

MSc Brain and Cognition

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Neural correlates of cognitive conflict during Binocular Rivalry

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The experiment used in this study was shared with Alba Sabaté, also in the MRG, for use in a parallel and separate study: “Individual Alpha Frequency as a marker for Binocular Rivalry dynamics”

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Abstract

In this study we investigated the EEG correlates of cognitive conflict and attentional processes during Binocular Rivalry (BR). Participants continuously reported perceptual fluctuations via keypress while EEG was recorded. The modulating effects of attention on BR dynamics have been the object of extensive investigation since the phenomenon first came under scientific scrutiny. The mechanisms of cognitive conflict have also been studied as a key factor in determining perceptual fluctuations. However, the bridge between these two processes is still somehow missing. Intriguingly, evidence supporting the necessity of attention for rivalry is as compelling as that denying it any involvement in rivalry whatsoever. It has been suggested that the necessity for the involvement of attention in BR depends on the degree of conflict between rivaling stimuli. However, research on purely stimulus-based conflict is scant. Using them respectively as markers of cognitive conflict and attention allocation, we tracked the fluctuations in mid-frontal Theta and occipito-parietal Alpha-band oscillations over the course of perceptual fluctuations in the BR task in order to investigate the occurrence of cognitive conflict and involvement of attention. We compared the power of each frequency band over the respective regions of interest right after and before perceptual switches and controlled for motor contamination due to behavioural report. In brief, we found that BR induces conflict-related activity due to competing percepts, reflected by an increase in mid-frontal Theta power right before perceptual switches and a decrease thereafter. Furthermore, while we predicted an inverse pattern for Alpha band oscillations, as we expected inhibition to be high in moments of perceptual stability (low conflict), we found this was merely a tendency. Finally we discuss possible interpretations of these results and suggest directions for future research.

Introduction

In this study we investigate the EEG correlates of Binocular Rivalry in search for the mechanisms governing perceptual fluctuations. In particular, we hypothesise that changes in perceptual experience are partially due to the detection of cognitive conflict occurring between competing stimuli. Furthermore, we hypothesise that this conflict invokes the need for attentional modulation of the competing stimulus. Provided below is the necessary theoretical background out of which these hypotheses were built, followed by an account of our experimental methodology and analysis as well as a discussion of our results.

1. Multistable perception

In everyday life, we are constantly bombarded by a vast amount of information. Through the integration, organisation and homogenisation of raw information arising from the senses, our brain activity mediates our unique and conscious perception of reality. However, the harmony of perceptual representation can be disrupted, failing to provide a coherent and unitary representation of the physical world either by appearing to distort the reality (Figure 1.A.) or to generate perceptions in its absence (Figure 1.C.). This disruption can take multiple forms such as misperceptions, hallucinations or illusions, the fabric of which is not always easy to differentiate. One famous example occurs when an image can be interpreted in multiple ways, either due to insufficient information preventing categorical inference or to conflicting information, permitting it in multiple ways (Figure 1.B.). This is known as multistable perception and is common both because it



Figure 1. A shows the café wall illusion where horizontal lines appear tilted, B the bistable image of a duck-rabbit and C the Kanizsa figure, yielding the non-existent illusory contours of a triangle

occurs spontaneously and is relatively easy to trigger, whilst being no less vivid. In the science of perception from neuroscience to philosophy, it has provided a case study for the striking variation in perceptual experience despite constant and unchanging physical stimulation, leading to speculation about the nature of the experience: ‘the flashing of an aspect on us seems half visual experience, half thought’ (Wittgenstein, 1953).

2. Binocular Rivalry

One dynamic case of multistable perception that has been particularly resistant to putative explanation is Binocular Rivalry (BR). Visual perception is normally derived from the two eyes which, under usual circumstances, combine their slightly different inputs in order to yield a unified, three-dimensional binocular scene. The neural mechanisms underlying this fusion enable humans to have a conscious and unitary visual experience by stifling local, inter-ocular conflicts and thus enabling the reconstruction of depth. However, when disparity between inputs becomes too great (resulting in overwhelming inter-ocular conflict), binocular fusion is disrupted giving rise to perceptual fluctuations between each input (Blake et al., 1978; Blake and Boothroyd, 1985). This phenomenon, albeit rare in non-experimental settings (Arnold, 2011) has become known as Binocular Rivalry, a term first coined by Wheatstone in 1838. Since then, perceptual rivalry has been reported in other sensory modalities, such as olfactory (Zhou et al. 2010) and auditory (Deutsch, 1974) and used (amongst others) for artistic purposes, for instance by Salvador Dalí or Memo Atken (Figure 2).



Figure 2. 'FIGHT': an interactive artwork by Memo Atken presented at Sonár+D 2017 projecting Binocular Rivalry in Virtual Reality

During experimentally induced BR, subjects simultaneously view a different stimulus through each eye but only consciously perceive one at a time. One of the many sources of wonder to this phenomenon is the entirely stochastic nature of perceptual fluctuations (Tong, Meng and Blake, 2006). As one image comes into awareness (the dominant percept), the other (the suppressed percept) falls below it in an alternating rhythm interspersed with unstable, patchy transitions that are best described as a piecemeal combination of both (the mixed percept). Unsurprisingly therefore, BR has attracted attention as a paradigm case in which phenomenological experience (i.e. the content of consciousness or to use Block's terms (2007), phenomenological consciousness) changes despite there being no variation in physical stimuli. However, which neural correlates of BR govern its dynamics?

3. What rivals and where?

Different schools of thought have sought to explain and locate the neural mechanisms behind BR dynamics: while some evidence suggests this process to be 'bottom-up' driven, other points instead to a 'top-down' interpretation, each locating the neural correlates of rivalry at different stages in the visual pathway. Despite (or in light of) the vast body of compelling evidence on both types of influence, it is generally agreed that rivalry occurs over a distribution of various, high and low levels of processing (Blake and Logothetis, 2002). I hereafter explain what is implied by these two types of influences.

