

Conscious perception and perceptual echoes: a binocular rivalry study

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Abstract

Alpha rhythms (~10Hz) in the human brain are classically associated with idling activities, being predominantly observed during quiet restfulness with closed eyes. However, recent studies demonstrated that alpha (~10Hz) rhythms can directly relate to visual stimulation, resulting in oscillations, which can last for as long as one second. This alpha reverberation, dubbed perceptual echoes (PE), suggests that the visual system actively samples and processes visual information within the alpha-band frequency. Although PE have been linked to various visual functions, their underlying mechanisms and functional role are not completely understood. In this study, we investigated the relationship between conscious perception and the generation and the amplitude of PE. Specifically, we displayed two coloured Gabor patches with different orientations on opposite sides of the screen, and using a set of dichoptic mirrors, we induced a binocular rivalry between the two stimuli. We asked participants to continuously report which one of two Gabor patches they consciously perceived, while recording their EEG signals. Importantly, the luminance of each patch fluctuated randomly over time, generating random sequences from which we estimated two impulse-response functions (IRFs) reflecting the PE generated by the perceived (dominant) and non-perceived (suppressed) stimulus, respectively. We found that the alpha power of the PE generated by the consciously perceived stimulus was comparable with that of the PE generated during monocular vision (control condition) and higher than the PE induced by the suppressed stimulus. Moreover, confirming previous findings, we found that all PEs propagated as a travelling wave from posterior to frontal brain regions, irrespective of conscious perception. All in all our results demonstrate a correlation between conscious perception and PE, suggesting that the synchronization of neural activity plays an important role in visual sampling and conscious perception.

Keywords: perceptual echoes; binocular rivalry, EEG oscillations; conscious perception; travelling waves

Introduction

The alpha rhythms (8–12 Hz) is the most prominent oscillation in the human brain, and the first one to be described in human electrophysiological recordings (Berger 1933). It involves most of the cortical regions, but it is most dominant in occipital and parietal areas. Its origin can be related to different processes: some studies pointed at the closed-loop interaction between cortical and thalamic regions, the latter acting as alpha pacemakers (Lopes da Silva et al. 1980, 1973; Bollimunta et al. 2011), but

recent evidence indicated uniquely cortical mechanisms as responsible for its generation (Halgren et al. 2019). Just like distinct sources can produce alpha-band rhythms, similarly these alpha-band oscillations are likely to serve different functions. On the one hand, alpha oscillations have been shown to strongly but negatively correlate with task demand and increasing attention, hence their presumed involvement in inhibitory functions (Jensen and Mazaheri 2010; Gazzaley and Nobre 2012; Klimesch 2012). On the other hand, alpha waves have been related to information processing, such as the temporal parsing of sensory information (Klimesch

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et al. 2007) or the perception of visual stimuli (VanRullen 2016). Regarding the latter, electrophysiological recordings demonstrate that visual stimuli reverberate in visual cortical areas around 10 Hz, producing what has been dubbed as perceptual echoes (PE) (Vanrullen and MacDonald 2012; VanRullen 2016).

PE are best observed by cross-correlating a non-periodic flickering stimulus, for example a disc whose luminance randomly varies over time, with the EEG signals recorded in occipital and parietal regions. The cross-correlation provides an impulse response function (IRF), which describes the brain response to each stimulus transient. Such response reveals a clear oscillation in the alpha band whose duration can last for as long as one second. A recent study ascribed the mechanisms generating the echoes to the interactions between brain regions within a predictive coding (PC) framework (Alamia and VanRullen 2019). However, whether PE are a by-product of cortical interactions or serve some specific cognitive function remains unclear. Experimental studies demonstrated that PE are enhanced when repetitions are embedded in the visual sequence, suggesting that they could reflect a role in regularity learning (Chang et al. 2017), whereas other evidence show that attended stimuli generate larger echoes than unattended ones, suggesting that attention allocation plays a role in modulating PE amplitude (Vanrullen and MacDonald 2012). In addition, PE have been characterized as travelling waves that propagate from occipital to frontal regions, thus including a spatial component that may reflect the hierarchical processing of visual information along the visual system (Alamia and VanRullen 2019; Lozano-Soldevilla and VanRullen 2019).

All these findings indicate that PE are relevant to different functional roles in visual information processing, suggesting that they may reflect some fundamental mechanism in cortical processing. In this study, we take one step further in this direction by exploring whether PE are modulated by conscious perception. In order to address this question, we tested a pool of participants within a binocular rivalry design, in which two different stimuli are shown separately to each eye, generating a rivalry that is resolved with the perception of only one of the two stimuli. In this experiment, a green and a red Gabor patch, respectively tilted by $\pm 45^\circ$, were displayed on the left and right side of the screen. We employed a dichoptic mirrors setup to project each stimulus separately to each eye. Importantly, the luminance of each stimulus varied over time in a random, non-periodic way, generating two flickering luminance sequences. Participants were instructed to continuously report which coloured Gabor patch was being perceived throughout the experiment, thus defining two sequences corresponding to the dominant and suppressed stimuli. Here, we aimed at computing the echoes by cross-correlating the EEG recordings with each sequence, to assess whether the generation and amplitude of PE are associated with conscious perception.

Materials and Methods

Participants and statistical power analysis

We estimated the number of participants via a statistical power analysis based on previously published data investigating PE in binocular vision (Brüers and VanRullen 2017). We determined the effect size as equal to 1.7, computed as the mean alpha power difference between the actual echoes and the ones obtained after shuffling the temporal sequences (i.e. surrogate echoes, see below). Setting the power level to 0.90 and the statistical threshold at 0.05, that effect size requires a number of participants equal to 4. However, we based our effect size estimates during binocular vision (i.e. both eyes fully perceiving the same stimulus), and we aimed at computing echoes in conditions of monocular vision and binocular rivalry (BR). Given these differences, we decided to increase the final number of participants, including 12 participants (7 females, mean age 26, SE = 0.9), which is comparable to previous studies investigating PE in various conditions of monocular vision (Benedetto et al. 2018; Schwenk

et al. 2020). All participants had normal or corrected-to-normal vision and gave written consent before the first session of the experiment, in accordance with the Declaration of Helsinki. This study was carried out in accordance with the guidelines for research at the 'Centre de Recherche Cerveau et Cognition' and the protocol was approved by the committee 'Comité de protection des Personnes Sud Méditerranée 1' (ethics approval number N° 2016-A01937-44).

