Title: Efficient prestimulus connectivity biases visual content

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Abstract

Ongoing fluctuations in prestimulus neural excitability and connectivity patterns influence near-threshold detection, or whether or not a stimulus is perceived. Do they also influence whether one or another stimulus is perceived? In this Magnetoencephalography study, we showed participants brief presentations of a bi-stable image consisting of a face superimposed with a house, and asked them to report which of the two contents of the image they perceived on each trial. Multivariate pattern analysis revealed that perceiving bi-stable faces and houses shared common neural substrates with perceiving unambiguous faces and houses. After source localizing the post-stimulus signals to the FFA, we analyzed oscillatory power and connectivity in FFA during a prestimulus interval. We found no differences in FFA power, but we did find differences in FFA connectivity prior to face vs house reports. Specifically, local graph theoretical measures showed that in the alpha frequency range (8-13 Hz), FFA was more efficiently and robustly connected to the rest of cortex prior to face reports. These prestimulus connectivity measures additionally predicted the accuracy of post-stimulus decoding. Our work suggests that object perception is shaped by ongoing network states captured with connectivity measures.

Introduction

Ongoing neural fluctuations interact with sensory inputs and influence perception (1, 2). These interactions can be captured by characterising prestimulus brain activity and the influence of that activity on upcoming perception and behavior. For example, prestimulus oscillatory power, an index of neural excitability, influences whether or not a near-threshold stimulus will be detected (3-6). Considering the complex spatio-temporal properties of ongoing neural activity, connectivity measures have been recently used to better understand prestimulus brain states. As a result, prestimulus connectivity was also shown to influence near-threshold perception (7-10).

The functions of sensory systems are not restricted to stimulus detection. In fact, one of the most important functions of the visual system is categorising objects to build the contents of visual experiences (11-13). Given that prestimulus neural excitability and connectivity bias stimulus detection ('*Did you see anything?*'), here we ask whether they also bias perceptual content ('*What did you see?*'). To distill the neural correlates of visual content, researchers have employed bi-stable perception paradigms in which the perceived category of an ambiguous but invariant stimulus can switch over time (14). Examples of bi-stable stimuli include the Necker cube (15), the Rubin vase (16), and binocular rivalry (17).

When presented briefly, only one of the two possible interpretations of the ambiguous image is perceived. Over multiple presentations, perception of the stimulus will vary between the two interpretations. This trial-by-trial variance in perception can then be used to assess the prestimulus mechanisms that might have influenced perception of one or the other stimulus category (18). As such, briefly presented bi-stable images are unique tools to probe the influence of prestimulus neural activity on subsequent perception.

Studies that have used bi-stable stimuli with semantic content, such as the faces and vase of the Rubin vase, have reported the involvement of temporal cortical regions known to be involved in non-rivalrous object perception. For example, an fMRI study using the Rubin vase illusion reported increased prestimulus Fusiform Face Area (FFA) activity prior to face (vs vase) reports (19), and a Magnetoencephalography study using the same stimulus reported increased prestimulus connectivity between the Fusiform Face Area (FFA) and early visual cortex prior to face (vs vase) reports (18).

Based on the "Windows to Consciousness" framework (10, 20), fluctuating connectivity levels influence upcoming perception and neural signals associated with perception. In the present MEG study, we used a brief-presentation binocular rivalry set-up similar to the aforementioned MEG study. We asked whether prestimulus neural excitability and/or connectivity influenced the perceptual report of the rivalrous stimuli, and whether this prestimulus activity also influenced post-stimulus neural activity.

Results

We showed 21 people an ambiguous image consisting of a red or blue face superimposed with a blue or red house. We recorded MEG and presented the image briefly and repeatedly while they wore red/blue glasses, and asked them to report the content of their percept (face or house) on each trial. To confirm that the response choices were stochastic trial-by-trial, we fit the pattern of response repetitions to a binomial distribution. The distribution accounted well for both face and house repetitions (R^2 face = .92, R^2 house = .79). In other words, participants were equally as likely to report face or house on each trial, regardless of their responses on previous trials. Face reports constituted

40% of overall reports, so face and house trials were equalized for each participant for all subsequent analyses.

