Unconscious perception can be predicted from prestimulus activity

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Abstract
A fundamental open question is why humans can make accurate guesses about stimuli they do not consciously see. This phenomenon is known as "unconscious perception." We asked human participants (N = 31) to discriminate the location of a briefly presented low-contrast visual stimulus, and then rate how well they saw the stimulus. The behavioral accuracy of discriminating the location of a subjectively unconscious stimulus could be predicted in a trial-by-trial manner from lateralized low frequency (1–15 Hz) electroencephalographic (EEG) activity before the stimulus. This effect was observed up to 1 s before the stimulus was presented. Lateralized occipital prestimulus EEG power modulated the stimulus-evoked activity in a complex manner, but the amplitude of the stimulus-evoked electrophysiological response was not strongly modulated by unconscious objective discrimination accuracy. Signal detection analyses indicated that the participants' capacity to discriminate unconscious stimuli lay on the same continuum as conscious vision. The results suggest that unconscious perception is not an automatic stimulus-evoked process but relies on perceptual decisions about weak perceptual signals that may be available for introspection.

Key words: Unconscious perception, subliminal perception, consciousness, blindsight, prestimulus, oscillations, EEG

Introduction

One of the major aims of visual neuroscience is to uncover which neural processes enable a person to consciously experience and respond to stimuli in their environment. Interestingly, the visual stimuli that individuals report as not consciously perceiving can influence their behavior, a phenomenon known as "unconscious perception" (Hannula, Simons, & Cohen, 2005). The neural mechanisms that enable this unconscious capacity are not well understood. Traditional models of unconscious perception emphasize stimulus-evoked activity, but here, we draw attention to the possibility that fluctuations in spontaneous neural activity before stimulus onset may be important for unconscious vision.

According to the currently popular models of vision, the feedforward sweep of stimulus-triggered activation through cortical areas happens outside of one's consciousness, but this activation is assumed to have the power to influence behavior (Vanrullen, 2007; VanRullen & Koch, 2003). The extent to which feedforward processes enable unconscious contents to influence behavior may depend on selective attention: the attended stimuli may produce stronger activation, thereby increasing the likelihood of correct behavioral response (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). Similarly, feedforward activation may trigger the formation of recurrent activity loops between different cortical areas, enabling stronger unconscious perceptual capacity (Dehaene et al., 2006). These conclusions are supported by studies that show that under certain conditions where the participants report not seeing a stimulus, early visually evoked activation is preserved (Gaillard et al., 2009; Kouider, Dehaene, Jobert, & Le Bihan, 2007; Salti et al., 2015; Supèr, Spekreijse, & Lamme, 2001). Widespread cortical activation is assumed to enable full-fledged conscious perception, allowing the participant to guide behavior based on the conscious contents and, for example, report what they perceived (Dehaene & Changeux, 2011; Lamme & Roelfsema, 2000).

Preserved early visual cortical activation in unconscious trials may not alone explain why in some unconscious trials the participant responds correctly but not in other trials. If the accuracy of unconscious perceptual responses depends on the strength of the early visual activation (Dehaene et al., 2006), then visually evoked activation should be higher in the trials where the participants provide a correct answer. Some studies that show enhanced event-related potentials (ERP) around 200 ms after stimulus onset in occipitotemporal electrodes when the participants correctly discriminate a target despite claiming that they do not consciously see it, support this conclusion (Koivisto & Grassini, 2016; Lamy, Salti, & Bar-Haim, 2009). However, because reports of conscious vision correlate with ERP amplitude in the same time window—an effect known as visual awareness negativity (Förster, Koivisto, & Revonsuo, 2020; Railo, Koivisto, & Revonsuo, 2011)—this putative correlate of unconscious perceptions could reflect degraded conscious perception. Koivisto and Grassini (2016) reported that the ERP correlate of unconscious discrimination also correlated with conservative response criterion, suggesting that what the participants labeled "unconscious" may have been severely degraded conscious perception. This is consistent with the results of Peters and Lau (2015), suggesting that when perception is measured using a procedure that minimizes the influence of criterion setting, no evidence for strictly unconscious perception is observed.

In contrast to the idea that the strength of early visually evoked responses correlates with the likelihood of correct behavioral responses within reportedly unconscious trials, Salti et al. (2012) found that only the late P3 wave correlated with the accuracy of unconscious discrimination, showing no difference between the ERP amplitudes of trials where the participants provided correct versus incorrect responses when only unconscious trials were considered. This could mean that unconscious perception may be less influenced by the strength of the visually evoked response than currently assumed. Possibly, the trial-by-trial variation in behavioral performance on unconscious trials relates not to the strength of visual-evoked response but to how well decision-making processes can "access" the visual stimulus–related information.

Instead of directly examining visually evoked activity, we reason that unconscious perception could be explained by spontaneous variation in neural activity before stimulus presentation; indeed,

recent views have emphasized the importance of top-down modulation of visual cortical activity on visual processing (Muckli & Petro, 2013). Prestimulus oscillations may bias the processing of a stimulus by modulating how excitable cortical neurons are, for instance, in response to an incoming visual stimulus (Samaha, Iemi, Haegens, & Busch, 2020). Prestimulus oscillations could influence whether unconscious stimuli elicit the correct behavioral response for at least two reasons. First, if unconscious perception can be explained in terms of the strength of the early evoked response, this effect could be driven by the prestimulus brain state: in trials where the participant's attentional state before stimulus presentation is optimal, the stimulus may trigger stronger visually evoked responses, thereby enabling more successful behavioral performance, even if the participants reported not seeing the stimulus. Numerous studies have shown that conscious visual perception is strongly influenced by low-frequency oscillations, especially the alpha (8–13 Hz) oscillations, before stimulus presentation (Bareither, Chaumon, Bernasconi, Villringer, & Busch, 2014; Jensen, Bonnefond, & VanRullen, 2012; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Samaha, Iemi, & Postle, 2017; Schroeder & Lakatos, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). Benwell et al., (2017) reported that prestimulus power modulated specifically conscious perception and not objective behavioral performance.

Second, prestimulus neural activity could explain variations in perceptual decision making instead of directly influencing the visually evoked neural response. Baria, Maniscalco, and He (2017) showed that when the prestimulus activity patterns resemble a pattern evoked by the visual stimulus, correct behavioral discrimination is more likely, even when the participants report not consciously perceiving the stimulus. This type of explanation builds on the idea that when the participants report not seeing a stimulus—that is, when they subjectively have no stimulus-related information on what to base their response on—the response is determined largely by the prestimulus state. This reasoning is very different from current models of (un)conscious vision (Dehaene et al., 2006; Lamme & Roelfsema, 2000), which attribute the differences in responding to stimulus-evoked response strength.

