


Conflict monitoring and attentional adjustment during binocular rivalry

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Abstract

To make sense of ambiguous and, at times, fragmentary sensory input, the brain must rely on a process of active interpretation. At any given moment, only one of several possible perceptual representations prevails in our conscious experience. Our hypothesis is that the competition between alternative representations induces a pattern of neural activation resembling cognitive conflict, eventually leading to fluctuations between different perceptual outcomes in the case of steep competition. To test this hypothesis, we probed changes in perceptual awareness between competing images using binocular rivalry. We drew our predictions from the conflict monitoring theory, which holds that cognitive control is invoked by the detection of conflict during information processing. Our results show that fronto-medial theta oscillations (5–7 Hz), an established electroencephalography (EEG) marker of conflict, increases right before perceptual alternations and decreases thereafter, suggesting that conflict monitoring occurs during perceptual competition. Furthermore, to investigate conflict resolution via attentional engagement, we looked for a neural marker of perceptual switches as by parieto-occipital alpha oscillations (8–12 Hz). The power of parieto-occipital alpha displayed an inverse pattern to that of fronto-medial theta, reflecting periods of high interocular inhibition during stable perception, and low inhibition around moments of perceptual change. Our findings aim to elucidate the relationship between conflict monitoring mechanisms and perceptual awareness.

Abbreviations: ACC, anterior cingulate cortex; BR, binocular rivalry; DICS, dynamic imaging of coherent sources; DLPFC, dorsolateral pre-frontal cortex; EEG, electroencephalography; *fdr*, false detection rate; *fm*, fronto-medial; *fMRI*, functional magnetic resonance imaging; OKN, optokinetic nystagmus; *po*, parieto-occipital; ROI, region of interest.

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alpha oscillations, attention allocation, binocular rivalry, bistable perception, cognitive conflict, EEG, functional inhibition, theta oscillations, visual awareness

1 | INTRODUCTION

Few perceptual phenomena have aroused as much curiosity as binocular rivalry (BR) and done so consistently over more than 400 years. In 1593, the Neapolitan savant Giambattista della Porta noticed that he was unable to read two books simultaneously, presented independently to his right and left eye. Instead, ‘the power of seeing is taken from the right eye and borrowed by the left’ and perception alternates between one book and the other (Porta, 1593). In more contemporary terms, BR arises when two disparate images are presented separately to each eye, disrupting the typical process of binocular fusion and producing stochastic perceptual alternations between both images. Despite its wide appeal in laboratory studies, BR is rarely experienced in real life (Arnold, 2011). However, it has been of continual interest for the study of the mechanisms underlying visual perception and awareness, as it induces striking fluctuations in perceptual experience despite constant physical stimulation (Baker, 2010; Blake et al., 2014; Doesburg et al., 2009). In the present study, we aimed to test a neurophysiological link between perceptual ambiguity and cognitive control mechanisms. We reasoned that the competition between alternative perceptual interpretations of sensory input might activate a similar brain network as that in cognitive control tasks. Despite being a predicted outcome of one of the earliest and most influential computational accounts of anterior cingulate cortex (ACC) function, the conflict monitoring theory (Botvinick et al., 2001), a neurophysiological link between perceptual ambiguity and conflict has not yet been established.

Cognitive control refers to a set of functions that allow us to perform tasks flexibly, according to instructions, internal goals and changes in the environment. Botvinick et al. (2001, 2004) proposed that the ACC, a fronto-medial (fm) brain area, is responsible for the detection of conflict during information processing (i.e., when two

incompatible representations are simultaneously active). The role of the ACC in conflict detection and monitoring has since been corroborated by evidence from functional magnetic resonance imaging (fMRI) studies using classic conflict-inducing paradigms such as the Stroop (Kerns et al., 2004), Simon (Kerns, 2006) and Flanker tasks (Botvinick et al., 1999). Evidence from electroencephalography (EEG) and modelling suggests that conflict detection is also reflected by increases in oscillatory power within the theta band (5–7 Hz) over frontal electrodes, originating in the ACC (Cohen, 2014). These studies show an increase in theta power following novel events, reinforcement learning and errors (Cavanagh & Frank, 2014), during incongruent trials in a response-priming task (Pastötter et al., 2013) and other classic, conflict-inducing paradigms (Cohen & Ridderinkhof, 2013). Frontal theta increases have also been observed prior to a perceptual transition in bistable images (Necker cube), both when participants’ perception spontaneously switched between perceptual interpretations and when these switches were induced by presenting biased cubes (Nakatani & van Leeuwen, 2005). Taken together, a robust, accepted finding in the area is that the involvement of conflict monitoring is typically associated to frontal oscillations in the theta band. Although the conflict monitoring theory is firmly grounded on response-conflict protocols (i.e., when a prepotent automatic response must be overridden in order to make way for the correct response, as in conflict-inducing paradigms), it acknowledges that conflict may occur at various stages of information processing including perceptual representation and stimulus categorisation (verbatim from Botvinick et al., 2001, p. 464; ‘If the ACC does respond to stimulus conflicts, one might expect this area to become active under conditions of binocular rivalry or in viewing ambiguous figures’). Despite receiving increasing attention (Nigbur et al., 2012), stimulus conflict, unlike response conflict, remains a lesser explored phenomenon.

The conflict monitoring theory also suggests that one of the functions of the ACC is to trigger strategic adjustments (i.e., attention orienting) in other brain structures (e.g., the dorsolateral pre-frontal cortex DLPFC) for conflict resolution (Botvinick et al., 2001). In the case of BR, attention allocation becomes relevant insofar as there is conflict to be resolved due to sustained visual competition (Dieter & Tadin, 2011). Furthermore, the dynamics of BR have proved particularly sensitive to attentional modulation, slowing down significantly when attention is directed away from the rivaling stimuli (Alais, van Boxtel, et al., 2010; Brascamp & Blake, 2012; Carter et al., 2005; Paffen et al., 2006; Zhang et al., 2011). Alpha oscillations reflect attentional selection via functional inhibition of irrelevant information across the sensory cortices (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2011; Van Diepen et al., 2019) and have been related to attentional adjustments after errors in a Stroop task (Carp & Compton, 2009) and to the destabilisation of multistable percepts (Strüber & Herrmann, 2002). We predict that if BR induces perceptual conflict between stimuli, periods of low inhibition between percepts (low alpha power) would co-occur with stronger competition and periods of high inhibition between percepts (high alpha power) with weak competition.

1.1 | Hypotheses

The theoretical framework of this study along with the hypotheses, the analysis pipeline and the experimental procedures described below were set up a priori and pre-registered on the Open Science Framework (<https://osf.io/g4hzp/>). Prompted by the aforementioned passage from Botvinick et al. (2001, p. 464) and drawing on the two complementary and foundational processes of the conflict monitoring theory, namely, conflict signalling and attention adjustment, we hypothesised that, first, if BR leads to stimulus-based conflict, then this conflict would be reflected by an increase in mid-frontal theta power shortly before the moment of conflict resolution occurring during perceptual switches, and second, if BR dynamics are linked to fluctuations in the excitability of occipital visual cortical areas via inhibitory regulation, then these dynamics will be reflected by decreases in occipital alpha power prior to perceptual switches, mirroring attention allocation via functional inhibition in the sensory cortices (cf. Figure 1d. for an illustration of these hypotheses).