We first asked what were the similarities in temporal dynamics between perceiving a non-rivalrous face or house image and perceiving a face or house from a rivalrous image. For this reason we had presented participants with unambiguous face and house images prior to the main experiment. The motivation was two-fold. First, we wanted to be confident that participants actually reported what they had perceived. Second, we wanted to know whether a rivalrous image took longer to mentally process compared to an unambiguous image. For this purpose, we trained a classifier on the broadband MEG signals resulting from the unambiguous images, and tested it on the signals resulting from the rivalrous images using the temporal generalisation method (21). The classifier performed significantly above chance (Fig 1B, masked at $p < .005$), meaning that the two conditions shared decodable neural representations. The signals from the non-rivalrous condition at 85ms onwards could predict those of the rivalrous condition from 120 ms onwards. The difference in the latency of maximum decodability was on average 36 ms and it was significant ($T=6.8$, $p < .0001$). Overall, this analysis gave us confidence that participants truly reported what they had perceived, and showed that visual content in ambiguous stimuli is decodable from brain responses to unambiguous stimuli, but with a delay.

To answer our main question of whether prestimulus activity in category-sensitive brain regions biases upcoming perceptual content, we first searched for such a region in our data to see whether we would obtain what is reported in the literature (temporal cortex; specifically the FFA). We source localized activity at the latency of the peak difference between face and house grand-averaged evoked activity (165 ms; Fig 1A) to the left fusiform gyrus (Fig 1A inset; FFA; MNI coordinates: $[-28, -58, -8]$ mm), consistent with literature reports on face perception (22, 23). For the subsequent analyses, we used FFA as our region of interest.

Figure 1. Post-stimulus data: evoked responses, source localisation, and decoding. A) Whole-brain grand-averaged source-level evoked responses of face and house trials from the binocular rivalry task. The maximum difference between the responses was at 165 ms (marked with a vertical dotted line). This difference was localised to the left FFA (inset). B) Face vs house decoding of sensor-level data using the time-by-time generalisation method, obtained from training a classifier on evoked responses to unambiguous face and house images, and testing on evoked responses to the bistable face/house images. Decodability of the bistable data was shifted by 36 ms compared to decodability of the unambiguous data. Accuracy scores are masked at $p_{cluster} < 0.005$.

After having localised our region of interest, we asked whether its prestimulus oscillatory power, particularly in the alpha band (8-13 Hz), was different between trials where people reported face and

those where people reported house. Alpha oscillations are known to be inhibitory and are therefore an index of neural excitability (24, 25). We used a cluster-based permutation approach (26) (clustering over the alpha frequencies 8-13 Hz) to contrast prestimulus FFA alpha band activity between face and house trials. The frequency spectra from both trial types showed clear alpha band peaks, but we found no statistical differences in prestimulus alpha power between face and house trials (Fig 2A). Overall, this analysis showed that prestimulus neural excitability in category-selective regions is unlikely to be a factor in biasing upcoming perceptual content.

Next, we asked whether the connectivity patterns of FFA influenced the perceptual reports. To assess connectivity, we used two local graph theoretical measures (27). The first was 'local efficiency', a measure of how well-integrated a node is to the rest of the network. The second was the 'local clustering coefficient', a measure of the robustness of the region's local network. We computed these measures in a frequency-resolved manner, and used a cluster-based permutation approach (clustering over the frequencies 8-13 Hz) to contrast prestimulus efficiency and clustering of FFA between face and house trials. We found that FFA had increased prestimulus efficiency and clustering in the alpha range on face trials compared to house trials (Fig 1B, efficiency: $p_{\text{cluster}} = 0.017$; Fig 1C, clustering: $p_{\text{cluster}} = 0.024$). The difference was most pronounced in the frequencies 8-9 Hz in both cases. In other words, FFA was more efficiently connected to its local network in a robust manner prior to face (vs house) responses.

