DOCTORAL THESIS

The role of the frontal lobe in attention and conscious perception processes in healthy population and patients with acquired brain injury

(El papel del lóbulo frontal en los procesos de atención y percepción consciente en población sana y pacientes con daño cerebral adquirido)

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Chapter 1: Resumen y conclusiones en castellano

La atención es un proceso psicológico básico cuyo funcionamiento se considera clave para el desempeño de otros muchos procesos cognitivos, tales como la percepción, el aprendizaje o la memoria. Desde las disciplinas de la Psicología Cognitiva y la Neuropsicología se ha concebido la atención como un sistema complejo y heterogéneo, conformado a su vez por diferentes subsistemas (Posner, 1975; Sohlberg & Mateer, 1987). Estudios con técnicas de neuroimagen y en pacientes con daño cerebral adquirido han mostrado que la atención requiere el funcionamiento coordinado de estructuras subcorticales y corticales (Posner, Sheese, Odludaş, & Tang, 2006), especialmente en áreas fronto-parietales (Posner & Dehaene, 1994); no obstante, las diferentes estructuras del lóbulo frontal participan en casi todas las funciones atencionales propuestas.

El objetivo de esta tesis doctoral es explorar el papel del lóbulo frontal en el control ejecutivo de la atención, centrándonos en dos contextos diferenciados. Por un lado, estudiamos el papel de las estructuras frontales en la relación entre el control ejecutivo y la percepción consciente de estímulos visuales en la población sana. Por otro lado, investigamos las funciones atencionales relacionadas con el daño en estructuras frontales en pacientes con confabulaciones como consecuencia de un daño cerebral adquirido, un síndrome clínico caracterizado por la producción de falsos recuerdos que suele ir acompañado de la falta de conciencia de los pacientes sobre su propio déficit (Dalla Barba, 1993; DeLuca, 2009).

De esta forma, este trabajo parte del modelo de las redes atencionales de Posner y Petersen (1990), que divide la atención en tres redes atencionales independientes tanto a nivel funcional como respecto a sus bases neuroanatómicas: la red de alerta, la red de orientación y la red de control ejecutivo. La red de alerta se relaciona con el mantenimiento de un estado de vigilancia (alerta tónica) o la capacidad para responder a cambios en el entorno (alerta fásica).

Por su parte, la red de orientación está asociada a la selección de determinados objetos o lugares, pudiendo ser guiada de forma voluntaria (de acuerdo a objetivos o metas) o de forma involuntaria (por las características físicas de los estímulos o su relevancia para el comportamiento). Por último, la red de control ejecutivo se encuentra especializada en la detección de conflicto (por ejemplo, entre la expectativa de un estímulo y el estímulo real, o entre la información proveniente de distintas dimensiones de un mismo estímulo), la detección de errores, la inhibición de respuestas automáticas y la flexibilidad cognitiva.

Estudios previos han puesto de manifiesto la capacidad de las redes atencionales de alerta y de orientación para modular la percepción consciente de información visual (Botta, Lupiáñez, & Chica, 2014; Chica, Bayle, Botta, Bartolomeo, & Paz-Alonso, 2016; Chica, Botta, Lupiáñez, & Bartolomeo, 2012; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011). Siguiendo esta línea de investigación, la primera serie experimental de esta tesis doctoral se enfoca en contestar a la pregunta científica sobre si la red de control ejecutivo también puede modificar nuestra capacidad para percibir estímulos visuales de forma consciente. Para ello, se llevaron a cabo dos experimentos conductuales en los que se presentaban dos tareas: una tarea de conflicto tipo Stroop, ideada para cargar la red de control ejecutivo, y una tarea de detección de estímulos, en la que se presentaba un estímulo en el nivel del umbral perceptivo (Gabor) y después se analizaba la sensibilidad perceptual y el criterio de respuesta adoptado por los participantes al responder al mismo.

En dichos experimentos se manipuló la proporción de ensayos congruentes e incongruentes, de forma que un experimento indujera la adopción de estrategias de control reactivo (ante una mayor proporción de ensayos congruentes, el control se ejecutaría tras la detección del conflicto en un determinado ensayo), mientras que el otro experimento propiciaba el mantenimiento de estrategias de control proactivo (ante una menor proporción de ensayos congruentes, el control se mantendría de forma anticipatoria durante toda la tarea) (Braver, 2012). Asimismo, se manipuló el tiempo de presentación de los estímulos de la tarea Stroop y la tarea de detección consciente, de forma que el Gabor y el estímulo Stroop podían aparecer de forma concurrente (una condición en la que se asume un alto grado de conflicto), o de forma secuencial (una condición que supondría un menor nivel de conflicto). Los resultados de estos experimentos mostraron que cuando la tarea poseía una alta proporción de estímulos Stroop congruentes, y el Gabor se presentaba al mismo tiempo que el estímulo Stroop (tarea concurrente), los participantes tendían a adoptar un criterio de respuesta más conservador para responder al Gabor en los ensayos Stroop incongruentes en comparación con los ensayos congruentes, probablemente debido a la utilización de estrategias de control reactivo. Estos resultados indican que la activación de la red de control ejecutivo en situaciones de alto nivel de conflicto (ensayos incongruentes e infrecuentes en una tarea concurrente) modula la percepción consciente de estímulos presentados en el umbral de la consciencia en la etapa de la toma de decisiones (criterio de respuesta). Asimismo, en estos experimentos se observó que la comisión de un error en la tarea Stroop (otra condición en la que se activa la red de control ejecutivo) se relacionaba con una menor capacidad para detectar el Gabor (menor sensibilidad perceptual) cuando éste se presentaba una vez que el participante había cometido el error en la tarea Stroop (en la tarea secuencial). De esta forma, estos resultados muestran una interacción a nivel conductual entre el control ejecutivo de la atención y la percepción consciente de estímulos en el umbral perceptivo.

En esta misma línea de investigación, la segunda serie experimental tiene como objetivo explorar las bases neurales de la interacción observada a nivel conductual entre el control ejecutivo y la percepción consciente. Para ello, se utilizó un paradigma experimental similar al de la serie experimental anterior, en la que los estímulos Stroop y Gabor se presentaban de forma concurrente, y donde la proporción de estímulos congruentes e incongruentes de la tarea Stroop fue manipulada entre sesiones, de forma que en una de las dos sesiones del experimento los participantes eran más propensos a emplear estrategias de control reactivo (mayor proporción de ensayos congruentes), mientras que en la otra tendían a emplear estrategias de control proactivo (mayor proporción de ensayos incongruentes). Al igual que en el estudio anterior, a nivel conductual se analizó la sensibilidad perceptual y el criterio de respuesta al Gabor. Además, se empleó la técnica de electroencefalografía de alta densidad para observar la actividad neuronal relacionada con los procesos de control ejecutivo y percepción consciente.

A nivel conductual, los resultados mostraron de nuevo que los participantes tendían a adoptar un criterio más conservador para detectar el Gabor en ensayos infrecuentes, esta vez asociado al empleo de estrategias de control proactivo (ensayos congruentes en la sesión de baja proporción de congruencia). A nivel neural, se observó una mayor amplitud del potencial evocado N2 al estímulo Stroop, relacionado con la detección de conflicto (Luck, 2012; Yeung, Botvinick, & Cohen, 2004), asociada a los ensayos de conflicto en los que el Gabor se había percibido de forma consciente, en comparación con los ensayos de conflicto en los que el Gabor no había sido percibido de forma consciente. Este efecto en el componente N2 fue encontrado en los ensayos incongruentes e infrecuentes de la sesión en la que se hacía un mayor uso del control reactivo (al igual que el efecto conductual de la primera serie experimental). Esta modulación del componente N2 fue observada también en los ensayos congruentes e infrecuentes de la sesión en la que se esperaba un mayor uso del control proactivo. Un análisis de localización de fuentes confirmó que, de forma coherente con la literatura previa (Botvinick, Cohen, & Carter, 2004), el componente evocado N2 tenía su origen principalmente en la activación de la corteza anterior del cíngulo. Por lo tanto, los resultados de este estudio demuestran la existencia de una interacción a nivel neural entre el control ejecutivo y la percepción consciente, respaldada por la activación de estructuras frontales relacionadas con la detección de conflicto como el cíngulo anterior. En resumen, la primera línea de investigación da respuesta a una cuestión que hasta ahora no se había tratado en la literatura científica, a saber, cuál es la naturaleza de la relación entre el componente de interferencia de la red de control ejecutivo y la percepción consciente de estímulos visuales, y cuáles son las bases neurales que subyacen a dicha relación.

La segunda línea de investigación de la presente tesis doctoral se centra en estudiar la implicación de regiones frontales en los procesos de atención y su relación con la consciencia desde una perspectiva neuropsicológica. Para ello, se analizó el grado de preservación de las redes atencionales tanto a nivel comportamental como a nivel de redes neurales en una muestra de pacientes que presentaban confabulaciones como consecuencia de un daño cerebral, a menudo afectando áreas frontales como la corteza orbitofrontal (A. Schnider, Nahum, & Ptak, 2017). El síndrome confabulador se caracteriza por la generación de falsos recuerdos, sin que los pacientes confabuladores sean conscientes de dicho déficit. Aunque el perfil neuropsicológico del confabulador se ha relacionado tradicionalmente con déficits mnésicos y/o ejecutivos (Fischer, Alexander, D'Esposito, & Otto, 1995; Stuss, Alexander, Lieberman, & Levine, 1978), estudios recientes han observado que diversos procesos atencionales tienen la capacidad de modular la presencia o ausencia de confabulaciones (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997; Ródenas, Lupiáñez, Arnedo, & Triviño, 2016; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017). El presente trabajo realiza una aportación novedosa en este campo de estudio, puesto que analiza los procesos atencionales en una muestra de pacientes confabuladores mediante el uso de tres tareas experimentales (de alerta, orientación espacial, e inhibición Go-NoGo), cuyos resultados complementan los obtenidos mediante pruebas neuropsicológicas, en comparación con una muestra de pacientes no confabuladores y una muestra de controles sanos. Además, en este estudio analizamos las lesiones en sustancia gris y sustancia blanca de los dos grupos de pacientes con daño cerebral adquirido, y su relación con su ejecución en las tareas atencionales.

Los resultados de la evaluación neuropsicológica evidenciaron, tal y como ha mostrado la literatura previa, déficits mnésicos (baja capacidad de recuerdo, presencia de numerosas intrusiones en recuerdo libre y con claves, y falsos positivos en reconocimiento) y ejecutivos (baja fluidez, abstracción y memoria de trabajo) en los pacientes confabuladores de nuestro estudio. No obstante, nuestra muestra de pacientes confabuladores presentó además alteraciones en diversas funciones atencionales, tales como la atención selectiva, atención alternante, y la capacidad de inhibición. Dichos déficits atencionales fueron corroborados por un patrón de rendimiento afectado en las tareas empleadas para evaluar las tres redes atencionales. Los pacientes confabuladores mostraron una afectación de la red de control ejecutivo, siendo especialmente vulnerables al conflicto tipo Simon (mostrando una mayor interferencia estímulo-respuesta que los pacientes no confabuladores y los controles sanos) y a la manipulación de la frecuencia de ensayos Go en la tarea Go-NoGo (siendo los únicos participantes que presentaron tiempos de reacción más cortos en el bloque con una mayor proporción de estímulos objetivo Go que en el bloque con igual proporción de estímulos Go y NoGo). Los análisis de sustancia gris revelaron que, de forma consistente con estudios previos, las lesiones en regiones del lóbulo frontal como el giro frontal inferior derecho o la corteza orbitofrontal se relacionaron con un patrón afectado de respuestas en la tarea de inhibición Go-NoGo (Aron, Robbins, & Poldrack, 2014; Sharp et al., 2010). Respecto a la tarea de alerta, los pacientes confabuladores se mostraron más sensibles a la presentación de la clave de alerta que el resto de participantes, beneficiándose o dependiendo más de dicha clave para un buen desempeño en la tarea, lo que podría indicar déficits en la capacidad de inhibición de señales salientes pero irrelevantes. Este patrón de resultados se relacionó con lesiones en la ínsula anterior, y estructuras subcorticales como el putamen, que han sido señaladas en estudios previos como fundamentales para un buen funcionamiento de la red de alerta (H. Kim, 2014; Sturm et al., 1999; Yanaka, Saito, Uchiyama, & Sadato, 2010). Por último, los pacientes confabuladores mostraron los efectos típicos de orientación espacial (validez, predictibilidad, y SOA) en una tarea de orientación con claves periféricas dividida en un bloque en el que las claves eran predictivas (señalaban la localización del estímulo objetivo en un 70% de los ensayos) y otro bloque en el que las claves eran no predictivas (señalaban la localización del estímulo objetivo en el 50% de los ensayos). Sin embargo, tanto los pacientes confabuladores como los no confabuladores (y al contrario que los participantes sanos) presentaron un mayor efecto de validez en el bloque predictivo que en el bloque no predictivo, sugiriendo que el comportamiento de ambos grupos de pacientes dependía más de las claves periféricas que el comportamiento de los controles sanos. El rendimiento en la tarea de orientación se relacionó con la integridad de los tractos medio y ventral del fascículo longitudinal superior en el hemisferio derecho (SLF II y SLF III, por sus siglas en inglés), de forma que una mayor integridad en esos haces de sustancia blanca se relacionaba con una mejor ejecución general en la tarea. Este dato es coherente con la literatura previa que destaca la importancia de las conexiones frontoparietales en el hemisferio derecho en los déficits de atención visoespacial, tales como la heminegligencia espacial unilateral (Bartolomeo, Thiebaut De Schotten, & Doricchi, 2007; Thiebaut de Schotten et al., 2014).