3. 1. Bottom-up contributions to BR dynamics

Proponents of bottom-up accounts of BR have provided evidence of activity in early stages of the visual pathway (Blake, 1989). For instance, fMRI studies observe changes in neural activity in the primary visual cortex (V1) during BR (Heeger et al. 2000; Tong et al. 2001). Tong et al. (1998) also used fMRI to monitor activity in stimulus-selective brain areas using face and house stimuli which are famously specific to the fusiform face area and the parahippocampal place area (FFA and PPA respectively). They measured activity during rivalry as well as in a replay condition (simulating the experience of alternation between stimuli without inter-ocular competition) in order to identify rivalry-specific activity. The pattern of activity was the same in both conditions (higher FFA activation when perceiving the face and similarly with PPA and the house). This result supposedly suggested that the competition between percepts is resolved before reaching higher levels of the pathway, representing faces and houses separately. Another study by Zou et al. (2016) induced BR dynamics below levels of awareness using counterphase flickering

to mask the competing stimulus-patterns, making subjects unaware of the conflicting features between images. In the absence of visible fluctuations between percepts, they found evidence of rivalry-related activity in the early visual cortex but minimal activation of the frontoparietal cortex, thereby making the case against its necessary engagement in BR dynamics as well as against a consciousness related top-down feedback process. The bottom-up theory of BR stimuli therefore suggests that resolution of the competition between incompatible images has already been resolved in early stages of visual processing based on information arriving to each eye separately. However, there are other conflicting theories.

3. 2. Top-down influences on BR dynamics

The opposite case has chiefly been made by research on BR in monkeys (Leopold and Logothetis, 1996). These studies show that changes in the visual experience of monkeys were only weakly correlated with changes in patterns of neural firing in V1 but strongly correlated with those in later visual areas, such as the inferior temporal cortex (IT). Other such studies (Logothetis and Schall 1989; Leopold and Logothetis 1996; Sheinberg and Logothetis 1997) used single-cell recording in monkeys while presenting rivaling stimuli (such as horizontal and vertical gratings) and looked at neuronal activity in V1, IT as well as the superior temporal sulcus (STS). The cells in V1 unsurprisingly correlated with the direction of the gratings (cells responsive to both horizontal or vertical directions) and hence to both stimuli, but did not provide any evidence of activity uniquely relating to the visual experience. However, the correlation increased in IT, with almost exclusive firing of vertical cells when the monkey was perceiving vertical gratings and likewise for the horizontal percept. Of course, this doesn't entirely preclude speculation as to which area of the visual pathway is the best candidate for a correlate of the changes in perceptual experience during BR, but it does provide evidence in favour of later areas. Ultimately, evidence for both accounts pave the way for a model of competition occurring over a distribution of the visual hierarchy and processed at different levels therein rather than being unique or locally-specific (Wilson, 2003). However, over and beyond the location at which BR is resolved, one might also ask which mechanisms stand behind perceptual fluctuations.

3.3 Reciprocal inhibition during BR

Despite the robust evidence pointing to contributions of high and low-level processes to rivalry dynamics, one point of consensus seems to be that BR is due to one or various mechanisms of reciprocal inhibition between competing neural populations governing each percept (Levelt, 1965), which can play out at different stages in the visual pathway. The outcome of the visual competition fluctuates over time. According to this view, these neural populations will be activated by the inputs (the stimuli) and send reciprocal inhibitory signals to each other. The activation of the population with the strongest signal then determines which percept becomes dominant. After a while, however, it becomes subject to neural adaptation, thereby weakening inhibition over the competing population whose inhibitory signal strength in turn increases until it eventually takes over as the dominant percept (Blake & Logothetis, 2002). Another more recent theory of visual competition in BR suggests that rivalry is closely linked to attention: according to the model of Li et al. (2017) attention amplifies visual competition by biasing gain toward one of the rival stimuli. But do inhibition and attention suffice to entirely explain fluctuations in BR?

4. Attention and cognitive conflict

The extent to which attention can influence perception becomes all the greater when sensory information is ambiguous. BR dynamics have proved particularly sensitive to attentional modulation which have been addressed extensively, some evidence going so far as to suggest that rivalry does not happen in its absence (Zhang et al. 2011; Brascamp and Blake, 2012). Most BR paradigms (as indeed, does ours), involve constant reporting of the perceptual experience and perceptually distinct stimuli (unless in masked or 'no-report' conditions), making attention unequivocally present during task performance. However, studies involving distractors have succeeded in directing attention away from the rivaling stimuli such as auditory distractions (Alais et al. 2010), secondary visual tasks (Paffen et al. 2006), or meditation (Carter et al. 2005), resulting in an overall slowing-down of fluctuations (some Tibetan Buddhist Monks reportedly being able to hold a percept for up to five minutes). Helmholtz (1925) famously claimed he could completely control the nature of his perception during BR while he performed a parallel task such as counting the Gabor gratings. In an attempt to provide a unifying framework for the range of findings on the effects of selective attention on rivalry dynamics (meaning the cases in which attention can prolong the dominance of the dominant percept and decrease that of the suppressed) Dieter and Tadin (2011), reason that attention is relevant

to BR insofar as there is conflict to be resolved due to sustained visual competition. Furthermore, they draw on studies to argue that the degree of stimulus conflict determines the magnitude of attentional effects, therefore, need for the involvement of attention depends on the degree of conflict between stimuli. Therefore, in order to understand the attentional control and modulation of rivalry, it is no less important to investigate the nature of stimulus conflict during BR, a hitherto lesser explored aspect. In our study, we attempt to probe the relationship between attention and cognitive conflict further. In the next sections, I give a brief overview of these processes as well as introduce their EEG correlates. Before, however, a brief overview of how EEG works is necessary.

5. Electroencephalography

Electroencephalography (EEG) is a neuroimaging technique that non-invasively measures the local field potentials (LFP) generated by neural populations from scalp electrodes. Neurons are interconnected by synapses that either help to propagate information across them (thus excite them) or prevent it (thereby inhibiting them). Either of these activities generate a postsynaptic electrical potential that can be recorded as neuronal populations fire in synchrony. The signal, when sufficiently strong to permeate tissue, skull and scalp can then be measured with surface electrodes placed on the scalp. Cortical pyramidal cells are thought to produce the most EEG signal as a result of their alignment, synchronicity and the perpendicular position of their synapses to the scalp. As local field potentials spread instantaneously, EEG is reputed for its excellent temporal resolution. However, due to having to pick up on signal beyond the tissue, bone, skull and scalp its spatial resolution is relatively poor. EEG is usually either used to measure event-related potentials (ERPs) to investigate fluctuations in cerebral activity time-locked to an experimental event or for spectral analysis of the oscillatory activity during a period of time. Here, we tracked the fluctuations in oscillations over the course of perceptual fluctuations in the BR task in order to investigate the occurrence of cognitive conflict and involvement of attention.