Experimental procedure

Each participant completed two sessions on two different days. One session consisted of 10 blocks, each composed of 10 trials. A trial lasted for 30 s each. The design consisted of two conditions: in half of the blocks, including the first one, participants performed BR trials, whereas on every other block they performed physical alternation (PA) ones. In BR trials, two Gabor patches, each encircled by a square frame (visual angle of the patch: 11.9 degrees, visual angle of the frame: 11.9 degrees), were shown separately to each participant's eyes. Patches were different in colour and inclination, either red or green, $\pm 45^\circ$, the colour-inclination associations were kept constant throughout each experiment, but randomized between participants. The spatial frequency of the Gabor was ~ 2.1 cycles/degree (~ 5.8 cycles/stimulus), with green/red-tilted bars, and the Gaussian full-width at half-maximum was ~ 2.8 degrees, and the background was black. The colour and orientation of the stimulus served mainly to help identify the perceived stimulus and thereby facilitate the perceptual reports from the participants; however, the main experimental variable was the stimulus luminance. The luminance of the Gabor patches changed randomly over time with a refresh rate of 160 Hz, and this random sequence was designed to have the same spectral power at every frequency (Fig. 1A, see also Vanrullen and MacDonald 2012). Importantly, the range in the two colours luminance was carefully calibrated and equalized to avoid any perceptual biases. Specifically, photometer measurements (Konica Minolta, LS-100) carried out before the study were used to linearize luminance values for each RGB channel separately. After the luminance linearization, the RGB value ranges for red (from (0,0,0) to (255,30,30)) and green (from (0,0,0) to (0,110,0)) colours were chosen based on their equal luminance ranges. The goal of this procedure was to prevent the occurrence of drastic biases in favour of one of the two bistable percepts. The physical position on the screen of the two Gabor patches was switched on each trial (i.e. either the left or the right side). The task was to report which patch was perceived by moving a joystick either to the left or the right (e.g. one participant instructions were to lean the joystick to the left when green was perceived and to the right when red was perceived). The colour-side associations were pseudorandomized between participants. Importantly, participants were encouraged to account continuously for their visual perception, reporting intermediate joystick positions when the perception of both patches overlapped. Each trial started by pressing a joystick button, and participants were encouraged to rest between trials. Each BR block was followed by a PA one. Only one Gabor patch at a time was displayed in PA blocks, replaying the exact sequence of Gabor patches reported in the previous BR block. Notably, PA blocks' stimuli were identical in duration and luminance values to those consciously perceived in the past BR block. In PA blocks, stimuli were presented to the same eye that was dominant during the BR block, thus switching between eyes according to the subject's joystick report. When participants reported intermediate joystick positions (i.e. overlapped perception of both patches), we did not show any stimulus, as we could not determine the exact fused perception. The task's instructions were the same, with the exception that participants were no longer performing a binocular rivalry task. The goal of such replays was to estimate precisely the reaction time (RT) in each trial and correctly segment the actual perception in the BR blocks before computing the echoes. Although there may be different mechanisms eliciting motor responses between the newly presented stimuli (PA condition) and

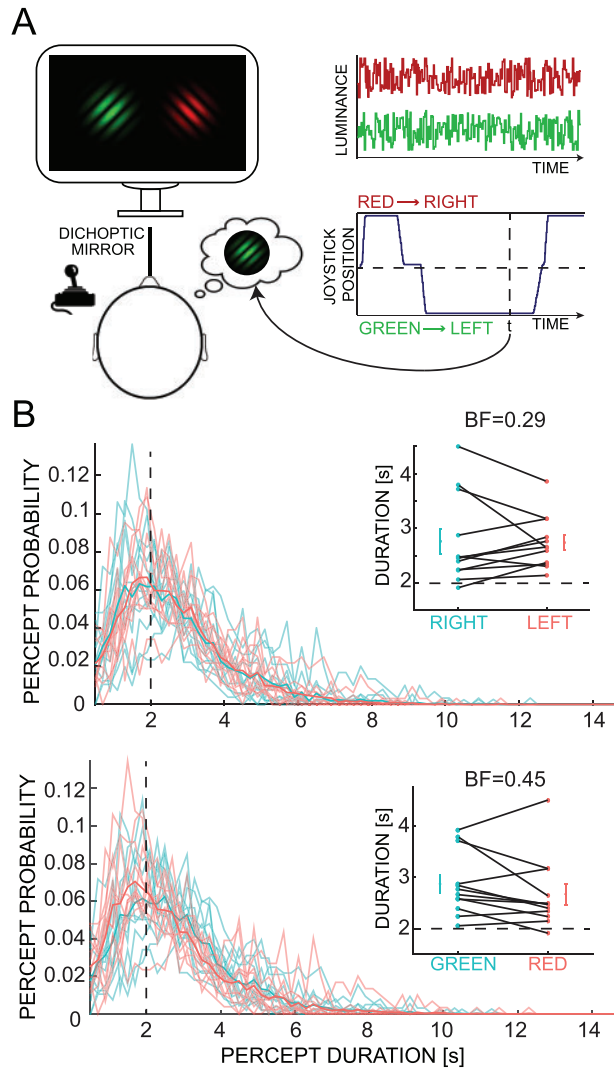


Figure 1. Experimental design

(A) Participants stared at the screen through a set of dichoptic mirrors that projected the left and right side of the screen to the left and right eye, respectively. Two stimuli, placed on the two sides of the screen, were Gabor patches of different colour and orientation, either red or green with a $\pm 45^\circ$ angle. Participants reported which patch they perceived by moving a joystick to either side, each one associated with a stimulus (pseudo-randomly between participants, consistent across blocks and sessions). (B) Distribution of percept duration in seconds, grouped for the left-right response (upper panel) and colour (lower panel). On average, participants perceived one or the other stimulus for 2 s. We discarded percepts below this threshold (indicated by the black, dashed lines). Overall, there was no difference in the duration of stimuli placed to the left and to the right (Bayesian t-test, $BF_{10} = 0.29$, error = 0.02%), and between green and red stimulus (Bayesian t-test, $BF_{10} = 0.45$, error = 0.03%).

present but suppressed stimuli (BR condition), we consider this correction as a useful approach in reducing such differences. Moreover, PA blocks served as a control condition to assess PE in condition of monocular vision, without rivalry.