In the current study, we randomly presented participants with a threshold-level low-contrast stimulus on either the left or right visual field and asked them to report in which visual hemifield the stimulus was presented and then rate how well they saw it (Figure 1A). We reasoned that we would have the highest chance of observing unconscious perception using this type of simple location discrimination task. Moreover, the left versus right location discrimination task allowed us to take into account if the lateralized EEG activity predicts performance in unconscious trials. We used single-trial analyses to test whether EEG predicts trial-by-trial variation in behavioral performance.

Materials and Methods

Participants

Thirty-four students (3/34 males, 3/34 left-handed) with a mean age of 24.4 (SD = 3.6) years and no neurological disorders participated in the experiment. Three participants were excluded before the EEG preprocessing because of a high false alarm rate (participants with false alarm rate > 0.3 were excluded; mean false alarm rate of the excluded participants was 0.59, SD = 0.26). The participants were students at the University of Turku. Each participant gave written informed consent. The study was conducted in accordance with the Declaration of Helsinki and was approved by the ethics committee of the Hospital District of Southwest Finland.

Stimuli

The experiment was run in MATLAB (version R2014b) using the Psychophysics Toolbox (Brainard, 1997). Stimuli were presented on an VIEWPixx/EEG LCD monitor with a 120 Hz refresh rate. The stimuli were Gabor patches (a diameter of 6.5° of visual angle and a frequency of 0.7 cycles/degree; the phase and orientation of the Gabor patch was randomly varied on each trial) presented on a gray 50% background (45.57 cd/m^2). On two-thirds of the trials, a low-contrast Gabor patch was presented.

The intensity of this low-contrast Gabor was individually adjusted to be near a 50% subjective detection threshold using a QUEST staircase (Watson & Pelli, 1983). On one-sixth of the trials, a high-contrast Gabor with three times higher contrast than the contrast of the low-contrast Gabor was presented. The high-contrast stimuli were presented to allow the participant to clearly see the stimuli every now and then, meaning they could use the whole visibility rating scale. Both low-contrast and high-contrast stimuli were presented for a duration of two frames (16.6 ms in total). One-sixth of the trials did not have any stimulus (catch trials), instead containing a blank screen with the fixation point lasting two frames. Only trials with the low-contrast stimuli were included in the statistical analysis.

Experimental design

The stimulus was presented after a fixation period that varied from 668 ms to 1332 ms from trial to trial to prevent the participant from learning to expect the stimulus at a specific delay. In addition, 250 ms after the Gabor was presented (or catch trial), the fixation point turned into an arrow pointing left and right, indicating that the participant should try to report the side of the target. After this, the numbers "0-1-2-3" were presented on the center of the screen to prompt a visibility rating response. Both responses were given by pressing a key on a numpad. The participants were told to try to give their best guess about stimulus location, even when they felt they did not see any stimulus. The visibility rating was given using a four-step scale where the alternatives were as follows: 0) "did not see stimulus at all," 1) "not sure but possibly saw something," 2) "pretty sure I saw it," and 3) "saw the stimulus clearly." The difference between alternatives 0 and 1 was stressed to the participant; that is, we emphasized that if they felt that they saw any glimpse of the stimulus, even an extremely weak one, they should select the second lowest alternative. The rating task was preferred over a yes/no task to make sure that the participants used a strict criterion for reporting stimuli "unconsciously." Throughout the present study, a participant is assumed to be unconscious of a stimulus only when she/he chose the lowest visibility rating (the three higher alternatives are all counted as conscious). No instruction was given about the response speed (of either response). The participants were also told that in some trials, the stimulus would not be presented, and they were told that on these trials, the correct response was to report that they did not see the stimulus. The experiment comprised a total of 400 trials per participant, subdivided into 10 blocks of 40 trials each.

EEG recording and preprocessing

A 64-channel EEG was recorded at a 500 Hz sampling rate (NeurOne Tesla amplifier). Before the recording, electrode impedances were brought near 5 kΩ. Two additional electrodes were used to record electro-oculograms (EOG): one electrode was placed beneath and the other beside the participant's left eye.

Preprocessing was carried out with MATLAB (version R2016b) using the EEGlab toolbox (version 14.1.1b). For each participant, bad channels (channels with no response or very noisy signals) were manually checked and interpolated. EEG data were rereferenced to the average of all electrodes. A 0.25 Hz high-pass filter and an 80 Hz low-pass filter were applied to the data. Line noise was cleaned up using the CleanLine EEGlab plugin. Data were epoched from -2000 ms to 1500 ms relative to the stimulus onset. Trials with eye movements (EOG electrodes) within -500 ms to 500 ms relative to the stimulus onset were discarded (on average, 24 trials, SD = 37 trials were rejected per participant). The locations of the electrodes were transposed so that the left hemisphere was always contralateral and the right hemisphere always ipsilateral relative to stimulus presentation. A time frequency analysis was performed on single trials using complex morlet wavelets (frequency range: 1–30 Hz with 2 Hz step size, with the number of cycles increasing linearly from 1 to 12). No baseline correction was applied because we examined the prestimulus oscillations.

Statistical analysis

Behavioral signal detection measures of sensitivity (d') and criterion (c) were calculated from binarized subjective visibility ratings. A hit was defined as a visibility rating of 1–3 when a stimulus was presented. False alarms were trials where the participant reported seeing a target (rating 1–3) when no stimulus was presented.

Time points between 1000 ms before stimulus onset in steps of 24 ms were statistically analyzed to examine if prestimulus oscillatory power predicted perceptual performance. These analyses were performed in a mass univariate manner (Maris & Oostenveld, 2007), analyzing all the time points and all frequencies between 1 and 30 Hz. Statistical analyses were performed on the single-trial data. We used mixed-effects logit models to test whether log transformed oscillatory power at specific time points and frequencies were predicted by the accuracy of the response (correct/incorrect) or subjective visibility (saw/did not see). In the mass univariate models, the participants were defined as random factors, and the intercepts were allowed to vary between participants. More complicated models often failed to converge, and the models also took very long to compute. Log transformed power was used as the predictor because untransformed data were strongly right skewed.

Statistical significance was assessed using permutation testing by randomly shuffling condition labels (1000 iterations). We used threshold free cluster enhancement (TFCE) to take into account the clustering of effects in neighbouring electrodes and time points (Smith & Nichols, 2009). Maps of the t values obtained from the mass univariate analyses were TFCE transformed using a function from the Limo EEG package (Pernet, Chauveau, Gaspar, & Rousselet, 2011). TFCE was also performed after each permutation, and the highest TFCE score ($TFCE_{max}$) of each permutation was saved to obtain a null distribution. TFCE values with the probability < .05 when compared with the $TFCE_{max}$ distribution were considered statistically significant. This type of analysis was performed on five different clusters of electrodes (see below).

