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Neural dynamics of breaking continuous flash suppression

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A B S T R A C T

Sensory input to the human visual system often becomes accessible to cognition and overt report during processing. We investigated neural precursors of conscious vision using EEG recordings and the popular breaking continuous flash suppression (bCFS) paradigm. In this technique, a mask consisting of high-contrast dynamic patterns is presented to one eye, predominating over a target stimulus presented to the other eye. The time needed for the target stimulus to overcome the suppression is thought to reflect the transition from unconscious to conscious perception. In bCFS trials with slow responses, indicative of potent suppression, a time-frequency analysis showed reduced occipital gamma power (33–38 Hz) contralaterally to the visual hemifield where the target was presented 0.27 to 0.21 s prior to the behavioral response. This neural activity was concurrent with a local phase reset and enhanced long-range phase synchronization in the theta band (7 Hz). Such a pattern did not arise in a control condition in which suppression was not induced. Thus, the theta phase reset and synchronization in bCFS trials precede a break from suppression, likely initiating a re-routing of information such that the neural representation of the target is updated more efficiently than that of the competing mask. Overall, these findings mark the emergence of a binocularly integrated percept that can be consciously selected for a behavioral response.

Introduction

How is the content of conscious perception determined in the brain? A popular method in consciousness research is Tsuchiya and Koch's (2005) potent and controllable interocular suppression technique, continuous flash suppression (CFS). A continuous stream of high-contrast Mondrian-like patterns is presented to one eye while the other eye is presented with an unchanging image. Observers will generally report becoming aware of this image only after a prolonged yet variable period of suppression.

Thus, breaking CFS (bCFS; Jiang et al., 2007) allows us to examine spontaneous changes in the contents of consciousness during constant physical stimulation conditions. CFS is generally considered to be a variant of binocular rivalry (e.g. Stein et al., 2011), and is therefore likely to be driven by analogous mechanisms, to the extent that competition between neural ensembles takes place. Shimaoka and Kaneko (2011) were indeed able to reproduce the principal features of CFS using a network with inhibition and adaptation which included parameters representing the stimulus feature dimension. The dominant activity would thus determine the subjectively perceived stimulus through adaptation-driven, noise-driven or hybrid processes (Panagiotaropoulos et al., 2014) occurring at multiple distributed stages along the visual

hierarchy (Blake and Logothetis, 2002).

Activity in the visual cortex on its own, however, does not appear to suffice to give rise to a conscious percept, as the emergence of consciousness has been linked to synchronous activity over distributed areas in the brain including anterior regions (Crick and Koch, 1998; Dehaene et al., 1998; Dehaene and Changeux, 2011). Such synchronous activity could provide a global neuronal workspace (Dehaene and Naccache, 2001) that enables the flexible sharing of information throughout the brain (Baars, 1990). More recently, Northoff and Huang (2017) have proposed the temporo-spatial theory of consciousness, which attributes the emergence of consciousness to the temporo-spatial features of the brain's neural activity. They postulate different neuronal mechanisms to account for the various dimensions of consciousness: temporo-spatial nestedness, alignment, expansion and globalization.

Building on a growing body of evidence, two major theories have developed to explain how cross-frequency coupling between neural oscillations could enable information transfer in the brain (Canavier, 2015; McLelland and VanRullen, 2016). The theta-gamma neural code, originally based on rat hippocampus recordings (Lisman, 2005), was later extended to serve as a more general mechanism in the brain (Jensen et al., 2014). Essentially, a slow oscillation imposes a rhythmic inhibition that segregates spatial representations according to a temporal phase code. As

inhibition decays and the duty cycle of the slow oscillation begins, stimuli are processed sequentially in the order of their excitability. Neuronal excitability can be modulated by bottom-up and top-down effects, such that more salient stimuli are processed earlier in the duty cycle. Additionally, decreasing the power of the slow oscillation would allow for more processing to occur per perceptual cycle. The communication through coherence theory proposes that stimulus representations are selectively transmitted by entraining post-synaptic neuronal ensembles (Fries, 2005, revisited in 2015). Synchronized neuronal groups also create sequences of restricted output and sensitivity to input as defined by the rises and troughs of the oscillations. However, only the entrained representation is transmitted to the higher brain area and maintained until the end of the cycle of the slow oscillation - meanwhile, other representations can be kept locally available, yet invisible to more distant brain areas. Accordingly, phase-resetting, i.e. the advance or delay of the phase of an oscillation, and phase-locking, which refers to the consistent phase relationship between two oscillations, are important concepts for the encoding of information in these frameworks (Canavier, 2015).