EEG recording and analysis

Recording and preprocessing

EEG signals were recorded using a 64-channel active BioSemi EEG system (1024 Hz sampling rate), and three additional ocular electrodes were used. The preprocessing was performed in EEGlab (Delorme and Makeig 2004) and consisted first in downsampling the data to 160 Hz followed by a high-pass (>1 Hz) and a notch (47–53 Hz) filter. Data were then average re-referenced and segmented from 200 ms before trial beginning until its end (–200 to 30,000 ms). Each epoch was then baseline corrected by subtracting the average between –200 ms and stimulus onset.

Perceptual echoes

PE are computed by cross-correlating the luminance sequences with the corresponding EEG signal. As reported in previous studies, PE are stronger in occipital and parietal regions (Vanrullen and MacDonald 2012; VanRullen 2016); hence, we focussed our analysis on signals recorded in POz (note that similar results are obtained when using the electrodes Oz and Pz). Firstly, for each response in the PA condition, we estimated the RT as the time between the onset of the stimulus (which we know and control) and the beginning of the joystick movement. We then used these RT estimates to improve the measure of the perceptual switch timing in the BR condition, that is we shifted backward the responses in BR to account for the RTs. Next, we segmented the EEG signals and the corresponding sequences according to participants' perceptions. In order to identify the temporal segments in which participants reported a full perception (either left or right), we normalized joystick responses between –1 (left) and 1 (right), and we included all the sequences in which the response was above a threshold set to ± 0.95 and longer than 2 s to ensure the sequences were long enough for the reliable estimation of PE (Fig. 1B). In BR blocks, for each segment we cross-correlated the EEG signal with the sequence of the perceived patch (i.e. dominant) and the non-perceived patch (i.e. suppressed). In PA blocks, we cross-correlated the EEG signal with the one sequence shown. In both conditions, the cross-correlation was computed on lags between –0.5 and 2 s. The module of the PE spectra was computed with a Fast Fourier transform over the delays between 0.25 and 1 s. From each spectrum, we extracted the average power in the alpha band (8–12 Hz). To estimate a baseline for comparison, we computed the same power spectra in surrogate echoes, obtained by cross-correlating the EEG signals with the luminance sequences after having shuffled their temporal order. Lastly, we compared the amount of alpha power in the echoes between conditions (dominant, suppressed and physical alternation) by means of a Bayesian ANOVA having CONDITION as a fixed factor and subject as a random term. For dependent variable, we considered the amount of alpha power computed in decibel [dB] as follows:

$$\text{echoes [dB]} = 10 \cdot \log_{10} \left(\frac{\text{alpha power}}{\text{surrogate alpha power}} \right).$$

Regarding the time-frequency analysis, we computed the power-spectra using a wavelet transformation (1–40 Hz, in log-space frequency steps with 1–20 cycles) of each IRF (i.e. the result of cross-correlating each luminance sequence and the temporally aligned EEG signal). We applied a baseline correction by subtracting the average activity 200 ms prior to 0 lags, and we extracted the mean value in the alpha range (8–12 Hz) in the time window between 250 and 850 ms. As previously said, for each condition, we computed the point-by-point difference in decibel between the power spectra and its surrogate. We then performed a point-by-point two-tailed t-test to identify the time-frequency regions significantly different from zero, and we applied a cluster-based permutation test (Maris and Oostenveld 2007). Regarding the t values clusters, we set a threshold at $t > 2.5$ ($P < 0.01$), and we compared the global sum for each cluster with the null distribution estimated over 200 iterations

following the same procedure, after having shuffled the conditions (i.e. dominant, suppressed, PA). For each cluster, we set the significance threshold at 0.05.

Travelling waves analysis

We eventually assessed how PE propagate through cortex as a travelling wave. As in our previous studies (Alamia and VanRullen 2019; Pang et al. 2020), we computed the echoes in seven midline electrodes (Oz, POz, Pz, CPz, Cz, FCz, Fz), and we created 2D maps by stacking signals from those electrodes (see Fig. 4A). From the 2D map, we computed a 2D-FFT, in which the power of the upper left quadrant represents the amount of waves travelling in a forward direction (FW—from occipital to frontal electrodes), whereas the lower left quadrant quantifies the amount of waves travelling backward (BW—from frontal to occipital). Note that the same values can be found in the right quadrants, since the 2D-FFT is symmetric around the origin. Since we investigated the propagation of the alpha-band echoes, we extracted the maximum values within the alpha range (8–12 Hz). In order to quantify the amount of waves above chance level, we computed a surrogate distribution of values by shuffling the electrodes order before quantifying the 2D-FFT (obtaining FW_{ss} and BW_{ss} for forward and backward waves, respectively). Similar to the previous analyses, we computed the amount of waves in decibel [dB] for FW and BW waves according to the following formula:

$$\begin{aligned} \text{FW waves [dB]} &= 10 \cdot \log_{10} \left(\frac{FW}{FW_{ss}} \right); \text{ BW waves [dB]} \\ &= 10 \cdot \log_{10} \left(\frac{BW}{BW_{ss}} \right). \end{aligned}$$

Statistical analyses

All statistical tests were performed within the Bayesian framework, assessing the likelihood of a model given the data. This analysis produces a Bayes factor (BF), which quantifies the ratio between models testing the alternative over the null hypothesis. Throughout the paper, all BFs comply with this convention—that is the probability of the alternative hypothesis over the null hypothesis, usually indicated as BF_{10} . In practice, a large BF ($\sim BF > 3$) provides evidence in favour of the alternative hypothesis, whereas low BF ($\sim BF < 0.3$) suggests a lack of effect (Bernardo and Smith 2001; Masson 2011). All analyses were performed in JASP (Love et al. 2015; JASP Team 2018). Data are available upon request to the corresponding author.

