Unconscious 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 subjectively unconscious stimulus can be predicted in trial-by-trial manner from low frequency (1–15 Hz) electroencephalographic activity present before the stimulus. Accurate discrimination of unconscious stimulus location was supported by lateralized 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 perceptual capacity lied on the same continuum as conscious vision. The results indicate that unconscious perception is not a distinct capacity, but relies on the same top-down mechanisms as conscious vision.

Key words: Unconscious vision, subliminal vision, blindsight, prestimulus, oscillations, EEG

Introduction

Visual stimuli that individuals report not consciously perceiving can influence their behavior, a phenomenon known as “subliminal” or “unconscious perception” (Hannula, Simons, & Cohen, 2005). Blindsight, observed in patients who are blind due to a lesion to their visual cortex, is the hallmark example of unconscious perception (Azzopardi & Cowey, 1997; Weiskrantz, Warrington, Sanders, & Marshall, 1974). Researchers have suggested that such capacity also exists in neurologically healthy individuals (Boyer, Harrison, & Ro, 2005; Merikle, Smilek, & Eastwood, 2001). Although there is abundant research into the neural correlates of conscious vision (Dehaene & Changeux, 2011; Koch, Massimini, Boly, & Tononi, 2016), surprisingly little is known about the neural correlates of unconscious vision in neurologically healthy participants. This imbalance is problematic because the neural processes that enable the putative unconscious visual capacity to influence behavior is the benchmark against which the processes that enable conscious vision are compared to: What does conscious vision enable that is not unconsciously possible? Here, our aim is to elucidate what explains above-chance objective performance when participant report not seeing a stimulus.

Unconscious processing is often characterized as a discrete capacity: that once a certain processing threshold is crossed, the brain “knows” that a stimulus was presented (see “high-threshold model” in (Morales, Chiang, & Lau, 2015) for discussion). 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)(Campion, Latto, & Smith, 1983; Hannula et al., 2005; Peters & Lau, 2015). The latter view suggests that what we label “unconscious” and “conscious” vision are two extremes of a single continuum. We tested this question in the present study by comparing objective discrimination accuracy to the sensitivity and criterion of subjective perception. If unconscious vision is indeed a capacity which can be strictly dissociated from

conscious vision, then the behavioral measure of unconscious vision (e.g. objective response accuracy) should be independent from the measure of conscious vision (e.g. subjective perception). In contrast, the continuum-view implies that if discrimination is impossible at the level of subjective reports, then objectively measured discrimination should not exceed chance-level either.

In addition to examining behavioral performance, we studied what neural mechanisms explain the trial-by-trial variability in objective performance when participants report not seeing a stimulus. Unconscious perception has been explained by referring to stimulus-evoked processes, either anatomic pathways such as the visual pathway through the superior colliculus (Danckert & Rossetti, 2005) or modes of neural activity (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006) which do not trigger consciousness. Koivisto and Grassini (2016) showed that when only trials where participants report not seeing a target are considered, correct discrimination of stimulus location was associated with stronger event-related potentials (ERP) around 200 ms after stimulus onset (Koivisto & Grassini, 2016). This effect correlated with conservative response criterion (Koivisto & Grassini, 2016), suggesting that "unconscious visual perception" was in fact severely degraded conscious perception. Subjective reports of perceptual consciousness correlates with ERP amplitude in the same time-window, while later correlates of conscious vision may reflect cognitive, "postperceptual" manipulation of these contents (Andersen, Pedersen, Sandberg, & Overgaard, 2016; Eklund & Wiens, 2018; Grassini, Railo, Valli, Revonsuo, & Koivisto, 2019; Mazzi, Tagliabue, Mazzeo, & Savazzi, 2019; Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014; Railo, Koivisto, & Revonsuo, 2011; Railo, Revonsuo, & Koivisto, 2015).

Instead of examining poststimulus activity, 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 on visual processing (Muckli & Petro, 2013). Many studies have shown that 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; Benwell et al., 2017; Jensen, Bonnefond, & VanRullen, 2012; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Samaha, Iemi, & Postle, 2017; Schroeder & Lakatos, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). 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). If large variation of trial-by-trial variability in unconscious perception is explained by prestimulus factors, it means that unconscious visual perception is under similar top-down influences conscious vision. Alternatively, top-down modulation could serve to selectively influence conscious vision, and not objective visual performance (e.g. Benwell et al., 2017).

