Forward modelling reveals dynamics of neural orientation tuning to unconscious visual stimuli during binocular rivalry

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Abstract

When different visual stimuli are presented to the two eyes, they typically compete for access to conscious perception, a phenomenon known as *binocular rivalry*. Previous studies of binocular rivalry have shown that neural responses to consciously suppressed stimuli are markedly diminished in magnitude, though they may still be encoded to some extent. Here we employed multivariate forward modelling of human electroencephalography (EEG) data to quantify orientation-selective responses to visual gratings during binocular rivalry. We found robust orientation tuning to both conscious and unconscious gratings. This tuning was enhanced for the suppressed stimulus well before it was available for conscious report. The same pattern was evident in the overall magnitude of neural responses, and it emerged even earlier than the changes in neural tuning. Taken together, our findings suggest that rivalry suppression affects broadband, non-orientation selective aspects of neural activity before refining fine-grained feature-selective information.

There is considerable evidence that the human brain can encode sensory events that elude conscious detection, either following acquired lesions of the sensory or association areas[1,2], or due to masking[3] or attentional manipulations of relevant stimuli[4,5]. A particularly striking example occurs during binocular rivalry, in which the presentation of different images to the two eyes leads to alternating periods during which the image to one eye is clearly perceived while the other is suppressed from awareness. One reason for the continued interest in binocular rivalry is that it provides a window onto the neural bases of consciousness[6-8] by allowing investigators to compare patterns of brain activity elicited by pairs of stimuli that are held constant while conscious perceptual reports alternate stochastically over time. Although previous research has shown that neural responses to suppressed stimuli are reduced in overall amplitude, no study to date has determined how the basic features that define such stimuli, such as their colour or orientation, are affected under conditions of binocular suppression. Here we addressed this question directly by recording neural activity with electroencephalography (EEG) while observers viewed rivalrous displays in which differently coloured and oriented gratings were projected to each eye. We used frequency tagging to track neural activity to each grating over time, and applied multivariate forward encoding modelling to recover orientation tuning profiles for the two stimuli as they alternated between conscious and unconscious perception.

A persistent question in the literature on binocular rivalry concerns the extent to which the brain represents stimuli that are currently suppressed from awareness. Invasive recordings in macaques[9,10] have shown that neurons in early cortical areas continue to respond to stimuli that are under binocular suppression. For some neurons,

61 firing rates appear to track the animal's perceptual reports, becoming lower when the
62 stimulus is suppressed and higher when it is perceived. Likewise, human neuroimaging
63 studies[6,11-15] have shown that the overall magnitude of neural responses in early cortical
64 areas is modulated according to observers' subjective perceptual report. For example,
65 studies using EEG to track the time course of neural activity during binocular rivalry
66 have revealed that response profiles to perceived and suppressed stimuli are anti-
67 correlated, and that perceived stimuli elicit a larger neural response overall[13,14,16,17].
68 Studies using functional magnetic resonance imaging (fMRI) have localised these
69 effects to relatively early cortical areas[6,11,18]. In higher areas, activity induced by
70 suppressed inputs may still be present, if for example the stimuli carry biologically
71 salient information (e.g., fearful faces[19,20]), while it can be completely absent in other
72 brain regions[6,19] This work suggests that any neural activity elicited by the suppressed
73 stimulus is simply too weak to cross the threshold for conscious report.
74 All previous studies in humans have focused exclusively on the overall *level* of
75 neural activity during binocular rivalry, rather than on the time-varying patterns of
76 activity associated with changes in the features of suppressed visual inputs. However,
77 other aspects of the stimulus' representation, in addition to the overall magnitude of
78 response, are known to be critical for conscious detection of targets[21]. Here we asked
79 whether orientation selectivity, which can be defined along several dimensions,
80 including the amplitude or gain of stimulus evoked activity as well as the fidelity or
81 sharpness of neural tuning, is modulated for a fixed stimulus as it alternates between
82 periods of conscious perception and suppression. Behavioural work in humans has

83 suggested that stimulus selectivity is affected during rivalry[7,22], but no study to date has
84 examined how rivalry affects neural representations of specific stimulus features.

85 To address this question we used multivariate forward modelling[23-26] of human
86 electroencephalography (EEG) data to quantify orientation-selective responses to
87 visual gratings that were undergoing changes in awareness during binocular rivalry. To
88 anticipate the results, we observed robust orientation tuning to both conscious and
89 unconscious gratings. Strikingly, orientation tuning began to increase for the currently
90 suppressed stimulus more than 300 ms before observers were aware of it, while at the
91 same time orientation tuning began to decline for the currently perceived grating that
92 was about to be suppressed from awareness. The same pattern was evident for the
93 overall magnitude of neural responses, and this effect emerged even earlier than the
94 changes in neural tuning (~800 ms before observers' button press indicating a switch
95 in percept). Taken together, our findings suggest that rivalry suppression first affects
96 the broadband, and non-orientation selective aspects of the neural information, before
97 refining the fine-grained feature selective information.