Results

Echoes

The main goal of this study was to determine whether PE are influenced by conscious perception. Firstly, we estimated the averaged alpha-band power of the PE generated by the dominant and suppressed stimuli, along with those measured during the PA task. Each PE was obtained by cross-correlating the EEG recording (POz electrode) with the corresponding luminance sequence (Fig. 2). In order to quantify the power in the alpha range in each condition (Fig. 3A), we computed the corresponding surrogate values after shuffling the temporal order of the sequence, thus expressing the PE alpha amplitude as a ratio measured in dB (see Methods for details). The graph in Fig. 3B reveals strong evidence in favour of a difference between conditions, as confirmed by a Bayesian ANOVA (CONDITION factor: $BF_{10} = 9.442$, error = 0.411%). A post hoc Bayesian t-test comparison confirms very strong difference between dominant and suppressed echoes ($BF_{10} = 23.926$, error < 0.001%). Not surprisingly, we also found echoes larger than zero in the PA conditions, that is when only one Gabor was displayed ($BF_{10} \gg 100$, error < 0.001%), confirming the results of a recent study (Schwenk et al.

2020) showing that PE, although strongly reduced, can still be observed in conditions of monocular vision. Additionally, echoes generated in the PA conditions were larger than the one generated by the suppressed sequence ($BF_{10} = 3.276$, error < 0.001%), but we observed no difference between PE generated by the dominant sequence and in the PA conditions ($BF_{10} = 0.159$, error < 0.001%). Interestingly though, both dominant and suppressed echoes proved to be larger than zero (Bayesian one sample t-test, both dominant and suppressed $BF_{10} \gg 100$, error < 0.001%), suggesting that PE can also be elicited without conscious perception. At last, we investigated the correlation in alpha power between EEG signals and PE. A previous study, using lateralized stimuli, demonstrated a negative correlation between EEG signals and PE due to spatial attentional mechanisms: attention decreases EEG alpha amplitude, but increases PE amplitude (Vanrullen and MacDonald 2012). Although our stimuli were not lateralized, we tested such correlation for each participant on a trial-by-trial basis. If the PE increase during dominant periods was caused by increased attention, we should observe a concurrent decrease in alpha power, and thus a negative correlation between the two measures. Instead, we found strong evidence for a positive correlation in alpha power across participants (t-test of correlation coefficients against zero, in all conditions $BF_{10} > 100$). This result provides strong albeit indirect evidence against the hypothesis that attention may be a confounding factor in our findings.

Time frequency

In order to assess the temporal dynamics of the PE in each condition (i.e. dominant, suppressed and physical alternation), we performed a time-frequency analysis on the echoes. In line with our previous results, Fig. 3C reveals a stronger effect in the alpha band in the dominant and PA conditions than the suppressed condition. This was confirmed by a cluster-based permutation test, which showed significant clusters in the alpha band starting from 250 ms in all conditions, but lasting longer and with higher values in dominant and PA. Overall the time-frequency analysis confirmed the previous results, indicating that PE elicited in the dominant and PA conditions are larger than in the suppressed condition.

Travelling waves

Finally, we investigated whether PE elicited during binocular rivalry propagate through cortex as forward travelling waves (i.e. from occipital to frontal regions), as recently shown in the case of binocular vision (Alamia and VanRullen 2019; Lozano-Soldevilla and VanRullen 2019). We quantified the amount of forward and backward waves as shown in Fig. 4 obtaining for each participant a value in dB for each condition (see methods for details). Interestingly, a Bayesian ANOVA performed with factors DIRECTION (FW and BW) and CONDITION (dominant, suppressed and PA) revealed a substantial difference between FW and BW waves ($BF_{10} = 3.963$, error = 0.001%) but neither a difference between conditions ($BF_{10} = 0.100$, error = 0.007%), nor an interaction ($BF_{10} = 0.097$, error = 0.012%). A Bayesian t-test comparing the amount of FW waves against zero confirmed that PE propagates from occipital to frontal regions when elicited by dominant ($BF_{10} = 6.783$, error < 0.001%), suppressed ($BF_{10} = 18.907$, error < 0.001%) and monocular sequences (PA, $BF_{10} = 3.655$, error = 0.001%).

Discussion

Previous studies showed that visual information reverberates in posterior brain regions in the alpha-band frequency range, as observed by cross-correlating white noise luminance sequence with EEG recordings (Vanrullen and MacDonald 2012; VanRullen 2016). Such reverberation, dubbed as PE, proved in several studies to be related to various cognitive functions, such as attention (Vanrullen and MacDonald 2012) and