2 | METHODS

2.1 | Participants

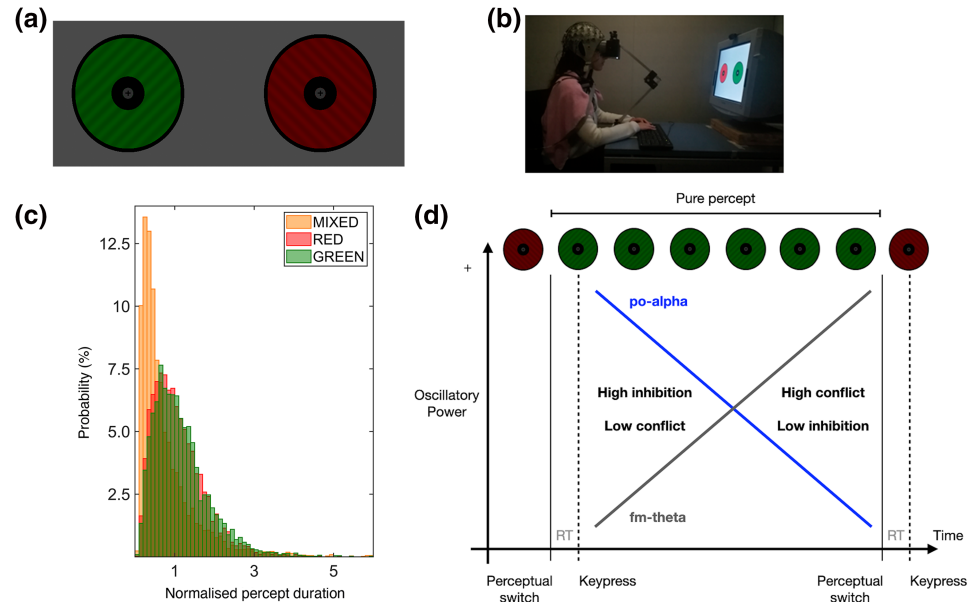
Although 25 was the pre-registered sample size, we recorded 32 participants (15 female, aged between 18 and 34 years, mean age of 23) as this was the required sample size for a parallel study, using the same experimental design and data. The following data presents the 32-participant sample (cf. Supporting Information for further information). Inclusion criteria comprised normal or corrected to normal vision and no medication. Participants received €10 per hour in return for their participation. They all provided written informed consent prior to the study and were naive to the purpose of the experiment. One participant was excluded before starting the experiment due to line noise in the EEG recording. The study was run in accordance with the Declaration of Helsinki and the experimental protocol approved by the local ethics committee in Parc de Salut Mar (Universitat Pompeu Fabra, Barcelona, Spain). Following the criteria for the EEG analysis (cf. Section 2.5), one participant was excluded from the main analysis, and two participants' data were discarded in the time-shifted control analysis, resulting in 30 subjects for the main analysis and 29 in the control analysis.

2.2 | Apparatus and stimuli

Participants were presented with two static circular rival Gabor patches (11.5° diameter; .1 contrast and .73 cycles/cm of spatial frequency and gratings oriented at $\pm 45^\circ$) and different colours: red and green. Images were presented on a 19.8-inch CRT monitor (1024 × 768; 120-Hz refresh rate) with a grey background (10.7 cd/m²) displayed at 80 cm from the participants' eyes. Each image was presented to a different eye by means of stereoscope mirror glasses (Figure 1b). Visual stimuli were created using the Matlab Psychophysics Toolbox (RRID: SCR_002881) and Matlab version R2017b (9.3.0.713579). These parameters gave us a BR paradigm in which percepts can last longer than 1 s when active behavioural report is requested from the participants.

The green RGB value was matched to the subjective luminance of the red Gabor using an up/down procedure adapted from Cavanagh and colleagues (Cavanagh et al., 1987), in order to minimise the flickering between red and green RGB Gabors at a rate of 60 Hz. To achieve this, participants were instructed to regulate the flickering until it had stopped completely, indicating that the colours had been matched. This served to prevent

FIGURE 1 (a) Competing stimuli: a representation of Gabor patches used as stimuli in the experimental protocol. (b) An image of the experimental setup: a participant performs the binocular rivalry task. (c) Distribution of normalised individual mean percept durations calculated for all percepts. (d) Sketch of predictions for the evolution of fronto-medial (fm) theta and parieto-occipital (po) alpha oscillations throughout a pure percept according to hypotheses



potential dominance of one percept based on stimulus features (Levelt, 1965) (cf. Section 3.1.1).

2.3 | Procedure

Prior to the experiment, participants were dark adapted for 5 min. The stereoscope mirrors were calibrated for stimuli to appear at the same retinal location of each eye, by ensuring monocular vision. Subjective luminance of stimuli was matched. During the BR blocks, stimuli were presented continuously throughout a block. Because the rival Gabors had dissimilar colours (i.e., red and green) and grating orientation ($\pm 45^\circ$ tilt), observers experienced rivalry as perception alternated between the two gratings.

Participants were seated in a dimly lit and sound-attenuated room and asked to keep movements (including eye movements and blinks) minimal during each block. The experiment consisted of 13 blocks lasting 120 s each. Before the experiment, participants performed two training blocks to become familiar with the task (training data were not analysed). Experimental blocks were interleaved with breaks (the duration of which was self-paced by participants) to limit fatigue. Unbeknownst to them, the task was divided into two conditions: nine blocks of a BR and four blocks of a replay condition (cf. Section 3.3), with one replay block following two consecutive rivalry blocks (in an AAB alternation pattern, plus one additional rivalry block at the end). As our study mainly targeted rivalry blocks, we included the replay condition only to have an estimate of the ability to report alternations in the BR blocks and reaction time. Data

from the replay condition were not analysed for oscillatory modulations given the impossibility of truly knowing participants' phenomenological experience during rivalry and the difficulty of correctly emulating rivalry dynamics with replay conditions (cf. Section 4). In the replay condition, the same image was presented to both eyes, and we recreated the perceptual fluctuations, akin to those in the BR condition, by physically alternating between the images (including pure and mixed percepts). The temporal dynamics of the fluctuations were determined individually by the participants' cumulative distribution of percept dominance from all previous rivalry blocks. The mean and standard deviation of percepts (mixed, green and red) were used to generate three gamma distributions of percept durations from which the simulated percepts durations were drawn. Importantly, the total percentage of time spent in the 'Null percept' during replay was low, ($2.24\% \pm 2.91\%$) indicating a behavioural performance in line with the expectation.