6. Alpha Oscillations in the EEG

The discovery of rhythmic oscillations in the human brain marked the beginning of a search for ways to unequivocally attribute functions or behavioural correlates to each.

Alpha-band oscillations were the first to be discovered by Hans Berger in 1929, oscillating at a frequency range of 8-12Hz and long considered as a ubiquitous marker of wakeful resting states. In fact, they were dubbed the rhythm of 'cortical idling' due to their observed increase in the absence of engagement in any task.

More recently however, Alpha oscillations have become recognised as an active player in perceptual and cognitive processes (Klimesch et al., 2007). Their putative modulation by both extrinsic and intrinsic factors has given rise to numerous studies searching for the mechanisms responsible for such modulation. More specifically, it has been shown that Alpha power can be affected by endogenous shifts in attention despite the absence of physical stimulation (i.e. such as BR, when the physical properties of a stimulus remain constant) and can reflect the focus of attention in the visual system (Thut et al. 2006). Since external stimuli are unchanging, the variability of perception can only be attributed to endogenous, spontaneous and intrinsic modulations of brain states. The most compelling attempts at delineating the nature of the relationship between attention and Alpha oscillations come from Foxe and Snyder (2011), Mathewson et al. (2011) and Jensen et al (2012) who put forth a sensory gating hypothesis whereby Alpha oscillations reflect a mechanism for selective attentional suppression due to functional inhibition across the sensory cortices. According to this view, a decrease in Alpha power is mirrored by a decrease in inhibitory processes. Lange et al. (2014) further show that Alpha oscillations influence perception of illusory stimuli by regulating the excitability of sensory cortices and the neuronal information flow within and between them. In this study, we shall therefore investigate Alpha-band oscillations as an EEG marker of attentional processes. However, in order to monitor conflict beyond attention, it is necessary to take into consideration another frequency band.

7. Theta Oscillations in the EEG

In recent years, evidence has accrued for the relation of Theta oscillations (between 4-7Hz) to cognitive conflict. Botvinick et al. (2001) propose models purporting to show that the necessity for the invocation of cognitive control is 'decided' as a result of constant conflict-monitoring by the anterior cingulate cortex (ACC) during informational processing. Pastötter et al. (2013) show EEG correlates of conflict to be reflected in mid-frontal Theta power, generated by the ACC, where an increase in conflict is mirrored by an increase in Theta power. In 2014, Cavanagh & Frank make a compelling case that Theta

oscillations over the mid-frontal cortex are a prime candidate reflecting the neural computations needed for the realisation of cognitive control (such as reinforcement learning, punishment or conflict between response and stimulus). However, whilst stimulus-response conflict has been the subject of much investigation (for instance in the Stroop-task) revealing its relation to frontal Theta and ACC activation, purely stimulus-based conflict (i.e. stimulus-stimulus, such as in the phenomenon of BR) remains a lesser explored field. Importantly, it has been stipulated that both conflicts may operate in a similar vein: *“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”* (Botvinick et al. 2001). This project was born out of the curiosity to investigate this stipulation as the combination of the aforementioned mechanisms relating to attention and inhibition.

8. Perception below levels of awareness

A final relevant point of discussion should be introduced before outlining our hypotheses. BR remains elusive due to the fact that both stimuli are presented continuously to subjects even though they only report seeing one percept or the other alternatively. Somehow therefore, the visual system receives signals from both inputs but only one at a time reaches conscious awareness, raising the question of what happens to the other stimulus and which properties of suppressed percepts nevertheless enable their processing, albeit below levels of awareness. Processing below awareness, also known as subliminal processing, is defined by Dehaene et al. (2006) “(etymologically ‘below the threshold’) as a condition of information inaccessibility where bottom-up activation is insufficient to trigger a large-scale reverberating state in a global network of neurons with long range axons”. In other words, stimuli are subliminal if they are attended to by the brain but not consciously perceived. One point of uncertainty concerns the occurrence of cognitive conflict below levels of awareness (Desender and Van Der Bussche, 2012). Dehaene et al. (2006) show that ACC conflict-related activity was only present during conscious processing of conflicting stimuli in a subliminal priming task implying that the ACC requires a conscious appraisal of conflicting stimuli. Similarly, Wu et al. (2015) used a flanker task with masked and unmasked primes (using interocular suppression) and showed that the typical conflict effect observed in unmasked conditions was absent when the primes were masked, suggesting that blocking awareness of competing stimuli prevents the involvement of executive control of attention. As mentioned above, Zou et al.

(2016) found little conflict-related activity in the absence of awareness during BR and Brascamp et al. (2015) also reported negligible fronto-parietal activity during BR when rivalry switches were masked to become unreportable. However, against this evidence, an implicit learning-rule study by Ursu et al. (2009) showing heightened ACC activation during subliminally processed conflict. Brooks et al. (2012) in a meta-analysis of the evidence, confirm activation of the ACC when exposed to subliminal conflicting stimuli. These conflicting pieces of evidence are relevant to the present study since the conflict between rivaling stimuli in BR takes place below levels of awareness (even though perceptual processes can still benefit from attention without being aware). Therefore, our findings will provide evidence in favour of either one or the other bodies of literature.

In light of the above overview, we used Theta and Alpha-band oscillations as respective markers of cognitive conflict and selective attentional modulation. Here, we tracked the fluctuations in Alpha and Theta-band oscillations over the course of perceptual fluctuations in the BR task in order to investigate the occurrence of cognitive conflict and involvement of attention.

Scope of the study and hypotheses

As we have seen, attentional modulation of rivalry dynamics during BR has been tested extensively. However, despite the explicit suggestion of the possibility of stimulus conflict during BR in the first formulation of the cycle of cognitive control and conflict monitoring by Botvinick (2001), this remains largely overlooked, despite many studies investigating conflict between stimulus and response. In our hypotheses, we attempt to address cognitive conflict and attentional allocation via inhibition as common mechanisms and, furthermore, do so below levels of awareness. Not only will this aim to unite two hitherto separated mechanisms, but will also provide evidence in favour of a relationship between attention, awareness and cognitive conflict.