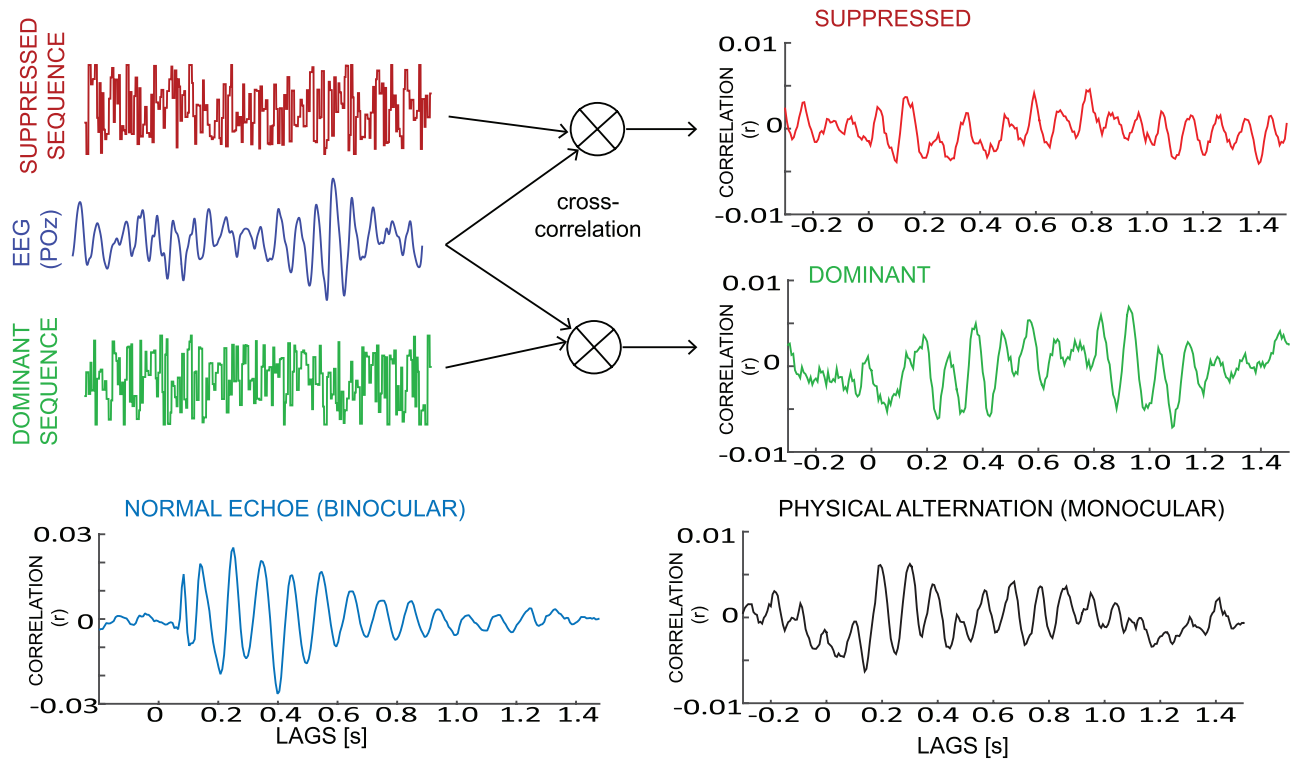


Figure 2. Computing perceptual echoes

Two random (independent) temporal sequences of luminance were displayed on opposite sides of the screen. Given the dichoptic mirror setup, each sequence was perceived by one eye only, producing a binocular rivalry that was resolved with one perceived sequence (i.e. dominant, in green) and one non-perceived (i.e. suppressed, in red). We computed PE by cross-correlating each sequence and the corresponding EEG signal (POz electrode), revealing a reverberation in the alpha-band interval. The same procedure was used to compute the PE in the physical alternation condition (in black). The bottom-left panel shows for comparison a PE computed in case of binocular vision (Brüers and VanRullen 2018). Note the difference in the y axis.

statistical learning (Chang et al. 2017). In this study, we investigated the link between PE and conscious visual perception using a binocular rivalry design. Our results indicate that PE can be generated by both consciously perceived and suppressed stimuli, but the former elicit larger PE than the latter, and of comparable amplitude as the PE generated during monocular vision. Moreover, we reported that the PE generated by both conscious and unconscious visual perception propagates as a travelling wave from occipital to frontal regions, possibly reflecting bottom-up processing in the visual system (Alamia and VanRullen 2019; Lozano-Soldevilla and VanRullen 2019; Pang et al. 2020).

Similar to the finding that PEs are enhanced by attention (Vanrullen and MacDonald 2012), we found that PEs generated by the consciously perceived sequence (i.e. the dominant stimulus) contain larger alpha power. One could wonder whether there is a link with attentional mechanisms. A previous study using a frequency-tagging technique demonstrated that participants need to attend the binocular rivalry stimuli to observe the dominant tagging frequency in the EEG recordings, arguing that attentional mechanisms might modulate binocular rivalry (Zhang et al. 2011). Conversely, in our study, participants were instructed to attend to both stimuli (which were superimposed at the same spatial location) during the whole experiment's duration, thus reducing any confound due to attentional mechanisms. Yet, we can de facto assume that the attentional focus is driven to the stimulus perceived as conscious, thus increasing the PE alpha power as compared with the suppressed one. Indeed, previous studies reported the opposite effects of attention on alpha power: while attention decreases stimulus non-specific alpha power, it nonetheless increases the spectral (alpha band) power of PE

(Worden et al. 2000; Thut et al. 2006; Vanrullen and MacDonald 2012). Importantly, our data show a positive correlation in alpha power between EEG signals and PE, thus suggesting that our findings are not a modulation due to attentional mechanisms. It could be interesting then to test the hypothesis that conscious perception plays a similar role in the modulation of alpha power. One possible experimental approach would be to lateralize the suppressed and dominant stimulus, thus assessing whether conscious perception modulates the alpha power in each occipital hemisphere similar to attention. Further experiments will shed light on this interesting hypothesis.

The enhancement of PE alpha power in the dominant condition together with the previous finding that attention enhances PE is reminiscent of the application of frequency tagging in binocular rivalry. Previous studies revealed that both conscious perception and attention allocation increase the spectral power corresponding to the steady-state visually evoked potential (SSVEP) (Tononi et al. 1998; Srinivasan et al. 1999; Ding et al. 2006). Even though SSVEP showed similar effects as PE in binocular rivalry and attention tasks, their underlying mechanisms are likely different. SSVEP is a passive brain response to a rhythmic stimulation, reflecting the spectral characteristics of the generating stimulus, whereas PEs are characterized by a clear 10 Hz oscillation without a corresponding 10 Hz peak in the visual stimulus, possibly reflecting computational cortical mechanisms (Alamia and VanRullen 2019). Despite the functional differences, it is tempting to speculate that in both SSVEP and PE, conscious perception modulates the amount of synchronized activity in brain regions: the higher alpha power in dominant PE might be associated with a larger synchronization of local neural activity, which might