Figure 2. Prestimulus MEG connectivity, but not power, biases upcoming perception. Shaded error regions represent SEM for within-subject designs (28). A) No difference in prestimulus spectral power between face and house trials. B) Prestimulus efficiency the alpha range (8-13 Hz) was increased on

face trials compared to house trials. C) Prestimulus clustering in the alpha range (8-13 Hz) was increased on face trials compared to house trials.

In light of a recent study similar to the current one, which reported increased connectivity between FFA and primary visual cortex (V1) prior to face reports (18), we additionally investigated the prestimulus coherence between FFA and V1. We calculated coherence in a frequency-resolved manner and used a cluster-based permutation approach (clustering over the frequencies 8-13 Hz) to contrast prestimulus coherence between FFA and V1 on face vs house trials. We found increased prestimulus coherence in the alpha range on face (vs house) trials (Fig S1, $p_{\text{cluster}}=0.021$). This effect was most pronounced in the frequencies 10-11 Hz. Consistently with the aforementioned study, FFA and V1 were more strongly connected prior to face (vs house) responses.

Finally, we asked whether prestimulus connectivity was related to post-stimulus activity. We extracted from each participant the maximum decoding accuracy from the time generalization decoding results, as well as the maximum differences between face and house trials in prestimulus efficiency and clustering (8-13 Hz). Maximum decoding accuracy was correlated with both prestimulus efficiency ($r=.53$, $p=.014$) and prestimulus clustering ($r=.49$, $p=.023$). So in addition to being predictive of upcoming perceptual reports, prestimulus connectivity was also predictive of the strength of post-stimulus signals associated with those percepts.

Figure 3. Prestimulus connectivity is correlated with post-stimulus decoding accuracy across participants. *r* values represent Pearson's correlation coefficients. Shaded areas represent 95% confidence intervals. A) Maximum prestimulus efficiency (8-13 Hz) differences between face and house trials are correlated with maximum post-stimulus decoding accuracy. B) Maximum prestimulus clustering (8-13 Hz) differences between face and house trials are correlated with maximum post-stimulus decoding accuracy.

Discussion

While the prestimulus requisites of near-threshold conscious perception have been widely studied (1, 3-10), only a few recent studies have investigated the influence of prestimulus activity on object perception (19, 29). These fMRI studies reported increased activity in category-selective extrastriate regions prior to object perception, but these prestimulus BOLD activations could represent increased local excitability of a cortical region, or they could be a product of increased connectedness of that region. In fact, a recent MEG study has reported that increased prestimulus connectivity between

striate and extrastriate regions, but not local excitability of these regions, predicted upcoming object perception (18).

Here we aimed to add to this emerging literature by employing a paradigm similar to the one in the aforementioned MEG study and investigating possible influences of prestimulus excitability and connectivity on object perception. We showed people a bi-stable face/house image whose perceptual content would vary trial-by-trial, and asked them to report their percept on each trial. We source-localised the post-stimulus activity to FFA and subsequently focused on differences between face-report and house-report trials in prestimulus FFA activity. We found no differences in FFA oscillatory alpha-band power prior to trials perceived as face vs house. Nevertheless, we did observe differences in FFA connectivity states prior to trials perceived as face vs house. Specifically, FFA was more efficiently and robustly connected to the rest of cortex in the alpha frequency range prior to face (vs house) perception of the bi-stable face/house image. These connectivity differences were correlated with post-stimulus decoding accuracy across subjects.