Along this trail of thought therefore, we ask the following questions:

1. Does Binocular Rivalry induce cognitive conflict from purely stimulus-based (i.e. conflict between stimuli) processes?
2. Do perceptual fluctuations during Binocular Rivalry correlate with the involvement of attention via inhibitory processes in order to resolve this conflict?

3. Do the above mechanisms occur below levels of awareness?

We hereby hypothesise that 1) BR dynamics induce cognitive stimulus-based conflict, reflected by an increase in mid-frontal Theta power at (or shortly before) the moment of conflict resolution occurring during perceptual switches and that 2) BR fluctuations are linked to fluctuations in the excitability of occipital visual cortical areas, reflected by decreases in occipital Alpha power prior to perceptual switches mirroring either the inhibitory process or the involvement of attention.

Materials and Methods

Observers. 32 naïve observers (15 female and 17 male; aged between 18 and 34) participated in the experiment. All were required to have normal vision, not wear glasses or contact lenses and not be under any particular medication. Participants received 10€/hour in return for their participation. One participant was discarded before the start of the task due to noise in the EEG signal.

Ethics statement. All participants gave written consent to take part in the study by filling out an Informed Consent form in accordance with the Declaration of Helsinki prior to the experiment. Furthermore, the experimental protocol was approved by the Ethics Committee in Parc de Salut Mar (Universitat Pompeu Fabra).

Apparatus and Stimuli. The binocular rivalry paradigm used was adapted from that of Pápai and Soto-Faraco (2017) with the experimental construct provided by the MRG group and adjusted to present needs based on feedback from 10 pilot studies. Visual stimuli were created using the MATLAB Psychtoolbox toolbox (Pelli, 1997) on a 19.8-inch CRT monitor (1024x768; 120 Hz refresh rate) with a grey background (10.7 cd/m²) displayed at 80cm from the participants' eyes and consisted of two circular rival images (11.5° diameter) with symmetrically opposed orthogonally oriented gratings ($\pm 45^\circ$). Initially of different shades of grey, we opted for coloured Gabors (red and green) based on feedback from pilot studies. Both stimuli were centred on a black fixation cross surrounded by a grey circle. Stimuli were presented to each eye through a stereoscope mirror in order to ensure monocular vision of each and were presented continuously throughout the trials of this condition.



Figure 3. A participant performs the Binocular Rivalry task with the EEG configuration

Pre-experiment adjustments and measurements. The green Gabor was adjusted to each participants' subjective isoluminance, for its RGB value to match the luminance of the red Gabor. This was adjusted with up/down key presses regulating the flickering between red and green Gabors at a rate of 60Hz until the flickering stopped (meaning the luminance had been matched). This served to avoid biases derived from percept dominance. This adjustment was provided by the MRG. Prior to the onset of the experiment, participants were dark-adapted to the room during a 5minute 'relaxation' session whereby their Individual Alpha Peak at rest was recorded (these data were used in a parallel study using the same experimental design and participant data. The stereoscope mirrors were calibrated for stimuli to appear at the same retinal location of each eye. Dominant eye and hand were noted for each participant. Eye dominance was recorded using a distance-hole-in-the-card test (Durand & Gould, 1910). Two training blocks were run in order for participants to become familiarised with the task.

Procedure. Participants were seated in a dimly lit and sound-attenuated room (Figure. 3) and asked to keep all movements minimal during each block and to rest in between blocks. The task required them to monitor perceptual fluctuations between the red and green Gabor patches and report them via keypress. Participants were instructed to fixate their gaze on the fixation cross. The keys used for the task were X and D on a QWERTY

keyboard: with one key for the green stimulus, another the red stimulus, both keys to report a mixed stimulus and neither to report none of the three aforementioned percepts. Left and right indexes was placed on each key throughout the experiment. The mapping was randomised across participants (X for red/D for green; X for green/D for red). The hemifield of each stimulus was also randomised across participants in order to avoid biases due to eye dominance (red left/green right; green left/red right). Unbeknownst to the observers, the task was divided into two conditions: a binocular rivalry task (9 blocks) and a replay condition (4 blocks) in a 2-1 alternation pattern (Figure. 4). The length of blocks (120s) was adjusted from 10 pilot studies. In the replay condition, matched physically changing stimuli were presented to both eyes that simulated rivalry by the physical alternation of gratings (in this case, the same grating was presented to both eyes). The temporal dynamics of these physical alternations were determined by each individual participants' keypress distribution from the cumulated previous blocks during rivalry with active report. In this way, the fluctuations of BR were mimicked unbeknownst to the observers, despite there being no competing stimuli.

EEG recording. During all experimental sessions, electroencephalography (EEG) data were acquired using a configuration with actiCAP (Brain Products GmbH, Munich, Germany) system and electrodes placed on 64 scalp sites in accordance with the 10-10 international system was used to record cerebral activity. The ground electrode was placed on AFz and online reference on the tip of the nose. Offline references 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, both being subsequently used for offline artefact rejection. All electrodes were filled with saline conductive gel and their impedance kept below 10k Ω . Brain Vision Recorder (Brain Products, GmbH, Munich, Germany) was used for cerebral signal recording.

Analysis

Behavioural analysis. The main information to derive from behavioural data was that participants were performing the task correctly and that their data could be used for subsequent EEG analysis. In order to confirm the above, we filtered out percepts shorter than 300ms which are more likely to be a perceptual switch than a percept itself, since this duration corresponds to the latency of motor evoked potential from human

movement such as keypresses (Halgren, 2011). The following information was extracted