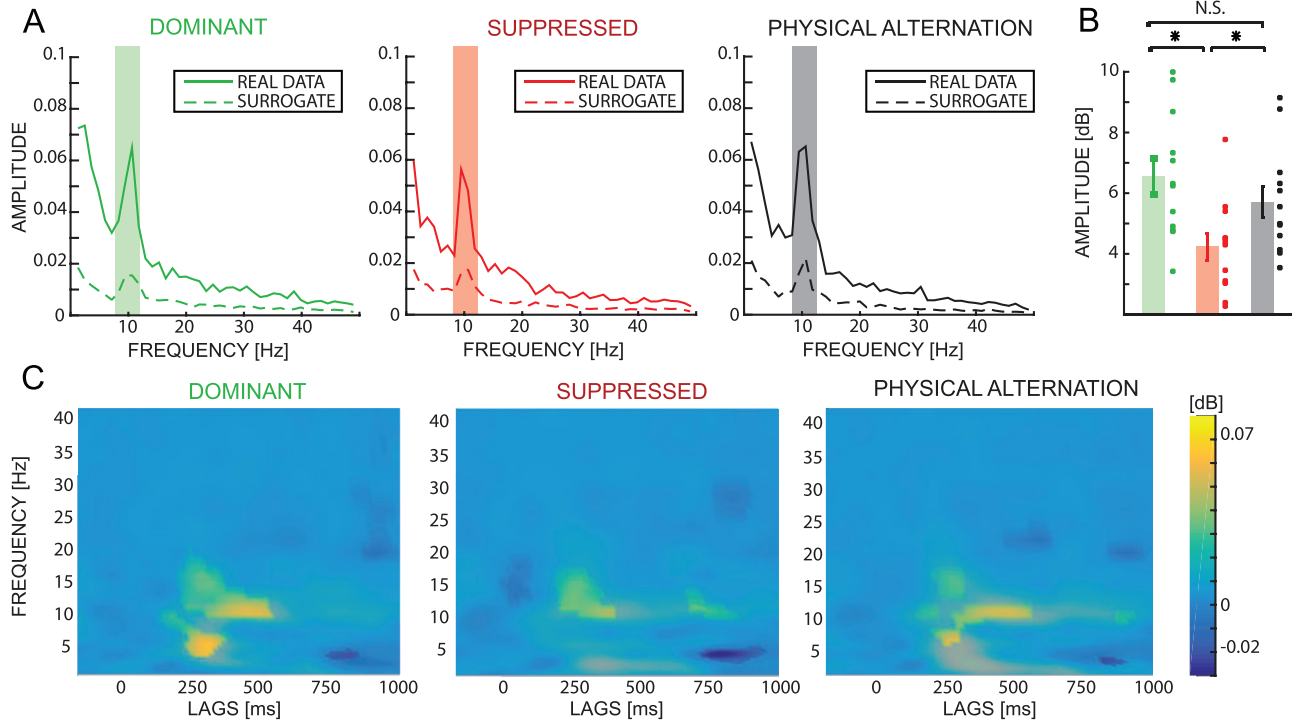


Figure 3. Echoes and time-frequency results

(A) The figure shows the power spectra of the PE obtained in the dominant (green), suppressed (red) and PA (black) condition. The dashed line is the spectra obtained in the surrogate echoes, that is computed after having shuffle the temporal order of the luminance sequence. We focussed the analysis in the alpha range (shaded in each panel). (B) The difference in the power spectra in the alpha range expressed in dB. The plot reveals a substantial difference between suppressed and both dominant and PA conditions, revealing that conscious perception increases the amplitude of the PE. However, all the conditions have PE larger than chance. Bars and error bars represent averages and standard errors respectively, while asterisks represent substantial difference (as indicated by Bayes Factor larger than 3, [Bernardo and Smith 2001](#)). (C) Time-frequency spectrogram for each condition (colour-code as in A). The non-transparent data reveal a difference larger than zero, as assessed by a cluster-permutation test (see results). Dominant and PA show longer and larger amplitude values than in the suppressed condition.

be akin to the increase in the power of the SSVEP related to conscious perception.

Besides their oscillatory temporal dynamics, PE elicited in conditions of binocular vision have been described in view of their spatial component, characterized as a travelling waves propagating from occipital to frontal regions ([Alamia and VanRullen 2019](#); [Lozano-Soldevilla and VanRullen 2019](#)). In this study, we replicate a similar pattern of results, as we observed the same amount of forward travelling waves in both dominant and suppressed conditions, as well as during the PA task (i.e. monocular vision). Surprisingly, the difference in PE amplitude observed between dominant and suppressed conditions was not reflected in the waves' directional power, as waves seem to propagate from lower to higher brain regions with the same strength irrespective of conscious perception. Possibly, the relatively poor spatial resolution of EEG recordings prevents us from accurately comparing the two conditions, and different experimental techniques will be required to reveal different directional strengths in the propagation of dominant and suppressed travelling waves. However, one could speculate that PE generated by the consciously perceived sequence (i.e. dominant) propagate further in the visual hierarchy, reaching frontal regions, which are supposedly involved in conscious perception ([Miller 2011](#); [Koch et al. 2016](#)), whereas the oscillatory waves of PE generated by the suppressed sequence vanish at an earlier stage of visual processing. Further studies will be needed to fully address this hypothesis.

Several previous studies investigated conscious perception in the light of the PC framework ([Hohwy et al. 2008](#); [Seth et al. 2012](#); [Lamme 2015](#); [Weinhammer et al. 2017](#)). PC is an influential scheme in cognitive

neuroscience that describes the brain as a hierarchical system, in which higher regions generate predictions about the activity of lower ones, and the difference between predictions and actual activities (i.e. the prediction error) is used to update the upcoming predictions ([Huang and Rao, 2011](#)). Is it possible to combine within the same framework PC, conscious perception and PE? In a previous study, we demonstrated that a simple model simulating the interaction between brain regions and based on PC principles can account for the generation and propagation of PE as travelling waves ([Alamia and VanRullen 2019](#)), under the assumption of plausible biological constraints (i.e. communication delays and time constants). Interestingly, additional experimental evidence supporting the tie between conscious perception, PC, and travelling waves was recently reported in another study investigating how psychedelic drugs altered travelling waves, supposedly by relaxing the weighting of top-down predictions, thereby releasing the bottom-up flow of information carried out by sensory input ([Alamia et al. 2020](#)). On the other hand, other studies have characterized conscious perception within a PC framework as the consequence of prediction-error minimization ([Hohwy et al. 2008](#); [Hohwy, 2012](#); [Friston, 2013](#); [Strauss et al. 2015](#)): this compelling hypothesis advocates that predictions are generated to efficiently explain and interpret the causes underlying our sensory information, thus generating our conscious perception of the world ([Panichello et al. 2013](#)). All in all, the result that PE correlates with conscious perception—as we demonstrated in this study—leads to the compelling speculation that PC is pivotal in the generation of both PE (as demonstrated in our previous computational study [[Alamia and VanRullen 2019](#)]) and conscious experiences.