Los resultados de este último estudio aportan evidencia concreta sobre la naturaleza de los déficits atencionales que presentan los pacientes confabuladores como consecuencia de un daño cerebral adquirido, y apuntan a las áreas y redes neurales implicadas en dichos déficits. Además, los datos de este estudio sugieren, de acuerdo con evidencia reciente (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997; Ródenas, Lupiáñez, Arnedo, & Triviño, 2016; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017), que estos problemas atencionales podrían estar a la base de la producción de confabulaciones en este tipo de pacientes.

En resumen, el trabajo de la presente tesis doctoral investiga la relación entre el componente ejecutivo de la atención con la percepción consciente, descubriendo la naturaleza de dicha relación y sus sustratos neurales, y explora la afectación de las tres redes atencionales en el síndrome confabulador como consecuencia de un daño cerebral adquirido, dando pie a la realización de nuevos estudios que analicen la importancia de dichos déficits atencionales en la producción de confabulaciones.

Chapter 2: Introduction

Imagine that you are driving on a four-lane highway to Granada. You have to manage the heavy traffic while keeping an eye on the road signs that would indicate you the highway exit to your destination. Even if the road is unfamiliar to you, it is very likely that you head Granada safe and sound. Furthermore, you may overtake some trucks on your way, monitor your car speed, and take a look at the beautiful landscapes surrounding the highway. But how can we efficiently manage this stimuli complexity and get to achieve our goals? Attention is thought to intervene in these situations in three different ways: 1) maintaining an alertness state, 2) focusing on relevant information, and 3) inhibiting competing responses.

Attention is a heterogeneous cognitive process that involves the operation of diverse brain networks, mostly relying on frontal lobe areas. In the last decades, numerous studies have pointed to the existence of an intimate relationship between attention and conscious perception, following the intuition that we usually perceive stimuli that are being attended. In the first section of this introduction, I will review the literature describing the different mechanisms of attention and their main neural bases. Next, I will address the literature on the relationship between attention and conscious perception, reviewing evidence in favor and against the interaction of both cognitive processes. In the third section, I will introduce confabulations after acquired brain injury, a syndrome characterized by the production of false memories in which patients are unaware of their deficit, and that is thought to involve damage to the orbitofrontal cortex. Finally, I will describe the main aims of this thesis, and the specific objectives of each of the experimental series presented in Chapters 2, 3, and 4.

2.1. Attention

2.1.1. First theoretical models of attention

The first models in Cognitive Psychology considered attention as an information filter which selects the information to be processed, in order to prevent overloading a limited-capacity system. However, when does this filter operation take place has been a matter of debate for a long period of time. Whereas some models proposed attention as an early-selection mechanism that would avoid sensory information to be processed (Broadbent, 1958), other models suggested that attention operated after stimulus processing and categorization (Deutsch & Deutsch, 1963). Later on, a flexible model for information filtering was proposed (Treisman, 1969), posing that this filter could adopt different attentional strategies.

The appearance of flexible filter models (Johnston & Heinz, 1978; Treisman, 1969) pointed out to the necessity of including a control-system into the conceptualization of attention, which would establish the criteria for the use of different strategies in the selection of information. Kahneman's model of attention incorporated this concept of a central executive that coordinates different cognitive systems and distributes the attentional resources among the tasks at hand in order to optimize behavior (Kahneman, 1973). This deployment of cognitive resources would take into account the arousal of the subject (i.e. the level of attention) and task difficulty. The concept of a central executive was reformulated by Norman and Shallice (1986), who postulated the existence of a Supervisory Attentional System that would intercede in certain circumstances to control cognitive processing. The situations that will require the activation of the Supervisory Attentional System would be those involving a) action planning and decision-making, b) error correction, c) novel, dangerous or complex situations, and d) situations requiring to overcome a habit. According to Norman and Shallice, in the absence of control, stimuli activate certain response schemas based on previous situations. These schemas are in local competition, and the function of the Supervisory Attentional System is to favor the appropriate response schema.

Although some of the ideas that formed these models are no longer considered accurate (e.g. the view of early versus late selection of attention as a dichotomy), they built the bases of the three main components of attention for an adaptive and efficient behavior: attention as a state, attention as a selection mechanism, and attention as a control system (Posner & Boies, 1971). These three functions were comprehensively addressed in Posner and Petersen's model of attention, in which the authors postulated the existence of three independent neural networks, each one related to a different attention mechanism (S. E. Petersen & Posner, 2012; Posner & Petersen, 1990).

2.1.2. The Attention Networks model

According to Posner and Petersen's model (Posner and Petersen, 1990), attention is not a unitary system. They propose that the concept of attention can be divided into three main subsystems that are implemented into three different networks of anatomical areas, involved in different cognitive functions. The three systems, performing separate but interrelated functions, are the alerting network, the orienting network, and the executive control network.

2.1.2.1. Alerting

The alerting network regulates the ability to prepare and maintain an optimal vigilant state that enables both responding to changes in the environment and sustaining a particular activity in time. Alerting has been studied by presenting a warning signal prior to a target, which produces a phasic change in activation (S. E. Petersen & Posner, 2012). Warning signals increase the speed of orienting attention and thus detecting and responding to the expected target, although this preparation can produce trade-off in response accuracy (Posner, 1994). On the other hand, the tonic aspect of alertness has been studied through long low-demanding tasks to measure sustained vigilance. In addition, studies of circadian rhythms have demonstrated that this general alertness state fluctuates during the day, increasing over the course of the day and going down again during the night and the early morning (Posner, 1975).

Concerning the neural bases of alertness, both classical lesion studies and recent imaging evidence support that tonic alertness is lateralized to the right hemisphere (S. E. Petersen & Posner, 2012), whereas phasic alertness activates bilateral brain structures (Jin Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). Specifically, tonic alertness has been associated to a network of fronto-parietal and thalamic-brainstem areas in the right hemisphere, including the anterior cingulate cortex (ACC) and the dorsolateral prefrontal cortex, the inferior parietal lobe, the pulvinar nucleus of the thalamus, and the ponto-mesencephalic tegmentum in the brainstem, possibly involving the locus coeruleus (Sturm et al., 1999; Sturm & Willmes, 2001). In addition, neuroimaging studies prompting phasic alertness have found activations of this midbrain-thalamic-anterior cingulate cortex (ACC) circuit as well as the bilateral cortical involvement of a ventral network of frontal and parietal areas (Chica et al., 2017; Corbetta and Shulman, 2002; Kim, 2014; Martín-Signes et al., in press; Sturm et al., 1999) (see Figure 1). Cortical areas involved in phasic alertness include the ACC, and supplementary motor area (SMA) in the frontal lobe, and bilateral inferior parietal lobule

(IPL) and superior parietal lobule (SPL), whereas subcortical regions include midbrain, caudate and thalamus (Jin Fan et al., 2005; Sturm & Willmes, 2001; Yanaka, Saito, Uchiyama, & Sadato, 2010). Coherent to neuroimaging evidence, phasic alertness has been proven to depend on the brain's norepinephrine system, arising in the midbrain and making contact with frontal and parietal areas (Posner, Rothbart, Sheese, & Voelker, 2012).

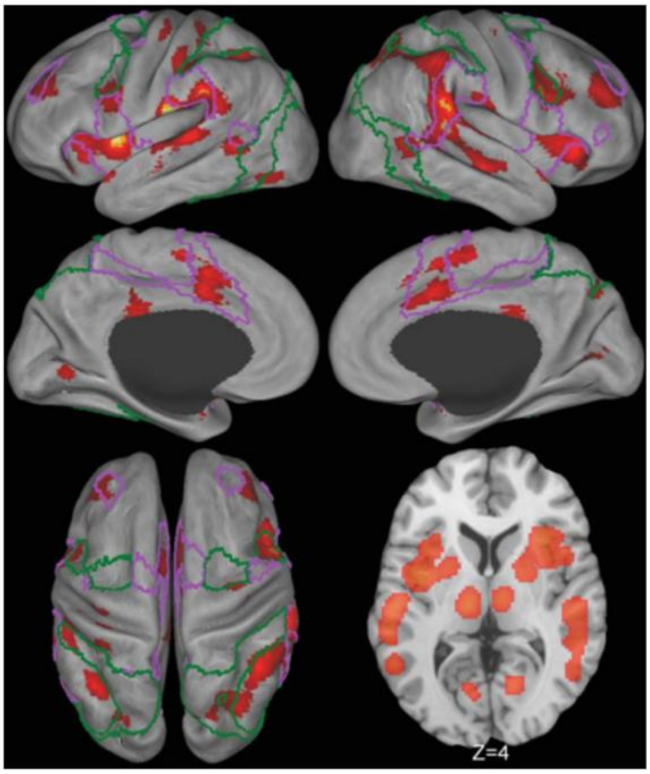


Figure 1. Brain regions associated with visual and auditory oddball effects (responses to deviant stimuli) in a meta-analysis of 75 individual fMRI studies (reproduced with permission from Kim, 2014). Green- and violet-colored borderlines mark estimates of the dorsal and ventral attention networks. Results from this meta-analysis suggest an implication of frontal and parietal areas from the ventral network in a supramodal alerting system. This comparison also showed activation of the sensory cortex regions, and subcortical regions involving the putamen, and the thalamus.

Recently, neuroimaging techniques such as Diffusion Weighted Imaging (DWI) have enabled neuroscientist to study the anatomical connections underlying cortical and subcortical regions. The relevance of these studies lies in their capacity to explore how brain regions are interconnected, and therefore suggest a possible functional association between them. Studies exploring the white matter bases of alertness in patients with neglect syndrome have suggested a link between tonic alertness and the inferior fronto-occipital fasciculus (IFOF), proposing that damage to this tract might prevent top-down modulation of visual cortex activity, or alternatively decrease the influence of visual input on the right ventrolateral prefrontal cortex (VLPFC) (Urbanski et al., 2011). Consequently, injury to the IFOF might contribute to impair patients' level of arousal (Doricchi, Thiebaut de Schotten, Tomaiuolo, & Bartolomeo, 2008; Urbanski et al., 2008) or sustained attention (Singh-Curry & Husain, 2009). By contrast, phasic alertness has been associated to the left (Niogi, Mukherjee, Ghajar, & McCandliss, 2010) and right (Yin et al., 2012) posterior limbs of the internal capsule, possibly due to its connections between the supplementary motor area and the thalamus (Yin et al., 2012). Phasic alertness has also been related to the ventral branch of the superior longitudinal fasciculus (SLF III) in the left hemisphere (Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2017), probably due to its overlap with the ventral network of attention (Corbetta & Shulman, 2002; Thiebaut de Schotten et al., 2011).

Changes in electrical brain activity as a consequence of the level of alertness have also been explored. For example, the awake-asleep transition, which is thought to depend on multiple brainstem–thalamo–cortical pathways, is associated with an increment of slow wave activity in frontal and central regions, and with the subsequent appearance of sleep spindles and/or K-complexes (Oken, Salinsky, & Elsas, 2006). Tonic alertness has also been associated to early event-related potentials (ERPs), such as the N1, whose amplitude decreases during sleep and low vigilance state (Fruhstorfer & Bergström, 1969; Kevanishvili & Von Specht, 1979), and the mismatch negativity component (MMN), which is also reduced when alertness decreases preceding sleep (Sallinen & Lyytinen, 1997). On the other hand, long latency ERPs, such as the

P3 wave, have been related to phasic alertness. Previous studies demonstrated that latency of the P3 component increases during sleep deprivation, while its amplitude decreases both during sleep deprivation and passive task conditions (García-Larrea, Lukaszewicz, & Mauguiére, 1992; Oken et al., 2006).