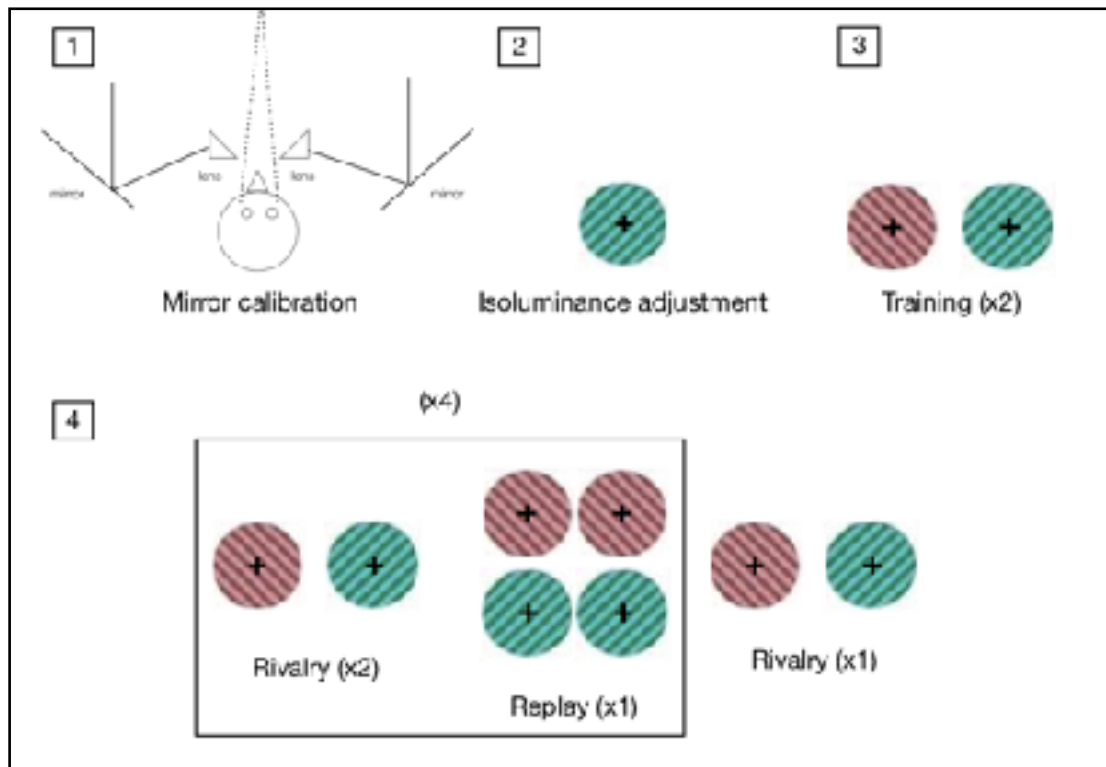


Figure 4. Shows the procedural flow of the experiment: **1.** Calibration of the stereoscope mirrors **2.** Isoluminance adjustment **3.** Two training blocks of BR of 120s **4.** 4 repetitions of two blocks of BR followed by one Blok of replay and **5.** A final BR block

for each participant using Matlab: mean lengths of percepts; total and percentage of time spent in the NULL percept condition during rivalry and replay; mean percentage of time spent in each percept across all participants, in order to check for dominance-bias. The alternation of percepts was then matched to cerebral activity to determine the presence of the possible EEG modulations that are correlated to changes in subjective perception.

Pre-processing of EEG data. All pre-processing and analyses were achieved using the Fieldtrip Toolbox (Oostenveld et al., 2011) and custom-made code provided by the MRG group. Data was segmented into trials corresponding to perceptual switches based on the moment of keypresses. EEG trials corresponding to switches between pure red and green percepts were included, as well as trials initiating with a pure percept and ending with a mixed percept. For a trial to be included in the main analysis, it had to be free from artefact-contamination and have a minimum duration of 1.5s: the time necessary to ensure analyses of the intended time windows, at the intended frequency bands (see below). Single trial data was introduced in the artefact rejection protocol in order to reject artefacts of the following description: blinks, heartbeats, head movements and noise from

electrooculogram upon visual inspection. Had subsequent analysis revealed any misconduct (task not properly understood or noisy signal), the participants' data would have been discarded. However, in the present case, no participant was discarded.

Time-frequency analysis. By hypothesis, the analysis centred around two frequency bands: Theta (5-7Hz) and Alpha (8-12Hz) oscillations. We used a Fast Fourier transform on two 500ms windows (this window length was selected in order to include at least 3 cycles at the central frequency of the band of interest; a Hanning taper was applied to each window prior to transformation) for each trial: one window was located right after the switch (beginning of the trial, henceforth referred to as AFTER) and the other was located just before it (ending the trial, henceforth referred to as BEFORE). The oscillatory amplitude (power) was converted to decibels (dB), for each frequency band, across the electrodes of interest and for the time windows of interest. Activity was measured over the whole scalp, but regions of interest were pre-defined for each frequency band: Fz, FCz and Cz for mid-frontal Theta P7, P8, PO3, PO7, POz, P04, PO8, O1, O2, Oz for occipito-parietal Alpha. The trials included in the analysis were stable pure percepts (red or green) of 1.5s or longer. Only trials for which the next percept was pure or mixed were used. Null percepts were not analysed.

A control analysis was performed, using the same approach but by shifting the time-windows of interest in order to avoid contamination from motor evoked potentials in the AFTER window and activity due to the report (decision-making, motor preparation and motor execution) in the BEFORE window and thus disentangle this contamination from activity relating to endogenously driven perceptual switches *per se*. This motivated the inclusion of the replay condition from which we calculated the median response-time of participants to report perceptual transitions from pure to pure percepts (excluding mixed and null percepts). The response time across participants was then calculated, yielding a median of 446ms (std=103.1ms). Here, the BEFORE window was therefore shifted by the trials covered 446ms, while the AFTER window was shifted by the trials covered by 300ms, the duration of a motor-evoked potential from human movement such as keypress (Halgren, 2011).

Statistical analysis. Ultimately, one power value was estimated per window of interest, per participant, averaged across all trials, then averaged across all frequencies of interest and across all electrodes of interest. These estimates were compared between the time

windows means of a one-tailed paired t-test. Given the directional hypothesis specified above, we expected Theta power to be higher when a switch is imminent, that is, in the BEFORE window right before the perceptual switch than when a perceptual switch is not upcoming, that is in the window right AFTER a perceptual switch. As for Alpha, the pattern was expected to be the inverse, that is, low right BEFORE a perceptual switch (indicating weak inhibition).

Results

Behavioural analysis. Descriptive statistics were derived for each participant. Analysis of behavioural data revealed percepts of interest to reach a mean duration superior to the minimal duration required of 1.5s (red percepts=2.34s [std=0.76] and green percepts=2.57s [std=0.83]). Furthermore, the mean number of red percepts was 140.71 ± 43.89 and of green percepts was 159.42 ± 44.09 . Individual participant data revealed no bias in dominance of red or green percept (mean percentage of red percepts of 29.12% and of green percepts of 35.44%). Importantly, the total and percentage of time spent in the ‘Null percept’ in both rivalry and replay conditions were low (respectively 9.12s and 0.84% during rivalry; and, 1.89s and 0.39% during replay) indicating correct task performance since the replay condition included no null percepts. Based on these results, no participant was discarded.