98 **Results**

99 To quantify the time-course and extent of neural information processing of
100 conscious and unconscious stimuli, we presented spatially overlapping red and green
101 gratings dichoptically to the left and right eyes. (Figure 1A; Movie 1). Dichoptic
102 presentation causes interocular suppression, such that observers perceive a single
103 coherent image that oscillates stochastically between the two stimuli over time, with
104 occasional mixed percepts in between (Figure 1B)[27,28]. To measure time-resolved
105 neural responses to the stimuli, we recorded neural activity using EEG, while the two

orthogonally oriented gratings counter-phase flickered at two different frequencies (20 and 24 Hz). The two gratings generated distinct steady-state visual evoked potentials (SSVEPs) that were tracked continuously over each 30 s trial. As described in detail below, the orientations of the two gratings varied from 0° to 160° (in 20° steps) across the trials to enable modelling of orientation-selective responses as a function of perceptual awareness. Participants (N = 22) reported whether they perceived the red or green grating, or a mixed percept, while we measured SSVEP responses. The magnitude of SSVEPs generated by rivalrous gratings are typically anti-correlated, exhibiting a larger response to the grating that is consciously perceived than to the grating that is suppressed from awareness[16].

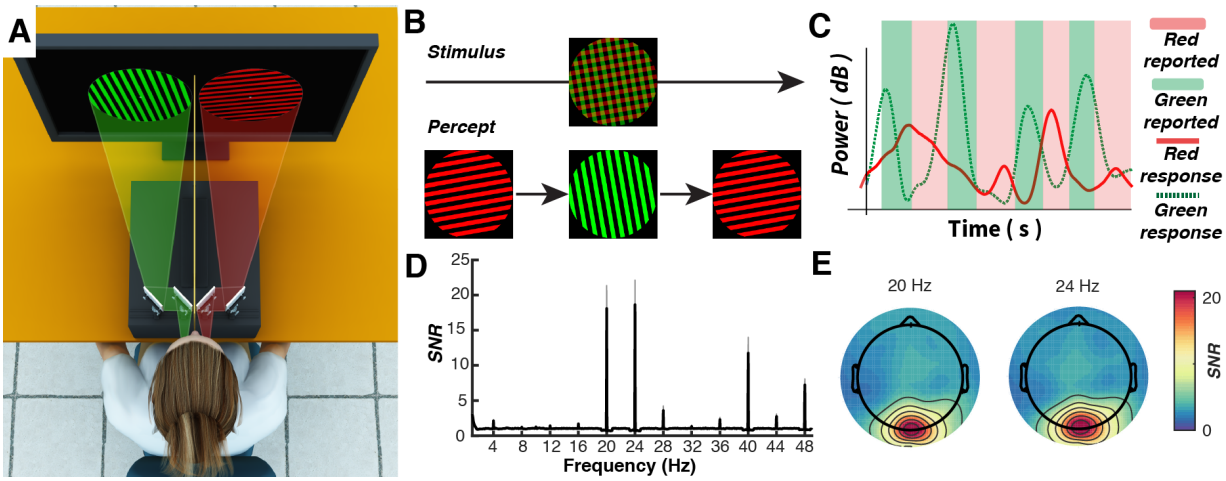


Figure 1. The SSVEP paradigm used to measure neural activity elicited by conscious and unconscious grating stimuli during binocular rivalry. **(A)** A red and green grating were presented on a computer screen while neural activity was recorded using EEG. A mirror stereoscope and a dividing board ensured that each eye received visual information exclusively from one of the two gratings, yielding binocular rivalry. **(B)** Under binocular rivalry observers typically perceive a slowly alternating percept in which one of the two gratings dominates in perception and the other is suppressed. Here observers occasionally reported a combination of either colour or orientation information (i.e., a mixed percept). **(C)** To separately track the brain's response to the gratings, the two stimuli counter-phase flickered at 20 and 24 Hz, producing unique frequency tags in the EEG. An illustrative segment from a typical trial of the rivalry task showing neural responses to the gratings (i.e. the power at the tagged frequencies) as a function of the participant's percept. **(D)** Mean frequency response for all participants across the entire 30 s trial (averaged over electrodes Oz, O1, O2, POz). Grey shading indicates ∓1 standard error of the mean. **(E)** Distribution of SSVEP responses for the 20 and 24 Hz gratings across the scalp for all participants.