Participants were instructed to fixate their gaze on the central fixation cross. The keys used for the perceptual report were X and D on a QWERTY keyboard which participants pressed with the left and right index fingers (i.e., continuously pressing X, D or both keys to report one colour, the other or a mixture, respectively). The assigned key for the green and red stimulus percepts was counterbalanced across participants. To report none of the three aforementioned percepts (null percept), they were instructed to depress both keys. Participants were instructed to report a red percept (for instance) whenever they perceived it 100% (i.e., a fully red Gabor with the corresponding orientation of the gratings); if this was not

entirely the case anymore, they would then report a mixed percept. The eye (left/right) in which each stimulus was physically presented was also randomised across blocks in order to avoid biases due to eye dominance (red left/green right; green left/red right).

2.4 | EEG recording

During the experiment, EEG data were acquired using a 60-electrode system (actiCAP, Brain Products GmbH, Munich, Germany) placed in accordance with the 10–10 international system. The ground electrode was placed on AFz and the online referenced on the tip of the nose. Electrodes for offline re-reference were placed on right and left mastoids. The vertical electrooculogram (Veog) was recorded by an electrode underneath the right eye and the horizontal electrooculogram (Heog) at the outer canthus of the right eye. Impedance was kept below 10 k Ω for all electrodes. The signal was recorded via BrainVision Recorder (Brain Products GmbH, Munich, Germany) at a sampling rate of 500 Hz.

2.5 | EEG pre-processing

Pre-processing and analyses of EEG data were done using Fieldtrip (RRID:SCR_004849) and custom-made code in Matlab. The pre-registered EEG analysis focused on periods of perceptual dominance bound between switches, that is, occurring between keypresses.

Data corresponding to these periods were separated into segments, hereby termed trials. We selected trials of 1.5 s or longer for the analyses (with an average number of trials per participant of 142 ± 48). The window length was selected to have one 500-ms window at the beginning of the trial (after one perceptual switch) and another at the end of the trial (prior to another perceptual switch) in order to include at least 3 cycles of the central frequency (6 Hz) in the slowest (theta) frequency band of interest in each of these 500-ms windows (cf. Figure 2a). Given the high proportion of mixed percepts that resulted from our stimulus size and luminance adjustment (Brascamp, Klink, & Levelt, 2015; Levelt, 1965), few trials included neat transitions from one pure percept to the other. Because we were interested in the time windows of dominance periods ending in a perceptual transition, the trials selected for analysis included periods of perceptual dominance leading to either another period of perceptual dominance or to a mixed percept (e.g., from red to green or red to mixed, cf. Figure 2a). Our focus centred around these periods of perceptual dominance because, according to the hypothesis under test, these must involve moments of low conflict (when the percept is stable) as well as moments of high conflict (when a transition is impending). This served to avoid conflating the uncertainty related to periods of binocular fusion (mixed percepts) with perceptual conflict because it is currently impossible, with the methods available, to know exactly what individual subjects are experiencing during mixed percepts.

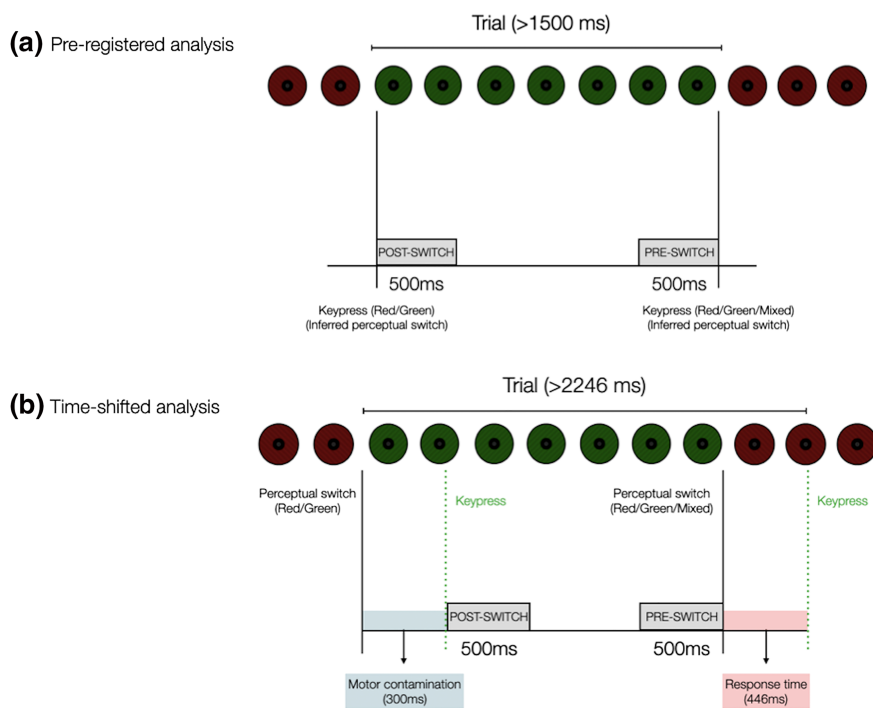


FIGURE 2 Schematic drawing of trial selection in the (a) pre-registered and (b) time-shifted analyses

Data were inspected for artefacts in order to manually reject segments contaminated by blinks, movements and noise upon visual inspection. Participants with fewer than 30 trials in at least one of the conditions of interest were excluded from analyses (i.e., the minimal amount required for a reliable estimation of power). One participant was excluded based on the criterion for the minimal number of trials in the main analysis (three trials), whereas data from two participants were discarded in the first control (time-shifted) analysis (three and 22 trials, respectively), resulting in 30 subjects for the main analysis and 29 in the first control analysis.

2.6 | Behavioural analysis

Percepts shorter than 300 ms (i.e., a rough estimation of the mean latency of motor-evoked potential from human movement such as keypresses; Halgren, 1990) were discarded. In order to check for dominance-bias and reliability of participants' report, we extracted for each participant the mean lengths of percepts, the total and percentage of time spent in the null percept condition during rivalry and replay conditions and the mean percentage of time spent in each percept. Evidence in favour of reliable report and against a bias towards one of the stimuli should be reflected by a similar duration of dominance for red and green percepts, due to the subjective isoluminance adjustment. Evidence in favour of the reliability of participants' report should be reflected by a low percentage of time spent in the null percept in both conditions (cf. Section 3.1.1). This is because in the rivalry condition stimuli were presented continuously to the eyes, whereas in the replay condition we did not include null percepts, therefore, correct reports should match the physical alternations presented. Given our efforts at tuning stimuli parameters to match the luminance of the stimuli, we did not expect the duration of mixed percept to exceed that of pure percepts. No participant was excluded based on behavioural performance.