Alpha oscillations are implicated in a variety of cognitive and perceptual phenomena (30) and act on neuronal populations by rhythmic inhibition (24). Their power can therefore be thought of as a proxy to neural excitability. If the prestimulus levels of excitation per se of the task-relevant sensory cortices influenced upcoming object perception, we would expect prestimulus alpha power in FFA to be different on face vs house trials. Yet we did not observe such a difference, and therefore found no evidence for that hypothesis. Despite this, we found differences between face and house trials in the prestimulus connectivity states of FFA. While prestimulus excitability of task-relevant sensory cortices influences simple perceptual operations such as near-threshold detection, our findings indicate that the connectivity states of these task-relevant regions are more relevant to understanding less simple perceptual operations, such as visual object perception.

Graph theoretical measures of network connectivity have provided important insights into properties of structural and functional brain networks, such as small-worldness and the existence of hubs (27, 31). Here we used the graph theoretical measures of efficiency and clustering coefficient to inform us about the connectivity states of FFA prior to face and house perception. We found increased prestimulus local efficiency in FFA on face (vs house) trials. This means that FFA was more highly integrated into the rest of the network prior to face (vs house) perception. In other words, when FFA was better integrated in cortex, people were more likely to subsequently perceive a face rather than a house. We additionally found increased prestimulus local clustering in FFA on face (vs house) trials. This means that FFA was more densely connected to its neighbors prior to face (vs house) perception. In other words, when the network to which FFA belongs was more robust, people were more likely to subsequently perceive a face rather than a house.

Our results provide further support to the Windows to Consciousness framework, which postulates that ongoing neural fluctuations impact pre-established connectivity pathways and influence upcoming perception. We now widen this view to include object perception, which is known to involve ventral stream activity, especially in the case of stimuli with semantic content. Since our time generalisation decoding analysis supported the notion that ambiguous and unambiguous perception share common neural substrates, we hypothesized that the ventral visual pathway be the candidate pre-established connectivity pathway (32, 33). In support of this hypothesis, we found increased coherence between V1 and FFA prior to face (vs house) perception. Despite the similarity in neural responses to bistable and unambiguous images, we found an interesting and unexpected difference between them. Decoding of responses to the bistable images was delayed with respect to those of the ambiguous images. This possibly relates to a delay in disambiguating the bistable image, before perceptual content becomes consciously accessible. In sum, the prestimulus activation of a pre-established connectivity pathway in the ventral stream might bias perception towards a face or a house, but the temporal dynamics of this activation seem to be perturbed at binocular rivalry onset.

Finally, if prestimulus connectivity biases upcoming perception, then it should also bias the post-stimulus signals associated with perception. We found that both prestimulus efficiency and clustering correlated well with decoding accuracy scores. The stronger the prestimulus effect was, the more decodable the post-stimulus signals were. This could indicate that participants who were more prone to the prestimulus connectivity effects were also better at subsequently disambiguating the bistable stimulus. Overall, it appears that prestimulus connectivity biases not only perceptual contents, but also content-related neural activity.

It is difficult to assign cognitive functions to the connectivity effects we detected, but at least two interpretations of these effects are plausible. One is that a conscious, top-down drive to perceive one of the contents of the stimuli leads to increased connectivity of the relevant cortical region, which in turn biases perception. The other is that spontaneous fluctuations in neural activity, which could randomly differ on a trial-by-trial basis, influence the connectivity state of the relevant cortical region, and in turn bias perception. The top-down interpretation is in line with a large body of literature suggesting that expectations, predictions, or context critically shape perception (34-38). That the effects were in the alpha frequencies might also support this interpretation, given the evidence from human and non-human primate studies showing that alpha oscillations subserve feedback connectivity in visual cortical areas (39, 40). However, a purely top-down interpretation is unlikely given our design and behavioral analysis: the prestimulus intervals were short (1 to 2 sec) and stimulus onset was jittered and difficult to predict within this range, and in addition, our behavioral analysis indicated that the response sequences were stochastic.

Figure 4. Example trial sequence.

Materials & Methods

Participants

21 volunteers with normal or corrected-to-normal vision participated in this experiment (11 m/10 f, 4 left-handed, mean age 26.3). During the course of the experiment participants wore non-magnetic clothes, and a questionnaire prior to the experiment excluded any metal artefacts on the participants being. The Ethics Committee of the University of Trento approved the experimental procedure and all participants gave written informed consent before taking part in the study.