Binocular rivalry affects the overall strength of neural responses

The median duration of perceptual dominance, during which one grating was perceived while the other was suppressed, lasted for 1390 ms (interquartile range = 1024 to 2349 ms; Figure 2A). To determine the effect of binocular rivalry on neural responses to the two gratings, SSVEP responses were epoched into bins that extended from 2s before the participant indicated a change in percept to 2 s after this response. The data were then combined across the flicker frequencies of the two

presented gratings to produce ‘aware’ and ‘unaware’ epochs (see Methods for further details). The label of the response (i.e., aware versus unaware) was defined relative to the percept reported at the time of the button press (0 ms). As shown in Figure 2B, the SSVEP elicited by the currently suppressed grating began to increase around 1500 ms before the stimulus was consciously perceived. At the same time, the SSVEP elicited by the currently perceived stimulus began to decline sharply after it had been reported, and the response to the suppressed stimulus began to rise. Thus, around 1000 ms after the observers’ button press, the neural response to the unaware stimulus was now larger than the response to the stimulus that was currently perceived. This timing fits with the behavioural observation that periods of stimulus dominance lasted on average around 1390 ms. As shown in Figure 2C, SSVEPs elicited by the grating stimuli were most pronounced over occipital-parietal electrode sites, as expected for such square-wave grating stimuli[6,16].

