to 1.38 from the first pentile to the fifth pentile ($F(4,76)=8.50$, $p < .001$, η_p^2 = .31). Together with other metrics of memory strength reported in the main manuscript, these results demonstrate the reliability of both the frontal positivity and the occipital alpha power as predictors of subsequent recognition memory when measured on each trial. In Experiment 2, we replicated the results from Experiment 1. That is, we found that for baseline items (i.e., not restudied), the memory strength was significantly weaker for the items that elicited a low frontal positivity and high occipital alpha power (i.e., poorly studied items) than the those studied with high frontal positivity and low occipital alpha power (i.e., well-studied items) ($t(19) = 2.83$, p =.01, 95% CI of difference = .05 ~ .33, Bayes factor = 6.0 for d_a, $t(19) = 4.22$, p <.0001). More critically, recognition performance was essentially identical across the two types of restudied items ($t(19)$ = 0.87, p >.3, Bayes Factor in favor of the null = 3.2 for d_a,), leading to a significant interaction between item category (poorly studied versus well studied) and study condition (baseline versus restudy) ($F(1,19) = 4.7$, $p < .05$, η_p^2 = .20 for d_a).

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Figure captions

Figure S1. The distribution of ERP responses during pre-encoding period across scalp.
The panel shows the distribution of ERP responses across 19 channels during pre-encoding period. The top row shows F3, Fz, and F4 channels from the left to right, the second row shows T3, C3, Cz, C4, and T4 channels from the left to right, the third row shows P3, Pz, and P4 from the left to right, the forth row shows T5, PO3, PO4, and T6 channels from the left to right, and the bottom row shows OL, O1, O2 and OR channels from the left to right. X-axis shows the time elapsed from the button press to initiate a trial. Y-axis shows the amplitude of the response with negative up and positive down. The red, green and blue lines show the ERP response for high-confidence hit (HC), low-confidence hit (LC), and miss (Miss) trials, respectively.

Figure S2. The distribution of ERP responses during encoding period across scalp.
The panel shows the distribution of ERP responses across 19 channels during encoding period. The channel labels are described in Figure S1. X-axis shows the time elapsed from the onset of the stimulus. Y-axis shows the amplitude of the response with negative up and positive down. The red, green, and blue lines show the ERP response for high-confidence hit (HC), low-confidence hit (LC), and miss (Miss) trials, respectively.

Figure S3. The distribution of time-frequency signals during the pre-encoding period. The panel shows the result of paired t-test ($p < .05$, uncorrected) between HC and Miss conditions across entire scalp channels for pre-encoding period. The channel labels are described in Figure S1. X-axis shows the time elapsed from the button press to start a trial. Y-axis shows the frequency (0-50hz). The color value at each time-frequency data point (i.e. 400ms time window starting from the time value indicated on the X-axis) indicates the p-value of the paired t-test.

Figure S4. The distribution of time-frequency signals for memory encoding during the encoding period. The panel shows the result of paired t-test ($p < .05$, uncorrected) between HC and Miss conditions across entire scalp channels for encoding period. The channel labels are described in Figure S1. X-axis shows the time elapsed from the button press to start a trial. Y-axis shows the frequency (0-50hz). The color value at each time-frequency data point (i.e., 400ms time window starting from the time value indicated on the X-axis) indicates the p-value of the paired t-test. The green and pink box highlights an example of the frontal low-frequency signal (0-3hz), and that of the occipital alpha (8-12hz) signal.

Figure S5. The frontal low-frequency power. The average power from 0-3hz at Fz channel. The red, green, and blue lines indicate the power measured from high-confidence hit (HC), low-confidence hit (LC), and miss (Miss) items. X-axis reflects the time elapsed after the stimulus onset. Of note, each time point reflects the 400ms window whose time value corresponds with the beginning of the window. The gray box highlights the time window that corresponds to that of the frontal positivity.

Figure S6. Individual scatterplots showing the relationship between the amplitude of the frontal positivity and the occipital alpha power across subjects. Each scatterplot shows the frontal positivity (x-axis) and the log-transformed occipital alpha power (y-axis) for an individual. As can be seen, the correlations between the two electrophysiological measures are negligibly weak though reliably negative.