Many electroencephalography (EEG) studies of visual awareness using methods that dissociate physical stimulation and conscious perception have concentrated on stimulus-locked time-frequency analysis or event-related potential analysis (for a review of the latter, see Railo et al., 2011). Oscillatory and coordinated network activity have been linked to the emergence of consciousness (e.g. Iemi and Busch, 2017; Ruhnau et al., 2014), leading for example to the window to consciousness framework (Weisz et al., 2014) and more recently to an interesting hypothesis which attributes a crucial role to the monitoring of visceral signals in the generation of a first-person perspective, essential for consciousness (Tallon-Baudry et al., 2017). Particularly the role of pre-stimulus alpha oscillations has been emphasized (e.g. Mathewson et al., 2011), but also frontal gamma band activity has been previously linked to states of perceptual reversal, e.g. using the static Necker cube paradigm (Strüber et al., 2001). As conscious perception does not co-occur with the stimulus presentation, response-locked activity should be more closely related to the specific perceptual cycle of interest, i.e. the break through CFS of the target, than stimulus-locked potentials. In fact, the study by Doesburg et al. (2009) on the EEG dynamics of perceptual switching during conventional binocular rivalry is in line with this perspective. Their results suggest that theta-modulated gamma synchronization across a prefrontal-parietal network is necessary for conscious perception. In the case of bCFS, this strategy is perhaps even more appropriate, as one of the advantages of the paradigm is that it can lead to extended periods of time between stimulus onset and its conscious detection, potentially allowing for the isolation of effects specific to the transition of a stimulus into consciousness.

In this study, we focus on the response-locked EEG correlates of conscious perception in trials with extended suppression periods to identify activity preceding the break from CFS. We use the reaction time (RT) distribution to select those trials with longer intervals between the physical presentation of the stimulus and its detection. This strategy excludes instances in which observers do not appear to undergo and then break from suppression, but instead appear to bypass this process altogether, perceiving the stimulus immediately. The selection should accordingly enhance any effects specific to the invisible stimulus overcoming suppression.

Our aim was to identify brain mechanisms related to the break from suppression of a previously "invisible" stimulus. Target stimuli were presented in the left or in the right visual hemifield (LVF/RVF) while recording oscillatory brain responses. Power differences between the activity recorded over the contralateral visual cortex (where the representation of the target would be processed) and the ipsilateral visual cortex (where only the mask is represented) in CFS versus control trials would reveal brain responses specific for target processing prior to the break from suppression. Lateralized occipital activity preceding the observer's reaction was thus identified and then placed in a broader context of phase-based information transfer by evaluating the concurrent

dynamics at lower frequency bands.

Material and methods

Participants

Twenty-four right-handed volunteers (5 male, mean age 21.83) with normal or corrected-to-normal vision participated in the experiment. They received course credits in return. The study protocol was approved by the local ethics committee (Universitätsklinikum Regensburg, reference number 13-101-0266). Written informed consent was obtained from all participants.

Sighting eye dominance was assessed for each subject using a variation of the Porta test (Porta, 1593, cited in Wade, 1996). Subjects were instructed to extend one arm and align the index finger with an object in the room with both eyes open and fixating on the index finger. They then alternately closed the right and the left eye and reported which caused the largest change in alignment between index finger and object. The dominant eye was determined to be the one that caused greater change when closed.

Subjects who did not display any behavioral differences between conditions, i.e. RTs during CFS and control trials did not differ significantly per a one-sample *t*-test (2 of 24), were excluded from the EEG analysis, as the suppression period would be negligible in these cases. RT was defined as the time between the target stimulus presentation (onset of the ramp) and the button press. While the cause of the ineffective CFS remains unclear, we were specifically interested in the EEG correlates of the break from a suppression which does not seem to have taken place in these cases.

Four additional subjects had to be excluded from the analysis entirely due to partial data loss. Thus, a total of eighteen subjects (3 male, mean age 21.67) were included in the EEG analysis.

Apparatus

Visual displays were generated with Matlab R2014b (The MathWorks, Natick, MA, USA) and presented on a 24-in. SONY GDM-FW900 monitor (1024 × 768 pixels, 120 Hz frame refresh rate) using the Psychophysics Toolbox (Brainard, 1997). The dichoptic images displayed on the monitor were fused using an in-house built mirror stereoscope mounted on a chinrest. To optimize the convergence of the two images, participants were requested to perform a short preliminary task in which the mirror angles and chinrest position were adjusted so that dichoptically presented complementary segments of a circle appeared as one continuous circle when viewed through the stereoscope. The location of the fixation point in this task corresponded to that of the fixation point in the experiment. The viewing distance was 81 cm.

Stimuli and procedure

During the entire experiment 2 black rectangular frames (4.15° × 9°) with a horizontal distance of 0.43° from each other were presented to each eye against a gray background. A black central fixation cross (0.38° × 0.38°) was located between these, equidistant from the center of each frame. The horizontal center-to-center distance between the dichoptic images was 13.84°. The frames therefore correspond to the left and right visual hemifields (LVF/RVF), conventionally defined as the visual field to the left or right of fixation and therefore projected left or right of the fovea. Participants were instructed to maintain fixation throughout each experimental block. The target stimuli consisted of 16 frontal photographs of caucasian faces with emotionally neutral expression (8 female), taken from the Radboud Faces Database (Langner et al., 2010). The outline of the rectangular images, sized 3° × 3°, was blurred using a Gaussian envelope with a standard deviation of 0.49°. The visible part of the image was approximately 2°, corresponding to four standard deviations of the