2.7 | Time-frequency analysis

According to the pre-registered hypotheses (<https://osf.io/g4hzp/>), the analysis was centred at two frequency bands: theta (5–7 Hz) and alpha (8–12 Hz) in two 500-ms time windows. Only segments that were free from artefacts and had a minimum duration of 1.5 s were included in the registered analysis. This segment length ensured the time necessary for analyses of the intended time windows, at the intended frequency bands. One time window

was located at the beginning of the segment, right after a keypress (henceforth referred to as post-switch), and the other was located at the end of the segment, just before a keypress (henceforth referred to as pre-switch). We used a fast Fourier transform with a Hanning taper zero padded up to a length of 1 s to extract the power in the frequency bands of interest in the pre-switch and post-switch windows.

The measure of interest was the power in the pre-switch versus post-switch, measured in decibels (dB). Activity was measured over the whole scalp, but regions of interest were pre-defined for each frequency band: a fm region (Fz, Cz) for the theta band and a parieto-occipital (po) region (P7, P8, PO7, PO3, POz, PO4, PO8, O1, Oz and O2) for the alpha band. The power contrast was calculated for each frequency and electrode of interest and, subsequently, averaged across frequencies and regions of interest (ROIs). Mistakenly (and noted a posteriori), data from FCz were not recorded during the experiment; therefore, data were acquired by pooling from Fz and Cz given the spatial resolution.

A first control analysis was performed trying to estimate the contamination from motor-evoked potentials in the post-switch window and from activity due to active report (decision making, motor preparation and motor execution of the keypress) in the pre-switch window. The response time of participants when reporting perceptual transitions (excluding mixed and null percepts) was estimated from the response latency in the replay condition (which resembled a visual detection task and was included specifically for this purpose, cf. Section 2.3). The median response time across participants in the replay condition was 446 ms ($SD = 103$ ms). In this control analysis, then, the pre-switch window was shifted by 446 ms, whereas the post-switch window was shifted by 300 ms, corresponding to the duration of a motor-evoked potential from human movement such as a keypress (Halgren, 1990) (cf. Figure 1b).

2.8 | Source localisation

The leadfield was calculated using a standard boundary element method available from Fieldtrip, version 20190203, the grid spacing was set to 10 mm. For each participant, frequency band (theta and alpha) and condition (pre-registered and time-shifted), power and cross-spectral density were calculated at the pre-switch and post-switch time windows with the same parameters as in the electrode level analysis. For each participant, frequency band and condition, we calculated the common filter for pre-switch and post-switch time windows using dynamic imaging of coherent sources

(DICS) with 1% regularisation, a spatial filtering technique operating in the frequency domain (Gross et al., 2001). We then used the common filter to obtain the power at the pre-switch and post-switch time windows for each frequency band and condition, and we computed the power differences (pre-switch vs. post-switch) in dB for each participant, frequency band and condition. Significant pre-switch versus post-switch window power differences at source level were assessed by means of one-tailed paired *t* tests for each frequency band and condition separately. Multiple comparison correction was performed by means of false detection rate (fdr) (Benjamini & Hochberg, 1995) procedure at an alpha level of .05.

2.9 | Evoked and ongoing theta activity

In order to evaluate whether motor contamination was reflected in the observed theta power increase, we disentangled ongoing and evoked theta activity, as theta activity related to movement preparation and execution has been observed to become phase locked to the movement (Kuo et al., 2014; Luu et al., 2004). We applied the method described by Cohen and Donner (2013) to calculate ongoing and evoked power on epochs reported as pure percepts exceeding a duration of 2246 ms (a duration determined by adding the durations of motor-evoked potential, 300 ms, and response time, 446 ms, to segments of at least 1,500 ms) by means of a short-time Fourier transform (500-ms windows, Hanning taper, 2 to 30 Hz in steps of 1 Hz, steps of 10 ms) for the interval -1750 to 500 ms relative to keypress. Only epochs corresponding to pure percepts ending in mixed percepts were considered. Epochs containing artefacts were discarded, and only participants with at least 30 epochs were selected for analysis (28 subjects). Power changes related to the baseline period (-1750 to -1250 ms) were calculated in decibels in the fm region (Fz, Cz). A one-tailed paired *t* test (right tail, alpha level .05) was used to detect significant theta changes relative to baseline period for times ranging from -1250 to 500 ms relative to the keypress. Multiple comparison correction across time was performed by means of a Monte Carlo randomisation procedure (10,000 iterations). In each iteration, the sign of a random subset of subjects was inverted and the *t* test performed. The maximum number of consecutive significant time points in each iteration was used to build a probability distribution of temporal cluster length. We set our significance threshold at 300 ms, which yielded a 5% probability of occurrence in the random cluster distribution.

2.10 | Time course of theta and alpha fluctuations

In order to observe the temporal evolution of theta and alpha activity during percepts, we selected the longer percept trials (trials of 2246 ms or longer) and calculated oscillatory power using 500 ms sliding windows (in steps of 2 ms) in the corresponding ROIs for the theta and alpha frequency bands. For each percept, the power was normalised with respect to the first 500 ms right after the keypress (in dB). For each trial, we selected the windows centred at -20% to 120% (in steps of 10%) of the total duration of the percept. Finally, we calculated the time courses of theta and alpha for each percept and participant.

3 | RESULTS

3.1 | Pre-registered analyses

3.1.1 | Behavioural report and trials of interest

Participants ($N = 30$ for the main analysis and $N = 29$ for the time-shifted control analysis) were asked to perform a BR task while EEG data were recorded. Dominance periods had a mean duration of $2.41 \pm .78$ s (red percepts), $2.63 \pm .83$ s (green percepts) and 1.94 ± 1.11 s (mixed percepts). The mean number of red percepts was 136.80 ± 42.80 ($28.76 \pm 9.23\%$), of green percepts was 155.27 ± 42.04 ($35.03 \pm 8.07\%$) and of mixed percepts (also known as piecemeal rivalry) was 203.23 ± 50.14 ($33.97 \pm 15.92\%$). The total percentage of time spent in the 'Null percept' (when participants perceived neither pure percepts nor mixed percepts) was low ($2.24 \pm 2.91\%$). The stimulus parameters were designed to induce percepts longer than 1 s, for purposes of analysis when active behavioural report is requested from the participants (cf. Section 2.2). BR dynamics, and particularly the latency between perceptual alternations, are known to be sensitive to various physical features that determine stimulus strength (Brascamp, Klink, & Levelt, 2015; Levelt, 1965). Using a large stimulus size (11.5° diameter, cf. Section 2.2) and the individual luminance adjustment, we minimised the salience of one stimulus over the other and reduced the speed of perceptual alternations.

3.1.2 | Modulation of theta power around perceptual switches

Our first hypothesis was tested on the 500-ms time windows at the beginning (post-switch window) and at the

end (pre-switch window) of the reported dominance period. Results showed an increase in fm theta power (5–7 Hz, cf. Section 2) before a perceptual switch compared with after a perceptual switch (Figure 3, left) ($t(29) = 3.2374$, one-tail, $\alpha = .05$; $p = .0015$; Cohen's $d = .59$), as predicted by the conflict monitoring theory (Botvinick et al., 2001).