We also analyzed ERPs and event-related spectral perturbations (ERSP) to examine how behavioral performance (subjective and objective measures) was associated with stimulus-evoked responses. These analyses were performed using a similar mass univariate approach as described earlier (mixed-effects logit models with random intercepts, 1000 permutations, and TFCE). Before ERP analysis, EEG was low-pass filtered at 40 Hz. Single-trial ERPs were baseline corrected to -200 ms. In standard ERSP analysis, multiple trials are averaged, and it is measured how EEG oscillatory power changes in response to a stimulus relative to some baseline state. Because we performed the ERSP analysis on single trials, we centered the oscillatory power at each poststimulus time point and frequency relative to the average power of a frequency band during the whole trial (-2 to 1.5 s relative to stimulus onset) (Grandchamp & Delorme, 2011).

Datasets are available for download at https://osf.io/xz8jr/.

Results

Behavioral results

On average, the participants reported seeing the target (visibility rating 1–3) in 51% of the trials (SEM = 14%) when the stimulus was presented. When the stimulus was not presented, they rarely reported seeing the target (9%, SEM = 8%). When the participants reported not seeing the target at all (visibility rating = 0), they nevertheless correctly reported the side of the stimulus in 60% of the trials on average (t test against chance-level: $t = 5.95$, $df = 30$, $p = 1.60 \times 10^{-6}$).

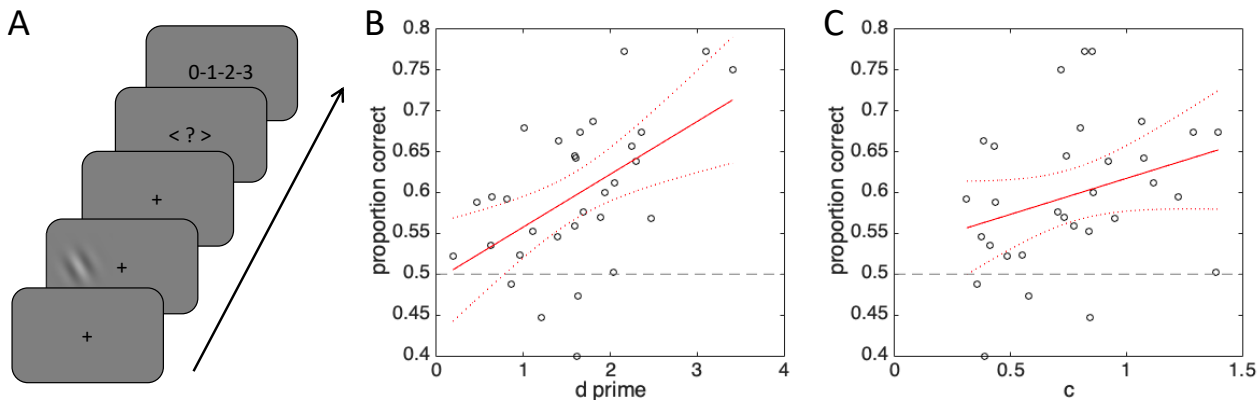

Figure 1. Behavioral paradigm and results. A) A schematic of a single trial: the participants gave a forced discrimination response and rated how well they saw the stimulus. B) Correlation between the sensitivity of subjectively detecting the stimulus and proportion correct (forced discrimination task) on subliminal trials. C) Correlation between criterion for reporting conscious perception and the correct proportion on subliminal trials.

Does accurate responses in the trials where the participants report no conscious perception reveal the existence of an unconscious perceptual capacity that functions independently of conscious perception? We calculated the participants' sensitivity and criterion for *consciously* detecting the target (i.e., the measures were calculated from subjective reports, not objective performance, using signal detection analyses). As shown in Figure 1B, the participants who were not sensitive to subjectively detecting the stimulus (d' ≈ 0) did not reveal subliminal perception (intercept of the linear model = .49). As shown in Figure 1C, the participants also tended to use a conservative criterion for reporting conscious perception. This is common with low-contrast stimuli because the participants try to minimize false alarms. Based on extrapolating the fitted linear model, if the participants used statistically optimal criterion (c = 0) for reporting consciousness, they would also have performed at near the chance level in discriminating the stimulus side of the subliminal trials (intercept = .53). These results indicate that correct discrimination performance is not fully separate from conscious vision but that the two phenomena lie on the same continuum.

Prestimulus correlates

We tested if prestimulus EEG power varied as a function of the participants' objective discrimination performance when they subjectively reported not seeing the target at all (the lowest visibility rating). Because the lateralization of cortical excitability varies depending on whether attention is focused toward the right or left visual hemifield (Thut et al., 2006; Worden, Foxe, Wang, & Simpson, 2000), we took this into account by transposing the electrode locations for each trial so that the left electrode locations represent electrodes that were contralateral with respect to the visual stimulus (and right electrodes were ipsilateral).

As shown in Figure 2A, objective performance on trials where the participants reported not seeing the stimulus at all predicted prestimulus power (i.e., lowest visibility rating). Oscillatory power at the occipital electrode clusters was predicted by the accuracy of responses up to 1 s before the stimulus was presented, even though the participants reported just guessing this. The effect is clearly lateralized: lower oscillatory power (1–15 Hz) contralateral to the stimulus and higher oscillatory power (1–5 Hz) in ipsilateral occipital electrodes predicts better performance. The strongest effects are observed in the occipital electrode clusters, but the frontal and central electrode clusters also show some effects. The results are relatively similar when consciously seen trials are included in the analysis (Supplementary Figure 1). When electrode locations were not transposed, only a weak prestimulus effect in the alpha band (up to 200 ms before stimulus onset) was observed (Supplementary Figure 2).

