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Research report

Arrhythmic activity in the left frontal eye field facilitates conscious visual perception in humans

Lorena Chanes [a], *Romain Quentin* [a], *Marine Vernet* [a] and *Antoni Valero-Cabré* [a,b,c,*]

[a] *Université Pierre et Marie Curie, CNRS UMR 7225-INSERM UMRS S975, Centre de Recherche de l'Institut du Cerveau et la Moelle (ICM), Paris, France*

[b] *Laboratory for Cerebral Dynamics Plasticity & Rehabilitation, Boston University School of Medicine, Boston, MA, USA*

[c] *Cognitive Neuroscience and Information Technology Research Program, Open University of Catalonia (UOC), Barcelona, Spain*

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ABSTRACT

The frontal eye field (FEF) is a brain region involved in several processes relevant for visual performance, including visuo-spatial attention, conscious access and decision-making. Prior research has causally demonstrated that high-beta FEF activity in the right hemisphere enhances conscious visual perception, an outcome that is in agreement with evidence of neural synchronization along a right dorsal fronto-parietal network during attentional orienting and a right-hemisphere dominance for visuospatial processing. Nonetheless, frontal regions in the left hemisphere have also been shown to modulate perceptual performance. To causally explore the neural basis of these modulations, we delivered high-beta *frequency-specific* bursts of transcranial magnetic stimulation (TMS) to the left FEF and report that, in this region, these patterns failed to modulate conscious perception. In contrast, *non-frequency-specific* TMS patterns yielded visual performance improvements similar to those formerly causally associated to the induction of high-beta activity on its right-hemisphere homotopic area. This noise-induced facilitation of conscious vision suggests a relevant role of the left frontal cortex in visual perception. Furthermore, taken together with prior causal right-FEF evidence, our study indicates that frontal regions of each hemisphere employ different coding strategies to modulate conscious perception.

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* *Corresponding author*. CNRS-INSERM-Université Pierre et Marie Curie. ICM, Equipe Cognition, Neuro-imagerie et maladies du Cerveau, Groupe de Dynamiques Cérébrales, Plasticité et Rééducation, Hôpital de la Salpêtrière, 47-boulevard de l'Hôpital, 75651 Paris Cedex 13, France.

E-mail addresses: avalerocabre@gmail.com, avalero@bu.edu (A. Valero-Cabré).

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1. Introduction

Research developed in the last decades has unveiled an important link between brain activity temporal dynamics and human cognition. Specific frequency bands on particular brain regions and their associated networks have been correlated to distinct cognitive processes. Interestingly however, differences or similarities in the modulation of behavioral correlates by characteristic spatiotemporal patterns in homotopic brain areas of opposite hemispheres have rarely been addressed.

In the current study, we focused on the frontal eye field (FEF), a cerebral region contributing in humans to the planning of eye movements, visuo-spatial attention, conscious access and decision-making [(Chanes, Chica, Quentin, & Valero-Cabre, 2012; Corbetta, Patel, & Shulman, 2008; Libedinsky & Livingstone, 2011; Moore & Armstrong, 2003; Paus, 1996), see also (Vernet, Quentin, Chanes, Mitsumasu, & Valero-Cabre, 2014) for a review)]. The right and left FEF are part of a bilaterally distributed dorsal attentional orienting network (Corbetta et al., 2008; Thiebaut de Schotten et al., 2011). However, interhemispheric differences regarding left and right frontal contributions to attention and other processes relevant for perceptual performance have also been reported. Indeed, a right hemisphere dominance for visuo-spatial attention (Bartolomeo, Zieren, Vohn, Dubois, & Sturm, 2008; Grosbras & Paus, 2002), and also a relevant role of the left hemisphere in visual awareness (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Rastelli et al., 2013) and decision-making (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006) have been shown.