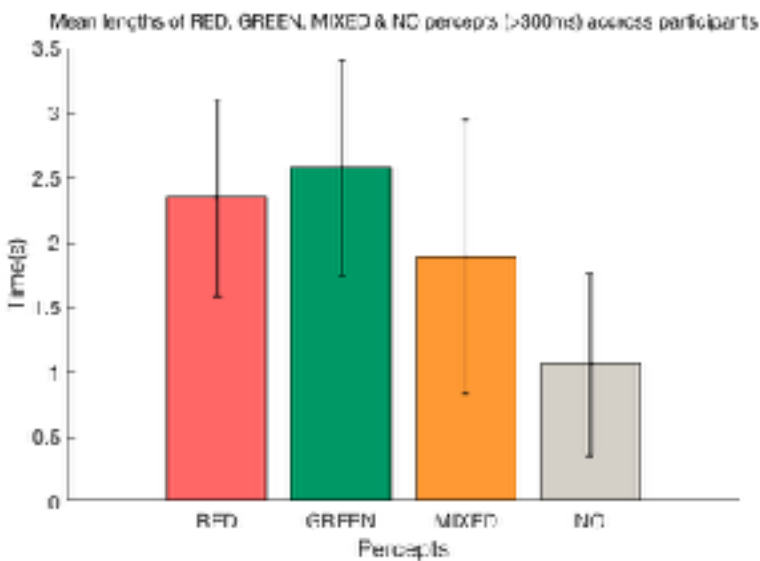


Figure 5. Bar chart representing the mean durations of percepts, after filtering out percepts > 300ms across participants.

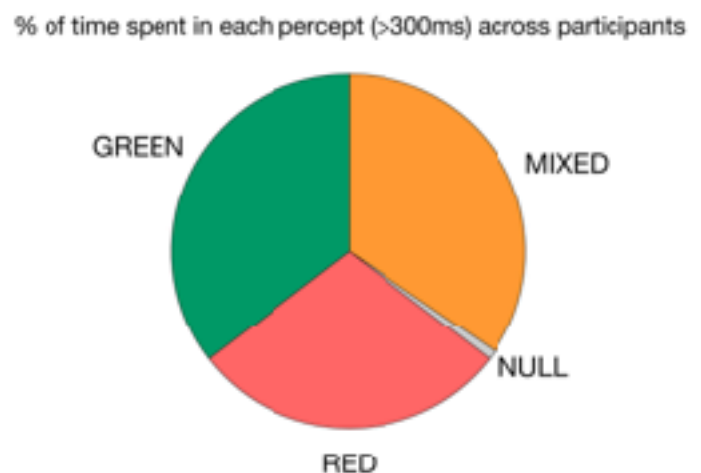


Figure 6. Pie chart representing the mean percentage of time spent in each percept across participants after filtering out percepts > 300ms.

Hypothesis-driven statistical analysis. Theta and Alpha power were compared in the AFTER and BEFORE time-windows and showed the expected pattern ($t_{stat}=-3.6158$; $p=5.4209e-04$ for Theta; $t_{stat}=2.7002$; $p=0.0056$ for Alpha) in the main analysis (Figure. 7). In the control analysis (Figure. 8), when windows of interest were shifted to control for contamination from the motor report, the results showed the expected pattern for Theta oscillations ($t_{stat}=-2.0649$; $p=0.0238$) but remained a tendency for Alpha oscillations ($t_{stat}=-0.5377$; $p=0.7026$).

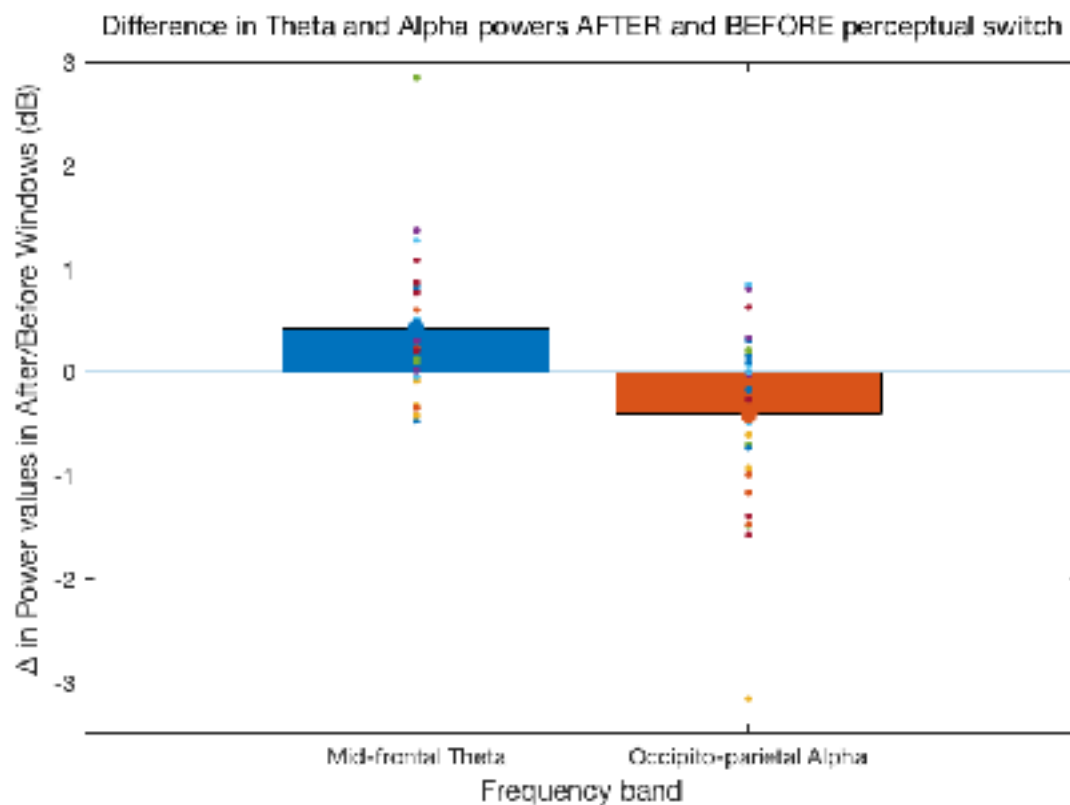


Figure 7. Bar plots of mean difference in power in windows BEFORE and AFTER perceptual switch in mid-frontal Theta and occipito-parietal Alpha oscillations, overlaid with scatter plots of this individual difference for each participant

