Subliminal perception can be predicted from prestimulus activity

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Abstract
A fundamental open question is vision science is why humans can make accurate guesses about stimuli they report not consciously seeing. We show that the objective accuracy of discriminating the location of a subliminal stimulus can be predicted in trial-by-trial manner from low frequency (1–15 Hz) electroencephalographic activity present before the stimulus. Accurate discrimination of subliminal stimulus location was supported by prestimulus neural activity that optimally suppressed non-relevant ipsilateral cortical signals or increased the excitability of contralateral visual cortex to weak stimuli. The effect was present up to 1 second before the stimulus was presented. Signal detection analyses indicated that this subliminal perceptual capacity lied on the same continuum as conscious vision. The results demonstrate that subliminal perception is not a distinct capacity, but relies on the same top-down mechanisms as conscious vision.

Visual stimuli that individuals report not consciously perceiving can influence their behavior, a phenomenon known as "subliminal perception" [1]. Previously, unconscious perception has been explained by referring to stimulus-evoked processes, either anatomic pathways[2] or modes of neural activity[3] which do not trigger consciousness. Another possibility is that subliminal vision reflects different sensitivities of measures subjective vision (e.g. a rating scale) and objective performance (e.g. a forced-choice response)[4,5]. All previous models of subliminal vision emphasize stimulus evoked activity, but neglect prestimulus activation. We reasoned that subliminal perception could be explained by spontaneous variation in neural activity before stimulus presentation as recent views emphasize the importance of top-down modulation of visual cortical activity[6]. Many studies have shown that visual perception is strongly influenced by low-frequency oscillations, especially the alpha (8–13 Hz) oscillations, before stimulus presentation[7–11]. These studies examined conscious visual perception. Here, we are specifically interested in what happens during those trials on which the participants report not seeing the stimulus subjectively (even though it was presented).

We presented participants (N = 31) with a threshold-level low-contrast stimulus randomly on either the left or right visual field, and asked them to report on which visual hemifield it was presented and rate how well they saw it (Fig. 1A). The participants reported seeing the target (visibility rating 1–3) on average on 51% of 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 on average on 60% of trials (t test against chance-level: $t = 5.95$, $df = 30$, $p = 1.60 \times 10^{-6}$). This capacity to objectively discriminate stimulus location above chance-level when the participant reports subjectively not seeing the stimulus at all is what we refer to as *subliminal perception*.

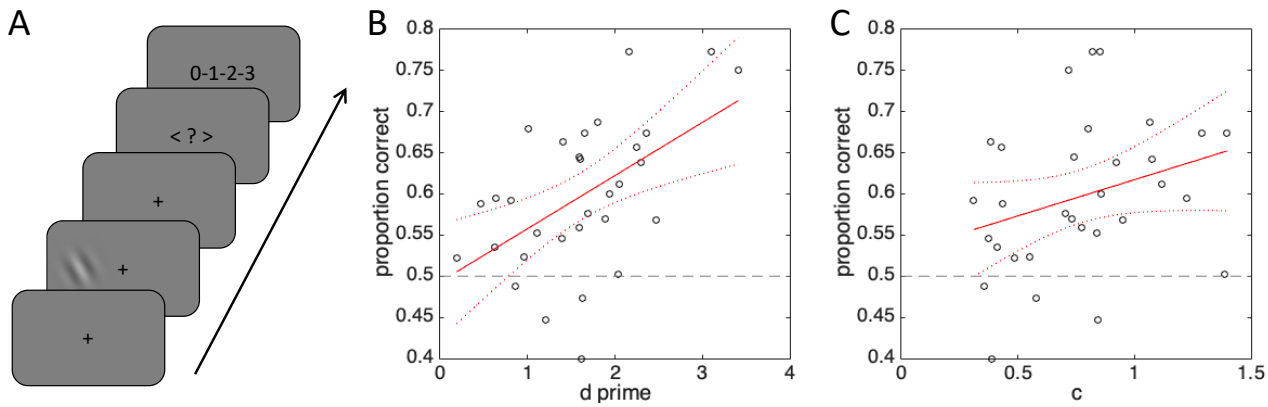

Figure 1. Behavioral paradigm and results. A) A schematic of a single trial: participants gave a forced discrimination response and rated how well they saw the stimulus. B) Correlation between sensitivity of subjectively detecting the stimulus and proportion correct (forced discrimination task) on subliminal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