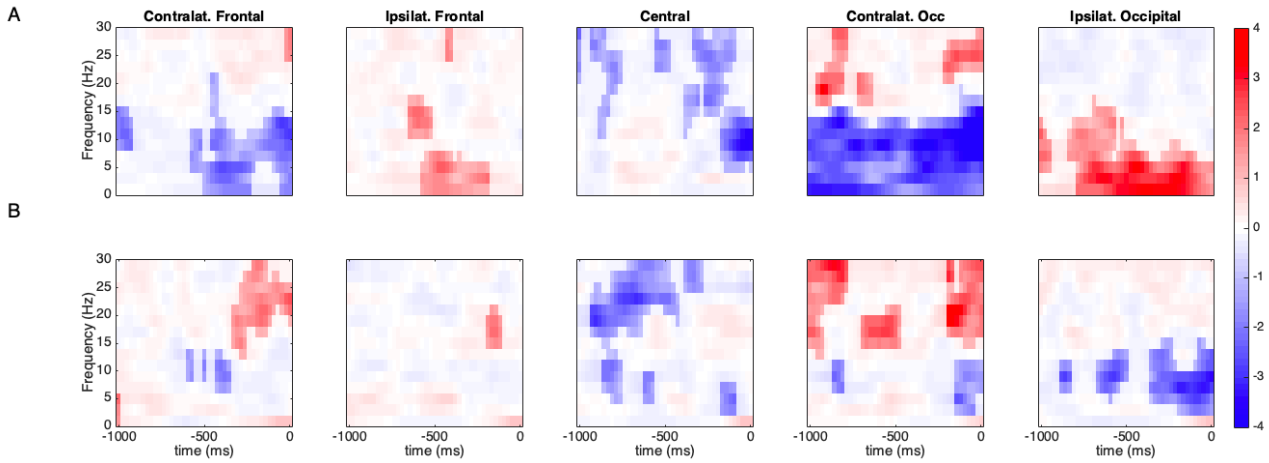

Figure 2. How behavioral performance predicts prestimulus oscillatory power. Results of mass univariate mixed-effects logit models where a single trial's prestimulus EEG power was predicted using A) the location discrimination accuracy on unconscious trials (visibility = 0) and B) binarized visibility ratings (did not see = 0; 1–3 = saw). Color is the t value of the mixed-effects logit model. The blue color denotes a negative correlation and red a positive correlation. The faint colors are time points/frequencies where the model does not statistically significantly predict EEG power. Bright colors show statistically significant modulation according to TFCE and permutation testing. Different columns represent different clusters of electrodes.

The prestimulus power in single trials was also associated with reported conscious visibility of the target in a trial-by-trial manner, as shown in Figure 2B. For instance, in the occipital electrode clusters, a lower power of around 5–10 Hz right before stimulus onset was predicted by conscious perception right before stimulus onset. Unlike in the case of accuracy of responding in unconscious trials, this effect does not show lateralization. A similar effect is also found when only trials with the correct objective discrimination accuracy are included in the analysis (Supplementary Figure 3).

The above results show that prestimulus power correlates with behavioral performance in reportedly unconscious trials. To see how well the participants' unconscious visual discrimination responses in single trials could be predicted based on the prestimulus oscillatory power, we ran a mixed-effects logit model that included the average power of the ipsilateral electrode cluster 668–190 ms before stimulus onset at 3 Hz and the average power in the contralateral electrode cluster 190–71 ms before stimulus onset across 5–9 Hz (but not their interaction). These frequencies/time windows were selected because the strongest prestimulus effects cluster around them. The time points right before or around stimulus onset were not included in these models to minimize the possibility that wavelet transformation "contaminated" the estimated prestimulus effects with visually evoked responses. The random subject structure of the logit model included separate intercepts for each participant. This classifier's area-under-the-curve (AUC) was 65%, which is very good performance given that the model was classifying the responses that the participants subjectively labeled as random guesses. Interestingly, the interaction between the contralateral and ipsilateral cluster predictors did not increase classifier performance (interaction t = -0.44). This suggests that the prestimulus power in the contralateral and ipsilateral sites contributed independently to discrimination accuracy.

Event-related potentials

What is the mechanism through which spontaneous prestimulus power influences the discrimination of reportedly unconscious stimuli? High-amplitude, low-frequency oscillations have been associated with suppressing the processing of nonrelevant signals, whereas low-amplitude, low-frequency power is associated with amplifying sensory input (Schroeder & Lakatos, 2009). The lateralized contribution of an occipital prestimulus oscillatory power on unconscious discrimination

performance suggests that successful behavioral responding to unconscious trials may be related to enabling strong responses to the (contralateral) visual stimulus while suppressing unwanted signals in the opposite (ipsilateral) visual field (where no target is presented). If this is the case, we should observe enhanced visually evoked responses to correctly discriminate unconscious targets (when compared with the trials of incorrect responses).

To examine how objective discrimination accuracy and subjective visibility of the stimulus influences stimulus-evoked activity, we analyzed ERPs in a single-trial manner. As in the prestimulus analyses, the electrode locations in these analyses were transposed so that in the scalp maps, the left hemisphere locations would correspond to the contralateral hemifield. As shown in Figure 3A, thee subjective visibility are associated with a strong increase of ERP amplitudes 275 ms after stimulus onset, here spanning most electrode locations. Nearly identical effects are produced by when objective discrimination performance is examined (all trials, Supplementary Figure 4). However, as shown in Fig. 3B, no strong effects are seen when the analysis is restricted to unconscious trials. The only (weakly) statistically significant effect is enhanced late ERPs (around 475 ms) to targets that were correctly discriminated, despite being reported unconscious. Therefore, these results do not support the conclusion that successful unconscious perceptual discrimination is enabled by a stronger visually evoked response.

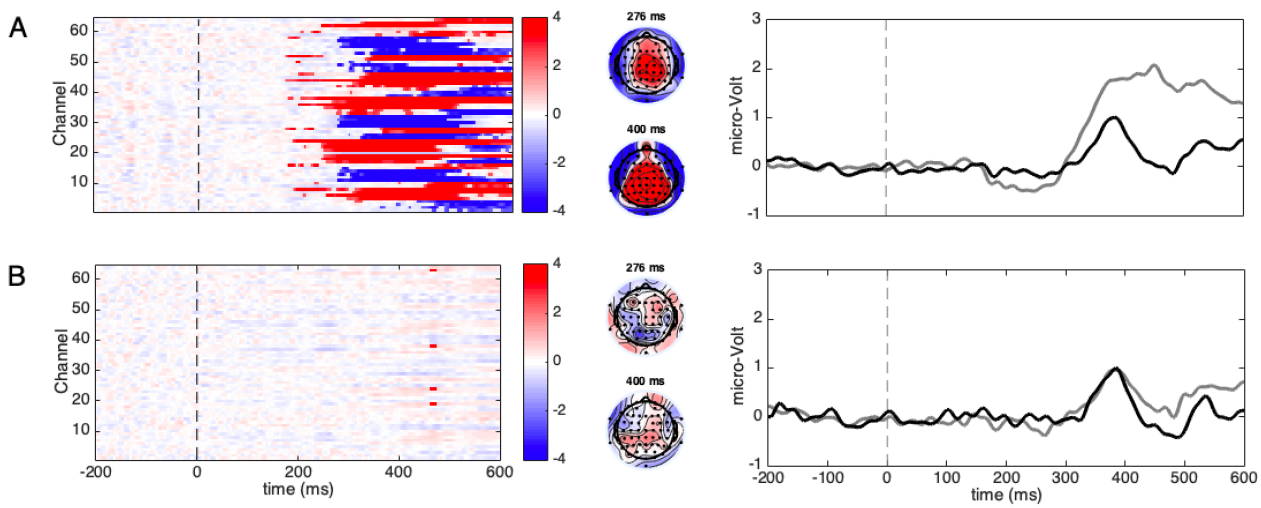

Figure 3. Event-related potentials. A) Single-trial visibility ratings (top panels) predicted ERPs 275 ms after stimulus onset. B) When only reportedly unconscious trials were included in the analysis (bottom panels), no strong effects were observed. The figures on the left show the results of the mass univariate mixed-effects regression models. Color denotes t value, and statistically significant effects (based on TFCE) are shown with a bright color. The middle panels show scalp topographies of the effects at 276 ms and 400 ms after stimulus onset (note that the electrode locations have been transposed: electrodes over the left scalp locations are contralateral to the stimulus). The rightmost panels show ERPs measured at the contralateral occipital cluster. The gray line depicts consciously seen (top panels) or correctly discriminated (middle/bottom panels) trials, and the black line depicts not consciously seen (top panels)/incorrectly discriminated trials (middle/bottom panels).