Materials and 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. The study was conducted in accordance with the Declaration of Helsinki and it 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. 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 (Watson & Pelli, 1983). 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.

Experimental Design

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 (Maris & Oostenveld, 2007). 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/.

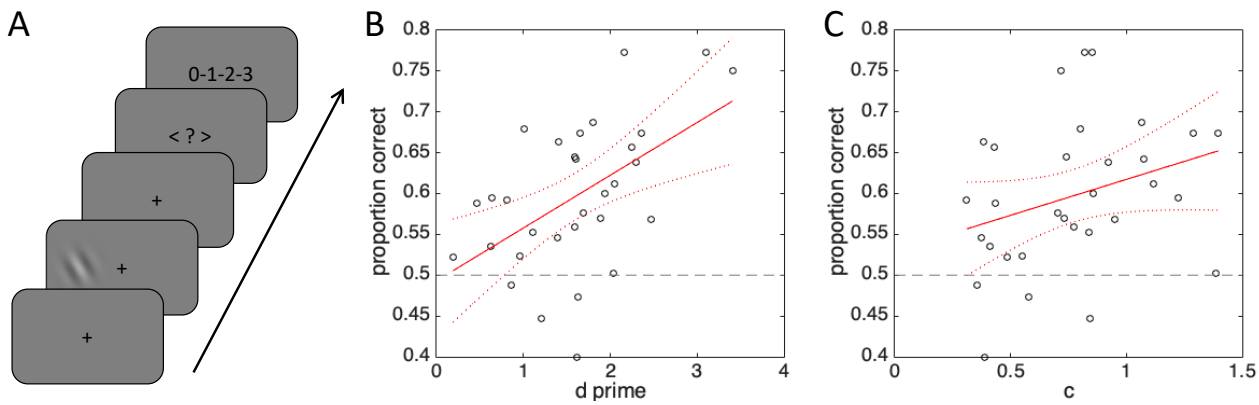


Figure 1. Behavioral paradigm and results. A) A schematic of a single trial: participants gave a forced discrimination response and rated how well they saw the stimulus. B) Correlation between sensitivity of subjectively detecting the stimulus and proportion correct (forced discrimination task) on subliminal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

Results

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*.

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 ($d' \approx 0$) 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 (Peters & Lau, 2015).

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 (Thut et al., 2006; Worden, Foxe, Wang, & Simpson, 2000), 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).

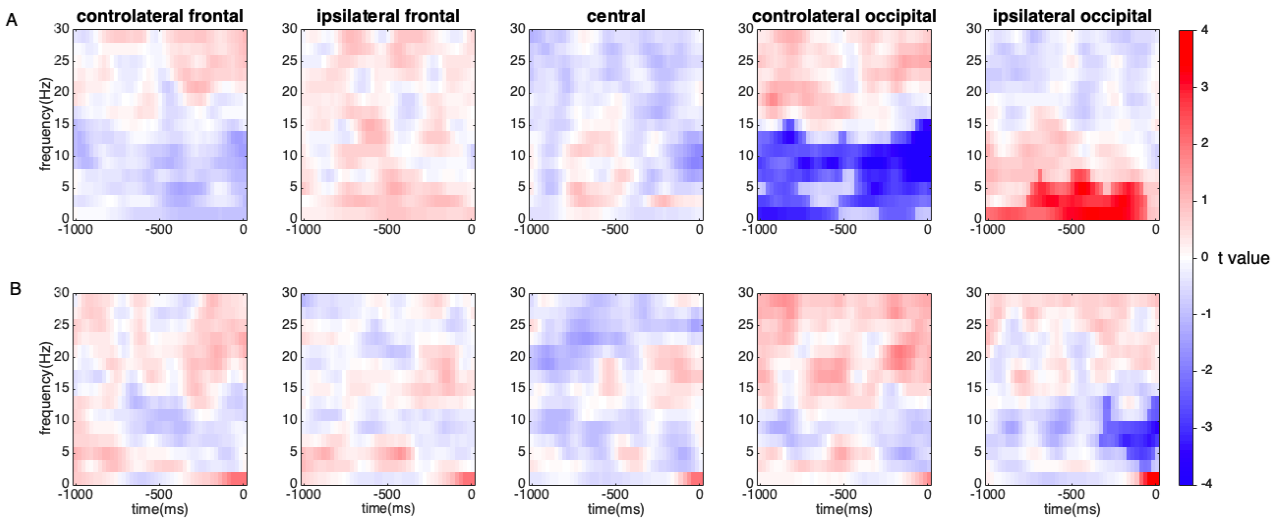


Figure 2. EEG results. Results of mass univariate mixed-effects logit models on single trials used to predict A) location discrimination accuracy on subliminal trials (visibility = 0), and B) binarized visibility ratings (did not see = 0; 1–3 = saw). Color is the t value of the mixed-effects logit model. 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.