Experimental Procedure

Participants were seated upright in the MEG system and we instructed them to keep fixation, and to avoid eye blinks and movements as best as possible during the experiment. To create rivalry, we used blue/red filter glasses which participants wore throughout. We took into account the colour filters and as such adapted the stimulus to suit the glasses. In between the blocks participants had a short break but remained seated in the MEG system. Visual stimuli were displayed via a video projector outside of the MEG chamber and projected to a screen in the MEG chamber. A camera allowed us to monitor participants during the experiment.

The experiment was divided into three different task types: staircase thresholding, passive viewing/oddball task, and onset binocular rivalry. All experiments were programmed and controlled in Psychtoolbox and the DataPixx I/O Controller and backprojected using the ProPixx Projector at 120Hz at 1980x1080 with the central images 400 x 400 in size and presented at a distance of 78cm.

Staircase thresholding

Due to the competing face/house stimulus properties, we wanted to ensure that participants perceived roughly equal amounts of houses and faces. As such we ran a staircase thresholding procedure with the Matlab toolbox Palamedes (41). Four staircase procedures controlled the brightness of the red house, blue house, red face, and blue face stimuli. The procedure was a simple 1 up 1 down with a step-size of 0.01, a start value of 0.5, a min/max of 0.95/0.05, and a stop-rule at 32.

Passive viewing/oddball task

To compare the neural responses to rivalrous and unambiguous stimuli, we presented participants with unambiguous house and face images (80 of each) prior to the main experiment. A stimulus would appear for 500 ms, followed by a jittered inter-stimulus interval of 1 to 2 sec, during which a fixation cross would appear. We required participants to report an oddball (inverted house or face) occurring on 10% of the trials to keep them engaged in the viewing task.

Onset binocular rivalry task

In the main experiment we presented participants with the rivalrous face/house images and required them to report their percept on each trial. A trial would begin with the presentation of a central fixation cross, followed by a blank screen for jittered interval of 1 to 2 sec. After the blank screen the bistable image would appear for 500 ms, and then a response screen 'House or Face?' would appear, the prompt for participants to respond with a right-handed button press to indicate their percept. The experiment consisted of 6 blocks of 80 trials each (total of 480 trials).

MEG Data Acquisition

We recorded MEG using a 306 channel whole head VectorView MEG system (Elekta-Neuromag, Ltd., Helsinki, Finland, 204 gradiometers and 102 magnetometers) installed in a magnetically shielded chamber (AK3b, Vakuumschmelze Hanau, Germany), with signals recorded at 1000 Hz sampling rate. We adjusted the hardware filters to band-pass the MEG signal in the frequency range of 0.01 Hz to 330 Hz. Prior to the recording, we recorded points on the participant's head using a digitizer (Polhemus, VT, USA). These points included the 5 Head Position Indicator (HPI) coils, the three fiducials (nasion, left and right pre-auricular points), and around 300 additional points covering the head as evenly as possible. We used the HPI coils to monitor head position during the experiment.

MEG Preprocessing and Source Projection

We pre-processed the data using the Fieldtrip toolbox (42). From the raw continuous data, we extracted epochs of 4 seconds lasting from 2.5 seconds before onset of the picture to 1.5 seconds after stimulus onset. This resulted in 400 trials per participant. We applied a high-pass filter on this epoched data at 1 Hz (IIR Butterworth 6- order two-pass filter with 36 dB/oct roll-off), followed by a

band-stop filter of 49–51 Hz to remove power line noise. We then down-sampled the data to 400 Hz. We visually inspected the trials for strong physiological (e.g. blinks) and non-physiological artefacts (e.g. channel jumps) and rejected the contaminated trials. For each participant, we then assigned the trials to the 2 conditions according to the participants' responses. Finally we equalised the number of trials in each condition to ensure comparable signal-to-noise ratio, which left us with 176 trials per condition on average.