Figure S1

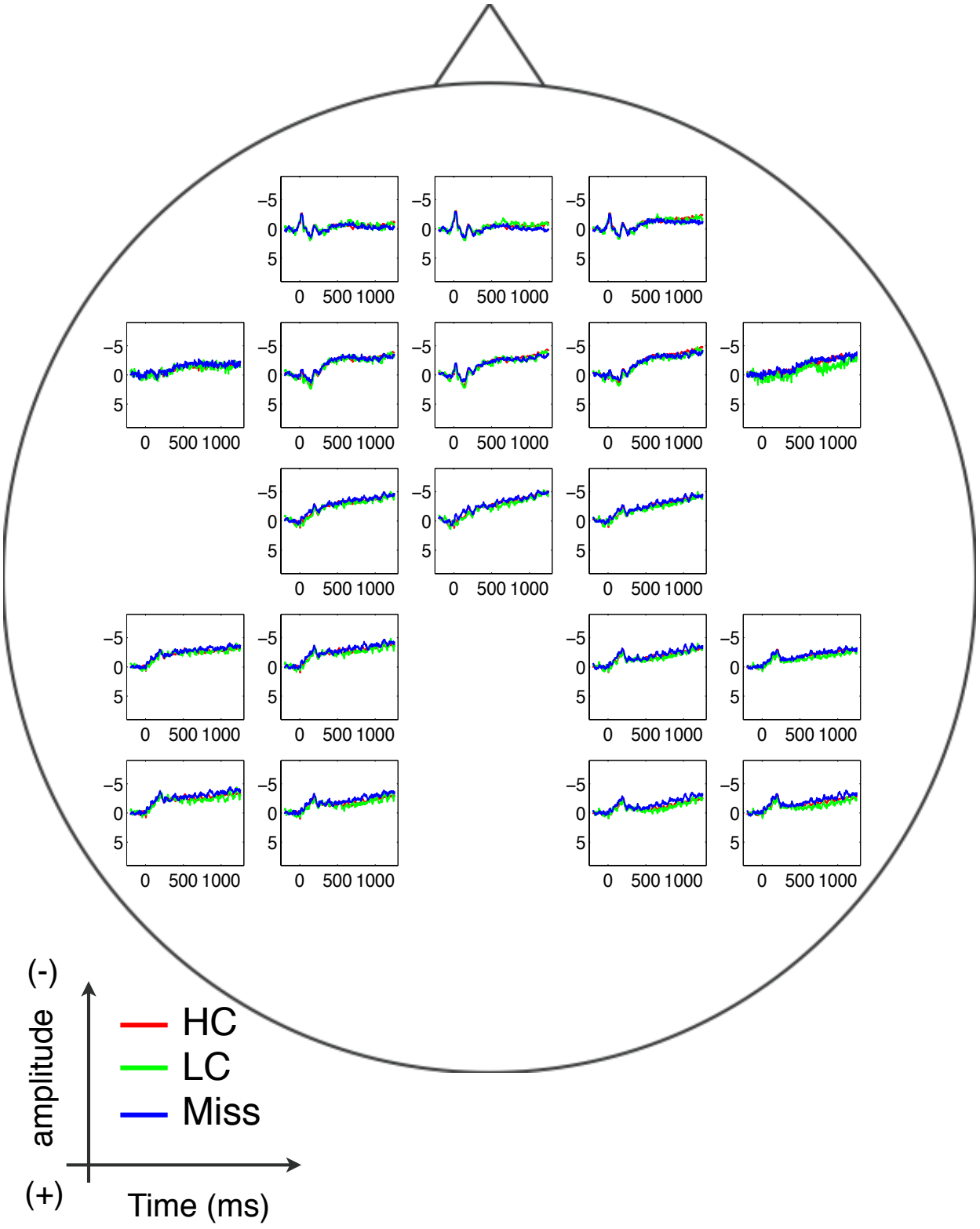


Figure S2

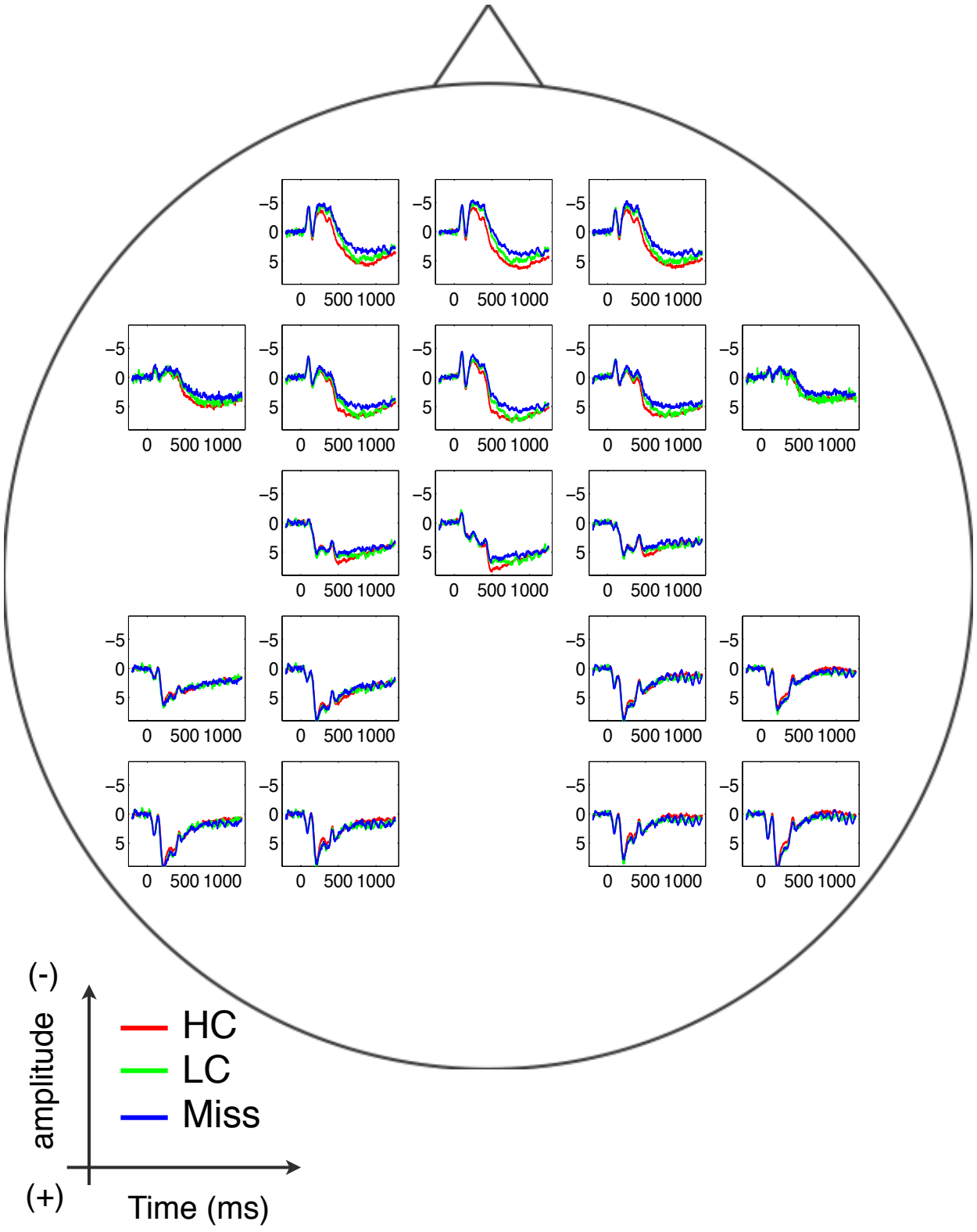