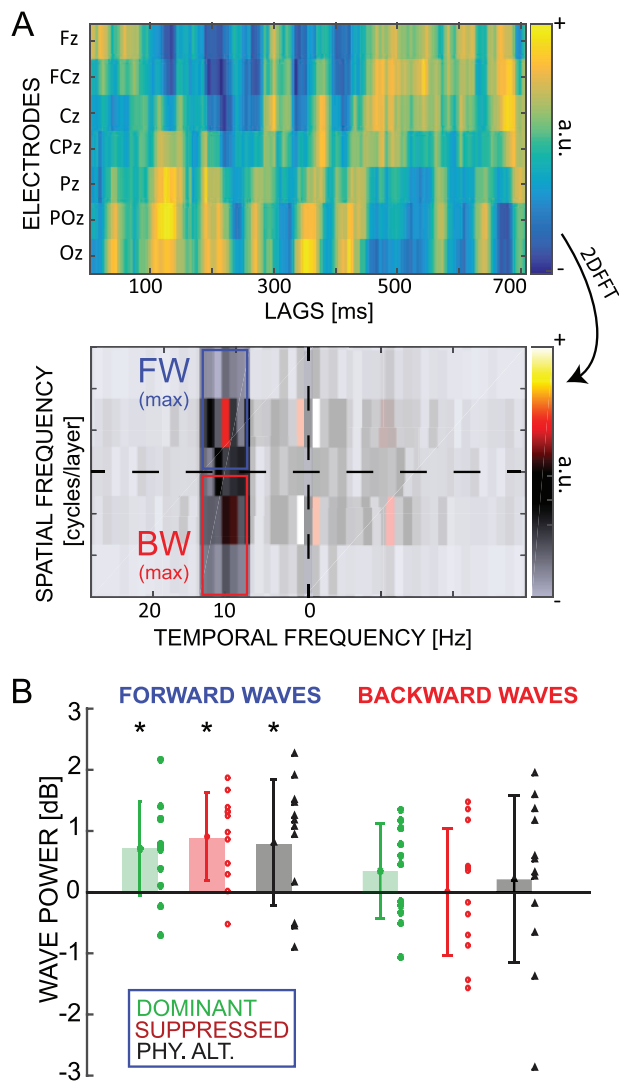


Figure 4. Travelling wave results

(A) We first obtain 2D maps stacking the PEs recorded over the seven midline electrodes. The colour code indicates the PE amplitude. From the 2DFFT, we computed the amount of FW and BW waves in each condition as the maximum amplitude value in the corresponding quadrant (restricted to alpha-band frequencies). (B) The results—expressed in dB, that is corrected using the surrogate, see methods—show that PE travel as FW waves in all conditions, irrespective of the conscious perception of the stimulus. Bars and error bars represent averages and standard errors, respectively, and asterisks represent substantial difference.

In conclusion, this study investigated PE by employing binocular rivalry, and revealed that these are modulated by conscious perception, but consciousness is not necessary to elicit them. In addition, PE evoked by both consciously and unconsciously perceived stimuli propagate from occipital to frontal regions as a travelling wave, irrespective of the conscious modulation.

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References

- Alamia A, Timmermann C, Nutt DJ, et al. DMT alters cortical travelling waves. *eLife* 2020;**9**:e59784. doi:10.7554/eLife.59784
- Alamia A, VanRullen R. Alpha oscillations and traveling waves: signatures of predictive coding? *PLOS Biol* 2019;**17**:e3000487. doi:10.1371/journal.pbio.3000487
- Benedetto A, Lozano-Soldevilla D, VanRullen R. Different responses of spontaneous and stimulus-related alpha activity to ambient luminance changes. *Eur J Neurosci* 2018;**48**:2599–608. doi:10.1111/ejn.13791
- Berger H. Über das elektroencephalogramm des menschen. *Arch Psychiatr Nervenkr* 1933;**99**:555–74.
- Bernardo AFM, Smith JM. Bayesian theory. *Meas Sci Technol* 2001;**12**:221. doi:10.1088/0957-0233/12/2/702
- Bollimunta A, Mo J, Schroeder CE, et al. Neuronal mechanisms and attentional modulation of corticothalamic alpha oscillations. *J Neurosci* 2011;**31**:4935–43. doi:10.1523/JNEUROSCI.5580-10.2011
- Brüers S, VanRullen R. Alpha power modulates perception independently of endogenous factors. *Front Neurosci* 2018;**12**:279. doi:10.3389/fnins.2018.00279
- Brüers S, VanRullen R. At what latency does the phase of brain oscillations influence perception? *eneuro* 2017;**4**:ENEURO.0078-17.2017. doi:10.1523/ENEURO.0078-17.2017
- Chang AYC, Schwartzman DJ, Vanrullen R, et al. Visual perceptual echo reflects learning of regularities in rapid luminance sequences. *J Neurosci* 2017;**37**:8486–97. doi:10.1523/JNEUROSCI.3714-16.2017
- Delorme A, Makeig S. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 2004;**134**:9–21. doi:10.1016/j.jneumeth.2003.10.009
- Ding J, Sperling G, Srinivasan R. Attentional modulation of SSVEP power depends on the network tagged by the flicker frequency. *Cereb Cortex* 2006;**16**:1016–29. doi:10.1093/cercor/bhj044
- Friston K. Consciousness and hierarchical inference. *Neuropsychanalysis* 2013;**15**:38–42. doi:10.1080/15294145.2013.10773716
- Gazzaley A, Nobre AC. Top-down modulation: bridging selective attention and working memory. *Trends Cogn Sci* 2012;**16**:129–35. doi:10.1016/j.tics.2011.11.014
- Halgren M, Ulbert I, Bastuji H, et al. The generation and propagation of the human alpha rhythm. *Proc Natl Acad Sci U S A* 2019;**116**:23772–82. doi:10.1073/pnas.1913092116
- Hohwy J. Attention and conscious perception in the hypothesis testing brain. *Front Psychol* 2012;**3**:96. doi:10.3389/fpsyg.2012.00096
- Hohwy J, Roepstorff A, Friston K. Predictive coding explains binocular rivalry: an epistemological review. *Cognition* 2008;**108**:687–701. doi:10.1016/j.cognition.2008.05.010
- Huang Y, Rao RPN. Predictive coding. *Wiley Interdiscip Rev Cogn Sci* 2011;**2**:580–93. doi:10.1002/wcs.142
- JASP Team. 2018. JASP (Version 0.8.6.0). [Computer software].
- Jensen O, Mazaheri A. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 2010;**4**:186. doi:10.3389/fnhum.2010.00186
- Klimesch W. Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci* 2012;**16**:606–17. doi:10.1016/j.tics.2012.10.007
- Klimesch W, Sauseng P, Hanslmayr S. EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 2007;**53**:63–88. doi:10.1016/j.brainresrev.2006.06.003