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.

Discussion

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 (Schroeder & Lakatos, 2009). Consequently, the lateralization of the prestimulus effect suggests that subliminal visual perception is explained by how successfully oscillatory activity suppresses unwanted neural activity (related to the information coming from the ipsilateral visual hemifield where no stimulus is presented) and amplitiess 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.

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. This effect is strongest over posterior sites, possibly reflecting visual cortical sources. Activity in visual cortex may be top-down modulated by frontal/parietal cortical areas (Koivisto, Lähteenmäki, Kaasinen, Parkkola, & Railo, 2014; Mathewson et al., 2014), or subcortical structures such as the pulvinar (Purushothaman, Marion, Li, & Casagrande, 2012; Saalmann, Pinsk, Wang, Li, & Kastner, 2012).

Signal detection analyses suggested that this capacity to discriminate the location of a subliminal stimulus was not independent of introspective access. Our results do not allow us to generalize that this applies to all visual tasks. We decided to use a location discrimination task as it is arguably the simplest possible visual task. However, also other studies suggest that that what are called "unconscious" and "conscious" perception lie on the same continuum. Peters and Lau (2015) who reported that when conscious and unconscious perception are measured using a sensitive "criterion-free" paradigm, participants could not discriminate the orientation of stimuli they had no introspective access to. Results of Koivisto & Grassini (2016) suggest that unconscious perception is best characterized as severely degraded conscious vision. Furthermore, the blindsight capacity of patients may not be observed when visibility is measured using a strict procedure (Mazzi, Bagattini, & Savazzi, 2016; Overgaard, Fehl, Mouridsen, Bergholt, & Cleeremans, 2008), and the unconscious capacity attributed to blindsight patients does not generalize to neurologically healthy patients (Hurme, Koivisto, Revonsuo, & Railo, 2017, 2019; Lloyd, Abrahamyan, & Harris, 2013; Railo, Andersson, Kaasinen, Laine, & Koivisto, 2014). Altogether the above findings challenge the assumption that unconscious/subliminal perception is a discrete perceptual capacity that is independent of conscious vision.

Some previous studies have reported that prestimulus power correlates with subjective visibility irrespective of objective accuracy (Iemi, Chaumon, Crouzet, & Busch, 2016; Samaha et al., 2017). 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 objective discrimination, which revealed a *positive* association (other electrode clusters show a more similar pattern, although not statistically significant for visibility). This shows that taking into account the lateralization of activity may uncover interesting effects, especially when lateralized stimuli are used. Some might argue that this shows that different neural processes underlie conscious and unconscious vision. In our view such interpretation is not warranted because the behavioral results show that the measure of unconscious vision cannot be dissociated from the subjective measure. That said, what explains the different prestimulus correlates of subjective and objective measures of vision need to be clarified in further studies. We suggest that the prestimulus correlate of visibility may reflect generally higher excitability in visual cortex (Iemi et al., 2016; Samaha et al., 2017), 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 (King & Dehaene, 2014).

Our results are also interesting when considered from the perspective of blindsight patients. The blindsight capacity—which is observed in only some patients with cortical blindness—has been traditionally explained by referring to 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 et al., 1974). Interesting open question is if prestimulus processes also contribute to blindsight. Our results suggest that in addition to considering which bottom-up visual pathways mediate blindsight, subsequent blindsight studies

should consider if top-down factors also play a significant role. Successful top-down modulation of externally triggered visual activity could help drive neural plasticity by triggering synchronized activity across different brain areas (Galuske, Munk, & Singer, 2019; Zanos, Rembado, Chen, & Fetz, 2018). If true, then e.g. visual stimuli triggered at specific phases of oscillatory power, or noninvasive brain stimulation could be used to trigger plasticity and behavioral change in patients.

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.

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.