Figure S3

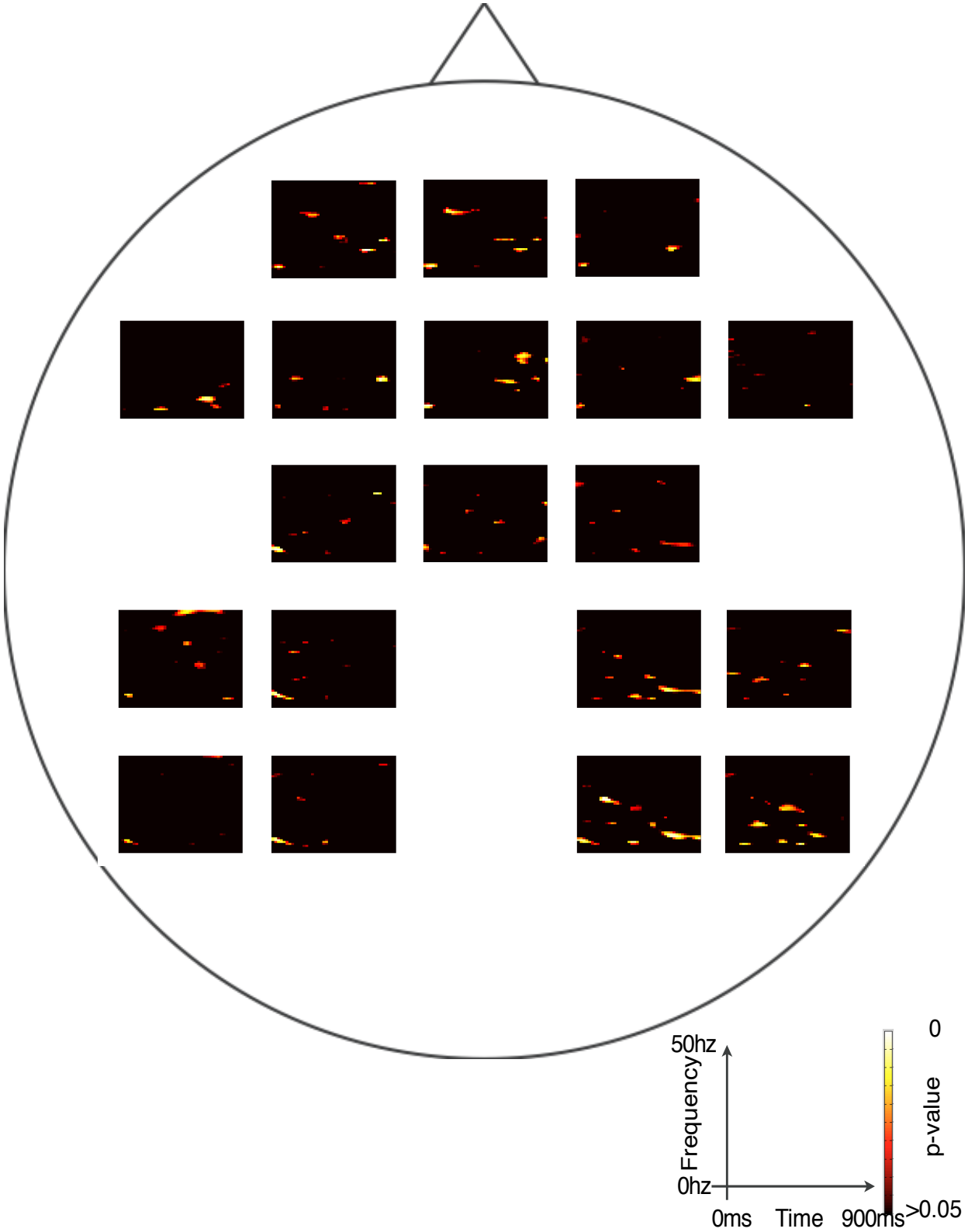


Figure S4

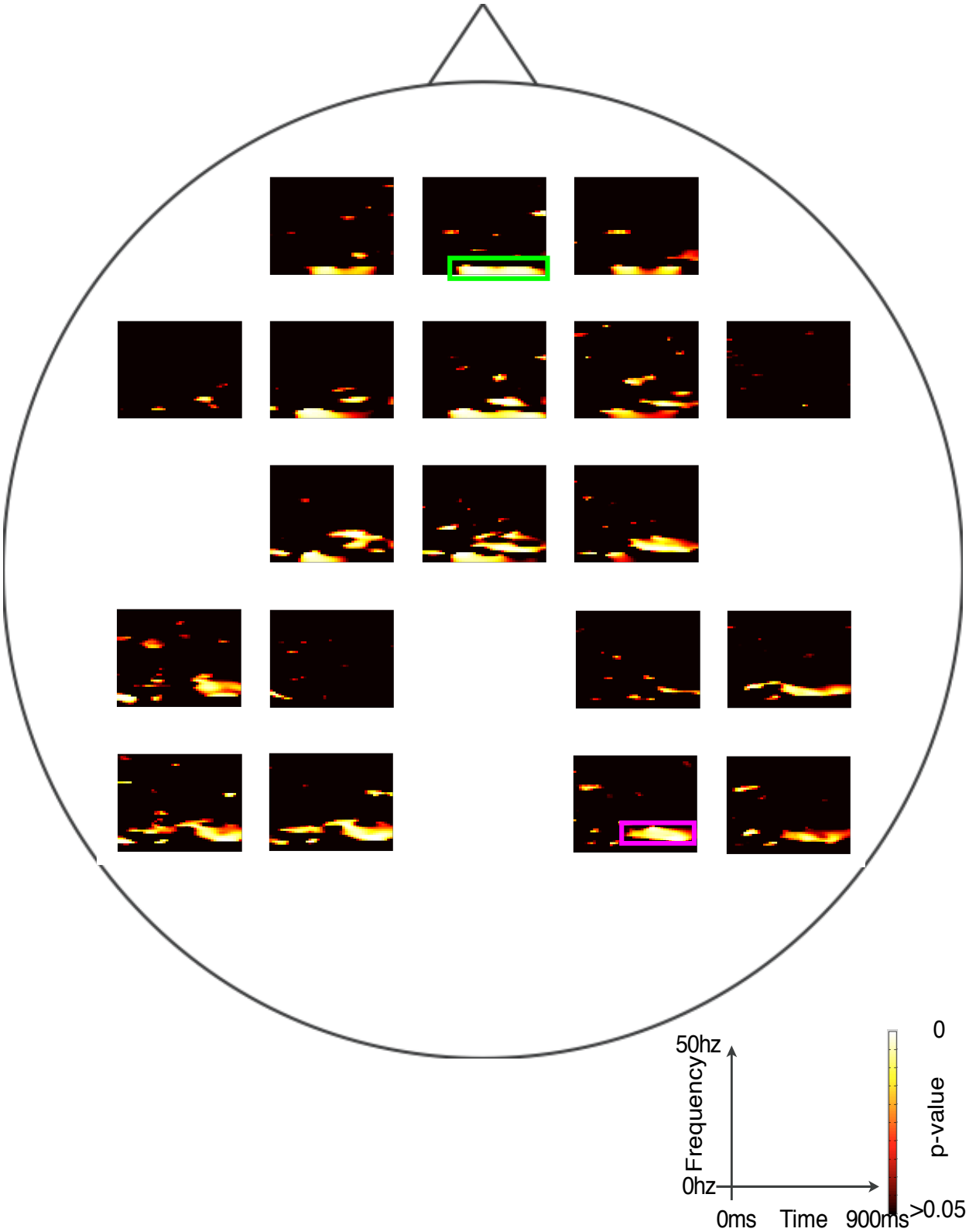