Next, we asked how prestimulus oscillatory power influences ERPs. If the prestimulus process that mediates accurate unconscious discrimination relates to fluctuations in cortical excitability, we should be able to observe that the contralateral occipital power is inversely related to ERP amplitude. We examined whether single-trial oscillatory power in the same frequencies/time windows that predicted objective behavioral performance (ipsilateral electrode cluster: 668–190 ms before stimulus onset at 3 Hz and contralateral electrode cluster: 190–71 ms before stimulus onset at 5–9 Hz) also

predicted ERP amplitude. We first included all trials (unconscious and conscious) in the analysis. These results are shown in Figure 4A. Contralateral occipital prestimulus power predicted ERP amplitude between roughly 0–400 ms after stimulus onset. Strong contralateral occipital power predicted more negative ERPs in frontal electrodes (i.e., negative correlation; blue color in Figure 4A) and more positive ERPs in contralateral occipital electrodes (positive correlation; red color in Figure 4A). This is consistent with the observed relationship between ERPs and visual behavioral performance. For example, as shown in Figure 3, better behavioral performance is associated with more positive ERPs in frontal sites between 275–400 ms. These observations suggest that fluctuations in prestimulus power do not directly predict stronger ERPs, but prestimulus EEG activity does modulate the activity in similar time windows and sites as conscious visibility. Ipsilateral occipital prestimulus power did not predict ERP amplitudes.

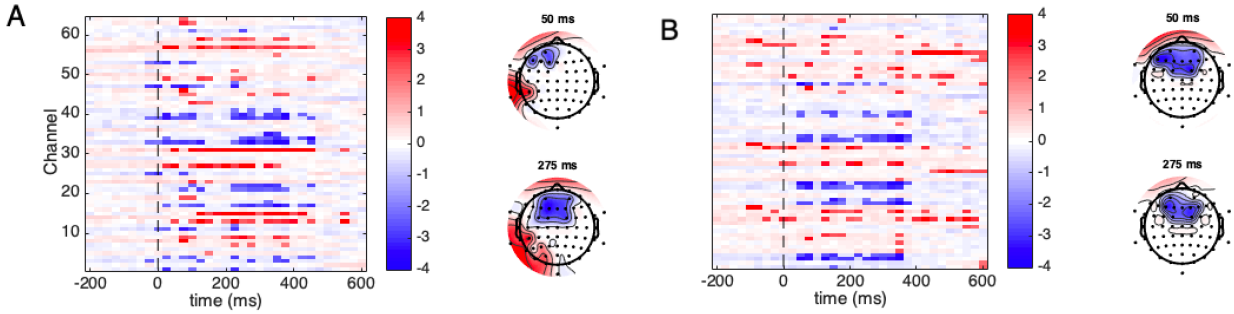

Figure 4. Influence of single-trial prestimulus oscillatory power on stimulus-evoked ERPs. A) Effect of contralateral occipital prestimulus power on ERPs when the analysis includes all trials. B) Same analysis when only reportedly unconscious trials are included. The rectangular colormap plot shows the results of the mass univariate linear mixed-effects models. Color represents the t value. A strong color represents statistically significant effects, as determined by TFCE. Scalp maps show the distribution of the effects at 50 and 275 ms (note that the electrode locations have been transposed: left "hemisphere" electrodes are contralateral to the stimulus).

Next, we tested whether any relationship between the prestimulus oscillatory power and stimulus-evoked ERPs would be observed if the analysis was restricted to trials where the participants reported not seeing the target at all. As shown in Figure 4B, stimulus-evoked ERP amplitude at the frontal electrodes was found to be modulated by prestimulus power in the same way as previously described. Ipsilateral occipital prestimulus power did not predict ERP amplitudes when only reportedly unconscious trials were included in the analysis. In sum, these results show that on trials where the participants reported not seeing a stimulus, fluctuations in prestimulus power (in frequency/time windows that predicted unconscious perception) modulated ERP amplitudes in the frontal electrodes.

Event-related spectral perturbations

We also examined how behavioral performance was related to stimulus-evoked changes in oscillatory power (ERSPs). As shown in Figure 5B (lower panels), single-trial ERSPs were strongly predicted by stimulus visibility (very similar effects were observed for objective discrimination performance, as shown in Supplementary Figure 5). Higher visibility of the stimulus was associated with higher ERSP responses 100–400 ms after stimulus onset. Around 300 ms after stimulus onset, stimulus visibility correlated negatively with ERSP amplitude (roughly frequencies 7–30 Hz). These observations replicate previous findings (Bareither et al., 2014; Li, Hill, & He, 2014).

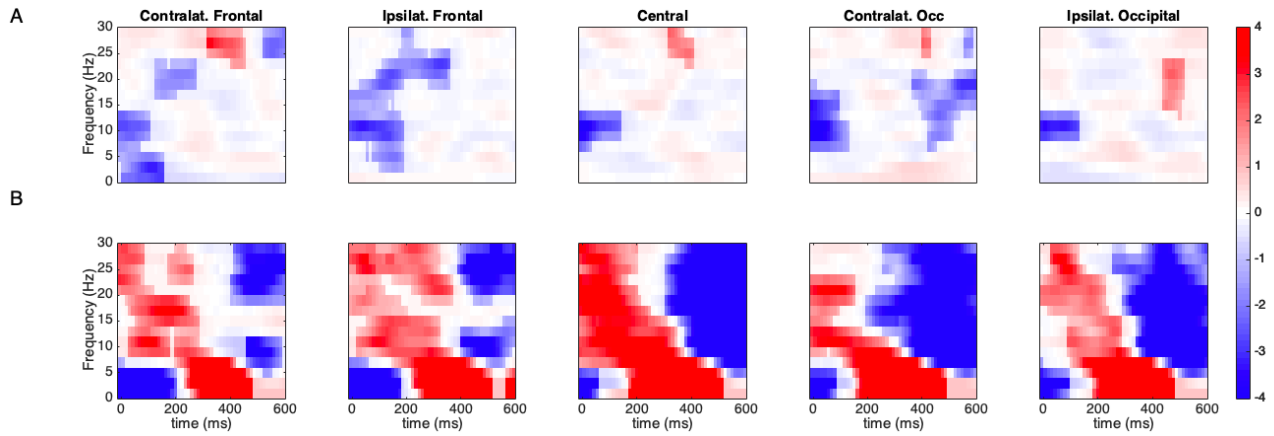

Figure 5. How behavioral performance predicts ERSP amplitude. Results of the mass univariate mixed-effects logit models where ERSP amplitude is predicted using single-trial A) location discrimination accuracy in subliminal trials (visibility = 0) and B) binarized visibility ratings (did not see = 0; 1–3 = saw). Color is the t value of the mixed-effects logit model. A blue color denotes a negative correlation and red a positive correlation. The faint colors are time points/frequencies where the model does not statistically significantly predict the behavioral outcome. Bright colors show statistically significant modulation according to TFCE and permutation testing. Different columns represent different clusters of electrodes.