2.1.2.2. Orienting

The orienting network of attention prioritizes sensory information processing by selecting a given sensory modality, an object, a location, etc. For this orienting system to be effective, it must be capable of guiding attention towards goals-directed information in a way that avoids distraction, but it also has to be sensitive to novel and salient stimuli which could be relevant for the task at hand, or become dangerous if ignored (Allport, 1989; see Chica et al., 2013, for a review). According to this prediction, Corbetta and Shulman's model of visual attentional selection (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) proposes the existence of two orienting systems of attention: a goal-directed or top-down attention system, and a stimulus-driven network responsible for the reorienting of attention to relevant stimuli. The top-down attention system is thought to select sensory information and responses based on cognitive factors, such as prior knowledge, expectations, and current goals (Corbetta & Shulman, 2002). This mechanism of spatial attention relies on the beforehand preparation of an "attentional set", involving the representation of the stimuli and responses relevant to the current task. By contrast, the stimulus-driven reorienting of attention relies on both stimulus salience (stimulus' physical properties in opposition to the background or the distracters) and behavioral relevance, being the latter a crucial factor for the activation of the ventral network (Jonathan Downar, Crawley, Mikulis, & Davis, 2001).

Nonetheless, in real life situations, the stimulus-driven orienting system is often influenced by cognitive goals. For example, if we are looking for mushrooms in the forest, our visual search is going to be shaped by our knowledge about the characteristics of these fungi, increasing the probability that we detect rounded, small, brown rocks or leaves in the weeds, in addition to real mushrooms. There is therefore wide consensus on the idea that the visual orienting system is modulated by the interaction between both bottom-up and top-down attention signals. In fact, this idea was proposed by Yantis and Egeth (1999), who demonstrated that highly salient stimuli do not always capture attention in visual search tasks, and that stimulus-driven attention is not always automatically-triggered. Moreover, although some authors postulated that exogenous and endogenous orienting represent two independent attention systems they sometimes interact for the control of behavior (Chica, Bartolomeo, & Lupiáñez, 2013).

Studies exploring the orienting of attention have employed cueing paradigms in which a cue is presented before a target (Posner, 1980). Cues could either be valid (signaling to target location), invalid (signaling a non-target location), or neutral (without spatial information about the target location). The difference between responses to valid and invalid cues as compared to neutral cues is referred to as costs and benefits in reaction times (RTs) and accuracy. Costs represent slower RTs and lower accuracy on invalid trials as compared to neutral trials, whereas benefits correspond to faster RTs or higher accuracy in response to valid cues as compared to neutral cues. Spatial cues can be symbolic and presented at fixation. These symbolic cues are usually spatially informative (i.e. indicating the target location with certain probability; e.g. 80% valid trials, 20% invalid trials), triggering top-down (or endogenous) attention. Cues can also be presented in the periphery (near the target location), assuming to trigger exogenous attention if they are not spatially informative (e.g. 50% valid trials, 50% invalid trials). If peripheral cues are spatially informative, they are assumed to trigger an initial exogenous capture and a top-down (or endogenous) maintenance of attention at the predicted location.

The endogenous orienting of attention driven by central symbolic cues is usually slower than exogenous orienting, but it can be sustained for longer periods of time (Müller & Rabbitt, 1989). In fact, the effect of exogenous attention reverses at long cue-target intervals: valid cues produce costs instead of benefits, a phenomenon known as inhibition of return (see Klein, 2000, for a review; Posner et al., 1985; Posner and Cohen, 1984). Exogenous attention cannot be voluntarily suppressed and is more resistant to interference (Jonides, 1981; Müller & Rabbitt, 1989). These observations took Jonides to conceive exogenous attention as an automatic mechanism, and endogenous attention as a mechanism under voluntary control.

Neuroimaging studies have highlighted the implication of a bilateral network in spatial attention, whose core regions are located in parietal and frontal areas (Hopfinger, Buonocore, & Mangun, 2000; Y.-H. Kim et al., 1999; Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999). As stated above, Corbetta and Shulman (2002) identified a dorsal frontoparietal network, including dorsal parietal regions such as the intraparietal sulcus (IPS) and the superior parietal lobule (SPL), and dorsal frontal regions such as the frontal eye field (FEF). This system would implement endogenous or top-down attention (see Figure 2A). In addition, it was observed that the preparatory activation of this dorsal network can sometimes extend to the visual cortex, most likely reflecting top-down modulation of sensory representations (Corbetta, Patel, & Shulman, 2008; Hopfinger et al., 2000). A second system, the ventral frontoparietal network, is found to activate along with the dorsal network when behaviorally relevant stimuli are detected, probably representing an exogenous or bottom-up capture of attention (see Figure 2A). Core regions of this right-lateralized ventral network include the right temporoparietal junction (TPJ), in particular the posterior sector of the superior temporal sulcus (STS) and superior temporal gyrus (STG), the ventral part of the supramarginal gyrus (SMG), and right ventral frontal cortex (VFC), including parts of middle frontal gyrus (MFG), inferior frontal gyrus (IFG), frontal operculum, and anterior insula (Corbetta et al., 2008). Concerning neurons' chemical communication, in the same way that the noradrenergic system and the neurotransmitter norepinephrine have an important role in the alerting network, the cholinergic system and the neurotransmitter acetylcholine seem to be crucial for the orienting of attention (Beane & Marrocco, 2004; Posner, Rothbart, Sheese, & Voelker, 2012).

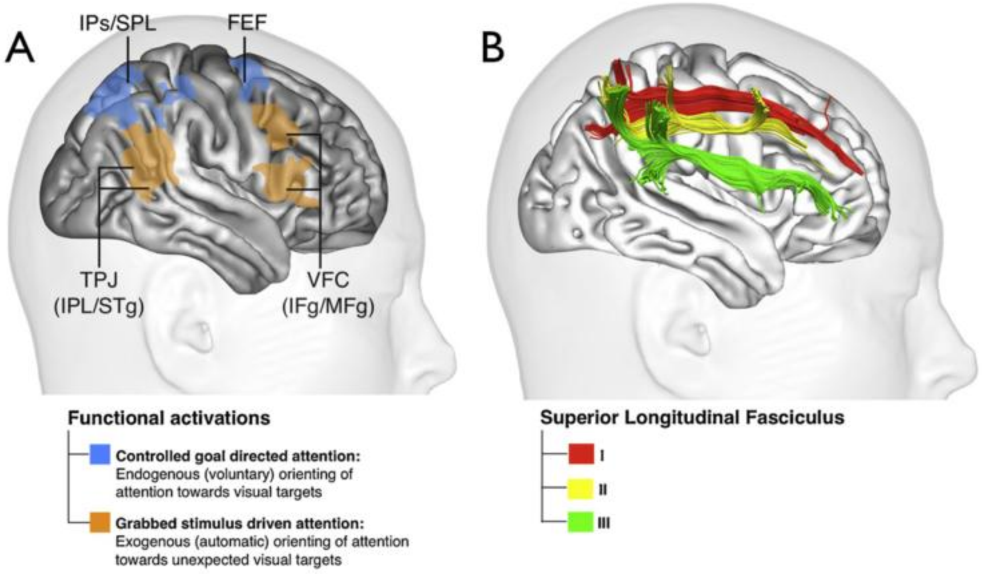


Figure 2. (A) Right-hemisphere view of spatial attention networks according to Corbetta and Shulman (2002). (B) The three branches of the Superior Longitudinal Fasciculus according to Thiebaut de Schotten et al. (2011). The figure represents the anatomical brain regions associated with spatial attention and the white matter branches that might connect them (reproduced with permission from Chica et al., 2013).

Studies on the white matter connections of the brain have proposed that visuospatial attention relies on the Superior Longitudinal Fasciculus (SLF), a white matter tract separated into a dorsal branch (SLF I), a middle branch (SLF II), and a ventral branch (SLF III) (Thiebaut de

Schotten et al., 2011). Importantly, the dorsal and ventral branches of the SLF have been proposed to lie beneath the dorsal and ventral orienting networks from Corbetta and Shulman's model of spatial attention (Thiebaut de Schotten et al., 2011). Projections of the SLF I to the cortex are symmetrically distributed between the left and right hemispheres, overlapping with the dorsal network of attention (Corbetta et al., 2008; Corbetta and Shulman, 2002; Thiebaut de Schotten et al., 2011) (see Figure 2B). The SLF III, which overlaps with the ventral attention network, is lateralized to the right hemisphere (see Figure 2B). Finally, the SLF II is also right lateralized, and it is thought to manage direct communication between ventral and dorsal attentional networks, as it overlaps with parietal regions of the ventral network of attention and prefrontal regions of the dorsal network of attention (Thiebaut de Schotten et al., 2011). The SLF has been largely implicated in the spatial orienting of attention, as its disconnection on the right hemisphere is related to spatial attentional deficits in spatial neglect (Thiebaut de Schotten et al., 2014).

Several ERP studies have shown that costs in orienting (attending to invalidly cued locations) produce a suppression of the P1 component to the target stimulus, whereas benefits (attending to validly cued locations) enhance the N1 component (Steven J Luck et al., 1994). These electrophysiological correlates of costs and benefits can be dissociated (Heinze, Luck, Mangun, & Hillyard, 1990; Lasaponara, Chica, Lecce, Lupianez, & Doricchi, 2011; Steven J Luck, Fan, & Hillyard, 1993; Steven J Luck, Heinze, Mangun, & Hillyard, 1990), supporting the existence of two independent processes contributing to validity effects. It has also been observed that inhibition of return (an above-described effect associated to exogenous orienting) affects both early (P1) and late (P3) ERPs, whereas endogenous attention produces stronger effects at late stages of processing (P3) (Chica & Lupiáñez, 2009). Finally, a component known as the N2pc (N2 posterior-contralateral) has been shown to be sensitive to spatial attentional selection (Eimer, 1996).

2.1.2.3. Executive control

In the first conceptualization of the Attention Networks model (Posner & Petersen, 1990), the third network referred to the monitoring process and awareness that encompasses target detection, also called focal attention. Therefore, the executive network of attention was conceived as a voluntary control mechanism that monitors and regulates sensory input, behavior, cognition, and emotion, and is associated to consciousness and to the on-line maintenance of information (Posner & Dehaene, 1994). Although the situations in which this system of control is involved are diverse, there seems to be enough convergence across data from different tasks on the activation of a frontal control system, involved in planning, error detection, task or stimulus novelty, difficult processing, or conflict (Posner & Digirolamo, 1998). In fact, executive control is a broad concept associated to conflict and error detection, inhibition of automatic responses, cognitive flexibility, and self-regulation.

Recently, Braver has postulated a dual mechanisms of control (DMC) framework, differentiating between proactive control, a goal-driven 'early selection' in which goal-relevant information is actively maintained in a sustained manner, and reactive control, a 'late correction' mechanism mobilized only as needed, such as after the detection of a high interference event (Braver, 2012). According to this framework, proactive control prepares the system priming task-relevant processing pathways prior to stimulus-onset, whereas reactive control suppresses the activation of task-irrelevant information in an online, trial-by-trial basis (De Pisapia and Braver, 2006). Reactive or proactive control mechanisms can be implemented depending on task characteristics. For example, in tasks with a high proportion of congruent stimuli (e.g., 75% congruent trials and 25% incongruent trials), in which expectancy for interference is low, participants' tend to rely on reactive control mechanisms. In contrast, low proportion congruent tasks (e.g., 25% congruent trials and 75% incongruent trials) induce a high expectancy for interference, making proactive control mechanisms more effective, and more likely to be recruited (Braver, 2012; De Pisapia & Braver, 2006).

In their review of the Attention Networks model (S. E. Petersen & Posner, 2012), two separate executive control networks were described: 1) a fronto-parietal network, including the precuneus, the middle cingulate cortex (mCC), the dorsolateral prefrontal cortex (dlPFC), the dorsal frontal cortex (dFC), the IPS, and the inferior parietal lobule (IPL), and 2) a cingulo-opercular network, constituted by the anterior prefrontal cortex (aPFC), the anterior insula/frontal operculum (aI/fO), the dorsal anterior cingulate cortex/medial superior frontal cortex (dACC/msFC), and the thalamus (see Figure 3). The fronto-parietal network (distinct to the orienting network) is thought to initiate and adjust control, whereas the cingulo-opercular network (partially overlapping with Posner and Petersen's original depiction of executive control network) affords 'set-maintenance' across the task (Dosenbach et al., 2007; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). Dosenbach and colleagues also found that the dlPFC and IPL in the fronto-parietal network and the thalamus in the cingulo-opercular network were connected to a cerebellar network. All these regions were characterized by error-related activity (feedback and adjustment), suggesting that the cerebellum either sends and/or receives error information from one or both of the control networks of the brain. The neurotransmitter dopamine is thought to intervene in the exertion of executive control, mainly by dopaminergic input from the ventral tegmentum (J Fan, Wu, Fossella, & Posner, 2001; S. E. Petersen & Posner, 2012; Posner, Rothbart, Sheese, & Voelker, 2012).