3.1.3 | Modulation of alpha power around perceptual switches

To address our second hypothesis on attention engagement in BR, we performed an analysis of po alpha power (8–12 Hz, cf. Section 2). As expected, according to the 'sensory gating hypothesis' (Foxe & Snyder, 2011), our results showed a decrease in alpha power before a perceptual switch compared with that after a perceptual switch ($t(29) = -2.2291$, one-tailed, $\alpha = .05$; $p = .0169$; Cohen's $d = -.41$), suggesting that attention engagement follows conflict detection as a result of the competition between perceptual interpretations (Figure 3, left).

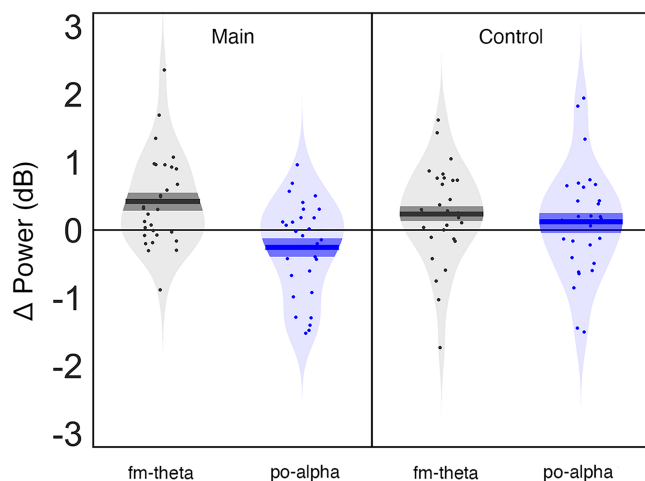


FIGURE 3 Left: Results for the main (pre-registered) analysis. The expected pattern can be observed: fronto-medial (fm) theta (5–7 Hz) power (dB) pre-switch was significantly higher than fm theta power post-switch (grey), whereas parieto-occipital (po) alpha (8–12 Hz) power (dB) pre-switch was significantly lower than po alpha power (dB) post-switch (blue). Right: Results from a control analysis, after time shifting our windows of interest. fm theta power (dB) pre-switch was still significantly higher than fm theta power (dB) post-switch (grey), whereas the effect for po alpha was not observed anymore (blue). Solid lines correspond to the group mean of each of the conditions, and dark shaded areas correspond to the mean \pm standard error of the mean. Light shaded areas correspond to the distribution of individual data and dots correspond to individual data. It should be noted that despite being shown in the same plot for purposes of illustration, theta and alpha frequency bands were analysed independently from each other

3.2 | Control analyses (not pre-registered)

3.2.1 | Possibility of motor contamination during perceptual switches

One concern is the possibility that the pattern of results just described was in part or in whole due to motor contamination from the keypress reports in the analysed time windows. Our paradigm involves decision making, motor planning and motor execution and performing the task requires participants to almost constantly be pressing at least one key. Furthermore, although frontal areas were once thought a prime candidate for spontaneous perceptual changes in multistable perception (Leopold & Logothetis, 1999; Lumer et al., 1998; Sterzer & Kleinschmidt, 2007), a possible confound between report and introspection-related activity has recently called this into question (Brascamp, Blake, & Knapen, 2015; Frassle et al., 2014; Zou et al., 2016), with competing interpretations of what frontal activity may represent (Block, 2019). To corroborate the robustness of our findings, we attempted to rule out contamination from report-related activity with three different approaches. One was to shift the time windows of analysis away from the moment of keypress, the second was to localise the sources of oscillatory activity and finally, given that theta activity related to movement preparation and execution has been observed to become phase locked to the movement (Kuo et al., 2014; Luu et al., 2004), we separated ongoing and evoked activity prior to a reported perceptual switch.

3.3 | Shifted time windows

The first control analysis was designed to bypass the period of potential motor contamination around reports of perceptual switches by shifting the windows of interest in time, away from the keypresses and the related activity. To do so we used trials of 2246 ms or longer (92 ± 40 trials per participant) (cf. Figure 1b). The pre-switch window was shifted by 446 ms before the switch (the average response time measured in a replay condition using physical alternations instead of BR, cf. Section 2). The post-switch window was shifted by 300 ms after the response, which was an estimated duration of the motor-evoked potential (Halgren, 1990). As in the main analysis, the fm theta power modulation was significant ($t(28) = 1.9809$; one-tailed, $\alpha = .05$; $p = .029$; Cohen's $d = .37$) when shifting the time windows; however, no reliable effect was seen in alpha oscillations: ($t(28) = .79$; one-tailed, $\alpha = .05$; $p = .8$; Cohen's $d = .16$) (Figure 3, right).

3.4 | Source localisation

The results of the time-shifted analysis above help separate fm theta changes from responses in the pre-registered analysis but leave open the possibility that the alpha modulation seen in the pre-registered analysis is conflated with response-related factors. In the analysis performed immediately surrounding perceptual switches, both the response-conflict and perceptual-conflict interpretations make indistinguishable predictions regarding alpha activity at the sensor level. However, strategic adjustments through attentional modulation via inhibitory processes may only be present in the immediate temporal vicinity of the perceptual switch, thus undetectable when shifting the windows of interest away from the reported moment of switch. It has in fact been suggested that the mechanisms for cognitive control operate according to a temporal hierarchy (Tang et al., 2016). In order to single out sensory-related activity from contamination by motor report in the vicinity of perceptual switches, we ran a second control analysis addressing the source localisation of the theta and alpha modulations reported in the main analysis. We used DICS, a spatial filtering technique operating in the frequency domain (Gross et al., 2001) (cf. Section 2.8). As expected, theta power modulation had a clear source consistent with fm areas, hence the predicted ACC generator (Figure 4). Therefore, the increase in theta oscillatory power in the initial results is unlikely to be attributed to motor components but can instead be attributed to perceptual conflict. Importantly, the source of alpha activity was localised in posterior occipital regions, consistent with visual attention processing in contrast to motor-related areas. This finding helped disentangle alpha modulations related to sensory inhibition from response-related factors.