Objective discrimination performance in single trials where the participants reported not seeing the target modulated ERSPs clearly to a lesser extent (Figure 5A). What is noteworthy is that an ERSP amplitude between 100–400 ms in occipital electrodes—where the strongest stimulus-evoked activation is expected—showed very weak modulation by unconscious discrimination accuracy. In occipital electrode clusters, the strongest effect was observed after 400 ms of stimulus onset in the contralateral cluster (around 15–20 Hz). As seen in Figure 5A, there were also some earlier effects in the frontal areas (e.g., ipsilateral cluster, roughly between 100–200 ms poststimulus).

Finally, we examined how single-trial variation in prestimulus power influenced ERSPs. As earlier, we restricted this analysis to the two prestimulus correlates that predicted behavioral performance in unconscious trials. Figure 6 shows the results when the analysis included only reportedly unconscious trials. Figure 6A shows how 5–9 Hz contralateral occipital prestimulus power influenced ERSPs. Remember that 5–9 Hz contralateral occipital prestimulus power was inversely related to behavioral performance in the unconscious trials (Figure 2): the lower the prestimulus power, the higher the likelihood of a correct response. As shown in Figure 6A (upper row), the pattern is different when the influence of the contralateral prestimulus power to ERSP is examined: the higher the prestimulus power, the higher the response to the stimulus is at the same frequency range (5–9 Hz) right after stimulus onset (0–200 ms). This correlation may be trivial in the sense that the result merely shows that when the power is high right before stimulus onset, it is also likely high right after stimulus onset. However, after about 300 ms after stimulus onset, the effect reverses into a negative correlation. Overall, the pattern of modulation by contralateral prestimulus power resembles the correlates of stimulus visibility (compare Figure 7 upper row to Figure 6 lower row). This finding is paradoxical because it seems to conflict with the relationship prestimulus power had with the behavioral discrimination accuracy: the higher the contralateral prestimulus power was, the less likely were the participants to correctly discriminate the location of an unconscious stimulus. However, paradoxically, the effect of high contralateral prestimulus power on poststimulus ERSP was comparable to the correlates of subjective visibility.

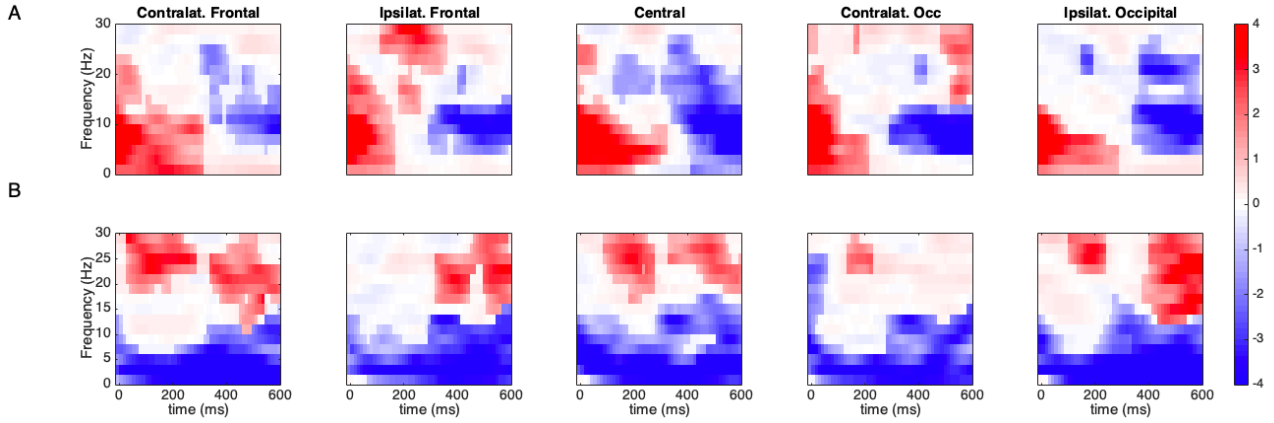

Figure 6. Influence of single-trial prestimulus oscillatory power on ERSP amplitude. A) How 5–9 Hz contralateral occipital prestimulus power influenced ERSPs. B) How 3 Hz ipsilateral occipital prestimulus power influenced ERSPs. Color is the t value of the mixed-effects logit model. A blue color denotes a negative correlation and red a positive correlation. The faint colors are the time points/frequencies where the model does not statistically significantly predict the behavioral outcome. The bright colors show statistically significant modulation according to TFCE and permutation testing. Different columns represent different clusters of electrodes.

Ipsilateral occipital 3 Hz prestimulus activity showed a different pattern: the higher the ipsilateral occipital prestimulus power, the weaker the ERSP response in low frequencies was (Figure 6B). Weak ERSP responses at low frequencies implies that stimulus-related processing was suppressed (strong low-frequency ERSP response was associated with high stimulus visibility, Fig. 5B). This is consistent with the idea that accurate discrimination of stimuli has to do with suppressing unwanted activation from the ipsilateral visual field.

Discussion

We investigated what factors may explain why behavioral visual discrimination accuracy can be on average above the level of chance, even though the participants subjectively report guessing. Our results reveal the following: First, unconscious perceptual performance was not completely independent of conscious introspection, as measured by the signal detection theory. Second, lateralized neural activity up to 1 s before stimulus presentation predicted behavioral performance even when the participants reported just making guesses (AUC = 65%). Interestingly, a similar effect was not observed for stimulus-evoked responses, although the visual stimuli participants reported not seeing still evoked clear electrophysiological responses (as measured by ERP/ERSP). Third, lateralized prestimulus activity in occipital electrodes was shown to influence stimulus-evoked electrophysiological responses in a complicated way. In part prestimulus activation may influence unconscious perception by suppressing stimulus evoked activation in the visual space where no stimulus was presented. However, by and large, the results do not support the view that trial-by-trial variation in behavioral performance in unconscious trials can be accounted for by variation in stimulus evoked response.