References

Ajina, S., & Bridge, H. (2018). Blindsight relies on a functional connection between hMT+ and the lateral geniculate nucleus, not the pulvinar. *PLoS Biology*. https://doi.org/10.1371/journal.pbio.2005769

Ajina, S., Pestilli, F., Rokem, A., Kennard, C., & Bridge, H. (2015). Human blindsight is mediated by an intact geniculo-extrastriate pathway. *ELife*. https://doi.org/10.7554/eLife.08935

Andersen, L. M., Pedersen, M. N., Sandberg, K., & Overgaard, M. (2016). Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhv108

Azzopardi, P., & Cowey, A. (1997). Is blindsight like normal, near-threshold vision? *Proceedings of*

the National Academy of Sciences of the United States of America. https://doi.org/10.1073/pnas.94.25.14190

Bareither, I., Chaumon, M., Bernasconi, F., Villringer, A., & Busch, N. A. (2014). Invisible visual stimuli elicit increases in alpha-band power. *Journal of Neurophysiology*. https://doi.org/10.1152/jn.00550.2013

Benwell, C. S. Y., Tagliabue, C. F., Veniero, D., Cecere, R., Savazzi, S., & Thut, G. (2017). Prestimulus EEG power predicts conscious awareness but not objective visual performance. *ENeuro*. https://doi.org/10.1523/ENEURO.0182-17.2017

Boyer, J. L., Harrison, S., & Ro, T. (2005). Unconscious processing of orientation and color without primary visual cortex. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.0505332102

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*. https://doi.org/10.1163/156856897X00357

Campion, J., Latto, R., & Smith, Y. M. (1983). Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behavioral and Brain Sciences*. https://doi.org/10.1017/S0140525X00016861

Cowey, A. (2010). The blindsight saga. *Experimental Brain Research*. https://doi.org/10.1007/s00221-009-1914-2

Danckert, J., & Rossetti, Y. (2005). Blindsight in action: What can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2005.02.001

Dehaene, S., & Changeux, J. P. (2011). Experimental and Theoretical Approaches to Conscious Processing. *Neuron*. https://doi.org/10.1016/j.neuron.2011.03.018

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious,

and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2006.03.007

Eklund, R., & Wiens, S. (2018). Visual awareness negativity is an early neural correlate of awareness: A preregistered study with two Gabor sizes. *Cognitive, Affective and Behavioral Neuroscience*. https://doi.org/10.3758/s13415-018-0562-z

Galuske, R. A. W., Munk, M. H. J., & Singer, W. (2019). Relation between gamma oscillations and neuronal plasticity in the visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1901277116

Grassini, S., Railo, H., Valli, K., Revonsuo, A., & Koivisto, M. (2019). Visual Features and Perceptual Context Modulate Attention Towards Evolutionarily Relevant Threatening Stimuli: Electrophysiological Evidence. *Emotion*. https://doi.org/10.1037/emo0000434

Hannula, D. E., Simons, D. J., & Cohen, N. J. (2005). Imaging implicit perception: promise and pitfalls. *Nature Reviews Neuroscience*. https://doi.org/10.1038/nrn1630

Hurme, M., Koivisto, M., Revonsuo, A., & Railo, H. (2017). Early processing in primary visual cortex is necessary for conscious and unconscious vision while late processing is necessary only for conscious vision in neurologically healthy humans. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2017.02.060

Hurme, M., Koivisto, M., Revonsuo, A., & Railo, H. (2019). V1 activity during feedforward and early feedback processing is necessary for both conscious and unconscious motion perception. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2018.10.058

Iemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2016). Spontaneous Neural Oscillations Bias Perception by Modulating Baseline Excitability. *The Journal of Neuroscience*. https://doi.org/10.1523/jneurosci.1432-16.2016

Jensen, O., Bonnefond, M., & VanRullen, R. (2012). An oscillatory mechanism for prioritizing salient

unattended stimuli. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2012.03.002

King, J. R., & Dehaene, S. (2014). A model of subjective report and objective discrimination as categorical decisions in a vast representational space. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2013.0204

Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: Progress and problems. *Nature Reviews Neuroscience*. https://doi.org/10.1038/nrn.2016.22

Koivisto, M., & Grassini, S. (2016). Neural processing around 200 ms after stimulus-onset correlates with subjective visual awareness. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2016.02.024