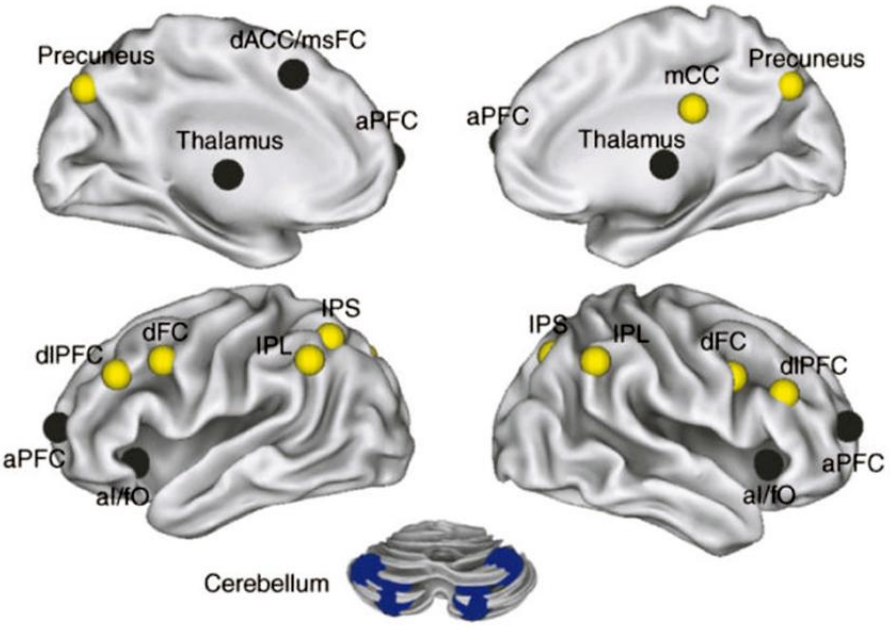


Figure 3: Fronto-parietal (with main regions in yellow) and cingulo-opercular (with main regions in black) networks of control (reproduced with permission from Dosenbach et al., 2008). Blue regions represent the cerebellar error network (Dosenbach et al., 2008).

The ERPs associated with the executive network of attention can be divided into conflict-related components and error-detection related components (Botvinick, Cohen, & Carter, 2004; Ullsperger & von Cramon, 2001). A great number of studies measuring conflict have reported modulations of an anterior fronto-central N2 component, reflecting template mismatch (i.e. expectancy violations) and response conflict in a variety of conflict situations, such as stimulus-stimulus or stimulus-response conflict, and inhibition of already planned responses (see Folstein and Van Petten, 2008, for a review). In addition, Luck and Hillyard (1994) proposed that the attentional selection N2pc component could also reflect attentional suppression of irrelevant or conflicting information interfering with target identification during visual search, which is thought to be mediated by the executive control network. On the other hand, an error-related negativity (ERN) component has been observed around the time of the emission of incorrect responses, also in fronto-central scalp sites (Yeung, Botvinick, & Cohen, 2004). This component has also been associated to error-correction, and it seems to require that the target is consciously processed, and the stimulus and response mismatch is detected (Woodman, 2010; Yeung et al., 2004). Both ERN and N2 are thought to reflect the operation of the same conflict detection system, by the activation of the ACC (Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; Yeung et al., 2004). In fact, the ACC seems to be activated prior to response during correct conflict trials, as reflected in the anterior N2, and immediately following error trials, as reflected in the ERN (V. Van Veen & Carter, 2002).

2.1.3. Neuropsychological Models of Attention

The study of attention in the discipline of Neuropsychology has also offered valuable insight into the understanding of the attentional functions and their neural bases. Neuropsychological models of attention also conceive this cognitive function as a selection mechanism, functionally complex, hierarchical, and involved in orchestrating other cognitive processes (Portellano, 2005). In neuropsychology, attention has been related to a variety of concepts, such as the speed of information processing, alertness or vigilance, sustained attention and executive attention. In this section, I will focus on Sohlberg and Mateer's model of attention, comparing this model with Posner and Petersen's Attention Networks model (S. E. Petersen & Posner, 2012).

Sohlberg and Mateer (1989; 1987) proposed an influential model which described different levels of attention based on clinical and experimental neuropsychology evidence. As a hierarchic model, each attentional level requires the correct functioning of the previous levels of attention. These levels are, from fewer to higher complexity: arousal, focal attention, sustained attention, selective attention, alternating attention, and divided attention. In this model, arousal would be equivalent to the general vigilant state, whereas focal attention would refer to the ability to attend to isolated sensory information. Sustained attention is the capacity to perform a task for a sustained period of time, and could refer to vigilance (in detection tasks) or focused attention (active maintenance of the information). On the other hand, selective attention corresponds to the inhibition of inappropriate stimuli or action schemas, whereas alternating attention permits the rapid and fluid change of attention among different tasks. Finally, divided attention is the capacity to carry out on more than one task simultaneously, distributing the attentional resources among them. This clinical proposal relies on the existence of dissociations between attentional functions in brain-damaged patients, which has led neuropsychologist to design specific tests to assess the different levels of attention in clinical settings. For example, sustained attention is assessed through continuous performance tests, which are usually low demanding and long-lasting (e.g. Auditory "A" Test). The evaluation of selective attention includes visual search tasks, in which patients have to find certain stimuli within visual scenes of diverse stimuli-complexity (e.g. Picture Completion test). Trail-type tasks (e.g. Trail Making Test or Color Trail Test), in which two different sets of stimuli are presented, are used to evaluate the alternating capacity of attention. On the other hand, Stroop-type tasks (e.g. 5 Digits Test), in which a dimension of the stimuli can interfere with the required response, provide an estimate of the ability to inhibit of both irrelevant dimensions of the stimuli and dominant responses. Finally, dual-tasks are used to evaluate the divided attention component (Lezak, 2012).

Interestingly, some levels of attention in Sohlberg and Mateer's model depend on the conjoint operation of more than one subsystem of the Posner and Petersen's Attention Networks model. Selective attention, for instance, would require the orienting network of attention in order to select relevant stimuli, but also would involve the executive network of attention, as it would inhibit both irrelevant stimuli and inappropriate dominant responses. In a similar manner, sustained attention could refer to both alertness and executive control networks, depending on task demands. On the other hand, low levels of attention in Sohlberg in Mateer's model would match the alertness network of attention in the Attention Networks model, as arousal and focal attention could correspond to tonic and phasic alertness, respectively; whereas higher levels of attention, such as alternating and divided attention, would match the executive control network.

2.2. Attention and conscious perception

The existence of a relationship between attention and conscious experience has been a recurrent claim even before Psychology was born as a discipline. William James (1890), for example, defined attention as “the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought”, pointing at the relationship between the current conceptions of two differentiated processes: attentional selection and conscious access (Dehaene & Changeux, 2011). Wilhelm Wundt (1912), by contrast, argued that attention and consciousness were different phenomena. However, he postulated that attention determined the degree of conscious access of a given stimulus, and that attended stimuli were perceived with clarity. As we stated above, Posner had related conscious experience to the executive control network of attention (Posner, 1994; Posner & Dehaene, 1994). Concretely, he claimed that one of the two main functions of executive attention was to monitor the processes taking place at a given moment. Therefore, this attentional system would have to be related to subjective experience, having access to both sensory and memory information (Posner & Dehaene, 1994). Milner and Goodale (1996), on the other hand, suggested that attention for object identification —as opposed to attention for action— is associated with consciousness.

During the last decades, a great research effort has been made to disentangle the role of attention mechanisms on visual conscious perception. Considering that our visual system is constantly exposed to large amounts of visual stimuli, and yet only a limited part of that information reaches consciousness, modulations of attention on conscious access have important implications in our understanding of the conditions eliciting conscious processing. In this section, current perspectives in the study of conscious perception are reviewed.

2.2.1. The study of consciousness: main aims, limitations, and empirical findings

As a complex high-level cognitive process, sometimes proposed to differentiate humans from the rest of non-human animals (see Roth, 2013), consciousness, its properties, and functions have always captured philosophers' and psychologists' interest. Conscious experience is a very familiar and conceptually simple experience, and yet, its empirical study remains challenging. In daily life situations, individuals acknowledge believing, making decisions, or acting upon a certain amount of information, corresponding to what we refer to as "being conscious". However, the definition of consciousness is not unitary, and many classifications can be made when it comes to types of consciousness. De Graaf and colleagues (De Graaf, Hsieh, & Sack, 2012) distinguish between self-consciousness (including self-recognition, agency, etc.), higher-order consciousness (i.e. reflexive thinking), state-consciousness (e.g. awake vs. asleep, healthy vs. comatose, etc.), and phenomenal consciousness (i.e. content-consciousness). In the present work we will only refer to phenomenal consciousness, that is, the subjective experience of a given content. One of the most important questions in the past decades regarding phenomenal consciousness has concerned its function, as it remains unclear what purpose raw conscious experiences serve (Tsuchiya, Wilke, Frässle, & Lamme, 2015). Some authors have proposed that consciousness allows for the integration of information from different brain systems, leading to high cognitive processes such as verbal report, evaluation, memory, planning, and intentional action (Baars, 1989; Dehaene & Changeux, 2011), whereas others claim that the ultimate adaptive function of consciousness is to make volitional actions possible (see for example Pierson and Trout, 2017). Another main challenge in neuroscience is to identify which mental representations and brain states are associated with phenomenal consciousness (Dehaene & Naccache, 2001; Searle, 1993), which has been called the "hard problem" of consciousness.

The study of consciousness differs from the study of other cognitive processes in one important aspect: conscious experience, the object of study, is not an objectively measurable response, but an introspective phenomenon. When conscious experience is assessed by subjective measures (i.e. self-report measures), a reasonable concern is that the subject's report could reflect other factors, such as decision making (Merikle, Smilek, & Eastwood, 2001). In order to overcome this problem, several studies have employed objective measures of awareness, for example, with forced-choice discrimination tasks, or with semantic priming paradigms. Studies using objective measures of conscious perception have demonstrated that a considerable amount of processing is possible without consciousness, from perceptual and motor levels of processing to semantic, emotional, and context-dependent levels of processing (Dehaene and Naccache, 2001; but see Peters and Lau, 2015).

In their theoretical framework for consciousness model, Dehaene and Naccache (2001) resumed the three major empirical observations that, in their opinion, any theory of consciousness should incorporate: 1) cognitive processing is not limited to conscious processing, that is, unconscious processing is possible, 2) attention is a prerequisite for consciousness, and 3) specific cognitive operations, such as information maintenance, novel combinations of operations, and deliberate behavior, require consciousness (Dehaene &

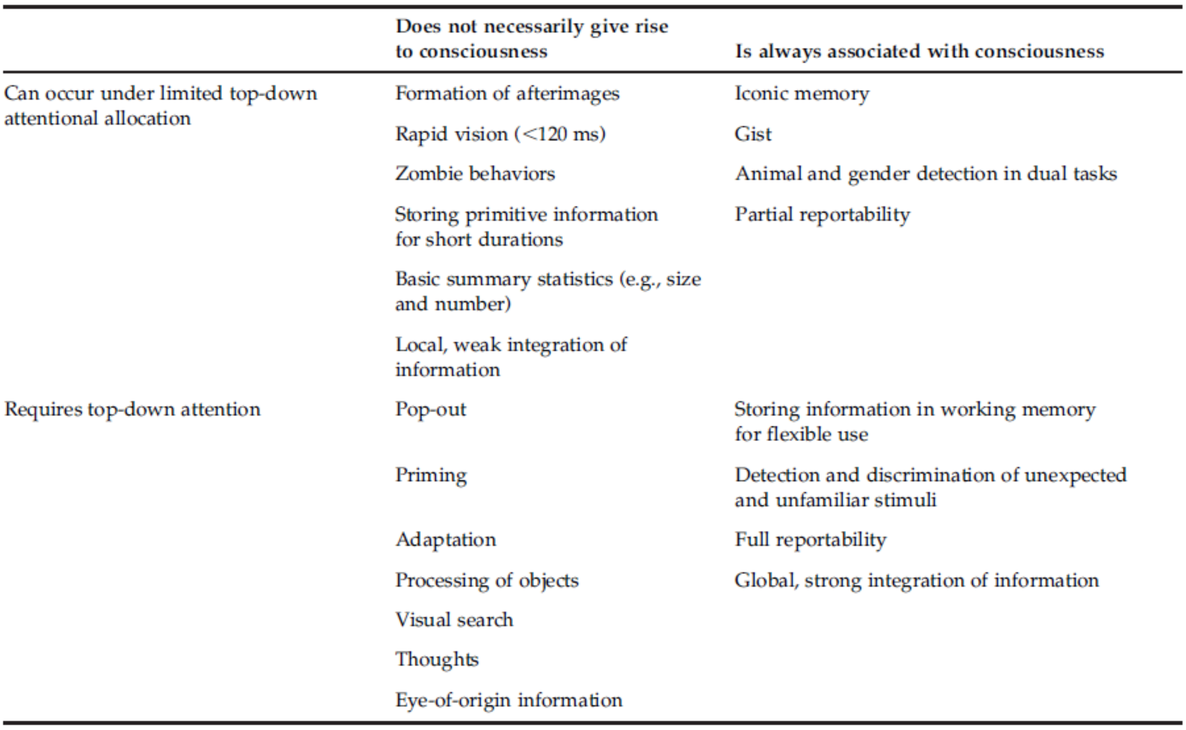
Naccache, 2001). As the interest of this thesis is to study the relation between attention and conscious perception, in the next paragraph we will go deeper into the second empirical observation.

