



Neural modulations of interference control over conscious perception

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ABSTRACT

The relation between attention and consciousness is a highly debated topic in Cognitive Neuroscience. Although there is an agreement about their relationship at the functional level, there is still no consensus about how these two cognitive processes interact at the neural level. According to the gateway hypothesis (Posner, 1994), attention filters the information accessing to consciousness, resulting in both neural and functional modulations. Contrary to this idea, the cumulative influence hypothesis (Tallon-Baudry, 2012) proposes that both attention and consciousness independently impact decision processes about the perception of stimuli. Accordingly, we could observe an interaction between attention and consciousness at the behavioral level, but not at the neural level. Previous studies have shown that alerting and orienting networks of attention modulate participants' ability to verbally report near-threshold visual stimuli both at behavioral and neural levels, supporting the gateway hypothesis over the cumulative influence hypothesis. The impact of the executive control network of attention on conscious perception, however, has only been explored behaviorally (Colás et al., 2017). In the present study, we employed high-density encephalography to investigate the neural basis of the interaction between executive attention and conscious perception. We presented a classical Stroop task concurrently with a detection task of near-threshold stimuli. In two separate sessions, we manipulated the proportion of congruent and incongruent Stroop stimuli. We found that the Stroop-evoked N2 potential (usually associated to conflict detection and localized in the anterior cingulate cortex) was modulated by both conflict detection and conscious perception processes. These results suggest that the relation between executive control and conscious perception lies in frontal lobe regions associated to conflict detection, supporting the gateway hypothesis over the cumulative influence hypothesis.

1. Introduction

We can only report a small portion of the information reaching our senses, but how this information is selected is still an open question in Cognitive Neuroscience. Attention has been proposed as the selection mechanism that filters the access of visual information into consciousness (Bartolomeo, 2008; Dehaene et al., 2006; Dehaene and Naccache, 2001; Posner, 1994). Dehaene et al. (2006, 2003), Dehaene and Changeux (2004), Dehaene and Naccache (2001) suggest that the extent to which a certain stimulus gains access to conscious processing depends not only on (bottom-up) stimulus strength but also on top-down attentional amplification. This idea follows the Global Neuronal Workspace model (Baars, 2005, 2002) of conscious access, which states that to be consciously perceived (and therefore accessible to higher order cognitive functions such as memory, language, and action-planning) the neural representation of sensory information has to propagate to distributed large-scale networks in the global neuronal workspace.

The model emphasizes the hierarchical organization of the brain, separating lower automatized and specialized systems from the supervisory executive system (Dehaene and Changeux, 2004). Other models also highlight the importance of attentional amplification for conscious perception (Petersen and Posner, 2012; Posner and Petersen, 1990), proposing attention as the gateway to consciousness.

The use of neuroimaging techniques in paradigms comparing conscious and unconscious processing of information has identified some key nodes in the frontal and parietal cortices that seem to be critically involved in conscious perception (for reviews, see Aru et al., 2012; Chica and Bartolomeo, 2012; De Graaf et al., 2012; Dehaene and Changeux, 2011). Given that the neural ignition of long-distance networks in the brain appears crucial for conscious perception, we could assume that changes in brain activity preceding the presentation of information also play an important role in conscious processing. In fact, existing evidence corroborates that conscious access can be predicted by pre-stimulus activation (Mathewson et al., 2009; Wyart and Tallon-

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Baudry, 2009). Accordingly, fluctuations in attention before stimulus presentation should modulate conscious perception.

The relation between attention and conscious perception has already been explored in the literature. Based on Petersen and Posner's theoretical model (Petersen and Posner, 2012; Posner and Petersen, 1990), attention can be divided into three functionally and anatomically distinct networks: alertness, orienting, and executive control. Behavioral studies have demonstrated that phasic alertness and exogenous spatial attention improve the conscious perception of visual stimuli (Chica et al., 2012, 2011; Kusnir et al., 2011; Petersen et al., 2017). However, interactions between both attentional systems and conscious perception occur through segregated brain networks. The interaction between phasic alerting and conscious perception is mediated through a fronto-striatal network including the anterior cingulate cortex, the supplementary motor area, the caudate, and the frontal eye-fields (Chica et al., 2016). The interaction between spatial attention and conscious perception is instead associated to the activity of the left frontal eye field, the bilateral superior and inferior parietal lobes, and the right inferior frontal gyrus (Chica et al., 2013).

Recently, interference control was demonstrated to modulate the conscious perception of near-threshold stimuli, making participants' decision criterion more conservative after incongruent as compared to congruent Stroop trials (Colás et al., 2017). Interference control is one of the three core components of executive function, that could be equivalent to executive control, as it enables us to attend selectively, focusing on some features or stimuli while suppressing attention to others (Diamond, 2013; Petersen and Posner, 2012). The present study addresses for the first time the neural mechanisms underlying the modulation of conscious perception by interference control. According to the cumulative influence hypothesis (Tallon-Baudry, 2012), the frontal lobes play a key role on the decisional stage of verbally reporting consciously perceived information. It is proposed that the information of attentional and perceptual systems is analyzed in different and independent brain networks, being integrated within the frontal lobe for decision-making (decision about reporting the stimulus presence or absence). Contrary, both the Global Neural Workspace model (Baars, 2005, 2002; Dehaene et al., 2006) and the gateway hypothesis (Petersen and Posner, 2012; Posner, 1994) state that attentional amplification should modulate conscious access in the prefrontal-parietal network. Therefore, attentional recruitments in conflict trials should result in a neural interaction (likely in frontal regions) between interference control and conscious perception.