Koivisto, M., Lähteenmäki, M., Kaasinen, V., Parkkola, R., & Railo, H. (2014). Overlapping activity periods in early visual cortex and posterior intraparietal area in conscious visual shape perception: A TMS study. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2013.09.051

Lloyd, D. A., Abrahamyan, A., & Harris, J. A. (2013). Brain-stimulation induced blindsight: Unconscious vision or response bias? *PLoS ONE*. https://doi.org/10.1371/journal.pone.0082828

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*. https://doi.org/10.1016/j.jneumeth.2007.03.024

Mathewson, K. E., Beck, D. M., Ro, T., Maclin, E. L., Low, K. A., Fabiani, M., & Gratton, G. (2014). Dynamics of alpha control: Preparatory suppression of posterior alpha oscillations by frontal modulators revealed with combined EEG and event-related optical signal (EROS). *Journal of Cognitive Neuroscience*. https://doi.org/10.1162/jocn_a_00637

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus α phase predicts visual awareness. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.3963-08.2009

Mazzi, C., Bagattini, C., & Savazzi, S. (2016). Blind-sight vs. degraded-sight: Different measures tell a different story. *Frontiers in Psychology*. https://doi.org/10.3389/fpsyg.2016.00901

Mazzi, C., Tagliabue, C. F., Mazzeo, G., & Savazzi, S. (2019). Reliability in reporting perceptual experience: Behaviour and electrophysiology in hemianopic patients. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2018.01.017

Merikle, P. M., Smilek, D., & Eastwood, J. D. (2001). Perception without awareness: Perspectives from cognitive psychology. *Cognition*. https://doi.org/10.1016/S0010-0277(00)00126-8

Morales, J., Chiang, J., & Lau, H. (2015). Controlling for performance capacity confounds in neuroimaging studies of conscious awareness. *Neuroscience of Consciousness*. https://doi.org/10.1093/nc/niv008

Muckli, L., & Petro, L. S. (2013). Network interactions: Non-geniculate input to V1. *Current Opinion in Neurobiology*. https://doi.org/10.1016/j.conb.2013.01.020

Overgaard, M., Fehl, K., Mouridsen, K., Bergholt, B., & Cleeremans, A. (2008). Seeing without seeing? Degraded conscious vision in a blindsight patient. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0003028

Peters, M. A. K., & Lau, H. (2015). Human observers have optimal introspective access to perceptual processes even for visually masked stimuli. *ELife*. https://doi.org/10.7554/eLife.09651

Pitts, M. A., Padwal, J., Fennelly, D., Martínez, A., & Hillyard, S. A. (2014). Gamma band activity and the P3 reflect post-perceptual processes, not visual awareness. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2014.07.024

Purushothaman, G., Marion, R., Li, K., & Casagrande, V. A. (2012). Gating and control of primary visual cortex by pulvinar. *Nature Neuroscience*. https://doi.org/10.1038/nn.3106

Railo, H., Andersson, E., Kaasinen, V., Laine, T., & Koivisto, M. (2014). Unlike in clinical blindsight patients, unconscious processing of chromatic information depends on early visual cortex in

healthy humans. *Brain Stimulation*. https://doi.org/10.1016/j.brs.2014.01.060

Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2011.03.019

Railo, H., Revonsuo, A., & Koivisto, M. (2015). Behavioral and electrophysiological evidence for fast emergence of visual consciousness. *Neuroscience of Consciousness*. https://doi.org/10.1093/nc/niv004

Saalmann, Y. B., Pinsk, M. A., Wang, L., Li, X., & Kastner, S. (2012). The pulvinar regulates information transmission between cortical areas based on attention demands. *Science*. https://doi.org/10.1126/science.1223082

Samaha, J., Iemi, L., & Postle, B. R. (2017). Prestimulus alpha-band power biases visual discrimination confidence, but not accuracy. *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2017.02.005

Schroeder, C. E., & Lakatos, P. (2009). Low-frequency neuronal oscillations as instruments of sensory selection. *Trends in Neurosciences*. https://doi.org/10.1016/j.tins.2008.09.012

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). α-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics*. https://doi.org/10.3758/BF03202828