Several experimental studies have found that non-attended information does not reach consciousness (Macdonald & Lavie, 2008; Mack & Rock, 1998; Raymond, Shapiro, & Arnell, 1992; Rensink, O'Regan, & Clark, 1997). For instance, Mack and Rock (1998) found that, when engaged in an attention-demanding task, participants failed to detect unattended salient changes in the features of visual stimuli, even when the stimuli were presented at the fovea (i.e. inattentional blindness). In a similar way, Macdonald and Lavie (2008) observed that high perceptual load in visual search impaired visual conscious perception of task-irrelevant stimuli presented at the periphery (i.e. load induced blindness). Attentional blink paradigms have demonstrated that when two masked targets are presented within approximately 500ms of each other, the second target often fails to gain conscious access when subjects are told to attend to the first target, but it can be consciously perceived when subjects are told to ignore the first target (Shapiro, Arnell, & Raymon, 1997). Finally, in visual change paradigms, detection of the changing object occurs easily when that object is given focused attention (for example, if it is verbally cued), but participants struggle to detect the same changing stimulus if attention has not been drawn to it, which is known as the change blindness phenomenon (Rensink, O'Regan, & Clark, 1997).

However, evidence on unconscious processing of attended information also exists (Kentridge, Heywood, & Weiskrantz, 1999; Naccache, Blandin, & Dehaene, 2002). It is known, for instance, that blindsight patients cannot consciously perceive visual stimuli presented in their blind fields, due to a lesion in the striate cortex. However, Kentridge and colleagues showed the case of a blindsight patient who could implement attention in the absence of consciousness. They demonstrated that peripheral cues could orient the patient's attention in his blind field without conscious perception of either the cue or the target (Kentridge, Heywood, & Weiskrantz, 1999). Another example is the priming effect (a benefit in the processing of stimuli congruent with a prime), which has been elicited for invisible (masked) words, but only when the subject was attending to the invisible prime-target pair (Naccache, Blandin, & Dehaene, 2002). Interestingly, attention here enhanced unconscious processing of the primes, because without attention, they failed to elicit priming. Therefore, although studies describing conscious perception when information is attended suggests attention as necessary for conscious perception, evidence on the unconscious processing of attended stimuli indicates that attention might not be sufficient for conscious perception (Chica & Bartolomeo, 2012; Posner, 1994).

In an attempt to disentangle which experimental conditions led to conscious perception of visual stimuli and which led to unconscious processing, Dehaene and colleagues (2006) proposed a taxonomy in which one could distinguish between conscious, preconscious (potentially conscious processing of strong bottom-up stimulation, but not accessible at the moment), and subliminal processing (unconscious processing elicited by weak bottom-up stimulation). Each one of these three levels of processing is proposed to be associated with distinct brain states, depending on the strength of bottom-up visual stimuli (weak or strong) and the deployment of top-down attention (absent vs. present). According to this taxonomy, conscious processing would result from the combination of both strong bottom-up stimulation and the operation of top-down attention, whereas strong bottom-up stimuli without top-down attention would result in preconscious processing. Alternatively, weak bottom-up stimulation would lead to subliminal processing, even if attended.

Nevertheless, other authors propose that attention is not always necessary for conscious perception to occur. Tsuchiya and Koch (2016), for example, presented a fourfold classification of percepts and behaviors depending on whether they require (or not) the operation of top-down attention, and whether they give rise (or not) to consciousness (see Figure 4). A significant difference between the two taxonomies is that Dehaene and colleagues' proposal did not contemplate conscious perception without the exertion of top-down attention, whereas Tsuchiya and Koch did consider this outcome (see the right upper panel in Figure 4). However, as the authors themselves specified, the examples from the upper row in Figure 4 are not the result of the complete absence of top-down attention processing, but rather of the limited availability of top-down attention. It is important to take this into account, as nowadays there is no objective psychophysical way to unambiguously determine a state of "complete absence of attention" (van Boxtel, Tsuchiya, & Koch, 2010). Moreover, the claim that when attention is focused in a given task or location no top-down attention resources can be allocated elsewhere implies the assumption that attention works as a lantern, and that the focus of attention cannot be divided. However, dual-task paradigms suggest that, although limited, top-down attention resources can be divided into more than one task and location (see Pashler, 1994, for a review on dual-task interference).



	Does not necessarily give rise to consciousness	Is always associated with consciousness
Can occur under limited top-down attentional allocation	Formation of afterimages	Iconic memory
	Rapid vision (<120 ms)	Gist
	Zombie behaviors	Animal and gender detection in dual tasks
	Storing primitive information for short durations	Partial reportability
	Basic summary statistics (e.g., size and number)	
	Local, weak integration of information	
Requires top-down attention	Pop-out	Storing information in working memory for flexible use
	Priming	Detection and discrimination of unexpected and unfamiliar stimuli
	Adaptation	Full reportability
	Processing of objects	Global, strong integration of information
	Visual search	
	Thoughts	
	Eye-of-origin information	

Figure 4: Fourfold classification of percepts and behaviors as a function of the allocation of top-down attention and the association with consciousness (reproduced with permission from Tsuchiya and Koch, 2016).

2.2.2. Theoretical frameworks of consciousness

The development of new experimental paradigms in cognitive psychology and brain imaging techniques, along with neuropsychological studies, has enabled a great body of research contributing to our current understanding of consciousness. As a consequence, in the past decades, some theoretical frameworks of consciousness have been proposed, taking this evidence into account (Crick & Koch, 2003; Dehaene & Naccache, 2001; Giulio Tononi, 2008).

One of these theoretical frameworks of consciousness is the Global Neuronal Workspace (GNW) framework (Dehaene & Naccache, 2001), which is based on Baars' global workspace theory of consciousness (Baars, 1989). This framework proposes that in unconscious processing, many modular cerebral networks are active in parallel, while conscious processing involves the top-down attentional amplification of the neural population representing the information and its mobilization into a brain-scale state of coherent and widespread activity. Although the GNW model posits that conscious experience requires a distributed brain activity rather than the activation of a fixed set of brain areas, it also proposes that workspace neurons (neurons providing long-distance and widespread connectivity) are particularly dense in the prefrontal and anterior cingulate cortices (Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001; Posner, 1994).

The integrated information theory (IIT) of consciousness (G Tononi, 2004; Giulio Tononi, 2008) posits that, at the fundamental level, consciousness results from the integration of information, and that its quality is given by the informational relationships generated by a complex of elements. Therefore, to generate consciousness, the system must be able to discriminate among a large repertoire of states (information), and should not be decomposable into a collection of causally independent parts (integration). Similar to the GNW model, the IIT claims that conscious processing requires functionally specialized networks, along with functional integration (i.e. many pathways for interaction between them).

On the other hand, Crick and Koch (2003) present a comprehensive framework of consciousness in terms of competing neural assemblies. According to these authors, consciousness depends on certain coalitions of neurons (competing neural assemblies) that rest on the properties of very elaborate neural networks. At any moment, the winning coalition is somewhat sustained, embodying the content we are conscious of. They propose that attention mechanisms can bias the competition among these nascent coalitions. Finally, they propose that the neural correlates of consciousness may be expressed by only a small set of neurons projecting from the back of the cortex to those parts of the front of the cortex that are not purely motor and that receive feedback from there.

2.2.3. The neural correlates of consciousness

Some authors have proposed that the main aim of cognitive neuroscience should be to identify which mental representations and brain states are associated with the subjective phenomenological experience of being conscious (Dehaene & Naccache, 2001; Searle, 1993), which is also known as the “hard problem” of consciousness (i.e. how does the brain create phenomenal consciousness?).

The majority of the abovementioned models of consciousness postulate that the visual neural correlates of consciousness (NCC) —the minimal neuronal mechanisms jointly sufficient for any visual conscious percept— involve the extra-striate visual cortex, having a reciprocal relationship which is mediated by long-range cortico-cortical feedforward and feedback projections (Baars, 2005; Crick & Koch, 2003; Dehaene, Sergent, & Changeux, 2003; G. Tononi & Edelman, 1998). The GNW posits that top-down attention amplifies the reverberation of the information, from occipito-temporal specialized brain regions to higher fronto-parietal areas, and back (Dehaene & Changeux, 2011) (see Figure 5). Similarly, Crick and Koch (1995) propose that attentional boost enables neurons in the ventral visual stream to establish a reciprocal relationship with neurons in the dorsolateral prefrontal cortex, leading to the reverberation of neural activity. These coalitions of neurons would be formed due to the projections of long-range axons of pyramidal neurons, possibly involving stages of the thalamus, such as the pulvinar (Crick & Koch, 1998), and the claustrum (Crick & Koch, 2005).

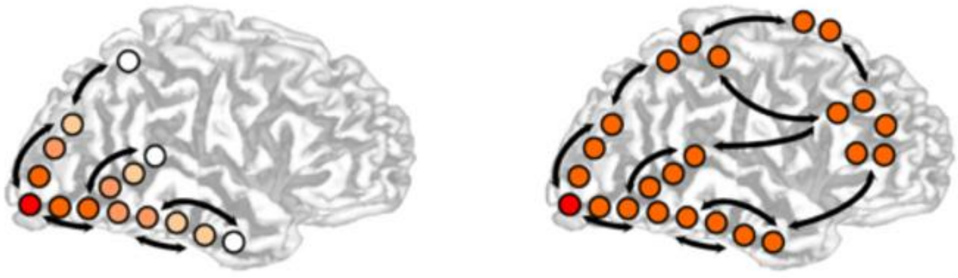


Figure 5. In the Global Neuronal Workspace model, unconscious processing (left) is associated with feedforward activity in sensory areas, whereas conscious processing (right) implies the reverberation of the information from sensory areas to higher fronto-parietal areas, and back (reproduced with permission from Dehaene and Changeux, 2011).

On the other hand, electrophysiological markers of visual conscious perception seem to depend on both stimulus (such as bottom-up strength) and cognitive variables (such as top-down expectations) (Aru, Bachmann, Singer, & Melloni, 2012). Several studies have shown a negative ERP deflection in posterior electrodes, peaking around 200ms from stimulus onset, only for the stimuli reaching conscious perception. This component is known as the visual awareness negativity (VAN), and has been observed in a large variety of paradigms studying conscious perception (Koivisto, Kainulainen, & Revonsuo, 2009; Wilenius-Emet, Revonsuo, & Ojanen, 2004). Usually, the VAN component is followed by a later positive amplitude enhancement (LP) to consciously perceived stimuli, peaking in parietal electrodes around 400ms, and overlapping with P3 component (Koivisto et al., 2009; Railo, Koivisto, & Revonsuo, 2011). In fact, the P3 potential has also been typically associated with conscious access (Dehaene and Changeux, 2011). However, a recent study showed no differences in this component when subjects already had a conscious working memory representation of the target stimulus (Melloni, Schwiedrzik, Muller, Rodriguez, & Singer, 2011). In addition, many studies have reported early markers of conscious perception as reflected by an enhanced amplitude of the P1 component. This modulation, however, may be reflecting fluctuations in attentional selection rather than conscious vs. unconscious processing (see Railo et al., 2011, for a review).