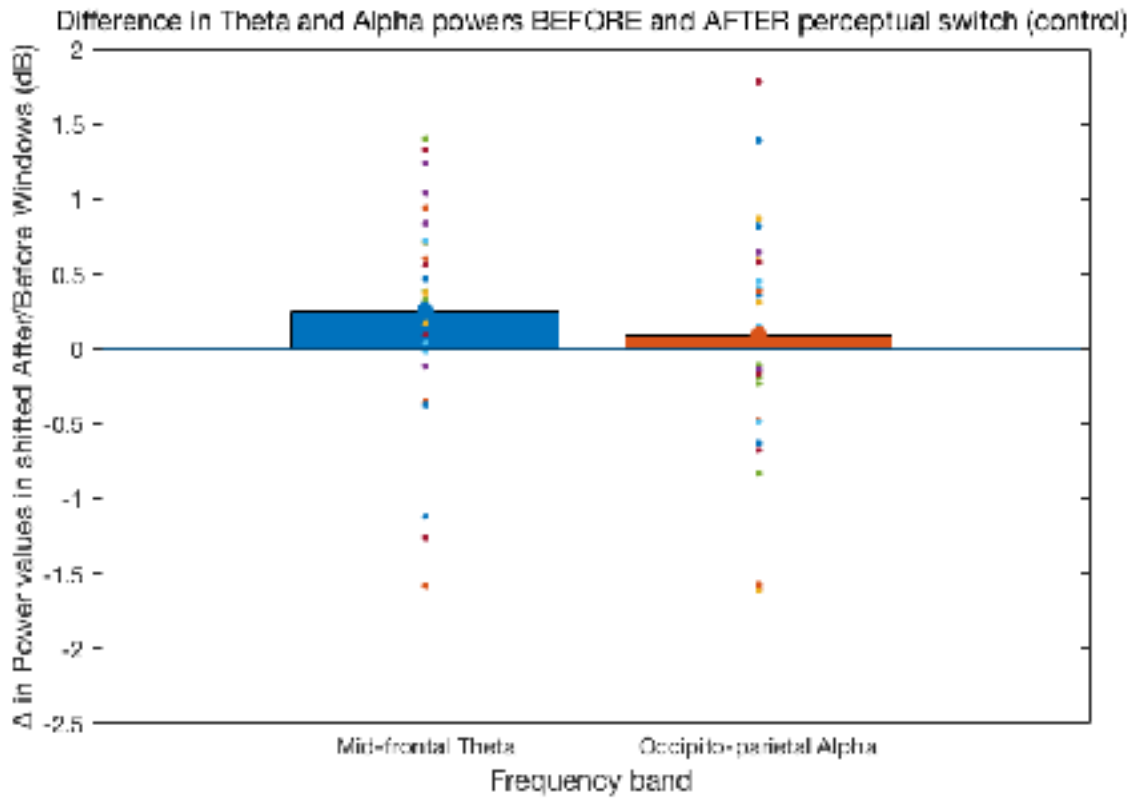


Figure 8. Bar plots of mean difference in power in windows BEFORE and AFTER perceptual switch, controlling for contamination from motor activity due to report in mid-frontal Theta and occipito-parietal Alpha oscillations, overlaid with scatter plots of this individual difference for each participant

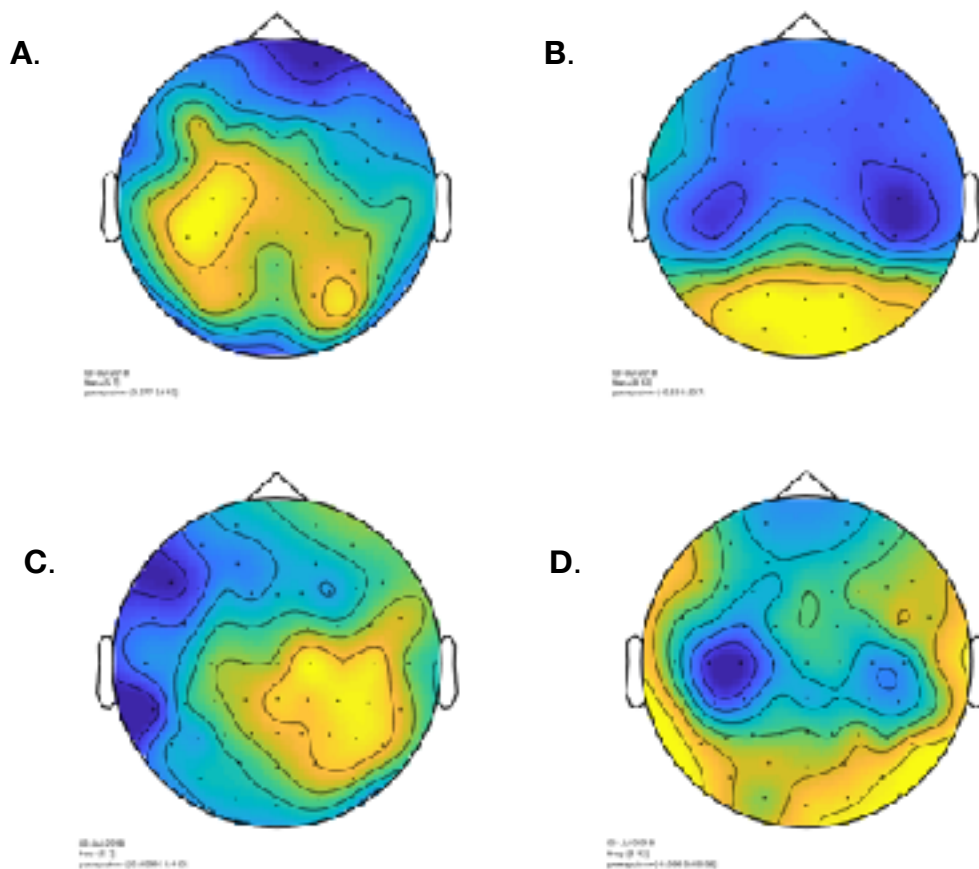


Figure 9. Topographic representations of difference in power AFTER and BEFORE perceptual switches in **A.** Mid-frontal Theta, **B.** Occipito-parietal Alpha, **C.** Mid-frontal Theta (control analysis) and **D.** Occipito-parietal Alpha (control analysis)

Discussion

In this study we used EEG to track oscillatory activity related to perpetual switches during BR. We found that the power in Theta-band oscillations increased right before a perceptual switch and decreased immediately after it, reflecting evidence of the mechanisms of cognitive conflict occurring between stimuli as the neural populations governing them engage in competition and reciprocal inhibition. This evidence is robust since the effect was present in the main analysis as well as that controlling for motor contamination. Furthermore, we found that Alpha oscillations decreased right before a perceptual switch and increased immediately after it, thus reflecting evidence in favour of the engagement of attention allocation via inhibition. However, this effect was only significant in the main analysis but remained a tendency when controlling for motor contamination.