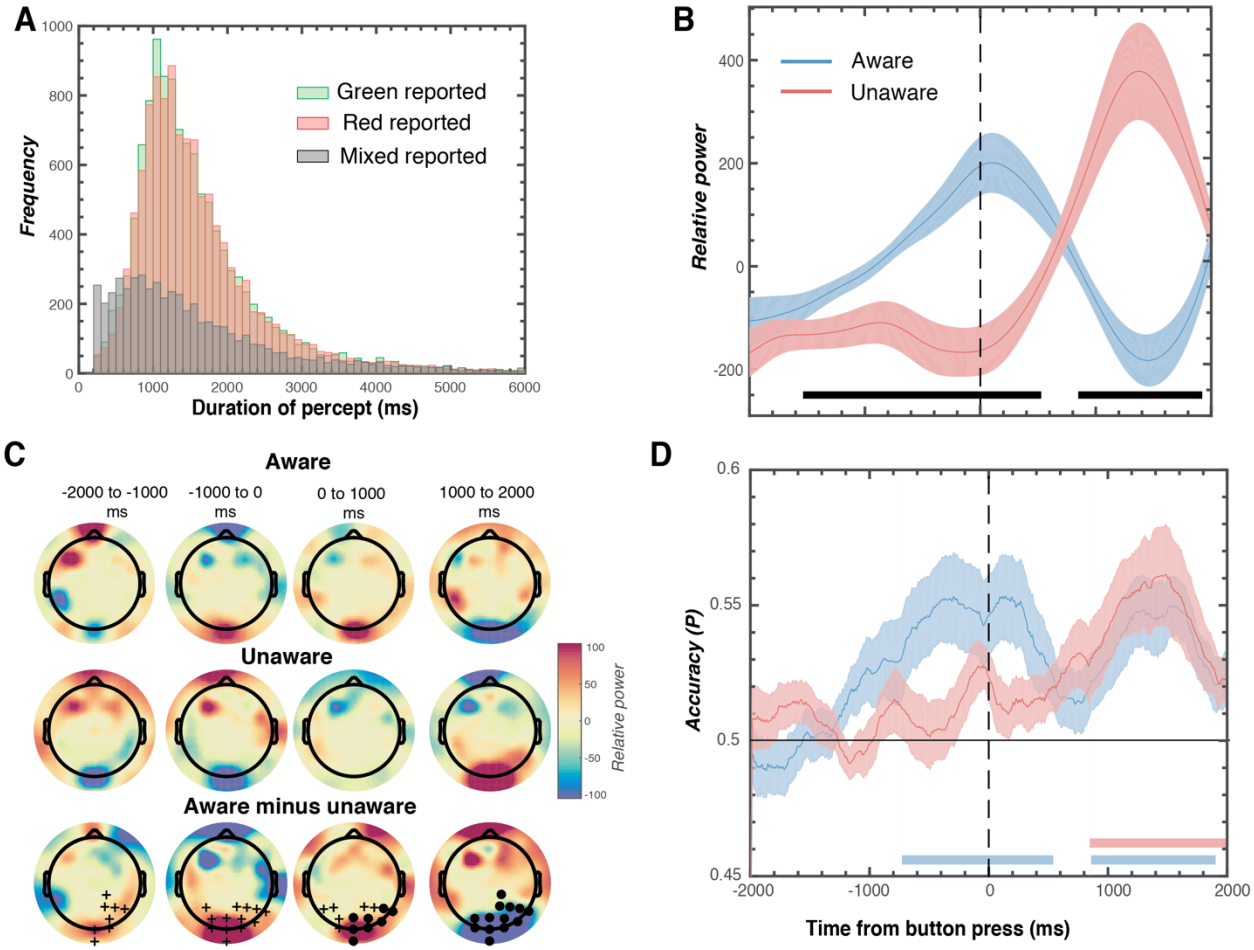


Figure 2. Behavioural and neural results associated with changes in awareness during binocular rivalry. **(A)** Distribution of durations of perceptual dominance across the 22 participants. **(B)** Time series of relative EEG power elicited by the grating stimuli, plotted separately for aware and unaware periods of the trial, averaged across three occipital electrodes (Oz, POz, Pz). The 'aware' response corresponds to the grating reported as the dominant percept at the time of the button press (0 ms), and the 'unaware' response corresponds to the suppressed stimulus at the same time point. The black horizontal lines indicate periods of significant difference between the conditions (two-tailed cluster-permutation, alpha $p < .05$, cluster alpha $p < .05$, N permutations = 20,000). **(C)** Headmaps of EEG data showing changes in relative power for periods in which gratings were consciously perceived (Aware, top row) and suppressed (Unaware, middle row), and the difference between these states (bottom row). Circles indicate clusters of electrodes with significantly lower activity, and crosses indicate clusters with significantly greater activity in the Aware vs. Unaware conditions (alpha $p < .05$, cluster $p < .025$, N permutations = 1500). **(D)** Accuracy of linear discriminant analysis used to predict observers' grating perception at time 0 ms (corresponding to the participants' button press). Coloured horizontal bars indicate times during which classification accuracy was significantly better than chance for Aware and Unaware epochs. Coloured shading in C and D represents ∓ 1 standard error of the mean.

179

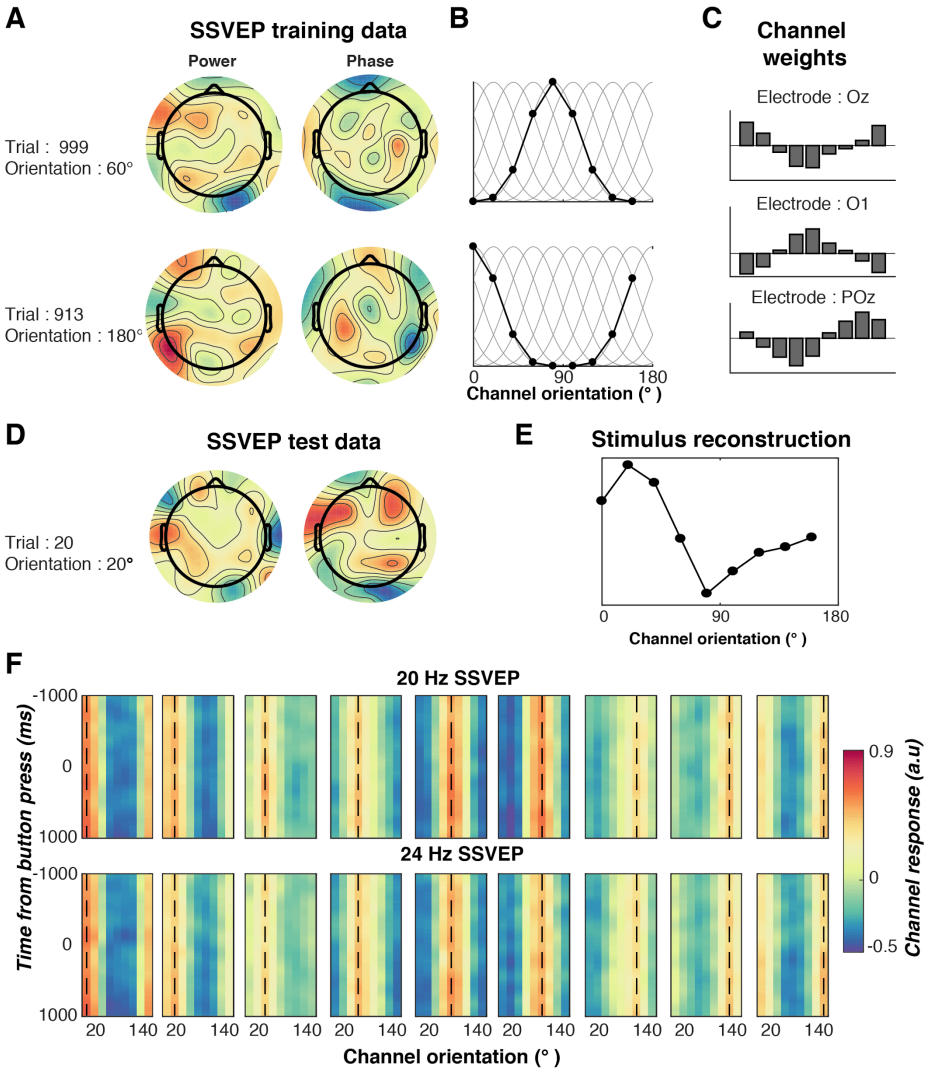
180 **Stimulus-evoked SSVEPs predict perceptual reports prior to awareness**

181 We next sought to determine whether SSVEPs could be used to predict which
182 percept the participant would report on a single-trial basis. To do this, we used a
183 multivariate linear discriminant analysis to determine whether there were patterns of
184 activity distributed across the scalp that predicted which grating was about to be
185 consciously perceived. Separately, for each SSVEP frequency and at each time point
186 across the epoch around when the percept changed, the classifier was trained on the
187 percept reported at time zero, which coincided with the participants' indicated
188 perceptual report. Again, the results were combined across frequencies to produce
189 unaware and unaware responses. Neural responses to consciously perceived gratings
190 predicted observers' perceptual reports around 800 ms before the report occurred
191 (Figure 2D), whereas neural responses to the unaware gratings did not reliably predict
192 observers' reports at this same time point. By contrast, at around 1000 ms after
193 observers made their response, SSVEP power was able to predict observers'
194 perceptual reports for both the aware and unaware stimuli.