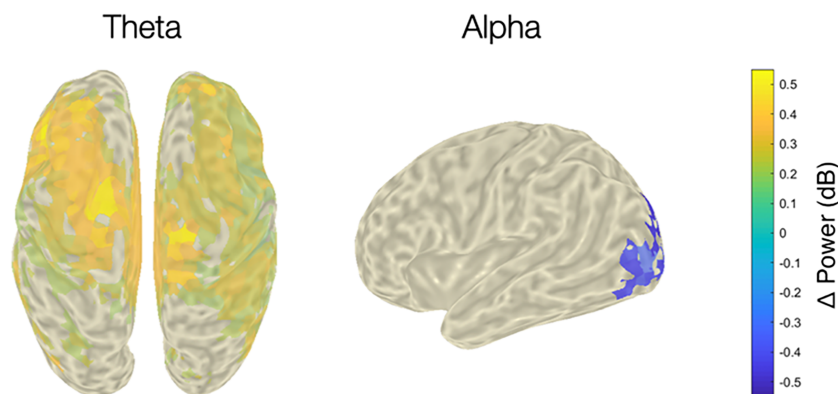


FIGURE 4 Brain topographies of source-localised activity for theta, 5–7 Hz (left) and alpha, 8–12 Hz (right) pre–post switch contrasts. Theta power modulation presents a clear source consistent with fronto-medial areas. The source of alpha activity is localised in posterior occipital regions

3.5 | Evoked and ongoing fm theta activity

In the third control analysis addressing the dissociation of conflict-related and motor-related activity, we attempted to single out ongoing theta activity, putatively associated to conflict detection, from theta activity evoked by the keypress itself (Kuo et al., 2014; Luu et al., 2004) following the approach of Cohen and Donner (2013) (cf. Section 2.9). The time-frequency map of ongoing fm activity (Figure 5a) displayed the well-known beta band (15–30 Hz) desynchronisation around keypress (0 s) (Cohen & Donner, 2013; Kuo et al., 2014).

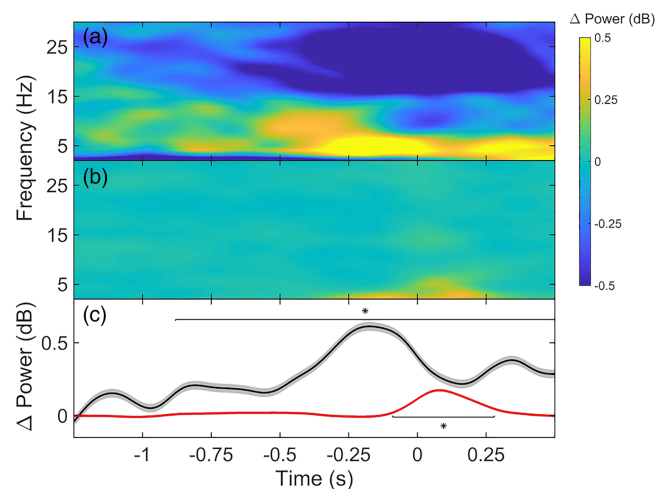


FIGURE 5 Ongoing and evoked fm theta activity. (a) The time-frequency map of ongoing activity. (b) The time-frequency map of evoked activity. (c) Theta band (5–7 Hz) power of the ongoing (black) and the evoked (red) activity. Significant increases relative to baseline period ($\alpha < .05$) are highlighted with black horizontal lines. Shaded areas around the ongoing activity of theta power (black line) indicate the standard error of the mean (SEM)

Importantly, we observed an increase in theta activity prior to a perceptual switch. The onset of this increase was earlier than the increase in evoked activity (Figure 5b), which was concentrated in the theta band and close to the perceptual switch. Statistical analyses confirmed a significant increase in ongoing fm theta activity, putatively related to conflict, from -880 to 500 ms relative to the keypress. Instead, evoked activity related to keypresses was significant at latencies closer to the keypress (-90 to 280 ms) (Figure 5c).

3.6 | Time course of theta and alpha fluctuations

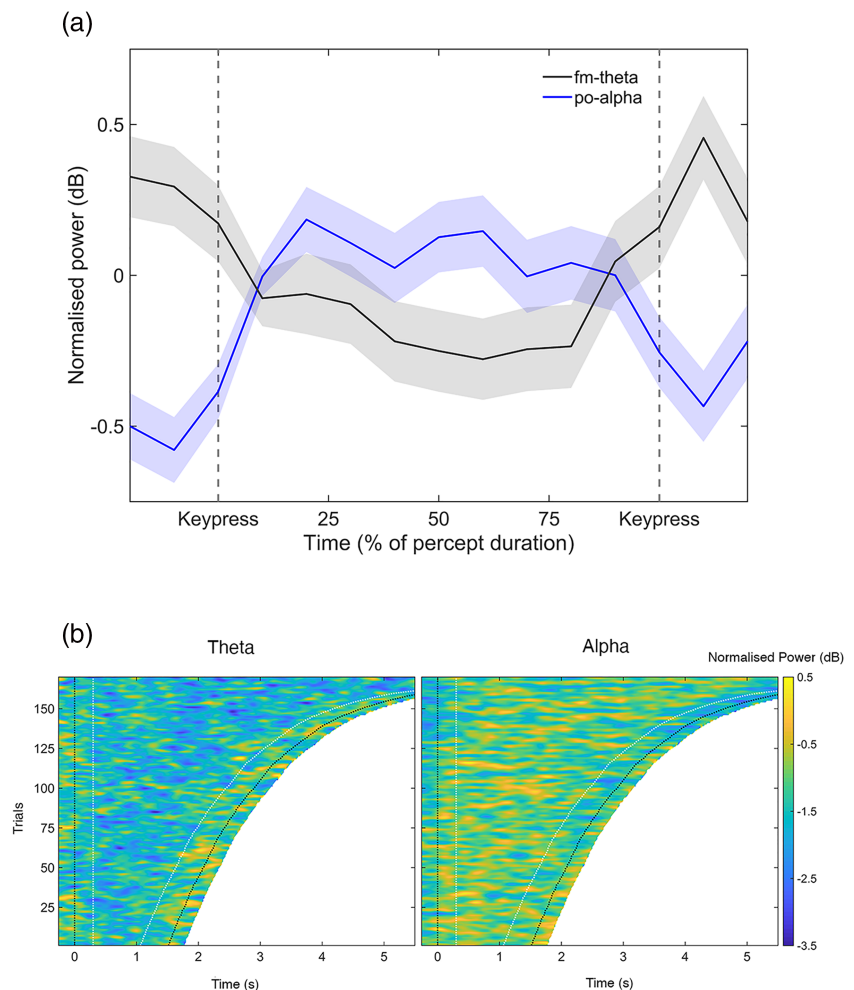
According to our hypotheses, the time course of theta and alpha oscillatory power should present opposing patterns throughout the duration of a percept. In order to appreciate this, we calculated the time courses of theta and alpha for each percept and participant (cf. Section 2.10). The resulting averaged time courses (Figure 6a) illustrate the antagonistic patterns of frontal theta and posterior alpha which can be observed on a

trial-by-trial basis in Figure 6b (trials ordered by duration). Together, the complementary time courses of frontal theta and posterior alpha endorse the hypothesised relationship between control mechanisms (conflict and attention) and perceptual processes.