We projected the data to source space by applying LCMV (linear constrained mean variance) beamformer filters (43) to the sensor level data. To create anatomically realistic head models (44), we used structural MRI scans and the Polhemus digitized scalp shape. We used individual MRI scans for the 5 participants for which the scans were available, and for the rest, we used a template MRI which was morphed to fit the individual's head shape using an affine transformation. We calculated a three-dimensional source grid (resolution: 8 mm) covering an entire MNI standard brain volume. For each of these points, we computed an LCMV filter using the individual leadfield and the data covariance matrix. We then multiplied the sensor-level signal to the LCMV filters to obtain the time series for each source location in the grid and for each trial. Finally, we used a parcellation scheme of 333 parcels (45) and averaged activity within each parcel.

To localise our region of interest, we first calculated the time-locked averages of the parcellated source-level signals (band-pass filtered between 1 and 30 Hz), normalized the responses across participants, and baseline-corrected them with a relative baseline of -200 ms to 0. We then computed the difference in the grand-averaged evoked responses between face and house trials (across participants and sources) to determine the time point at which there was the largest difference, which was at 165 ms. Finally, we contrasted face and house evoked response amplitude at that time point across participants with t-statistics for each parcel source and chose the parcel with the largest t-stat as our region of interest.

Multivariate Pattern Analysis (MVPA) decoding

We performed MVPA decoding on the post-stimulus period 0-800 ms based on normalized (z-scored) single-trial sensor data downsampled to 100 Hz. We used multivariate pattern analysis as implemented in CoSMoMVPA (46) to identify when a common network between perception of unambiguous and rivalrous stimuli was activated. The two classes were face and house; in the rivalrous case, we labelled trials as face and house according to the participants' responses. The training set were the unambiguous trials and the testing set were the rivalrous trials. We used a Naive-Bayes classifier with the temporal generalisation method (47) to assess the ability of the classifier across different time points in the training set to generalize to every time point in the testing set. We used local neighborhoods features in time (in each time step of 10 ms we included as additional features the previous and following time steps). We generated the time generalisation matrix for each participant and statistically tested for above-chance decoding (defined as >50% accuracy) significance with a cluster-based permutation approach (clustering over the two time dimensions between 0-800 ms).

Analysis of prestimulus power, graph measures, and coherence

We calculated spectral power, efficiency, the clustering coefficient in source-localised left FFA, as well as coherence between FFA and left V1 (defined by the parcellation scheme), in the prestimulus interval of -1 to 0 sec. We used multi-taper frequency transformation with a spectral smoothing of 2 Hz to get Fourier coefficients. From those we extracted power in FFA and computed coherence between FFA and V1.

For the graph analysis we computed the cross-spectral density (CSD) on source data and derived an all-to-all connectivity matrix of imaginary coherence, a conservative measure of phase synchronisation. We then took the absolute values of the connectivity matrix, calculated the adjacency matrix by thresholding the connectivity matrix. We set the thresholds by taking the maximum value across the first dimension of the (source x source x frequency x time) connectivity matrix, and then the minimum values of those maximum values across the 2nd dimension of the

matrix, obtaining a threshold per frequency and time -point. Finally, we used the connectivity matrix and thresholded adjacency matrix to calculate local efficiency and local clustering coefficient in FFA. We averaged all of the above measures over the prestimulus time interval, and contrasted face vs house estimates across participants with a cluster-based permutation approach (clustering over frequencies 8-13 Hz).

Author contributions

N.W., N.P., and E.R. conceived project and designed research. N.P. and E.R. collected data. E.R. analyzed data. E.R., N.P., and N.W. wrote the paper.

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Supplementary material

Figure S1. Prestimulus alpha band (8-13 Hz) coherence between V1 and FFA is increased prior to face vs vase responses. Shaded error regions represent the standard error of the mean for within-subject designs.