This can be interpreted in various ways. Firstly, it may be that the effect of attentional modulation is only present in the immediate temporal vicinity of the perceptual switch, thus disappearing when shifting the windows of interest in time. However, the current study does not allow us to verify this since the immediate window (in the main analysis) inevitably contains the possibility of contamination due to keypress report. Future research could replicate this study using no-report paradigms (these are discussed below). Secondly, the lack of significance of this result need not undermine the theory outlined in the introduction. According to Dieter and Tadin (2011), need for the involvement of attention should depend on the degree of stimulus conflict. Therefore, it may simply be that the stimuli used in our paradigm were insufficiently incompatible so as to warrant the involvement of selective attention. One way to address this in the future would be to replicate the study using various degrees and types of conflicting stimuli (different images, different luminance adjustments, etc.). Furthermore, their theory predicts a larger degree of attentional control in the onset and early stages of rivalry, due to the unresolved conflict when stimuli are initially presented. However, they claim that ongoing rivalry should be less susceptible to attentional control, due to the ongoing periods of clear conflict resolution. Therefore, this could also be investigated by comparing oscillatory dynamics in the Alpha band over different stages of the rivalry dynamics in time.

The contribution made by this study derives its main significance from the evidence it provides of the little-explored phenomenon of purely stimulus-based conflict. Additionally, our results provide an example of cognitive conflict below levels of awareness. Due to the discussed effect in the Alpha band, it is too early, however, to draw conclusions about the possibility of uniting the hypothesis of attentional modulation of BR through Alpha oscillations with that of cognitive conflict and Theta oscillations. However, if the effect are found in the future with the aforementioned suggestions of future research, it would not only unite these theories but also reveal the intriguing possibility of Theta and Alpha-band oscillations presenting inverse patterns despite oscillating at neighbouring frequencies (respectively 4-7 and 8-12 Hz).

Limitations to our study should be acknowledged. First of all, our paradigm involved continuous report via key-press. Despite our efforts at controlling for contamination from motor response, as well as all that it entails (decision-making, motor planning, motor execution), the motor-evoked potential remains a considerable artefact (Halgren, 2011). If executed correctly, our participants should almost constantly be pressing one key (as is indeed confirmed by our behavioural analysis). Indeed, despite finding statistical evidence of the increase in conflict-related Theta-power, the corresponding topographies (Figure. 9) do not yield quite the expected pattern of mid-frontal activation. Therefore, we cannot decisively eradicate the possibility of competing interpretations of our findings and further exploratory analyses may explain the patterns presented in the topographies. In order to decisively control for motor contamination, the same analysis could be carried out using non-behavioural reports such as optokinetic nystagmus (OKN) or pupil dilation as measures of perceptual switches. However, one practical constraint in our paradigm comes from the stereoscope mirror, which cannot be supplanted by an eye-tracking device, in order to measure the above indicators.

This leads me to a second limitation. Frässle et al. (2014), by using no-report paradigms for binocular rivalry with fMRI (with a sophisticated combination of OKN, pupil dilation, rivalry and replay conditions), showed that brain responses which were previously taken to reflect purely perceptual processes such as frontal BOLD activity are in fact correlates of introspection and activity related to stimulus-monitoring for decision-making and response purposes. Therefore, future research will help to disentangle the functional role of frontal areas during BR. Of course, as neuroimaging techniques essentially provide

correlational evidence, there is always the possibility of a confound between functions. It can, of course, not be excluded that other functional correlates of Theta-band oscillations (or indeed Alpha) be discovered in the future, thereby rewriting interpretations of the current study but such is the exploratory nature of scientific investigation.

A final note on the potential implications of BR for the neural correlates of consciousness. Perception, as a field of enquiry, has long sparked questions pertaining to the nature of conscious experience, and its implications for the science of consciousness, a field that has soared in recent decades. Perhaps more so than any other subfield in this pursuit, research on the neural correlates of visual consciousness has made particular progress. 'A neural correlate of consciousness (NCC) can be characterised as a minimal neural system that is directly associated with states of consciousness' (Chalmers, 2010). Given the vast amount of passing comments found in the literature about BR being useful to investigate the 'neural correlates of consciousness', it is interesting to highlight the following study. Tononi et al. (1998), used magnetoencephalography (MEG) during BR in order to probe the difference in brain states between suppressed and dominant percepts, which were both tagged to a different flickering frequency in order to exclude contamination from behavioural report. Fascinatingly, they observed that the specific subset of brain regions that varied with conscious perception differed for each subject, suggesting the intriguing possibility of locally specific, but widely distributed and individually specific correlates of conscious visual experience. Therefore, unlikely as it is that a single local mechanism will account for visual consciousness as a global state, future directions for the study of BR, beyond searching for correlations, could include probing the nature of representational content during BR itself: for instance, how does the representational content in the distributed task-responsive neural system during BR come to match that in visual consciousness?

Summary and Conclusion

In summary, we provide evidence of cognitive conflict occurring between stimuli and below levels of awareness during BR which is important for two reasons: firstly, there is little evidence of conflict purely between stimuli and secondly, there is debate as to the possibility of its occurrence below levels of awareness. We also find a potential attentional modulation of this conflict immediately prior to perceptual switches, but unable to preclude a confound from motor related activity, cannot draw conclusions purporting to

bridge processes of attention with cognitive conflict. However, our findings provide a step towards a broader understanding of the role of cognitive conflict in BR and future study will reveal its relationship, if any, to the numerous attentional effects on rivalry dynamics.

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