4 | DISCUSSION

To make sense of visual scenes, the brain must draw perceptual inferences from ambiguous and incomplete sensory inputs, in order for only one of several alternative perceptual interpretations to prevail in our conscious experience. BR is a valuable tool to study the mechanisms behind perceptual inference, as a paradigmatic case in which competing perceptual interpretations are constantly available but only one (the dominant percept) reaches awareness while the other (the suppressed percept) falls below it. One point of consensus is that in BR this fluctuation is due to one or more mechanisms of reciprocal inhibition between competing neural populations governing each percept at different stages in the visual pathway (Alais, Cass, et al., 2010; Levelt, 1965).

FIGURE 6 (a) Time course of fronto-medial theta (grey) and posterior alpha (blue) oscillatory power in the period between keypresses denoting perceptual switches, averaged across all trials of all participants. The activity has been measured in steps of 10% of total percept duration (the period between both dotted lines always contains a pure percept), with the time axis normalised to percept duration. (b) Left: Temporal evolution of theta power (normalised with respect to mean power during percept) for trials of all participants sorted from shortest to longest. Right: Temporal evolution of alpha power (normalised with respect to mean power during percept) for trials of all participants sorted from shortest to longest. Black lines correspond to keypresses and white lines to estimated motor-evoked potentials and response times. It should be noted that theta and alpha frequency bands were analysed independently from each other and are shown here in the same graph for the purpose of illustration



The population with the strongest signal determines the dominant percept until neural adaptation diminishes its responsiveness and the alternative population eventually takes over as the dominant percept (Blake & Logothetis, 2002). We postulated that these competitive dynamics involve the concurrence of two mechanisms: conflict processing in the frontal cortex and attention allocation via functional inhibition in sensory cortices.

We measured changes in fm theta power to address the hypothesis that if conflict mechanisms are involved in BR, then we should expect theta power increases as in typical conflict tasks (Cavanagh & Frank, 2014; Cohen & Ridderinkhof, 2013; Pastötter et al., 2013). The results confirmed our expectations: theta power selectively (in time and topography) increases before a perceptual switch compared with after it. Furthermore, the lower occipito-parietal alpha power right before the switch confirmed our hypothesis about the lesser involvement of inhibitory mechanisms when conflict is high.

We suggest that conflict in BR may result from the competition and reciprocal inhibition dynamics between the neural populations governing each percept, in line with current accounts (Blake & Logothetis, 2002; Levelt, 1965). In BR, conflict plays out continuously: When the competition has a strong winner, the conflict signal (and therefore theta power) is low, putatively during periods of stable percepts. On the other hand, when competition is steep, there is no strong winner, so conflict is stronger (hence, higher theta power), putatively in moments impending a change in percept. Furthermore, the outcome of this competition necessarily fluctuates over time because the conflict in BR can only be temporarily resolved until the inhibitory signal from the neural population governing the competing percept begins to weaken, calling the alternative representation to awareness.

We expected that alpha activity (classically interpreted as a marker of inhibitory processes; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2011; Van Diepen et al., 2019) would relate to BR dynamics and that its time course would present an inverse pattern to that of theta (i.e., less inhibition leads to more competition right before a switch, and vice versa after the switch; Figure 6a). Although we are unable to preclude alternative interpretations for the outcome in the alpha band based on the sensor-level results alone, the expected involvement of posterior alpha oscillations in BR fluctuations was confirmed with source localisation. We can therefore exclude the involvement of motor areas in the alpha power effect.

We can only speculate as to why the posterior alpha effect appeared only in the immediate temporal vicinity of the switches but not when shifting the time windows in the first control analysis. One possible simple

explanation, as we discussed earlier (cf. Section 3.4), could be that strategic adjustments through attentional modulation via inhibitory processes may only be present in the immediate temporal vicinity of the perceptual switches, but not identifiable during moments of relative resolution, in the shifted time windows. According to Dieter and Tadin (2011), the need for the involvement of attention should depend on the degree of stimulus conflict. The conflict between our stimuli was constant throughout the experiment, but independently from the physical stimulus characteristics, the amount of detected conflict by the conflict network necessarily fluctuates between moments of resolution.

In line with this, attentional modulation of rivalry predicts more attentional control at the onset and in early stages of rivalry (i.e., initial selection) than during ongoing dominance periods, due to the unresolved conflict when stimuli are initially presented. Therefore, as our paradigm presents ongoing rivalry throughout the experiment, it may not trigger the attentional mechanisms for conflict resolution in the same way that the onset of rivalry would.

Beyond conflict monitoring, the ACC has been characterised as a central hub for many of the computations implicated in flexible and adaptable behaviour from conflict to predictive processes such as reward prediction and prediction errors (Silvetti et al., 2013; Vassena et al., 2014) just to name a few. These have encouraged a parallel quest for a theoretical framework able to encompass and account for the range of findings concerning ubiquitous ACC functions (Vassena et al., 2017), with early computational models focusing on conflict (Botvinick et al., 2001), and prediction errors (Holroyd & Coles, 2002, 2008). Certain proposals such as the expected value of control framework (Shenhav et al., 2013) suggest that the ACC plays an overarching role that is at once strategic (able to anticipate a trade-off between effort and reward) and controlling (able to determine the appropriate action and degree of control). In our study, we propose a similar role for ACC function: When a mismatch occurs between inputs, conflict is detected and the necessary adjustments (through attentional adjustments via inhibition) are invoked in order to stifle the sustained visual competition during BR. Certain theories of perception, most famously seen in applications of the predictive coding theory for instance, make similar projections regarding processing mechanisms: As perceptual predictions are compared against incoming sensory input, ongoing inferences are constantly adjusted, in part due to prediction errors, which help to minimise the mismatch between internal predictions and incoming inputs (Friston, 2005; Hohwy et al., 2008). In everyday perception, there is a strong prior that both eyes will receive

fairly similar inputs (nearly identical images, slightly shifted due to the different location of each eye on the face), conducive to binocular fusion. In BR, this prediction is a constant failure and the prior remains unmet: According to our suggestion, when the visual system fails to reconcile the incongruent inputs (which happens continually here because both inputs are always present), conflict is signalled, and the relevant adjustments are invoked (Kerns et al., 2004 or Botvinick et al., 1999, for examples in sensorimotor conflict). While the link between the monitoring function of the ACC (conflict and error detection) and the subsequent modulation of behaviour remains currently unresolved, we believe that our study provides an initial example of two functions of the ACC acting in harmony in order to promote flexible processing, reflected by the antagonistic patterns of theta and alpha oscillations in different brain areas (Figure 6a).