The study of the electrophysiological correlates of conscious perception reveals one of the major challenges in the study of the NCCs: disentangling the neural prerequisites and consequences of consciousness from the real correlates of phenomenal consciousness (Aru, Bachmann, Singer, & Melloni, 2012; De Graaf, Hsieh, & Sack, 2012). Pre-requisites of consciousness are factors that modify consciousness thresholds, such as the minimal level of arousal necessary to process information, stimulus expectation, adaptation, working memory, or the allocation of attention. Consequences of consciousness refer to the cascade of cognitive processes that follow conscious processing and that are directly enabled by it. One possible solution to this problem could lie in the employment of no-report studies. These studies first assess the neural activity corresponding to subjective and objective measures of awareness for each subject, and then infer the subjects' phenomenological experience from the recorded brain activity on each trial (Tsuchiya, Wilke, Frässle, & Lamme, 2015). A combination of both report paradigms and no-report paradigms could significantly move forward the study of the neural correlates of consciousness.

2.3. Confabulation after brain damage

2.3.1. Definition and classification of confabulations

Confabulations refer to the generation of false memories without intention to deceive. These false memories can guide confabulators' beliefs, intentions, and behavior, and tend to be accompanied by a great feeling of rightness, making confabulators resist to abandoning them when confronted with the truth (Gilboa et al., 2006; Moscovitch & Melo, 1997). As a consequence, confabulations can have a huge impact on daily living, and some confabulators require permanent supervision (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017). Although primarily described in Korsakoff syndrome, confabulations have also been observed after acquired brain injury, such as aneurysms in the anterior communicating artery (ACoA), hypoxia, stroke in the right or bilateral middle cerebral arteries, limbic encephalitis, head injury, and brain tumors (for example, see Nahum et al., 2012). Several studies have also pointed to the presence of confabulations in Alzheimer's disease and other dementias (La Corte, Serra, Attali, Boissé, & Dalla Barba, 2010; Nedjam, Dalla Barba, & Pillon, 2000). Some authors have reported confabulation associated to psychiatric illnesses such as schizophrenia (Cunningham et al., 1997; Garrison, Bond, Gibbard, Johnson, & Simons, 2017), although other authors propose that these are delusional memories, i.e. true memories giving rise to a deluded interpretation, or false memories arising in the context of a psychosis (Buchanan, 1991; Kopelman, 1997), instead of confabulation (Langdon & Turner, 2010).

Several taxonomies of confabulations have been proposed, based on diverse aspects of confabulations such as content, the way in which they arise, the domains in which they may be manifested, and the clinical syndromes in which they appear (Lorente-Rovira, Berrios, McKenna, Moro-Ipola, & Villagrán-Moreno, 2011). The usefulness and meaningfulness of these distinctions have been called into question (Dalla Barba, Cappelletti, Signorini, & Denes, 1997; M K Johnson, O'Connor, & Cantor, 1997; Metcalf, Langdon, & Coltheart, 2007), and some authors argue that confabulation should be regarded as a continuum, ranging from minor distortions to the more fantastical ones (Dalla Barba, 1993; Fischer, Alexander, D'Esposito, & Otto, 1995; Kapur & Coughlan, 1980). However, the classification of confabulations proposed by Schnider (2008) has reached reasonable consensus and it is widely used in the literature. Schnider distinguished between four forms of confabulation: 1) intrusions in memory tests (provoked confabulations, see Kopelman, 1987); 2) momentary confabulations or false verbal statements in situations inciting a patient to make comments; 3) fantastic confabulations, which have no basis in reality, are nonsensical, and illogical; and 4) behaviorally spontaneous confabulations, which guide confabulators behavior. In addition to these four types of mnestic confabulations, associated with past memories or future plans, confabulators can show non-mnestic confabulations, frequently known as delusional misidentifications (Schnider, 2008). These can include reduplicative paramnesia (mental duplication of places or people), Capgras syndrome (misidentification of people), Fregoli syndrome (hyperfamiliarity of unknown faces), and pseudohallucinations (misidentification of objects). Although mnestic and non-mnestic confabulations use to co-occur, they can be dissociated, which suggests that different neural basis and different cognitive mechanisms underlie them (Schnider, 2008).

2.3.2. What causes confabulations? Theories on the nature of the deficit

There is no consensus regarding the cognitive deficits that lie beneath the appearance of confabulations. Traditional theories on the nature of the deficit have been divided into theories of temporal context and monitoring theories. These theories also differ on the stage of processing in which the core deficit causing confabulations takes place.

2.3.2.1. Temporality theories

The reality-filtering hypothesis, proposed by Schnider and colleagues (Nahum, Ptak, Leemann, Lalive, & Schnider, 2010; Nahum, Ptak, Leemann, & Schnider, 2009; A. Schnider & Ptak, 1999; a Schnider, 2001; a Schnider, Ptak, von Däniken, & Remonda, 2000), posits that confabulating patients fail to suppress previously activated memory traces that are not related to the ongoing reality, exhibiting a failure of personal temporality. Coherent to this claim, spontaneous confabulations can usually be traced back to real events from the patient's past (a Schnider, von Däniken, & Gutbrod, 1996). According to this model, confabulations would arise as a consequence of temporal context confusion, due to a malfunction of early processes of extinction of irrelevant memories. Following Schnider and colleagues' hypothesis, confabulators guide their behavior based on memories and habits that do not pertain to the present or that are currently inappropriate, due to their incapacity to filter the relevant representations for the ongoing reality. The failure of this reality filtering mechanism, which is hypothesized to rely on the posterior medial orbitofrontal cortex (OFC), is therefore posited as responsible for spontaneous confabulations (A. Schnider, Nahum, & Ptak, 2017; a Schnider, 2001).

Dalla Barba and colleagues, by contrast, argue that confabulations involve a distortion of temporal consciousness that hinders the organization of episodes, knowledge, and information into patients' past, present, and future (Dalla Barba & Boissé, 2010; Dalla Barba & La Corte, 2013; La Corte, George, Pradat-Diehl, & Barba, 2011). Therefore, according to this theory, confabulators present alterations of a determined type of consciousness (temporal consciousness), which impede the correct temporalization of the object in memory (Dalla Barba, 2002). According to these authors, the problem will not concern extinction of irrelevant memory traces, but the individual's entire subjective temporality. They describe temporal consciousness as a specific form of consciousness (different from perception or imagination) that allows individuals to remember their personal past, to be oriented in their present world, and to predict their personal future. Furthermore, they argue that temporal consciousness is experimentally measurable and dissociable from impersonal temporality, that is, the capacity to answer questions about others' past, present, and future. Finally, they point to the hippocampus as the brain center of temporal consciousness, as bilateral damage to the hippocampus leads to amnesia and absence of temporal consciousness, whereas confabulations or distorted temporal consciousness arise after an injury to structures connected to the hippocampus (Dalla Barba & La Corte, 2013).

2.3.2.2. Monitoring theories

In accordance with the dual monitoring deficit proposed by Moscovitch, Gilboa, and colleagues (Gilboa, 2010; Gilboa et al., 2006; Gilboa, Alain, He, Stuss, & Moscovitch, 2009; Gilboa & Moscovitch, 2002; Moscovitch & Melo, 1997), confabulations can arise in one of two ways: 1) after a deficit in the mechanism monitoring the relevance of memory associations and the generated feeling of rightness, at early, preconscious stages of memory retrieval, or 2) in later monitoring processes, as a consequence of deficits in strategic retrieval or verification. Strategic retrieval refers to situations where recall is not elicited by the cue, and memories are recovered through a strategic search process, similar to problem-solving. This strategic search is guided towards local, proximal cues that can activate associative memory processes. Then, strategic processes monitor the recovered memory and evaluate whether it is consistent with the memory task goals and with previous knowledge, determining whether it is likely to be true or false. These authors argue that Schnider's temporal context confusion or Dalla Barba's distorted temporal consciousness cannot account for confabulations, because confabulations can also involve content confusion (i.e. a higher probability to confabulate if the stimuli are similar in physical form or semantic category) rather than temporal confusion, as well as semantic memory (a type of information in which specific temporal context is not a factor) (Gilboa et al., 2006).

On the other hand, Johnson and colleagues’ source monitoring framework (M K Johnson, Hayes, D’Esposito, & Raye, 2000; M K Johnson, O’Connor, & Cantor, 1997; Marcia K. Johnson, Hashtroudi, & Lindsay, 1993; Marcia K. Johnson & Raye, 1998) proposes that confabulations are due to the inability to locate the temporal and contextual sources of each recollection. Again, according to this model, poor source monitoring can occur either as a result of a defective information encoding (early processing in memory) or as a consequence of a limited retrieval monitoring (later stages of memory verification). The source monitoring framework posits that memories are bound with perceptual and reflective information that can cue each other later in retrieval. When memories are not rich in those features (due to distraction, focusing on other types of information, etc.), they are more likely to try to access additional information, and therefore to be biased by prior knowledge, stereotypes, and social or cultural factors (M K Johnson, Hayes, D'Esposito, & Raye, 2000). This can lead to imperfect encoding, producing errors in reactivation or retrieval, or difficulties for the evaluation of those memories and their distinction from other mental experiences. According to Johnson and colleagues (2000), damage to three frontal-subcortical brain circuits (involving the dorsolateral prefrontal cortex, the orbitofrontal cortex, and the anterior cingulate cortex, respectively) would lead to impairments in the abovementioned processes, producing confabulations in memory.

2.3.2.3. Recent evidence

Confabulations cannot be solely explained by a memory deficit because some amnesic patients do not confabulate (Dalla Barba & La Corte, 2013). The combined deficit model proposed that confabulations are caused by a dysfunction in memory and in executive processes (Fischer, Alexander, D'Esposito, & Otto, 1995; Stuss, Alexander, Lieberman, & Levine, 1978). Recent studies, however, have demonstrated that attention can modulate the presence of confabulations, as it is shown in divided attention tasks (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997) and visual search tasks (Ródenas et al., 2016). Ciaramelli and colleagues demonstrated that false recognition in confabulators is in part due to the processing of irrelevant information during retrieval. They compared confabulating patients' recognition in divided attention and full attention situations, and observed that, contrary to non-confabulating patients, confabulators showed lower false recognition during divided attention as compared to full attention conditions. In light of this evidence, the authors suggested that the core deficit in confabulations is an excessive processing of task-irrelevant information that inflates the ‘feeling of rightness’, leading to an unsuccessful verification by later monitoring processes (Ciaramelli, Ghetti, & Borsotti, 2009). Cunningham and colleagues administered various neuropsychological tests to non-confabulators, low-confabulators, and high-confabulators, and observed that high-confabulators were significantly slower in the Trail Making Test (Part B) than both low-confabulators and non-confabulators (Cunningham et al., 1997). Finally, Ródenas and colleagues presented a visual search task to both confabulating and non-confabulating patients, and found that confabulators made more errors than non-confabulators in both target trials (making more commissions when searching the target among distracters in trials where the target was present) and catch-trials (committing more false positives when the target was absent). In addition, they observed that confabulators’ errors increased when attentional load was manipulated, and when the distractors were physically similar to the target (Ródenas, Lupiáñez, Arnedo, & Triviño, 2016).

Taking into account all the evidence reviewed above, Triviño and colleagues developed a behavioral treatment to reduce confabulations (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017), tapping on those processes whose impairment is thought to be responsible for confabulations according to the main theories: selective attention during encoding, monitoring during retrieval, and memory control after retrieval. Although this study does not determine the mechanisms involved in confabulations, the authors found that after the treatment confabulating patients not only reduced their confabulations, but also tended to improve in selective attention and planning as measured with neuropsychological tests. The reduction of confabulations after neuropsychological treatment was also associated to an improvement of patients’ performance in the visual search task (Ródenas, Lupiáñez, Arnedo, & Triviño, 2016). However, memory scores —with the exception of intrusions in recall and false positives in recognition— remained the same when comparing pre and post-treatment scores. This suggests that confabulations may be associated to impaired attentional processes, such as selective attention or early conflict detection (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017).

2.3.3. Cognitive processes affected in confabulators

Confabulators usually show impairments on both memory processes and executive functions (Bajo et al., 2017; Ciaramelli et al., 2006; Ciaramelli and Ghetti, 2007; Lavie, 2005; Nahum et al., 2012, 2009; Turner et al., 2008, 2007). Moreover, confabulations are usually presented along with behavioral disorders, such as impulsivity and disinhibition (Stuss, Alexander, Lieberman & Levine, 1978), and anosognosia, the lack of awareness of the deficit (Fischer, Alexander, D'Esposito, & Otto, 1995).