195 **Binocular rivalry affects visual orientation selectivity**

196 Next, we sought to answer the critical question of whether orientation selectivity
197 for the rivalrous gratings was influenced by observers' awareness of the frequency-
198 tagged stimulus. To do this, we applied forward encoding modelling, which has
199 previously been used to recover orientation selectivity from both EEG and MEG
200 activity[23-26,29]. Broadly, this technique identifies multivariate patterns of EEG activity that
201 are selective for defined stimulus features, in this case orientation (see Figure 3 for an

example). We convolved grating orientation in each epoch against a bank of nine canonical, orientation-selective tuning functions, each maximally sensitive to a different orientation, to produce regression coefficients for that trial (Figure 3B). Then at each time point in the epoch, multivariate regression was used to estimate the spatial map (or *weight matrix*) sensitive to orientation in a training set of data. This weight matrix (Figure 3C) was inverted and multiplied against a test set of data (Figure 3D) to determine orientation selectivity (Figure 3E) in the test data. The procedure was iterated over all time points in the epoch, and a cross-validation procedure was used such that all epochs served in both training and test data.



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213 **Figure 3.** Overview of the forward encoding modelling procedure used to measure
214 orientation selectivity in the binocular rivalry paradigm. **(A)** Patterns of SSVEP activity
215 (here separated into real and imaginary components) are measured in response to a
216 range of orientations. **(B)** Regression coefficients for the orientations are estimated for
217 each trial from orientation selective functions. **(C)** Least-squares regression is used to
218 estimate weights for all EEG electrodes for each of the channels in the orientation
219 model. The channel weights are shown here for three example occipital-parietal
220 electrodes. **(D)** The channel weights are inverted and multiplied against a set of
221 independent training data. **(E)** The model will reconstruct the presented orientation if
222 there is an orientation selective response. In this case, the stimulus reconstruction
223 shows a tuned response to a presented grating of 20° orientation. **(F)** Average
224 orientation reconstructions over time for the two SSVEP frequencies (collapsed across
225 aware and unaware conditions) for all participants for each of the nine presented
226 orientations, indicated by the black dotted line. These reconstructions were realigned
227 so we could combine the representations of the different orientations.

228 Figure 3F shows the results of the forward encoding modelling for each of the
229 presented orientations (20° to 180° in 20° steps) for the two SSVEP frequencies of 20
230 and 24 Hz. As shown, the forward encoding model successfully recovered the
231 presented orientation across all time points in the epoch. Because we were not
232 interested in any specific orientation, but rather in orientation selectivity in general, and
233 to increase the signal to noise ratio, we re-centred all the representations to the
234 presented orientation (0° for consistency) in that trial. To quantify orientation selectivity
235 between different conditions, these outputs were fit with a Gaussian function, with the
236 amplitude providing an index of orientation selectivity (see Methods for details).
237 The forward encoding model revealed a strong orientation-selective neural
238 response that was tuned to the presented orientation (Figure 4A). Strikingly, we found
239 orientation-selective response to both the currently perceived grating and to the
240 grating that was suppressed due to binocular rivalry. Critically, this result suggests that
241 the visual system encodes feature-selective information about the presented stimulus
242 even when that stimulus is not consciously perceived. Moreover, just prior to the
243 observers' button press indicating a switch in percept, the grating that was currently
244 suppressed but was about to be consciously reported was associated with
245 significantly greater orientation selectivity than the grating that was perceived (but was
246 about to be suppressed).