In recent years, Transcranial Magnetic Stimulation (TMS) has been successfully used to provide causal evidence on the involvement of cerebral oscillations in cognition (Chanes, Quentin, Tallon-Baudry, & Valero-Cabre, 2013; Romei, Driver, Schyns, & Thut, 2011; Romei, Gross, & Thut, 2010; Ruzzoli & Soto-Faraco, 2014). Using short bursts of TMS at different single frequencies (constant inter-pulse interval across the burst) and *non-frequency-specific* patterns (two or more different inter-pulse intervals embedded in the same TMS burst), cerebral oscillations in specific frequency bands have been shown to play a crucial role in perceptual processes. In particular, we formerly reported frequency-specific perceptual modulations by right FEF activity. Indeed, while high-beta frequency selectively enhanced perceptual sensitivity, higher (gamma) frequency selectively shifted response criterion (Chanes et al., 2013). Moreover, *frequency-specific* perceptual sensitivity increases correlated with the volume of the first branch of the superior longitudinal fasciculus linking this region with the intraparietal sulcus (Quentin, Chanes, Vernet, & Valero-Cabre, 2014). Taken together with electrophysiological work in monkeys and humans (Buschman & Miller, 2007; Phillips & Takeda, 2009), these studies suggest that such high-beta synchronization may reflect attention-related processes.

We here explored whether similar coding strategies exist in the left homotopic frontal area, the left FEF. To that end, we assessed the impact of high-beta *frequency-specific* and *non-frequency-specific* TMS bursts on the discrimination and conscious detection of low-contrast near-threshold targets. Similar results to those observed for the right FEF would indicate analogous coding strategies for the left and the right frontal cortices in the modulation of perceptual performance.

2. Materials and methods

2.1. Participants and consent

Twelve participants (7 women and 5 men) aged between 20 and 31 (mean ± SD, 24 ± 4) years old took part in the main experiment (left FEF *frequency-specific* and *non-frequency-specific rhythmic* patterns, Experiment 1). Eleven of them were naïve as to TMS and to the purpose of the experiment. Another group of 12 naïve participants (6 women and 6 men, 4 of them having participated in the main experiment) aged between 21 and 39 (25 ± 5) years old took part in the control experiment (left FEF *non-frequency-specific random arrhythmic* patterns, Experiment 2). All subjects participated voluntarily and reported no history of neurological or psychiatric disorders and had normal or corrected-to-normal vision. The protocol was reviewed by the Inserm (*Institut National de la Santé et la Recherche Scientifique*) ethical committee and approved by an Institutional Review Board (CPP *Ile de France 1*). The apparatus, visual stimuli and TMS procedure employed here on the left FEF were identical to those reported for the right FEF in a recent publication (Chanes et al., 2013).

2.2. Apparatus, stimuli and procedure

Visual stimuli were displayed on an eye-tracker screen (Tobii Technology AB 17″ wide, 1024 × 768) using a laptop computer (Dell Latitude E6400) and standard stimulus presentation software (E-prime). Each trial started with a gray resting screen (luminance: 75 cd/m2, 2500 msec), followed by a fixation screen (randomly lasting between 1000 and 1500 msec) (Fig. 1a). The fixation cross (0.5 × 0.5°) was displayed in the center, along with three black rectangular placeholders (6.0° × 5.5°): one central and two lateral ones (centered 8.5° to the left and right of the fixation point). Then, the fixation cross became slightly larger (0.7 × 0.7° for 67 msec) to alert participants of an upcoming event. After an inter-stimulus interval (233 msec), a target could appear or not at the center of one of the two lateral placeholders for a brief period of time (33 msec). The target consisted in a low-contrast Gabor stimulus (2 cycles/degree spatial frequency, 3° diameter, minimum and maximum Michelson contrast of .037 and .283, respectively) with its lines tilted 1°–10° clockwise or counterclockwise from the vertical orientation. The inter-trial interval lasted at least 4 sec.

Participants were asked to perform two tasks. First, they had to determine the orientation of the Gabor lines (*discrimination* task) by pressing the corresponding button on a computer keyboard (“1” for counterclockwise and “2” for clockwise) with the index and middle fingers of their right hand. They were encouraged to guess a response even when the target was not presented or they did not consciously perceive it and accuracy was collected as the outcome measure. Secondly, participants had to report whether they had consciously perceived the *Gabor* or not (conscious *detection*