We conducted an electroencephalography (EEG) study adapting the paradigm used in Colás et al. (2017), which combined a typical Stroop-task (with congruent and incongruent stimuli) with a conscious detection task of near-threshold stimuli (in which stimuli were individually titrated to achieve ~50% consciously reported Gabors). Both tasks were presented in a concurrent manner, so that trials could be sorted into congruent-seen, congruent-unseen, incongruent-seen, and incongruent-unseen. Participants conducted two separate sessions; in one of them, 75% of the Stroop trials were congruent and 25% of the trials were incongruent, a manipulation known to prompt reactive control due to the low expectancy of interference (Botvinick et al., 2001; Braver, 2012; De Pisapia and Braver, 2006). In the other session, 25% of the Stroop trials were congruent and 75% of the trials were incongruent, increasing the recruitment of proactive control as a consequence of the high expectancy of interference (Botvinick et al., 2001; Braver, 2012; De Pisapia and Braver, 2006). Following the dual mechanisms framework of control (Braver, 2012; De Pisapia and Braver, 2006), individuals can either rely on a reactive strategy of cognitive control, activated only after conflict detection, or employ a proactive control strategy which is maintained through the block of trials. The recruitment of these two mechanisms of control can depend on task contingencies or individual differences, or can just wax and wane spontaneously during a block of trials (Kalanthoff et al., 2014).

We analyzed the anterior N2 component locked to the appearance of

the Stroop word, a component that has been related to conflict solving (Folstein and Van Petten, 2008; Luck, 2012). We expected an overall enhanced N2 component when the Stroop word was incongruent as compared to congruent trials, due to interference control recruitment. We hypothesized that this difference would be larger when participants had to implement reactive control (on incongruent trials from the high proportion congruent session), because according to the dual mechanisms framework (Braver, 2012; De Pisapia and Braver, 2006), proactive control would be maintained across both congruent and incongruent trials in the low proportion congruent session. In addition, we conducted source-localization analyses, and we expected the N2 component to be localized in the anterior cingulate cortex (Van Veen and Carter, 2002). Moreover, if the interaction between interference control and conscious access was supported at the neural level, the N2 component should differentiate between consciously perceived and non-perceived near-threshold stimuli. We hypothesized an interaction between interference control and conscious perception, expecting a larger N2 component for incongruent seen as compared to incongruent unseen trials, especially in the high proportion congruent session. Results from this study will show for the first time the when and where of the neural basis of the interaction between interference control and the conscious perception of near-threshold stimuli.

2. Methods

2.1. Participants

Twenty-six students from the University of Granada (Spain) gave their signed informed consent to participate in the study in exchange of course credit. Five participants did not attend the second session of the study and were removed from the analyses. Therefore, data from twenty-one participants (3 men; mean age of 21 years, SD = 3.69) were included for the behavioral analyses. For the ERP analyses, data from four further participants were excluded because, after applying artifact detection tools, they had less than 15 trials per condition. The study was approved by the Human Ethical Committee from the University of Granada, in compliance with the ethical standards of the 1964 Declaration of Helsinki.

2.2. Apparatus and stimuli

E-prime software (Schneider et al., 2002) was used for the presentation of stimuli and behavioral data collection. Experiments were conducted using a 17" DELL monitor running at 85 Hz. Participants sat at approximately 57 cm from the screen. Two black markers and a centered fixation point (a black plus sign, $.3 \times .3^\circ$) were displayed at the beginning of each trial. The markers consisted of a black square outline (6° width \times 4.5° height), placed 8° to either the left or the right side of the fixation point (distance measured from the center of the fixation point to the center of the lateral marker). Spanish words for blue (*azul*, $1.5 \times .5^\circ$), green (*verde*, $2^\circ \times .5^\circ$), and yellow (*amarillo*, $4^\circ \times .5^\circ$) colors were presented 1° above fixation. Words were presented either in blue, green, or yellow ink, and could make a given trial congruent (when word meaning and ink color matched) or incongruent (when word meaning and ink color did not match). Inside the lateral markers, a Gabor stimulus could appear. Matlab 8.1 (<http://www.mathworks.com>) was used to create 100 Gabor stimuli (4 cycles/deg. spatial frequency, 2.5° in diameter, SD of $.3^\circ$), with a maximum and minimum Michelson contrast of .92 and .02, respectively.

2.3. Procedure

Fig. 1 shows the timing and sequence of events in a given experimental trial. The duration of the fixation display varied randomly between 1008 and 1752 ms. The Stroop word was then presented for 492 ms, and the Gabor stimulus (lasting 36 ms) appeared 252 ms after

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