Our behavioral results suggest that the performance on reportedly unconscious trials was not completely independent of the participants' introspective abilities, at least based on the signal detection theoretic metrics of sensitivity and criterion. By saying that "unconscious" perception may be accompanied by introspective (i.e., conscious) access to the visual information, we do not wish to imply that the participants simply saw the stimuli. Obviously, they did not. When they reported not seeing the stimulus, they also often did not know the location of the stimulus (unconscious discrimination accuracy was only 60% on average). This means that the participants were effectively

blind to the stimuli on most of the trials. However, our behavioral results suggest that the above chance behavioral performance on these "unconscious" trials may nevertheless be based on signals—barely different from the "noise"—that the participants could introspect and base their response to. Part of the difficulty in answering whether these signals were really unconscious or not is that it requires us to binarize (saw vs. did not see) a process that is continuous. Second, whether the nature of the information on what the participants based their decision on was visual or not could be debated, but this is mostly a semantical question: the key point is that on some trials, the percept seemed to be informative about the location of the stimulus. Finally, by and large "objective" visual discrimination behavior and subjectively experienced perception evoked nearly identical ERP/ERSP responses, suggesting that the two are not strongly dissociated.

Why did the accuracy of behavioral discrimination on unconscious trials not modulate ERP/ERSP amplitudes if prestimulus fluctuations in EEG power did influence them? This could be because the statistical power for detecting how prestimulus power influences ERPs/ERSPs is higher because the analysis was based on continuous regressors rather than on a categorical behavioral outcome (i.e., correct versus incorrect responses). Although we collected visibility ratings using a four-step scale, we decided to binarize the categories because the participants mostly used the two lower alternatives. Moreover, dichotomization of seen/not-seen ratings allowed for straightforward testing of the mechanisms of unconscious vision, which was the major goal. That is, we defined "unconscious" by equating it with the lowest visibility rating (Overgaard, 2011; Ramsøy & Overgaard, 2004).

Previously, Baria et al. (2017) showed that participants' behavioral responses on unconscious trials could be predicted from prestimulus activity patterns: when prestimulus activity resembled left stimulus-evoked responses, the participants were more likely to respond "left." Because we transposed our electrode locations to correspond to contralateral versus ipsilateral space, our analysis was sensitive to the spatial pattern of the evoked response. Our motivation to transpose electrode locations to contralateral versus ipsilateral space was partly that the lateralization of prestimulus power could explain how strongly the visual system responds to a visual stimulus in the contralateral visual field. This type of mechanism is unlikely to explain our findings because we did not observe differences in ERP/ERSP amplitudes 100–400 ms after stimulus presentation during the unconscious trials. That said, high ipsilateral prestimulus power was associated with weak low-frequency ERSP power, suggesting that accurate unconscious discrimination may in part be because of successful inhibition of noise in the ipsilateral (nontarget) hemisphere.

Based on previous studies (Koivisto & Grassini, 2016; Lamy et al., 2009) and models of (un)conscious vision (Dehaene et al., 2006; Lamme & Roelfsema, 2000), we expected that ERP amplitudes over visual cortical areas would correlate with both stimulus visibility and unconscious discrimination performance at around 200 ms poststimulus (i.e., VAN). The results do not support this conclusion because VAN did not reach statistical significance, and it also did not correlate with unconscious discrimination. Koivisto and Grassini (2016) observed that VAN amplitude correlated with discrimination performance when the participants reported not seeing the stimulus. Unlike in the present study, Koivisto and Grassini (2016) used a four-alternative discrimination task. The higher spatial uncertainty associated with four possible stimulus positions (in contrast to two positions in the present study) may have enabled the use of higher contrast stimuli, which could imply a higher power to detect amplitude differences in the VAN time window. Another interesting difference between many previous studies that have detected VAN and the present study is that previous studies that have observed a strong VAN have typically used a reference electrode in the nose (e.g., Koivisto & Grassini, 2016). Possibly, the noise reference allows for better sensitivity to detect occipital effects, such as VAN. Finally, unlike Koivisto and Grassini (2016), who performed their analysis on amplitudes averaged over a time window, we performed a mass univariate analysis, which somewhat weakens our statistical power for detecting small amplitude differences. In sum, we conclude that the absence of statistically significant associations between occipital ERPs and behavioral

performance/prestimulus oscillations should not be taken as evidence that such effects and mechanism do not exist.

Interestingly, contralateral occipital prestimulus power predicted ERP amplitude selectively in frontal areas, but not in occipital areas, when only the unconscious trials were included in the analysis. Although the location of ERP effects on the scalp do not allow for direct conclusions about the cortical generators of the effect, it is nevertheless noteworthy that the strongest association was observed in frontal electrodes (the strongest visual stimulus driven activity is typically observed in occipital electrodes). We suggest that this frontally localized effect may indicate that contralateral occipital prestimulus activity influenced how well the visual stimuli triggered activation in the frontal cortical mechanisms that underlie decision making. Because the location—and to some extent the timing—matches frequently observed neural correlates of conscious vision (P3 wave; Dehaene & Changeux, 2011; Förster et al., 2020), this could mean that contralateral occipital prestimulus fluctuations influenced how available the weak visually evoked activation was to frontal mechanisms underlying behavioral decisions. Prefrontal decision-making mechanisms can be activated by unconscious stimuli (Lau & Passingham, 2007; Van Gaal, Ridderinkhof, Scholte, & Lamme, 2010). Studies have also reported that activity in the frontal cortical areas correlates with unconscious behavioral performance (Lau & Passingham, 2006) and consciousness (Persaud et al., 2011) in blindsight patients.

Our results are interesting when considered from the perspective of blindsight patients. Blindsight capacity has been traditionally explained by referring to the anatomical pathways that bypass the primary visual cortex (Ajina & Bridge, 2018; Ajina, Pestilli, Rokem, Kennard, & Bridge, 2015; Azzopardi & Cowey, 1997; Cowey, 2010; Danckert & Rossetti, 2005; Weiskrantz, Warrington, Sanders, & Marshall, 1974). An interesting open question is to what extent prestimulus processes also contribute to blindsight. Previous studies on blindsight patients have focused on stimulus-evoked neural activation but have not considered what neural mechanisms modulate trial-by-trial variability in blindsight capacity. The present results resonate nicely with Ko and Lau (2012), who suggested that blindsight patients fail to adapt a proper criterion of conscious perception after a lesion. We suggest that unconscious perception in healthy individuals may similarly reflect fluctuations in how well visual perceptual information can be accessed by frontal decision-making mechanisms.

In conclusion, our results show that unconscious perception should not be seen as a passive, automatic perceptual capacity whose neural mechanism relates to how strongly the visual system responds to a stimulus. Instead, accurate objective visual discrimination of unconscious trials depends on the state of the brain right before the stimulus is presented.

Authors' roles

H.R. designed the experiment, supervised data collection, and wrote the manuscript. R.P. and H.R. analyzed the data. R.P. and K.L. collected the data and commented the manuscript.