Does subliminal perception reveal the existence of an unconscious perceptual capacity that functions independently of conscious perception? We calculated the participants' sensitivity and criterion to *consciously* detect the target (i.e. the measures were calculated form subjective reports, not objective performance) using signal detection analyses. As shown in Figure 1B, participants who were not sensitive to subjectively detect the stimulus (d' ≈ 0) did not reveal subliminal perception (intercept of the linear model = .49). As shown in Figure 1C, participants also tended to use 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, had the participants used statistically optimal criterion (c = 0) for reports of consciousness, they would also have performed near chance-level in discriminating stimulus side on subliminal trials (intercept = .53). These results suggest that subliminal perception is not an unconscious capacity that is separate from conscious vision, but that the two phenomena lie on the same continuum[12].

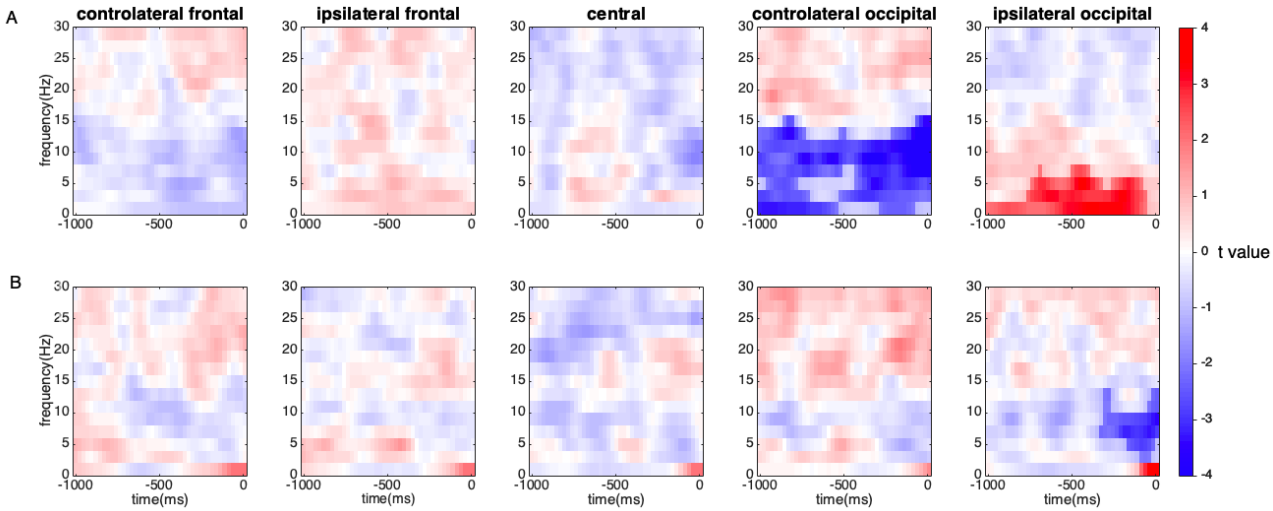

Figure 2. EEG results. Results of mass univariate mixed-effects logit models on single trials used to predict A) location discrimination accuracy on subliminal trials (visibility = 0), and B) binarized visibility ratings (did not see = 0; 1–3 = saw). Color is the t value of the mixed-effects logit model. Blue color denotes negative correlation and red color 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 the cluster mass permutation tests. Different columns represent different clusters of electrodes.

Next, we tested if prestimulus EEG power predicts the participants' objective discrimination performance when they subjectively report not seeing the target at all (lowest visibility rating). Because the lateralization of cortical excitability varies depending on whether attention is focused towards the right or left visual hemifield [13,14], we took this into account in our analyses by transposing electrode locations for each trial so that left electrode locations represent electrodes which were contralaterally with respect to visual stimulus (and right electrodes were ipsilateral). As shown in Figure 2A, prestimulus power predicts objective performance on trials where the participants report not seeing the stimulus at all (i.e. lowest visibility rating). Occipital electrode clusters predict accuracy of responses up to 1 second before the stimulus is presented. 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. Results are relatively similar when also consciously seen trials are included in the analysis (Supplementary

Figure 1). When electrode locations were not transposed, only a weak prestimulus effect in alpha band (up to 200 ms before stimulus onset) was observed (Supplementary Figure 2).