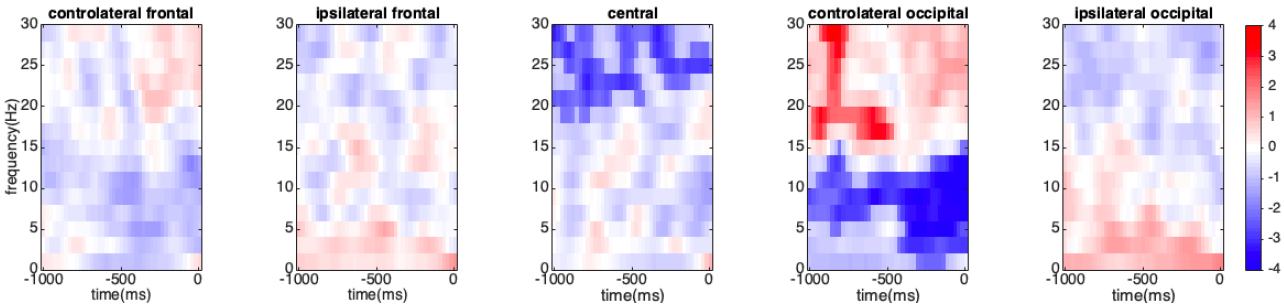
Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, *97*(4), 709–728. https://doi.org/10.1093/brain/97.4.709

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial

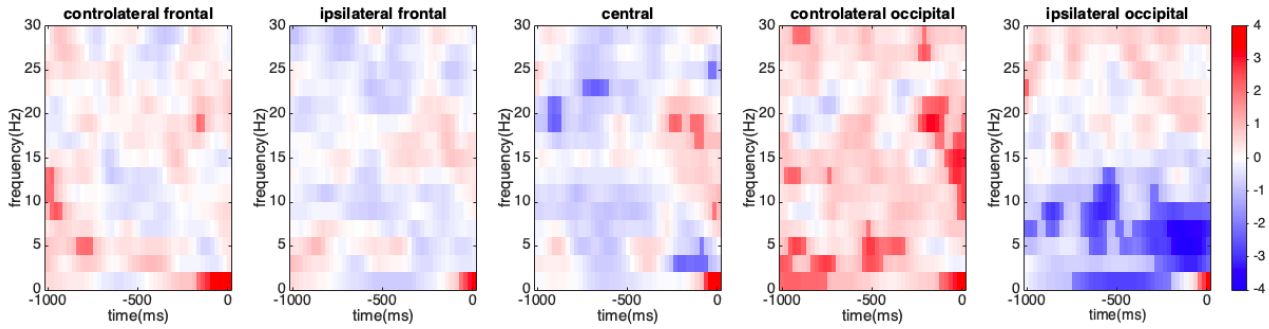
attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*. https://doi.org/10.1523/jneurosci.20-06-j0002.2000

Zanos, S., Rembado, I., Chen, D., & Fetz, E. E. (2018). Phase-Locked Stimulation during Cortical Beta Oscillations Produces Bidirectional Synaptic Plasticity in Awake Monkeys. *Current Biology*. https://doi.org/10.1016/j.cub.2018.07.009

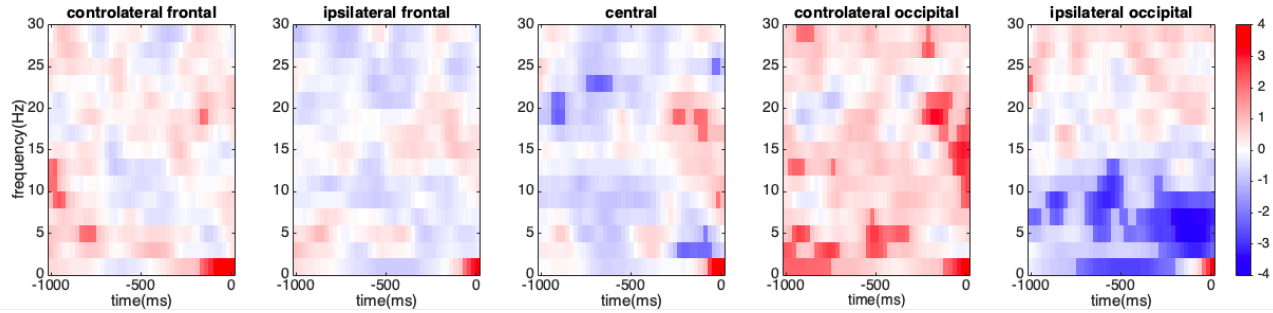
Supplementary information



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.