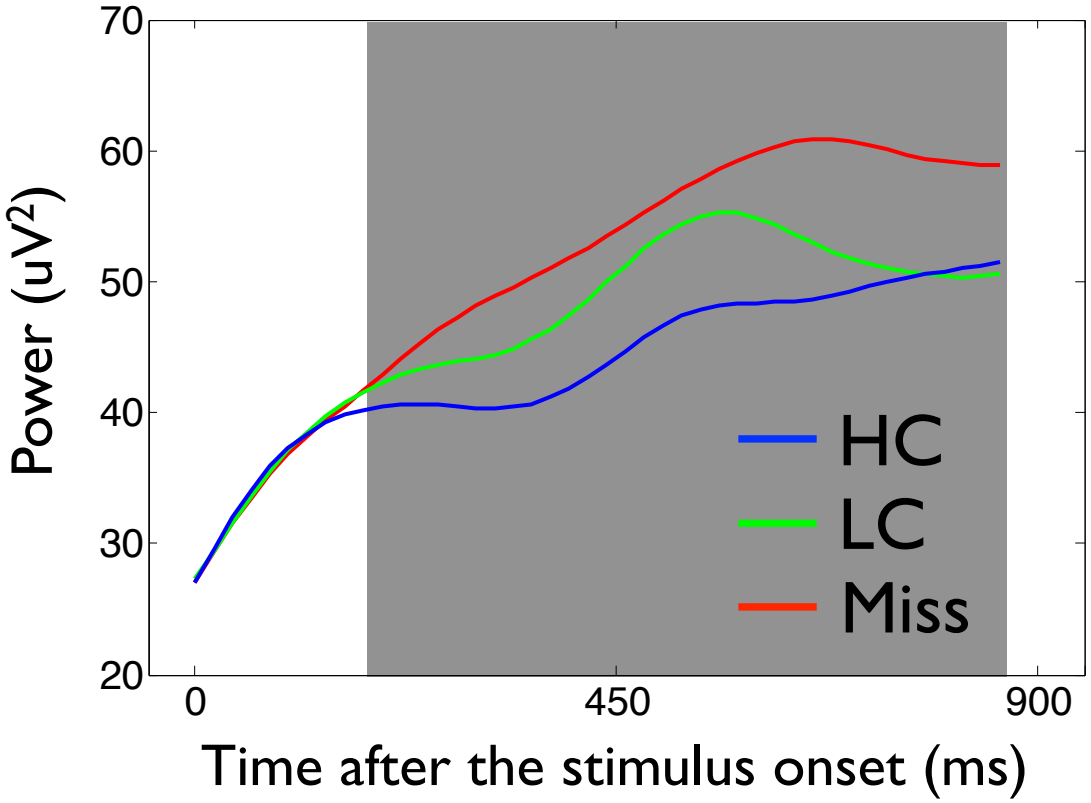
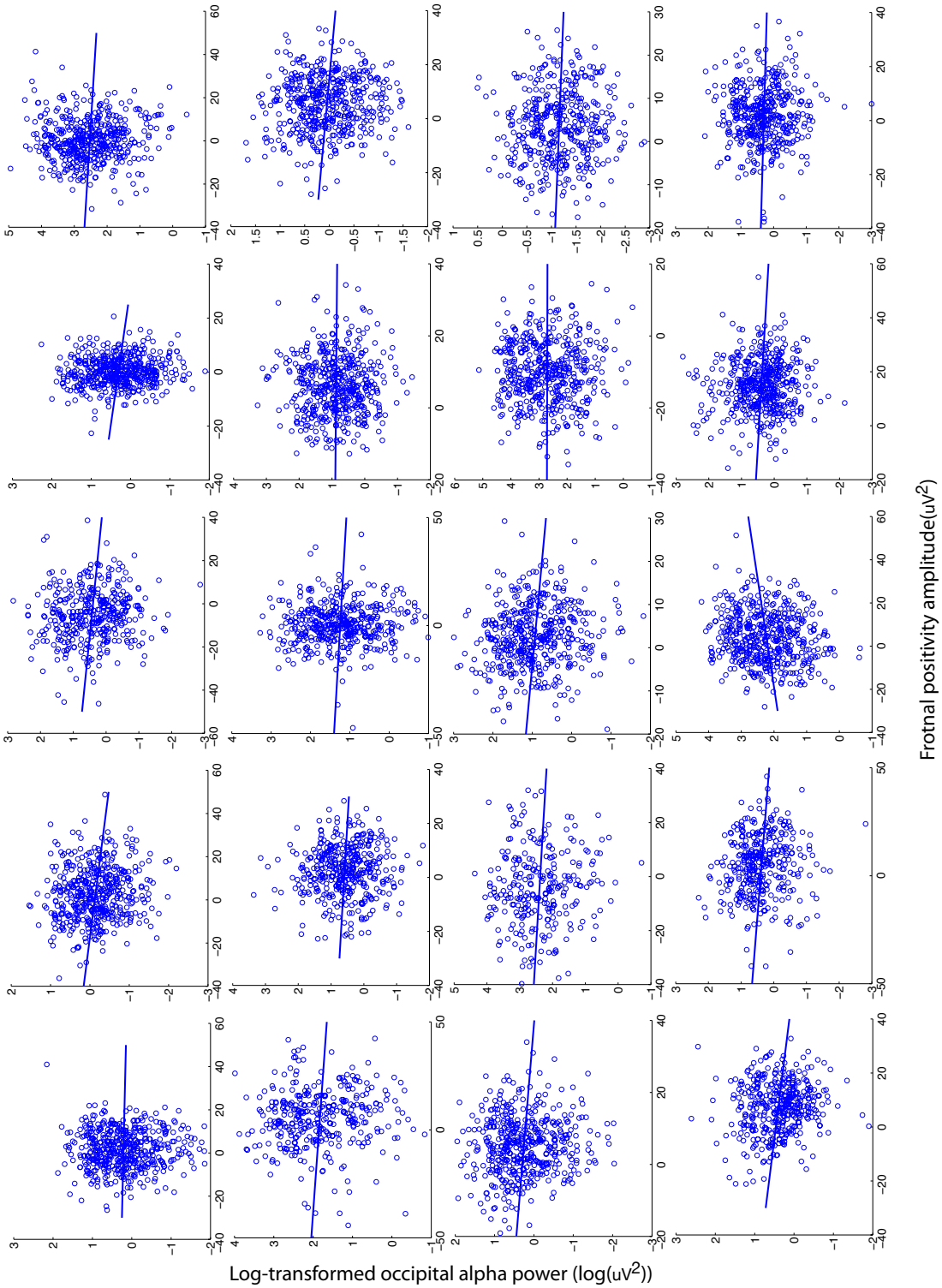


Figure S5


70
60
50
40
30
20
Power (uV2)
0
450
900
Time after the stimulus onset (ms)
HC
LC
Miss

Figrure S6


Log-transformed occipital alpha power (log(uV2))
Frotnal positivity amplitude(uV2)