NeuroImage 152 (2017) 1–11

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Deactivation in the posterior mid-cingulate cortex reflects perceptual transitions during binocular rivalry: Evidence from simultaneous EEG-fMRI

Abhrajeet V. Roy[a], Keith W. Jamison[a], Sheng He[b], Stephen A. Engel[b], Bin He[a,c,*]

[a] Department of Biomedical Engineering, University of Minnesota, USA
[b] Department of Psychology, University of Minnesota, USA
[c] Institute for Engineering in Medicine, University of Minnesota, USA

ARTICLE INFO

Keywords:
Binocular rivalry
Fronto-parietal network
EEG
fMRI
Simultaneous EEG-fMRI
Default mode network

ABSTRACT

Binocular rivalry is a phenomenon in which perception spontaneously shifts between two different images that are dichoptically presented to the viewer. By elucidating the cortical networks responsible for these stochastic fluctuations in perception, we can potentially learn much about the neural correlates of visual awareness. We obtained concurrent EEG-fMRI data for a group of 20 healthy human subjects during the continuous presentation of dichoptic visual stimuli. The two eyes' images were tagged with different temporal frequencies so that eye specific steady-state visual evoked potential (SSVEP) signals could be extracted from the EEG data for direct comparison with changes in fMRI BOLD activity associated with binocular rivalry. We additionally included a smooth replay condition that emulated the perceptual transitions experienced during binocular rivalry as a control stimulus. We evaluated a novel SSVEP-informed fMRI analysis in this study in order to delineate the temporal dynamics of rivalry-related BOLD activity from both an electrophysiological and behavioral perspective. In this manner, we assessed BOLD activity during rivalry that was directly correlated with peaks and crosses of the two rivaling, frequency-tagged SSVEP signals, for comparison with BOLD activity associated with subject reported perceptual transitions. Our findings point to a critical role of a right lateralized fronto-parietal network in the processing of bistable stimuli, given that BOLD activity in the right superior/ inferior parietal lobules was significantly elevated throughout binocular rivalry and in particular during perceptual transitions, compared with the replay condition. Based on the SSVEP-informed analysis, rivalry was further associated with significantly enhanced BOLD suppression in the posterior mid-cingulate cortex during perceptual transitions, compared with SSVEP crosses. Overall, this work points to a careful interplay between early visual areas, the right posterior parietal cortex and the mid-cingulate cortex in mediating the spontaneous perceptual changes associated with binocular rivalry and has significant implications for future multimodal imaging studies of perception and awareness.

Introduction

Bistable stimuli have long been used to investigate the behavioral aspects of consciousness, and more recently through the use of imaging, the neural correlates of consciousness. During binocular rivalry, one's conscious awareness spontaneously fluctuates between two different images that are presented simultaneously to the visual system, one to each eye (Tong, 2003). Low-level competition between eye-specific neurons in the lateral geniculate nucleus and primary visual cortex has been implicated in the resolution of binocular rivalry (Blake, 1989; Rees, 2007). Still other studies have suggested that binocular rivalry is the result of competition between conflicting neural patterns at later stages in the visual processing stream, versus simply being the result of competition between monocular neurons (Leopold and Logothetis, 1996; Freeman, 2005). Such theories of rivalry assume only partial suppression of eye-specific information at early visual processing levels, allowing for residual neural signals to reach brain regions involved in higher level, top-down cognitive processing (Wilson, 2003).

Indeed, increased fronto-parietal BOLD activity has been previously associated with binocular rivalry. Several studies have associated cortical activity in multiple regions of the posterior parietal cortex and prefrontal cortex with perceptual transitions during binocular rivalry (Knapen et al., 2011; Wilcke et al., 2009; Britz et al., 2011).

* Correspondence to: University of Minnesota, 312 Church Street, SE, Minneapolis, MN 55455, USA.
E-mail address: binhe@umn.edu (B. He).

http://dx.doi.org/10.1016/j.neuroimage.2017.02.041
Received 16 October 2016; Accepted 14 February 2017
Available online 20 February 2017

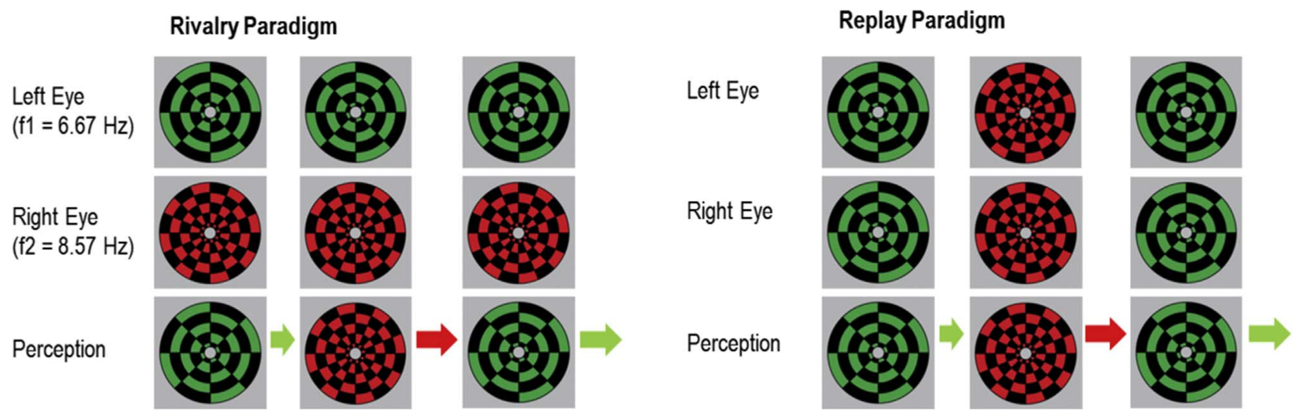

Fig. 1. Binocular rivalry stimulus design. During rivalry blocks (left) each eye was presented with a different flickering image in the center of the visual field. Replay blocks (right) simulated both instantaneous and smooth perceptual transitions for comparison with the rivalry condition. Green and red checkerboards were used to induce SSVEPs at 6.67 Hz and 8.57 Hz, respectively.