It is noteworthy that although research in sensory perception often exploits incongruences between inputs (Botvinick & Cohen, 1998; Ernst & Banks, 2002; Ernst & Bühlhoff, 2004; Lackner, 1988; McGurk & Macdonald, 1976), these incongruences have not been unified within the framework of cognitive conflict. Many examples can be found in cross-modal literature, where perceptual conflict is often used to create illusions like the McGurk effect, the rubber hand illusion and the ventriloquist illusion. In fact, recent studies have revealed that during the McGurk effect (i.e., when a visual speech stimulus is superseded with a non-matching auditory stimulus giving rise to an illusory auditory percept), theta oscillations and ACC activity reflect the discrepancy between auditory and visual inputs (Morís Fernández et al., 2017, 2018). While this phenomenon reflects prediction errors due to incompatible visual and auditory inputs, it can contribute to the generalisation of the role of theta oscillations in perceptual conflict detection when strong priors are not met. Other studies have addressed oscillatory responses to multistable stimuli (İşoğlu-Alkaç & Strüber, 2006; Nakatani & van Leeuwen, 2005), with similar patterns of oscillatory activity being reported. For instance, frontal theta power enhancements alongside posterior alpha power fluctuations were observed during perception of a Necker cube (Nakatani & van Leeuwen, 2005). In their study, participants who experienced frequent spontaneous perceptual switches between both possible interpretations of the cube showed characteristic activity in the same regions of interest and the same frequency band as our study: occipital alpha and frontal theta prior to perceptual switches. However, it must be noted that this activity was specific to participants who experienced frequent perceptual switches and was not generalisable to those who did not.

Consciousness research has shown sustained interest in the phenomenon of BR due to constant change in phenomenological experience to physically unchanging input. In particular, BR allows researchers to study both to the mechanisms behind perceptual switches (i.e., the neural processes governing transitions) as well as the neural bases of the perceptual content itself (i.e., the rivalrous images) and in so doing may shed some light on one debate that has existed in both consciousness and BR research: Is visual awareness rooted mainly in frontal or occipital areas of the brain (Block, 2019)? Replay conditions have provided hope to add to this debate: Because replay is designed to mimic the same conscious perceptual content, the difference between activity during rivalry and replay should inform us as to the activity governing solely the transitions between rivalrous images—thus the processes that governs what falls in and out of visual consciousness. In order to prevent our findings from being interpreted as reinforcing either side of the debate, two minor points should be noted. Replay conditions are relevant to visual awareness only insofar as they enable the comparison of activity during perceptual transitions (i.e., with the same perceptual content) and thereby extract that related purely to the transition itself. As we mentioned above, it is technically very difficult to emulate exact BR transitions during replay conditions, given the subjective and constantly evolving nature of BR (see Brascamp et al., 2018 for a discussion of these difficulties). It should therefore be emphasised that our replay condition was not designed to replicate BR transitions but purely to have an estimate of our participants' ability to report alternations in the BR blocks and the latency of this report (to be used later in our control analyses). Further, we do not consider our replay condition informative as to the extraction of purely transition-related activity and thus to the correlates of visual awareness during perceptual transitions, nor do we believe this question to have a place within the scope of this study.

One related limitation concerning our paradigm is the possible confound due to the effort exerted by task demands, that is, the continuous motor report of participants' perceptual experience. In conflicting or difficult tasks, participants are required to exert effort, which in turn increases cognitive load. Such processes are known to share neural correlates to those we discuss here: an increase in mid-frontal theta power and decrease in posterior alpha power, making cognitive load-related modulations a very possible confound in our results (Gevins et al., 1998; Pellouchoud et al., 1999). Our paradigm required continuous behavioural report involving motor action and thus also the continuous report of (and attention to) perceptual reversals. It is thus impossible to disentangle the correlates of perceptual fluctuations from

cognitive load-related modulations with our design because these will necessarily be confounded throughout the performance of the task. It should be noted that such an explanation is not incompatible with our proposed explanation involving conflict. However, alternative paradigms that minimise participant report could provide valuable information to help adjudicate between these confounding explanations. As mentioned above, (cf. Section 3.2.1) a possible confound between report and introspection-related activity has recently called into question the role of frontal activity during multistable perception (Brascamp, Blake, & Knapen, 2015; Frassle et al., 2014; Zou et al., 2016), with competing interpretations of what it may represent. In this ongoing discussion, ‘no-report’ paradigms, such as that proposed by Frassle et al. (2014), have been suggested to offer a promising alternative to paradigms involving behavioural report, decoding perceptual transitions from a combination of pupillometry and optokinetic nystagmus (OKN) instead. We believe that such a design would address the confound from cognitive-load-related modulations because effort exertion would be minimal in paradigms like these. Although report and no-report paradigms (or more recently yet, no post-perceptual cognition paradigms) present new possibilities to researchers, it will of course depend on the goals of each study whether participant report adds informative value or simply adds confounding noise to the recorded data. What each paradigm can contribute to research in perceptual awareness is an ongoing discussion in the BR literature (Block, 2019; Brascamp et al., 2018; Phillips & Morales, 2020).

The present study was based on a pre-registration and as such, the hypotheses tested, the protocol and analyses were designed a priori. One limitation, common to several neuroimaging methods, concerns the correlational nature of the EEG markers (changes in theta and alpha power) we used to signal conflict detection and attention deployment, respectively. Although these markers are well established in related literature, they may admittedly be seen as a case of reverse inference, because it is of course possible that theta and alpha power are associated to different mechanisms we did not consider in our hypotheses. For instance, the results presented here may be attributable (or linked) to violations of expectations or surprise, processes that are necessarily confounded in our protocol and also linked with theta and alpha oscillations (Cavanagh & Frank, 2014; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Mathewson et al., 2011; Pastötter et al., 2013; Van Diepen et al., 2019). It is not possible with our design to entirely dismiss that the observed increase in theta power is in fact independent from conflict-related processes. However, given the initial

suggestion for this study in Botvinick et al.’s (2001) paper and our a priori pre-registered hypotheses and analysis pipeline drawing on various empirical studies, we do not consider our findings to be inconsequential. Our study can be considered an informative first piece of evidence towards the testable hypothesis that cognitive conflict and attention can be seen as two sides of an adaptive mechanism serving flexible behaviour.

In conclusion, our findings provide a step towards a broader understanding of the role of cognitive conflict monitoring and resolution in perception. Should the role of conflict become generalised beyond these initial results, it will provide a promising way of understanding perception within and across sensory modalities in the dynamic, rapidly evolving and highly multisensory world that we live in.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Conceptualisation: M.R., M.T., S.S.F., A.D., L.M.F., M.S.P. and A.S. *Methodology:* M.R., S.S.F., M.T. and L.M.F. *Software:* M.T. and L.M.F. *Formal analysis:* M.T., L.M.F., A.D., and A.S. *Investigation:* A.D., A.S., and M.S.P. *Resources:* M.T., M.S.P. and L.M.F. *Data curation:* M.T., L.M.F. and A.D. *Writing—Original Draft:* A.D. *Writing—Review & Editing:* A.D., M.T., S.S.F., M.R., L.M.F. and M.S.P. *Project administration:* S.S.F., M.R., M.T., L.M.F., M.S.P. and A.D. *Supervision:* S.S.F., M.S.P., M.R., M.T. and L.M.F.

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DATA AVAILABILITY STATEMENT

Data and analysis script are publicly available at the following link: <https://osf.io/v5frc/>.

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