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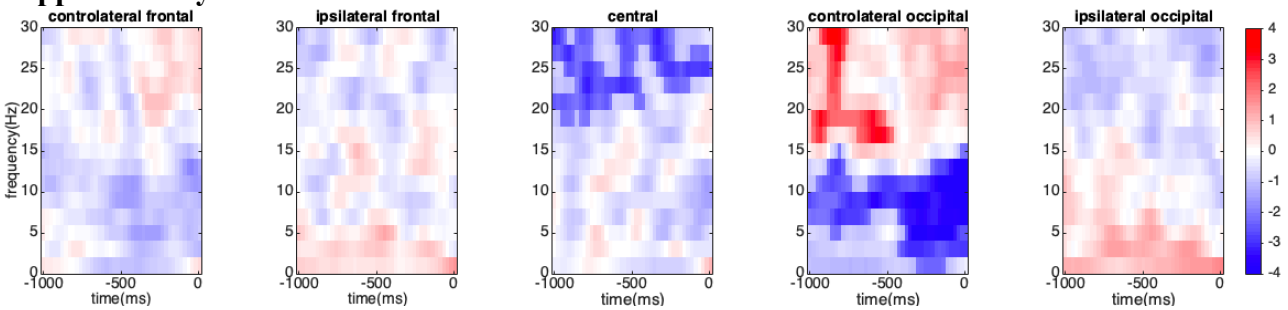
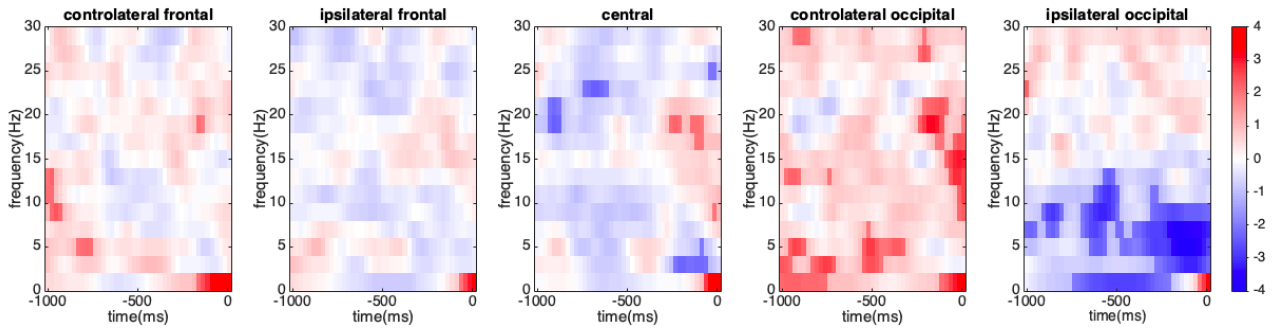
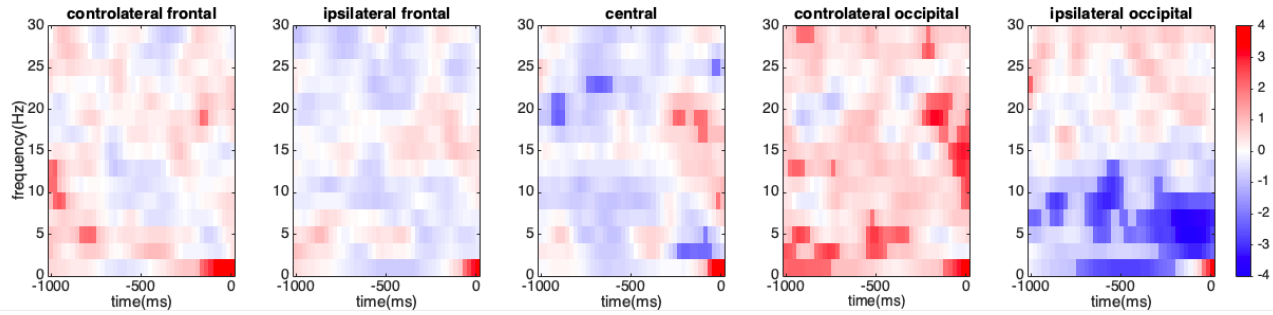
Supplementary information



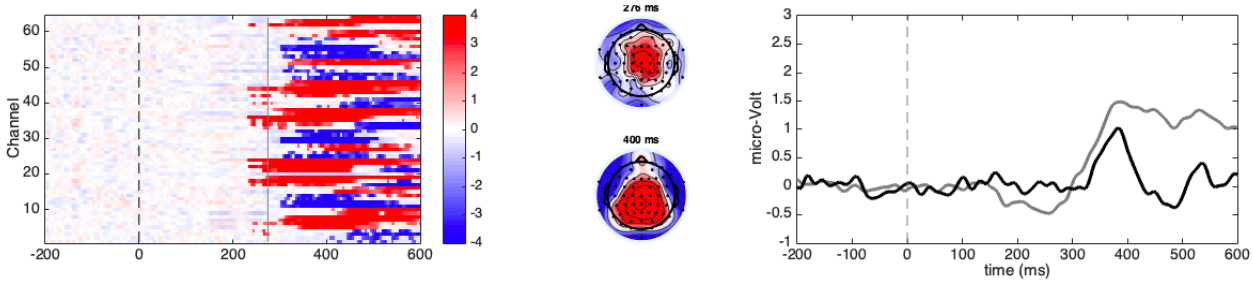
Supplementary Figure 1. Predicting prestimulus power using the accuracy of objective discrimination. This analysis includes trials where the participants reported seeing the target, along with the trials where they reported not seeing the target. Color represents the t value. A bright color represents statistically significant effects according to cluster mass permutations test.



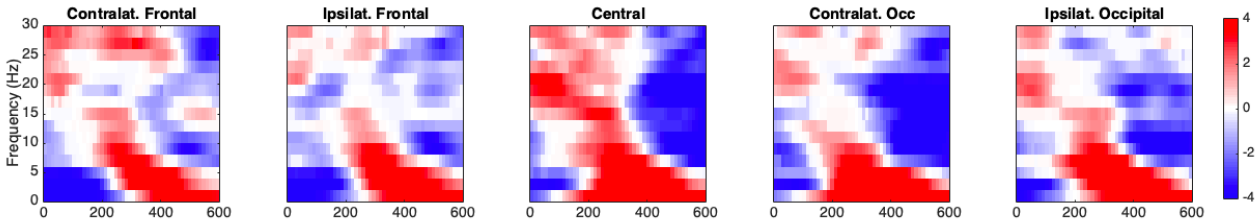
Supplementary Figure 2. Nontransposed stimulus locations: Predicting prestimulus power using response accuracy (only trials with visibility rating = 0 included). Not corrected for multiple comparisons.



Supplementary Figure 3. Predicting prestimulus power using visibility (unconscious vs. conscious) when only the trials where correct forced-choice answer was given are included. Not corrected for multiple comparisons.



Supplementary Figure 4. Objective discrimination performance, when both consciously seen and not seen trials are included in the analysis, modulates ERPs very similarly as subjective visibility.



Supplementary Figure 5. Objective discrimination performance, when both consciously seen and not seen trials are included in the analysis, modulates ERSPs very similarly as subjective visibility.