To see how well participants' subliminal visual discrimination responses can be classified based on the prestimulus oscillatory power, we ran a mixed-effects logit model that included average power on the ipsilateral electrode cluster 668–190 ms before stimulus onset at 3 Hz, and average power in the contralateral electrode cluster 190–71 ms before stimulus onset across 5–9 Hz (but not their interaction). Random-subject structure 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 responses which the participants subjectively labelled 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 prestimulus power in contralateral and ipsilateral sites contributed independently to discrimination accuracy.

High amplitude low-frequency oscillations have been associated with suppressing the processing of non-relevant signals, whereas low amplitude low-frequency power is associated with amplifying sensory input[9]. Consequently, the lateralization of the prestimulus effect suggests that subliminal visual perception is explained by how successfully oscillatory activity is in suppressing unwanted neural activity (related to the information coming from the ipsilateral visual hemifield where no stimulus is presented) and amplifying stimulus-relevant neural activity (related to contralateral hemifield where the weak stimulus is presented). Put differently, conditions that support discriminating signal from the background noise increase the probability of accurate subliminal forced-choice responses. Signal detection analyses suggested that this capacity to discriminate subliminal stimuli was not completely independent of introspective access[12].

The prestimulus correlates are “spontaneous” in the sense that they are not triggered by an external stimulus. However, the fluctuations in spontaneous activity could be “endogenously” under the participant’s voluntary influence. Phenomenologically, the fluctuations in the lateralization of low-frequency power may correspond to the participant subjectively focusing attention to either the left or the right visual field, trying to anticipate the location where the stimulus will be presented. While our results suggest that this effect is strongest over posterior sites, the top-down control of this activity may be influenced by frontal/parietal cortical areas [15,16], or subcortical structures such as the pulvinar [17,18].

Some previous studies have reported that prestimulus power correlates with subjective visibility irrespective of accuracy [7,19]. As shown in Figure 2B, this finding is replicated in our data: the power of 5–14 Hz oscillations ipsilateral to the stimulus 300–0 ms before stimulus onset were negatively associated with subjective visibility. Note that the direction of this correlation is opposite than what was observed for subliminal discrimination (other electrode clusters show a more similar pattern, although not statistically significant for visibility). As shown in Supplementary Figure 3, a similar but stronger effect of visibility was observed when the analysis was restricted to correct trials. The prestimulus correlate of visibility could reflect generally higher excitability in visual cortex[19], which could help drive recurrent activation with other brain areas assumed crucial for conscious perception, and cross the decision boundary participants use to report conscious perception[20].

In conclusion, our results show that subliminal perception should not be seen as a passive, automatic perceptual capacity. Instead, accurate objective visual discrimination is more likely when the brain state before the presentation of the stimulus is in position that favors suppression of non-stimulus related activity or amplification of stimulus-evoked activation.

Methods

Participants

Thirty-four students (3 males, 3 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 due to high false alarm rate (participants with false-alarm rate > 0.3 were excluded; mean false-alarm rate of excluded participants was 0.59, SD = 0.26). Participants were students at the University of Turku. Each participant gave written informed consent before the experiment.

Stimuli and procedure

The experiment was run in MATLAB (version R2014b) using the Psychophysics Toolbox [21]. Stimuli were presented on an VIEWPixx/EEG LCD monitor with a 120 Hz refresh rate. Stimuli were Gabor patches (diameter of 6.5° of visual angle and a frequency of 0.7 cycles/degree, phase and orientation of the Gabor patch was randomly varied on each trial) presented on a grey 50% background (45,57 cd/m^2). On 2/3 of trials a low contrast Gabor patch was presented. This intensity of this low contrast Gabor was individually adjusted to be near 50% subjective detection threshold using a QUEST staircase [22]. On 1/6 of trials a high contrast Gabor with three times higher contrast than the contrast of the low contrast Gabor was presented. High-contrast stimuli were presented to allow the participant to clearly see stimuli every now and then, which meant that they could use the whole visibility rating scale. Both low contrast and high contrast stimuli were presented for a duration of 2 frames (16.6 ms in total). 1/6 of trials did not have any stimulus (catch trials), but instead a blank screen with the fixation point lasting 2 frames.