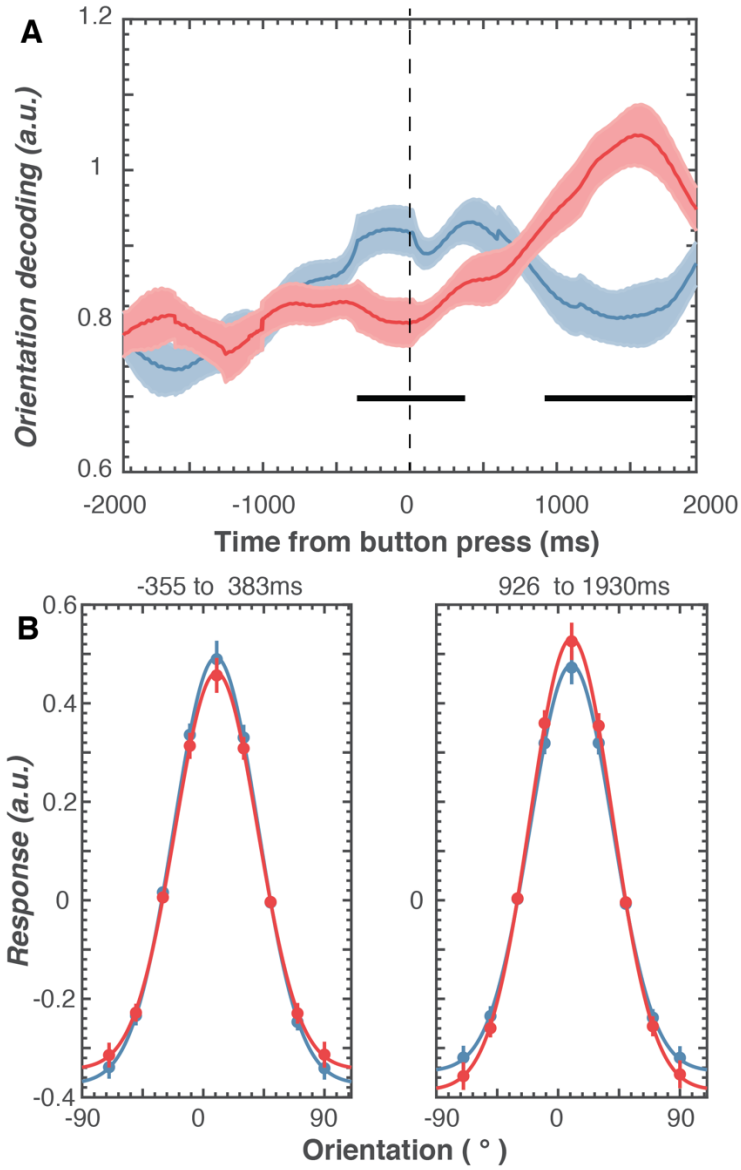

Figure 4. Results of forward encoding modelling for orientation selectivity under binocular rivalry. **(A)** Orientation decoding (given by height of tuning curves) over time for SSVEP responses elicited by aware and unaware gratings. The 'aware' response corresponds to the grating reported as the dominant percept at the time of the button press (0 ms), and the 'unaware' response corresponds to the suppressed stimulus at the same time point. The horizontal black bars indicate significant differences between the aware and unaware conditions (two-tailed cluster-permutation, alpha $p < .05$, cluster alpha $p < .05$, N permutations = 20,000). Coloured shadings show ∓1 standard error of the mean. **(B)** Orientation tuning curves collapsed across significant time points shown in A. Error bars show ∓1 standard error of the mean. The lines are fitted Gaussians (Equation 4) to data averaged across observers.

To further determine how orientation selectivity was affected by awareness, we averaged the time-resolved tuning curves over the significant time points (black lines in Figure 4A) to recover the tuning curve, and fitted Gaussian functions to quantify the change in neural representations (Figure 4B). This again revealed robust orientation-selective responses to both aware and unaware stimuli, shown by the tuned response at the presented orientation (0°). The analysis also confirmed that the amplitude of the orientation-tuning functions was reliably larger for grating stimuli when they were aware than when they were unaware (p = .01), suggesting that conscious perception is associated with a boost in the gain of orientation selectivity (or a suppression in the gain for suppressed stimuli). Crucially, however, at the same time points relative to observers' perceptual reports, there was no change in the width of the tuning functions (p = .37), suggesting that awareness does not alter the fidelity or tuning of the underlying neural representation (aware M = 33.70, SE = 2.97; unaware M = 31.58, SE = 1.25).

Discussion

We investigated how binocular rivalry affects the neural representation of visual orientation information in human observers. Previous work in non-human primates has shown that the selectivity of neurons in visual areas tracks changes in awareness, such that suppressed stimuli evoke a smaller selective response than dominant (perceived) stimuli. It has remained unclear whether the same changes in feature-selectivity occur in humans because conventional neuroimaging approaches focus on overall levels of activity, rather than tracking the time-varying changes in selectivity for elementary stimulus features. Here we used forward encoding modelling to determine how

283 orientation selectivity was influenced under conditions in which orthogonally oriented
284 pairs of gratings were presented dichoptically to induce binocular rivalry.

285 We found significant orientation selectivity in neural activity associated with both
286 aware and unaware gratings, and this response increased just before the reported
287 change in awareness. Forward encoding modelling allowed us to quantify orientation
288 tuning curves. These analyses revealed that while the gain (amplitude) of orientation
289 tuning was affected by rivalry, the fidelity (or sharpness) was not. We also found that
290 the overall neural response to the gratings, as indexed by the power of the frequency-
291 tagged SSVEP, began to increase ~1000 ms before orientation-selectivity changed. On
292 a single trial basis, from the power of the SSVEP response alone, it was possible to
293 predict an observer's choice ~800 ms before the individual reported the change. As
294 with most previous investigations of binocular rivalry[6,14,16,30], we used observers' button-
295 press responses to demarcate changes in awareness, and these perceptual switches
296 typically precede overt responses by 300 to 400 ms[30]. Such response time delays
297 cannot account for the current findings, however, as SSVEP power predicted
298 observers' percepts ~800 ms before their responses. This observation suggests that
299 during rivalry, alternations in awareness of rivalrous stimuli are initially signalled by
300 broadband changes which are not selective for orientation in neural activity, followed
301 by a change in fine-grained stimulus selectivity immediately prior to a change in
302 conscious report.