2.3.3.1. Confabulators' neuropsychological profile

When facing memory tasks, confabulators fail to learn information that has been presented repeatedly and forget it quickly, showing few correct responses in free recall and recognition tests (Johnson et al., 2000). Moreover, confabulating patients' performance differs from amnesic patients' performance in the number of intrusions and false positives that they commit in free recall (more intensively in cued recall) and recognition tests, respectively (Gilboa et al., 2006). Interestingly, confabulations have also been observed in visual memory tests, such as in Rey's Complex Figure recall (Pelati et al., 2011; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017). Figure 6 shows an example of a patient's confabulation in the immediate recall of the Rey Osterrieth's Complex Figure.

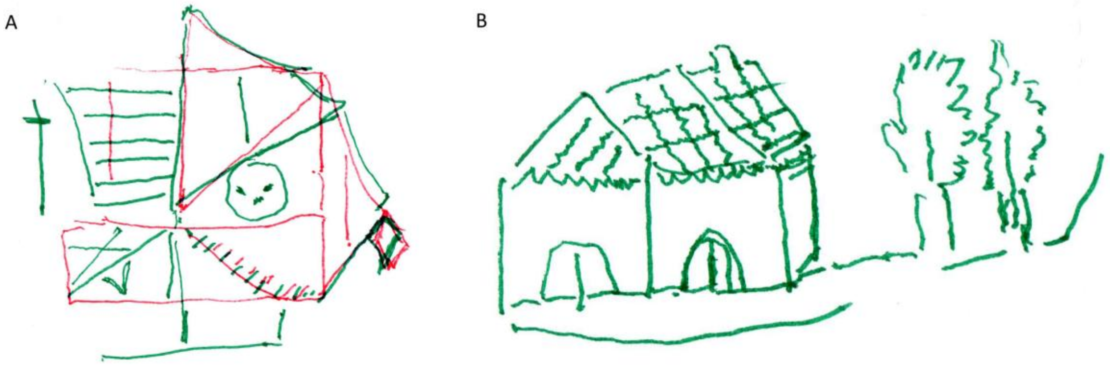


Figure 6. Copy and immediate recall (3 minutes after the copy) of the Rey Osterrieth's Complex Figure in a confabulating patient after acquired brain injury. Reproduced with permission of the patient and of her neuropsychologist, Dr. M. Triviño.

Concerning executive deficits, confabulating patients fail to inhibit verbal and motor responses. For example, Fotopoulou et al. (2007) found that confabulating patients committed more errors than amnesic patients when they had to inhibit a word triggered by a sentence in the Hayling test (e.g. "John nailed the nail with a..."). Confabulators also struggle to access the information, as demonstrated by a poor execution in fluency tests (a Schnider, von Däniken, & Gutbrod, 1996). Moreover, some confabulating patients demonstrate deficits in cognitive flexibility, as evidenced by their performance in the Wisconsin Card Sorting Test, with low scores in categorization and a high amount of perseverations (Johnson et al., 1997).

In addition to their mnestic and executive impairments, recent research suggests that confabulators tend to have difficulties in maintaining and changing their focus of attention, as demonstrated by their poor performance in divided attention and visual search tasks (Cunningham et al., 1997; Ródenas, Lupiáñez, Arnedo, & Triviño, 2016).

2.3.3.2. Confabulations and consciousness

As stated above, confabulations tend to co-occur with anosognosia, the impairment of awareness of one's own disabilities due to an altered brain functioning (DeLuca, 2009). Although the first psychiatric theories of confabulation recognized a conscious aspect to confabulation, by which confabulations were actively motivated, this idea is not well supported by empirical evidence. Nowadays, there is a wider consensus in regarding confabulation as an "unaware" process, as it was described in the neurological literature (DeLuca, 2009).

However, anosognosia is not a unitary construct, and confabulating patients can be unaware of their deficit in more than one way (DeLuca, 2009). For example, although confabulating patients can sometimes acknowledge that they have memory deficits, they usually are not conscious about the fact that they confabulate, neither are they aware of the situations in which they could probably confabulate, nor of their confabulations when actually engaged in such behavior (DeLuca, 2009). A rehabilitation strategy to reduce confabulations, as suggested by DeLuca (1992), could be to reduce anosognosia, that is, to improve patients' awareness of their production of confabulations. The rehabilitation programs that have been reported so far did not directly impact anosognosia, but rather indirectly addressed this aspect of confabulations, providing feedback of their errors (Dayus & van den Broek, 2000; Del Grosso Destreri et al., 2002; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017).

2.3.4. Neural bases of confabulations

Fotopoulou (2010) distinguishes between two forms of confabulations: "memory-related confabulation", which is our topic of interest and corresponds to the phenomenon that we have been describing along the text; and "awareness-related confabulation", which strictly refers to false statements regarding the patients' medical condition and abilities (e.g. anosognosia for hemiplegia). Although at the level of individual symptoms patients can show both types of confabulations, these two syndromes seem to rely on independent neural bases (Fotopoulou, 2010), and therefore we will describe them separately.

2.3.4.1. Memory-related confabulation

Confabulations can result from lesions located in more than 20 anterior and posterior brain areas (Dalla Barba & Boissé, 2010; Gilboa & Moscovitch, 2002). Many studies in confabulation after brain injury have described lesions to the frontal lobes, in particular to regions of the orbitofrontal cortex (Gilboa et al., 2006; A. Schnider, 2008) such as the ventromedial frontal cortex (Fotopoulou, 2010). In addition, damage to the anterior limbic system such as the genu of the internal capsule, the amygdala, the perirhinal cortex, and the medial hypothalamus also leads to the presence of confabulations (Schnider, 2003) (see Figure 7).

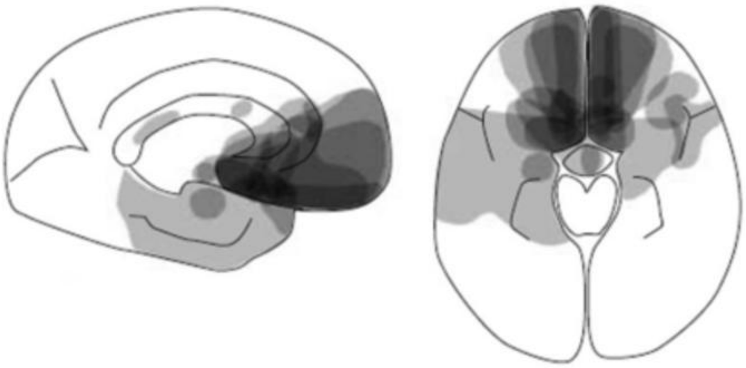


Figure 7. Lesion overlap of confabulating patients examined in different studies by Schnider and colleagues (reproduced with permission from Schnider, 2003). Lesions usually include the posterior medial orbitofrontal cortex and basal forebrain, but can also affect the amygdale, hippocampus, and perirhinal cortex.

Importantly, the anterior limbic system shares connections with the ventromedial prefrontal cortex and the posterior orbitofrontal cortex (see Figure 8), areas that also elicit confabulations when injured (Gilboa et al., 2006). In fact, frontal lobe areas maintain reciprocal connections with the medial temporal lobes both during encoding and remembering (Hirstein, 2005; Simons & Spiers, 2003).

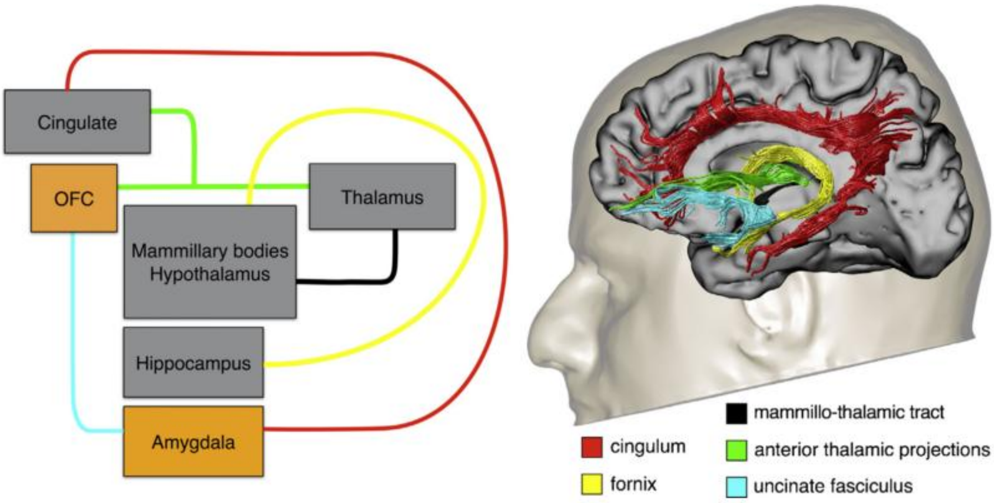


Figure 8. Representation of the limbic system and its main white matter pathways (reproduced with permission from Catani et al., 2013).

It has been proposed that the anterior limbic system and its connections to the prefrontal cortex are crucial for the appearance of confabulations (Gilboa & Moscovitch, 2002; A. Schnider, 2003; Turner, Cipolotti, Yousry, & Shallice, 2008). In this line, Dalla Barba and colleagues (Dalla Barba & Boissé, 2010; Dalla Barba & La Corte, 2013), have proposed that lesions to the hippocampus and the fornix lead to amnesia, whereas damage at any other point of both downstream and upstream pathways to the hippocampus produce confabulation (see Figure 9). From this observation, they argue that confabulation seems to occur when a preserved hippocampus receives distorted information from damaged areas located predominantly in the orbitofrontal cortex (Dalla Barba, Brazzarola, Marangoni, Barbera, & Zannoni, 2017).

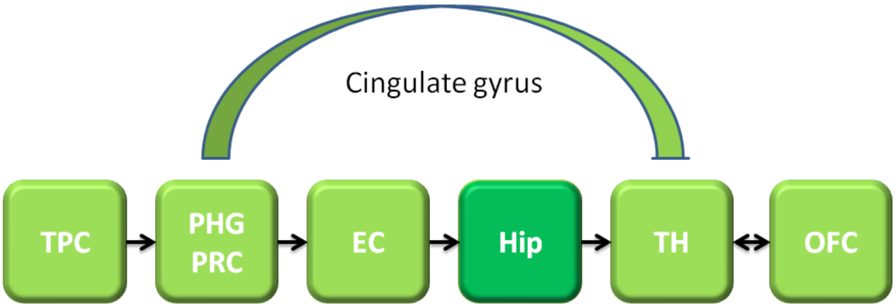


Figure 9. Schematic cognitive and neuroanatomical model of memory functioning (adapted with permission from Dalla Barba and La Corte, 2013). Confabulation would arise after damage to structures or pathways carrying information to an at least partially preserved hippocampus. Abbreviations: TPC, temporoparietal cortex; PHG, parahippocampal gyrus; PRC, perirhinal cortex; EC, entorhinal cortex; Hip, hippocampus; TH, thalamus; OFC, orbitofrontal cortex.

This evidence suggests that, as proposed for certain types of amnesia (Aupée et al., 2001; Nahum et al., 2014; Tucker et al., 1988; Warrington and Weiskrantz, 1982), confabulation could be considered as a disconnection syndrome. Moreover, a recent fMRI study found reduced functional connectivity between right inferolateral frontal cortex and right mediotemporal regions including the hippocampus, uncus, and amygdala in Alzheimer’s disease patients showing confabulating tendencies as compared with non-confabulating patients with Alzheimer’s disease (Venneri, Mitolo, & De Marco, 2017). They concluded that confabulatory tendencies appear in early Alzheimer’s disease as a result of the disconnection between crucial computational hubs in frontal and mediotemporal regions.

2.3.4.2. Awareness-related confabulation

Awareness-related confabulations have been described following perisylvian lesions to the right hemisphere, in relation to anosognosia for hemiplegia (unawareness of paralysis)

(Fotopoulou, 2010). Interestingly, anosognosic patients tend to produce confabulations when confronted with their deficits, stating that they can move their paralyzed limb, or confabulating about the reasons for which they cannot do it (Prigatano, 2009).

A recent review by Bartolomeo et al. (2017) demonstrated that damage to the right hemisphere can lead to space-related confabulations in relation to the patient's personal, peripersonal or extrapersonal space; and that, unlike left hemisphere lesions, these disorders are usually accompanied by confabulations. For instance, lesions in the right frontal lobe can also be associated with misidentifications of others' identity, as it happens in the Capgras and Fregoli syndromes (Bartolomeo, de Vito, & Seidel Malkinson, 2017). Moreover, extensive right fronto-temporo-parietal damage can cause somatoparaphrenia, i.e. confabulations regarding misidentification of the patients’ left limbs, which are no longer perceived as part of their body (Bartolomeo et al., 2017; Vallar & Ronchi, 2009). This evidence suggests that damage to the right hemisphere is crucial for the appearance of this form of confabulations.