- Koch C, Massimini M, Boly M, et al. Neural correlates of consciousness: progress and problems. *Nat Rev Neurosci* 2016;**17**:395. doi:10.1038/nrn.2016.61
- Lamme V. Predictive coding is unconscious, so that consciousness happens now. *Open MIND* 2015;**22**:1–4. doi:10.15502/9783958571105
- Lopes da Silva FH, van Lierop THMT, Schrijer CF, et al. Organization of thalamic and cortical alpha rhythms: spectra and coherences. *Electroencephalogr Clin Neurophysiol* 1973;**35**:627–39. doi:10.1016/0013-4694(73)90216-2
- Lopes da Silva FH, Vos JE, Mooibroek J, et al. Relative contributions of intracortical and thalamo-cortical processes in the generation of alpha rhythms, revealed by partial coherence analysis. *Electroencephalogr Clin Neurophysiol* 1980;**50**:449–56. doi:10.1016/0013-4694(80)90011-5
- Love J, Selker R, Verhagen J, et al. Software to sharpen your stats. *APS Obs* 2015;**28**:27–9.
- Lozano-Soldevilla D, VanRullen R. The hidden spatial dimension of Alpha: 10-Hz perceptual echoes propagate as periodic traveling waves in the human brain. *Cell Rep* 2019;**26**:374–380.e4. doi:10.1016/j.celrep.2018.12.058
- Maris E, Oostenveld R. Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods* 2007;**164**:177–190. doi:10.1016/j.jneumeth.2007.03.024
- Masson MEJ. A tutorial on a practical Bayesian alternative to null-hypothesis significance testing. *Behav Res Methods* 2011;679–90. doi:10.3758/s13428-010-0049-5
- Miller G. Feedback from frontal cortex may be a signature of consciousness. *Science* (80-) 2011; 779. doi:10.1126/science.332.6031.779
- Pang Z, Alamia A, Vanrullen R, 2020. Turning the stimulus on and off dynamically changes the direction of alpha travelling waves 1–18. doi:10.1101/2020.04.15.041756.
- Panichello MF, Cheung OS, Bar M. Predictive feedback and conscious visual experience. *Front Psychol* 2013;**3**:620. doi:10.3389/fpsyg.2012.00620
- Schwenk JCB, VanRullen R, Bremmer F. Dynamics of visual perceptual echoes following short-term visual deprivation. *Cereb Cortex Commun* 2020;**1**:tgaa012. doi:10.1093/texcom/tgaa012
- Seth AK, Suzuki K, Critchley HD. An interoceptive predictive coding model of conscious presence. *Front Psychol* 2012;**2**:395. doi:10.3389/fpsyg.2011.00395
- Srinivasan R, Russell DP, Edelman GM, et al. Increased synchronization of neuromagnetic responses during conscious perception. *J Neurosci* 1999;**19**:5435–48. doi:10.1523/jneurosci.19-13-05435.1999
- Strauss M, Sitt JD, King JR, et al. Disruption of hierarchical predictive coding during sleep. *Proc Natl Acad Sci U S A* 2015;**112**:E1353–62. doi:10.1073/pnas.1501026112
- Thut G, Nietzel A, Brandt SA, et al. α -Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J Neurosci* 2006;**26**:9494–502. doi:10.1523/JNEUROSCI.0875-06.2006
- Tononi G, Srinivasan R, Russell DP, et al. Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc Natl Acad Sci U S A* 1998;**95**:3198–203. doi:10.1073/pnas.95.6.3198
- Vanrullen R, MacDonald JSP. Perceptual echoes at 10 Hz in the human brain. *Curr Biol* 2012;**22**:995–9. doi:10.1016/j.cub.2012.03.050
- VanRullen R. Perceptual cycles. *Trends Cogn Sci* 2016;**20**:723–35. doi:10.1016/j.tics.2016.07.006
- Weilhammer V, Stuke H, Hesselmann G, et al. A predictive coding account of bistable perception - a model-based fMRI study. *PLoS Comput Biol* 2017;**13**:e1005536. doi:10.1371/journal.pcbi.1005536
- Worden MS, Foxe JJ, Wang N, et al. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J Neurosci* 2000;**20**:RC63. doi:10.1523/jneurosci.20-06-j0002.2000
- Zhang P, Jamison K, Engel S, et al. Binocular rivalry requires visual attention. *Neuron* 2011;**71**:362–9. doi:10.1016/j.neuron.2011.05.035