303 Our results are broadly consistent with findings from invasive recordings in
304 macaque visual cortex during binocular rivalry[10,31]. Around 300 ms before the currently
305 suppressed stimulus broke into awareness, we found that orientation selectivity for the

grating began to increase. This anticipatory neural response in humans is consistent with findings from neuronal recordings in macaque area V4, which have shown that the firing rate of neurons during binocular rivalry increases around 300-500 ms before the animal reports a change in the perceived stimulus. Our work goes beyond these findings by showing that, in humans, orientation-selective information is reliably available to the system even when a rivalrous stimulus is not consciously perceived.

More broadly, our findings are consistent with the influential global workspace theory of consciousness[32,33], which proposes that while all stimulus information is represented by early sensory regions, only those that get fed through to higher cortical regions activate a global brain network and thus reach awareness. On this account, stimuli reach awareness because they induce high synchrony within a global network of more local networks. Once an item has activated the global network, it can inhibit alternative and competing stimuli. Our results potentially add to this account, as we found that during rivalry broadband neural responses first change with awareness, and are followed several hundred milliseconds later by more fine-grained (feature-specific) changes in stimulus representations. One way this might occur is via feedback connections from higher brain areas, which are predicted to have access to the global workspace, to lower-level sensory regions which represent stimulus-selective information such as visual orientation. This idea could be tested by disrupting higher cortical areas – for example using transcranial magnetic stimulation – and measuring changes in orientation tuning to rivalrous stimuli. Future studies could also apply the forward encoding approach used here to assess feature-specific neural responses in different experimental paradigms in which conscious reports are altered, such as visual

329 masking[3], or in cases of neural pathologies such as blindsight [2] or unilateral spatial
330 neglect[1,34].

331 **Methods**

332 **Participants**

333 A group of 26 healthy adult observers (age range = 18 to 37 yr) participated in
334 exchange for partial course credit or financial reimbursement (AUD$20/hr). All
335 participants provided written informed consent, and all reported normal or corrected-
336 to-normal vision and normal colour perception. The study was approved by The
337 University of Queensland Human Research Ethics Committee and was conducted in
338 accordance with the Declaration of Helsinki.

339 **Experimental setup**

340 The experiment was conducted inside a dimly illuminated room with participants
341 seated in a comfortable chair. The stimuli were displayed on a 22-inch LED monitor
342 (resolution 1920 x 1080 pixels, refresh rate 120 Hz) using PsychToolbox presentation
343 software[35,36] for MATLAB (v7.3). Viewing distance was maintained at 54 cm using a
344 chinrest, meaning each pixel subtended 1.8’ x 1.8’.

345 **Task**

346 Prior to the start of the experiment, participants aligned the mirror stereoscope
347 (Fig 1A) so images presented to the left and right eyes appeared overlapping. Identical
348 circular checkerboards were placed around the stimulus in both eyes to encourage
349 fusion of the images. Each trial began with presentation of these checkerboards and a
350 central Gaussian fixation dot. After 1500 ms, green and red square-wave gratings were
351 presented to the left and right eyes, so that they appeared within the centre of the

352 surrounding checkerboards. The colours were presented at 100% luminance intensity.
353 To generate SSVEPs, the gratings counter-phase flickered at 20 and 24 Hz for 30 s.
354 Counter-phase flickering square-wave gratings were used because these produce
355 large SSVEP responses and produce orientation-selective neural activity that can be
356 tracked with EEG [13]. Participants indicated whenever the percept (red, green or
357 mixed) changed during the trial using separate keys on a standard keyboard. For half
358 the participants, the red gratings flickered at 20 Hz and the green gratings flickered at
359 24 Hz; for the remaining participants these contingencies were reversed.
360 Across trials the orientations of the gratings were varied between 0° and 160° (in
361 20° steps) so that forward encoding modelling could be employed to determine
362 orientation selectivity contained with the EEG data. The orientations of the pairs of
363 gratings presented in each trial were always perpendicular to ensure strong rivalry
364 between the stimuli[31,37,38]. There were 90 x 30 s trials in total across the experiment,
365 meaning that each orientation was repeated 10 times.