The stimulus was presented after a fixation period that varied from 668 ms to 1332 ms from trial to trials in order to prevent the participant from learning to expect the stimulus at specific

delay. 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, 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. Visibility rating was given using a four-step scale where the alternatives were: 0) "did not see stimulus at all", 1) "not sure but possibly saw something", 2) "pretty sure I saw it", and 3) is "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 extremely weak, they should select the second lowest alternative. Rating task was preferred over a yes/no task to make sure that the participants use a strict criterion for reporting stimuli “unconscious”. Throughout the present study a participant is assumed to be unconscious of a stimulus only when she chose the lowest visibility rating (the three higher alternatives are all counted as conscious). No instruction was given about response speed (of either response). Participants were also told that in some trials the stimulus is not presented, and they were told that on these trials the correct response is to report that they did not see the stimulus. The experiment comprised a total of 400 trials per participant, subdivided in 10 blocks of 40 trials each.

EEG recording and preprocessing

64-channel EEG was recorded at 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 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 signal) were manually checked and interpolated. EEG data was re-referenced to the average of all electrodes. A 0.25 Hz high-pass filter, and an 80 Hz low-pass filter was applied to the data. Line noise was cleaned using the CleanLine EEGlab plugin. Data were epoched from -2000ms to 1500ms relative to stimulus onset. Trials with eye movements (from EOG electrodes) within -500 ms–500 ms relative to stimulus onset were discarded (on average 24 trials, SD = 37 trials, were rejected per participant). Electrodes locations were transposed so that the left hemisphere was always contralateral and the right hemisphere always ipsilateral relative to stimulus presentation. Time-frequency analysis was performed on single-trials using complex morlet wavelets (frequency range: 1-30 Hz with 2 Hz step-size, and the number of cycles increasing linearly from 1 to 12). No baseline correction was applied because we examine 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 visibility rating 1–3 when a stimulus was presented. False alarms were trials where 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 analyzes were performed in mass univariate manner, analyzing all 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 if log transformed oscillatory power at specific time-point and frequency predicted the accuracy of response (correct/incorrect) or subjective visibility (saw/did not see).

Logit models was used to examine visibility ratings (although response was in ordinal scale) because now the results are more easily compared to analysis examining objective discrimination performance. In the mass-univariate models participants were defined as random factors, and 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 was strongly right skewed.

Statistical significance of the mixed effects analyzes was determined using cluster mass permutation testing to correct for multiple comparisons [23]. Statistically significant clusters refer to adjacent time/frequency points where power predicted accuracy of responding at the 5% alpha level. The t mass of each continuous cluster was computed. A null distribution of cluster masses was obtained by randomly shuffling the predicted categories (e.g. correct/incorrect response), and running the mixed-effects logit model 1000 times. After each model t values masses of statistically significant ($p < .05$) clusters were determined, and the cluster with the largest absolute mass was saved. The results of the mixed effects model run with non-shuffled data was compared to this null distribution. If the mass of a cluster was larger than largest 5% of the null distribution cluster masses, the effect was considered statistically significant.