Structural differences in the posterior parietal cortex have also been associated with individual differences in perceptual dominance durations during rivalry (Kanai et al., 2010). Furthermore, prefrontal regions that have been implicated in rivalry are generally associated with high level cognitive processes such as decision making, selective attention and goal selection. These top-down networks can modulate activation of neural populations in earlier visual processing areas through feedback projections (Tong et al., 2006). Thus, fronto-parietal networks may be important for integrating high level pattern representations of the visual stimuli with low level neuronal competition in early visual networks for the resolution of rivalry.

A number of studies have suggested a role of both bottom-up and top-down cortical networks in the processing and interpretation of bistable stimuli (Zhang et al., 2011; Meng and Tong, 2004). This bidirectional model emphasizes the recruitment of widespread neural networks during rivalry and reiterates the importance of fronto-parietal regions for its resolution. However, this view has been challenged by more recent work showing that much of the fronto-parietal activity associated with rivalry disappears when bistable changes in visual competition become perceptually invisible/unreportable (Zou et al., 2016; Brascamp et al., 2015). Additionally, it has been suggested that frontal activity during rivalry predominantly reflects introspection and action, not perception, using optokinetic nystagmus and pupil size to track perceptual alternations (Frassle et al., 2014). Given these findings, it is possible that fronto-parietal activity during rivalry lacks a causal role in driving visual competition and is more related to processes involved in visual awareness and attention. Regardless, the specific neural mechanisms of binocular rivalry and their spatiotemporal characteristics remain elusive.

The goal of this study was to delineate neural networks involved in rivalry using simultaneous EEG-fMRI functional imaging techniques. It was hypothesized that changes in BOLD activity during binocular rivalry could be directly correlated with simultaneous fluctuations in occipital EEG activity related to eye-specific competition of frequency-tagged steady-state visual evoked potentials (SSVEPs). Specifically, we predicted that fronto-parietal BOLD increases during rivalry would be greatest during perceptual transitions, as has been previously reported (Knapen et al., 2011). We employed a novel EEG-informed fMRI analysis approach for assessing event-related BOLD activity specifically correlated with SSVEP dominance, when one of the SSVEP signal envelopes peaked while the other was maximally suppressed, and SSVEP crosses, when the amplitudes of the two SSVEP envelopes were approximately equivalent. Using this integrative approach, we found that BOLD activity in a right-lateralized fronto-parietal network was differentially elevated throughout rivalry with peak activation during perceptual transitions, compared to both SSVEP peaks and crosses. In contrast, when we directly compared BOLD activity differences between SSVEP envelope peaks and crosses, this fronto-parietal activity disappeared, suggesting that rivalry is predominantly resolved within early visual regions. Additionally, we found strong deactivation in the posterior mid-cingulate cortex during rivalry-related perceptual transitions, suggesting that this region may be critical for mediating information transfer between early visual and fronto-parietal networks during visual processing. Overall, our findings reiterate that multiple cortical networks are differentially activated during binocular rivalry due to multiple cognitive processes operating concurrently for its resolution.

Methods

Subjects

All experiments were carried out following procedures approved by the Institutional Review Board of the University of Minnesota, Twin Cities. We recruited 20 healthy human subjects for simultaneous EEG-fMRI data acquisition during binocular rivalry. Prior to EEG-fMRI sessions, subjects were introduced to the binocular rivalry stimulus in EEG-alone sessions. This allowed us to evaluate subject-specific perceptual dominance durations prior to the main experiments, to ensure that they were of sufficient length for adequate SSVEP envelope extraction.

Stimulus paradigm

Subjects were presented with a dichoptic rivalry stimulus which consisted of a rotating green and black circular checkerboard presented to one eye, and a rotating (in the opposite direction) red and black checkerboard presented to the other eye as shown in Fig. 1. During replay blocks the same rotating image was presented to both eyes at any time. Subjects were instructed to report their current perceptual state using three different buttons: B1 for green, B2 for red and B1+B2 for perceptually mixed states (i.e. perceptual transitions). Images rotated at a rate of 11.25 degrees/second, and each image was presented flickering at a different frequency within an annular window from 0.5–3.75 degrees visual angle. The green and red images flickered at 6.67 and 8.57 Hz, respectively, and were presented on a gray background with a central fixation cross for subjects to attend to during experimental blocks. Stimulus frequencies were determined prior to EEG-fMRI experiments based on our group's experience with EEG-alone and behavioral studies of rivalry-related SSVEP stimuli (Zhang et al., 2011; Jamison et al., 2015). Frequencies were chosen to be perceptually similar in order to avoid potential stimulus bias that could arise from significantly different rates of contrast reversal. Tagged frequencies were implemented with the MR's stimulus pre-