366 **EEG acquisition and pre-processing**

367 Continuous EEG data were recorded using a BioSemi Active Two system
368 (BioSemi, Amsterdam, Netherlands). The signal was digitised at 1024 Hz sampling rate
369 with a 24-bit A/D conversion. The 64 active scalp Ag/AgCl electrodes were arranged
370 according to the international standard 10–20 system for electrode placement [26]
371 using a nylon head cap. As per BioSemi system design, the common mode sense and
372 driven right leg electrodes served as the ground, and all scalp electrodes were
373 referenced to the common mode sense during recording.
374 Offline EEG pre-processing was performed using EEGLAB in accordance with

375 best practice procedures[39,40]. The data were initially down sampled to 256 Hz and
376 subjected to a 0.5 Hz high-pass filter to remove slow baseline drifts. Electrical line
377 noise was removed using the *clean_line.m,* and *clean_rawdata.m* in EEGLAB [29] was
378 used remove bad channels (identified using Artifact Subspace Reconstruction), which
379 were then interpolated from the neighbouring electrodes. Data were then re-referenced
380 to the common average before being epoched into trials (-1 to 31 s). Systematic
381 artefacts from eye blinks, movements and muscle activity were identified and
382 regressed out of the signal using semi-automated procedures in the SASICA toolbox
383 [30]. After this stage, any trial with a peak voltage exceeding ±100 *uV* was excluded
384 from the analysis.

385 **Data analysis**

386 A wavelet transform (150 ms time-domain standard deviation) was applied to
387 the recorded EEG data in each trial to extract the neural response to the two gratings.
388 The data were then epoched into 4 s time periods symmetrically around each button
389 press (-2 s to + 2 s), which observers used to indicate a change in the perceived
390 grating. Epochs were only included if the preceding epoch was not a mixed percept, so
391 we were certain the preceding epoch was the previously aware stimulus. We did not
392 include periods with mixed percepts because these are by definition ambiguous with
393 respect to stimulus awareness (i.e., both stimuli are perceived to some extent). Epochs
394 were also only included if the button press occurred between 2 and 28 s into the trial
395 (thus ensuring a robust frequency tagged signal). To ensure the encoding reflected
396 periods of stable perception, only dominance periods lasting longer than 500 ms were
397 included. Two participants were excluded because most responses were between one

colour and mixed. Two further participants were excluded because they reported significantly fewer switch (<100, SD < 2 SD below average). This produced a mean of 1276 epochs for the remaining (N = 22) participants (range = 445 to 1963 across the participants). For each participant the periods of dominance were relatively evenly split between the two colors; there were relatively fewer periods in which the percept was mixed, and these tended to be shorter-lived in duration (Figure 2A). To maintain consistent phase information in the SSVEPs, we aligned the nearest counter-phase flicker within the epoch to the participants' button press, separately for the 20 and 24 Hz frequencies.

Forward encoding modelling

We used forward encoding modelling to extract the orientation selective response from the patterns of EEG activity. This technique transforms sensor-level activity distributed across the scalp into tuned 'feature-channels' that are selective for a specific feature dimension, in this case orientation[23,24,26,29]. To do this, we used the orientations of the epoched data segments (4 s each) to construct a regression matrix with 9 regression coefficients for each of the orientations. This regression matrix was convolved with a tuned set of nine basis functions (half cosine functions raised to the eighth power) cantered from 0° and 160° (in 20° steps). This tuned regression matrix was used to measure orientation at each time point in the 4 s epoched segments. This was done by solving the linear equation (1):

$$B_1 = WC_1 \quad (1)$$

Where B_1 (64 sensors x N training trials) is the electrode data for the training set, C_1 (9 channels x N training trials) is the tuned channel response across the training trials, and

W is the weight matrix for the sensors to be estimated (64 sensors x 9 channels). Following an approach recently introduced for the analysis of MEG data, we separately estimated the weights associated with each channel individually [31]. W was estimated using least square regression to solve equation (2):

$$W = (C_1 C_1^T)^{-1} C_1^T B_1 \quad (2)$$

Following this previous work[41,42] we also sought to remove the correlation between the sensors which hinders finding the true solution to the linear equation. To do this, we first estimated the noise correlation between electrodes and removed this component through regularisation[43]. The channel response in the test set C_2 (9 channels x N test trials) was estimated using the weights in (2), and was applied to activity in B_2 (64 sensors x N test trials).

$$C^2 = (W W^T) W^T B^2 \quad (3)$$

To avoid overfitting, we used a five-fold cross validation procedure in which 80% of epochs were used to train the model, and the remaining 20% of epochs were used for testing. This procedure was repeated until all epochs had served as both training and test trials. We repeated this procedure for both of the SSVEP frequencies and at each time-point in the epoch to produce a time-resolved orientation-selectivity function. We then shifted all trials to a common orientation, so that 0° corresponded to the orientation presented on each trial. These reconstructions were smoothed with a Gaussian temporal kernel to increase signal-to-noise[29].

To quantify orientation selectivity, we fit the results of the forward encoding model with a Gaussian function (4) using least square regression to quantify the amount of orientation selective activity.

$$G(x) = A\, exp(-\frac{(x-\phi)^2}{2\sigma^2}) + C \quad (4)$$

Where *A* is the amplitude representing the amount of orientation selective activity, ϕ is the orientation the function is centred on (in degrees), σ is the width (degrees) and *C* is a constant used to account for non-orientation selective baseline shifts.

Acknowledgements

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