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

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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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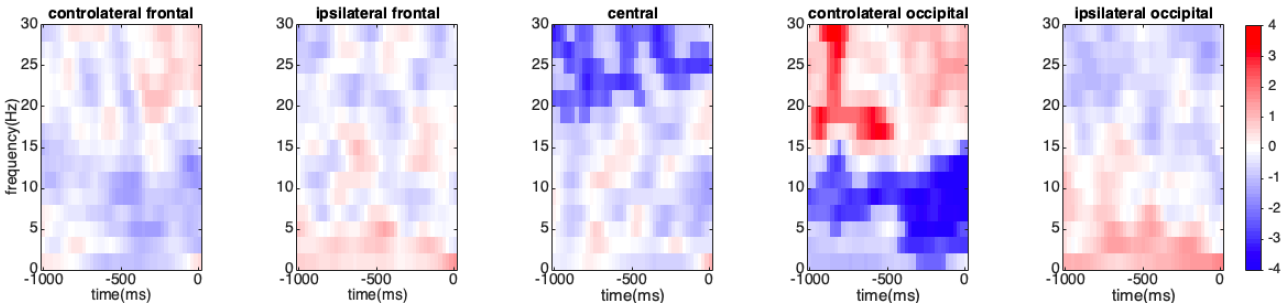
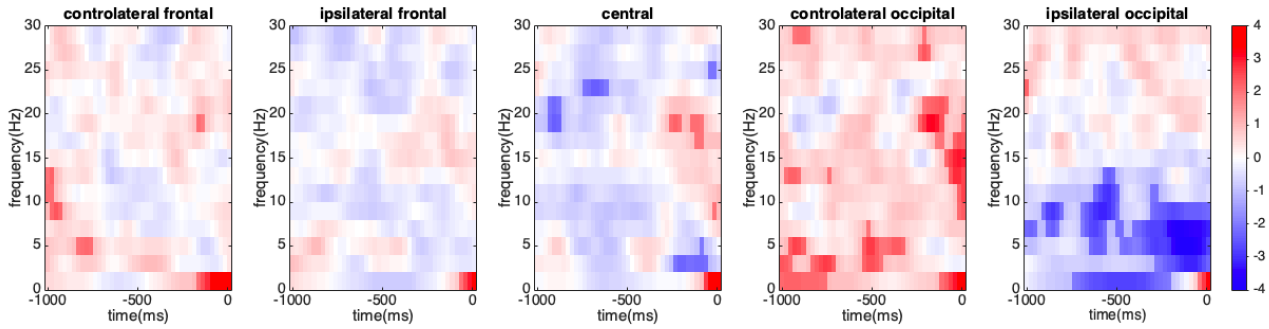
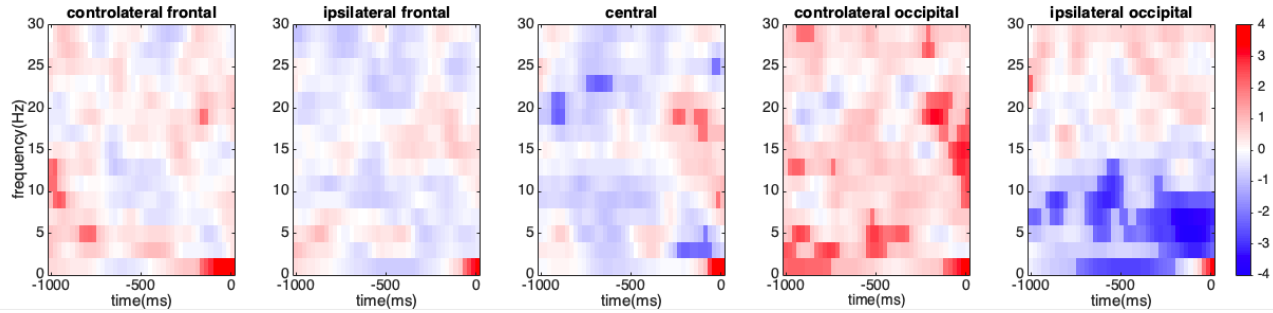
Supplementary Figures



Supplementary Figure 1. Predicting response accuracy based on prestimulus power. This analysis includes trials where participants reported seeing the target, in addition to the trials where they reported not seeing the target. Color represents t value. Bright color represents statistically significant effects according to cluster mass permutations test.



Supplementary Figure 2. Non-transposed stimulus locations: Predicting response accuracy based on prestimulus power (only trials with visibility rating = 0 included). Not corrected for multiple comparisons.



Supplementary Figure 3. Predicting visibility when only trials where correct forced-choice answer was given. Not corrected for multiple comparisons.