2.4. Summary and research aims

As we claimed above, attention is a heterogeneous and complex system, whose alertness, orienting and executive control networks rely mostly on frontoparietal brain networks. The main aim of this doctoral thesis is to explore the role of frontal lobe structures in the control of attention. We conducted our research through two series of studies, each of them engaging different approaches to address the topic of interest. One line of research focused on addressing the relationship between the executive control aspect of attention, a mechanism that mostly relies on frontal brain networks, and the conscious perception of visual stimuli. We performed both a behavioral and a high-density EEG study to explore the modulations of conscious perception when participants had to respond to a Stroop task involving both congruent and incongruent trials. We also manipulated the proportion of congruent trials to understand the contributions of reactive and proactive forms of control in both studies. The EEG study was developed to understand the neural basis of the interactions between executive control and conscious perception. We expected to observe modulations of components related to frontal lobe functioning such as the N2 component.

A second line of research addressed the implication of the frontal lobes in attention and consciousness with a different approach. Instead of manipulating attention and measuring consciousness and the neural activity associated to both processes, we measured attention in a clinical population known to have deficits in consciousness and frontal brain damage: patients confabulating as a consequence of an acquired brain injury. This second line of research was therefore centered in the study of attention processes in the context of confabulations, a clinical syndrome that usually appears as a consequence of brain damage to specific frontal lobe regions such as the orbitofrontal cortex, and in which one of its defining characteristics is the lack of consciousness about their generation of false memories (anosognosia), that persists even when the patients are confronted with evidence.

As summarized in the introduction chapter, the confabulating syndrome is usually considered a memory disorder, and a lot of research has focused on the assessment of memory processes in confabulating patients. In addition, confabulating patients usually show impairments of executive functions and some attentional processes. Therefore, we hypothesized that attentional networks would be impaired in confabulating patients, especially executive attention processes, which are thought to be crucial for the control of behavior and memory monitoring during recollection. We used three attentional tasks to explore alerting, spatial orienting, and executive control in confabulating patients, a control group with brain lesion without confabulations, and a healthy control group. The alerting task used an auditory stimulus (on 50% of the trials) that was not predictive of the location of the target or the time interval in which it will be presented. The orienting task used a peripheral cue that attracted spatial attention either exogenously or endogenously. In different blocks of trials we manipulated the predictability of the cue. It was not predictive of the future location of the target in one of the blocks, and it was predictive of the future location of the target in the other block of trials. In both tasks, participants had to discriminate an X/O stimulus presented in the left or right visual field by pressing either a left or a right situated key. This allowed us to measure a Simon-type conflict, as confabulating patients tend to be faster and more accurate when the response location matched the stimulus location as compared to conditions in which the response location does not match the stimulus location. Finally, we presented participants with a Go-No Go task to measure executive control. In different blocks of trials we manipulated the proportion of Go stimuli hypothesizing that the condition with a high proportion of Go stimuli will require more executive control (response inhibition) when a No Go stimulus was presented.

The next sections describe our research questions, and how we addressed them through the mentioned series of studies.

2.4.1. Does executive control modulate visual conscious perception at the behavioral level?

Our first aim was to explore the relationship between executive control processes and conscious perception of visual stimuli in healthy populations. Previous research had demonstrated behavioral and neural interactions between phasic alertness and spatial orienting (two of the three networks of attention from Posner and Petersen's model) (S. E. Petersen & Posner, 2012; Posner & Petersen, 1990) and visual conscious perception (Botta et al., 2014; Chica et al., 2012b; Chica et al., 2016, 2010; Kusnir et al., 2011). However, the modulations of executive attention (the third attentional network in Posner and Petersen's model) over conscious perception remained largely unexplored. Therefore, we conducted a behavioral study to determine whether executive control, an attentional process mostly implemented in the frontal lobes (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004; C S Carter, Botvinick, & Cohen, 1999; S. E. Petersen & Posner, 2012; Yeung, Botvinick, & Cohen, 2004), could impact conscious perception in a similar way than spatial attention and alerting networks do. Specifically, we tested whether interference control elicited by the Stroop conflict could affect conscious processing of near-threshold stimuli. We hypothesized that conscious perception will be altered when incongruent as compared to congruent trials were presented concurrently with the near-threshold target detection task. Following the dual mechanisms of control framework (Braver, 2012), this modulation should be greater in conditions of low interference expectancy as compared to conditions of high interference expectancy, due to the recruitment of reactive control.

2.4.2. Is the relationship between executive control and conscious perception supported by frontal mechanisms?

Our second specific aim was to prove whether this relationship between executive control and conscious perception relied on frontal lobe mechanisms. In order to explore this interaction at the neural level, we conducted an adaptation of the abovementioned behavioral experiment with high-density electroencephalography. We analyzed the amplitude of the conflict-evoked potential N2, associated to the activation of the anterior cingulate cortex, as a function of interference control and conscious perception. In addition, we conducted source localization analyses to confirm that the N2 component was originated in the anterior cingulate cortex. We hypothesized an interaction between interference control and conscious perception, expecting a larger N2 component for incongruent trials in which the near-threshold target was consciously perceived as compared to incongruent trials in which the near-threshold target was not consciously perceived. This effect was expected to be larger in the high proportion congruent session. Moreover, this N2 component should be source-located in the anterior cingulate cortex.

2.4.3. Do frontal attention networks preserve their functionality and integrity in the confabulation syndrome after acquired brain injury?

The third aim of this doctoral thesis was to explore attention mechanisms in the context of confabulations after acquired brain injury. Confabulations are thought to arise due to a dysfunction in memory or in monitoring processes. However, some studies have demonstrated that attention can modulate the presence of confabulations in divided attention tasks (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997) and visual search tasks (Ródenas, Lupiáñez, Arnedo, & Triviño, 2016). To deeper investigate the possibility that attention deficits significantly contribute to the presence of confabulations after acquired brain injury, we experimentally assessed the function and integrity of the three attention networks on a sample of confabulating patients, and compared their behavioral performance with a sample of matched non-confabulating patients, and a group of healthy controls. We expected to observe behavioral deficits in executive attention (both in response inhibition measured with the Go-No Go task and in the Simon effect) in the confabulating patients group as compared with the two control groups. Alerting and spatial orienting were expected to be relatively preserved in confabulating patients. Patients' brain lesions were explored by localizing their brain damage on grey matter, combined with MRI-based diffusion-weighted imaging (DWI) tractography to investigate long-range white-matter pathways. We concentrated in exploring the correlations between behavioral indexes in the three attentional tasks (alerting, orienting, and executive control) and the integrity of the superior longitudinal fascicule (SLF), a white matter track connecting the frontal and parietal lobes. The SLF is organized along three longitudinal fiber tracts separated into a dorsal branch (SLF I), a middle branch (SLF II), and a ventral branch (SLF III) (Thiebaut de Schotten et al., 2011). Projections of the SLF I to the cortex are symmetrically distributed between the left and right hemispheres, and it appears that they overlap with the dorsal network of attention (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Thiebaut de Schotten et al., 2011). The SLF III, which overlaps with the ventral attention network, is lateralized to the right hemisphere. Finally, the SLF II is also right lateralized, and it is thought to manage direct communication between ventral and dorsal attentional networks, as it overlaps with parietal regions of the ventral network of attention and prefrontal regions of the dorsal network of attention (Thiebaut de Schotten et al., 2011). The SLF has been largely implicated in the spatial orienting of attention, as its disconnection on the right hemisphere is related to spatial attentional deficits in spatial neglect. Recent research has also observed a correlation between the integrity of the left ventral branch of the SLF with alertness in healthy controls (Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2017). Less is known about the implication of the SLF in executive attention, although we could expect a correlation between executive attention and the dorsal branch of the SLF (the so-called SLF I), which is related to top-down attentional control.

The described studies are presented in different chapters along the manuscript (chapters II, III and IV). The first study has been published in a Q1 journal (Frontiers in Psychology), whereas the second is under review in another Q1 journal. The third study is currently in preparation for its submission for publication. The following chapters are structured as scientific manuscripts, each containing an introduction, methods, results, and discussion section.

Chapter 3: Behavioral Interactions between Executive Attention and Conscious Perception

The content of this chapter has been published as Colás, I., Triviño, M., Chica, A.B., 2017. Interference Control Modulations Over Conscious Perception. Front. Psychol. 8, 1–12. doi:10.3389/fpsyg.2017.00712

3.1. Introduction

The human brain is a complex system capable of processing, integrating, and acting upon an incredible amount of information. In everyday life, we perceive multiple stimuli at the same time, even if we might not be aware of all of them, that is, if we cannot report their perception. In fact, only a limited portion of the information we process becomes part of our conscious experience (see Tononi, 2008 for a review). But what exactly makes that information reportable? Attention has been postulated to act as that gateway for consciousness, enhancing sensory properties of the stimuli to access conscious perception. Numerous experimental studies in brain-damaged patients (Pöppel, Held, & Frost, 1973) and in the healthy population (Bar & Biederman, 1998) have demonstrated that both attended and unattended information can be processed to a certain extent. However, according to the gateway hypothesis (Posner, 1994, 2012), consciousness emerges after the attentional system has filtered out information from our crowded environment (for a review, see Dehaene and Naccache, 2001). This hypothesis considers attentional selection as a necessary although maybe not sufficient condition for consciousness (Chica & Bartolomeo, 2012).

Attention is a complex and heterogeneous system (S. E. Petersen & Posner, 2012; Posner, 1975; Posner & Petersen, 1990). In order to better understand how attention modulates consciousness, it is important to analyze the impact that different attention systems can exert on conscious processing. Following Posner and Petersen's model (S. E. Petersen & Posner, 2012; Posner & Petersen, 1990), attention can be dissected into alerting, orienting, and executive control networks. Previous literature has already explored alerting and orienting contributions to conscious perception (Botta, Lupiáñez, & Chica, 2014; Chica et al., 2011; Chica, Bayle, Botta, Bartolomeo, & Paz-Alonso, 2016; Chica, Lasaponara, Lupiáñez, Doricchi, & Bartolomeo, 2010; Chica & Bartolomeo, 2012; Chica, Botta, Lupiáñez, &

Bartolomeo, 2012; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; Valentin Wyart, Dehaene, & Tallon-Baudry, 2011; Valentin Wyart & Tallon-Baudry, 2008). For example, Kusnir and colleagues (2011) found that an auditory cue eliciting phasic alerting improved participants' ability to discriminate a near-threshold stimulus, especially when targets were temporally unpredictable. Concerning spatial attention, exogenous attention modulates conscious access (Chica et al., 2011, 2010), producing larger (and more consistent) effects than endogenous attention does (Chica, Botta, et al., 2012). In order to broadly complete the theoretical framework on the relation between attention and conscious perception, modulations of the anterior network of executive control (the third attention network in Posner and Petersen's model) over consciousness must also be explored.

The executive control network (Posner & Raichle, 1994) refers to a system involved in the voluntary control of processing in novel or complex situations. According to Norman and Shallice's model (1986), the executive control system is activated whenever an individual's acting schema fails to sort out a particular situation. This could happen when the situation is new, complex or dangerous, requires planning or decision making, implies the inhibition of an automatic or competing responses, or involves the detection or correction of an error. Although the term executive function has a much broader meaning in psychology (Diamond, 2013; S. E. Petersen & Posner, 2012), executive control could be equivalent to its interference component, which includes inhibitory control and interference control. Three core aspects of executive functions can be differentiated: the abovementioned interference control, working memory, and cognitive flexibility or set shifting (Diamond, 2013; Lehto, Juujärvi, Kooistra, & Pulkkinen, 2003; Miyake et al., 2000). Interference control enables us to selectively attend, focusing on some stimuli or features and suppressing attention to other stimuli.

Previous studies exploring the relation between executive processes and conscious perception have mainly focused on working memory, manipulating its load. High working memory load affects conscious perception, reducing visual processing of attended stimuli, and inducing inattentional blindness (Fougnie & Marois, 2007; Scalf, Dux, & Marois, 2011). Active working memory load also influences the attentional blink magnitude (Akyürek, Hommel, & Jolicoeur, 2007), and operation span correlates with the size of the blink (Colzato, Spapé, Pannebakker, & Hommel, 2007). Moreover, working memory load has been demonstrated to increase the threshold of subjective visibility, modulating the impact of a prime stimulus on the response to the target (De Loof, Verguts, Fias, & Van Opstal, 2013). Some studies have distinguished between working memory components (executive and visuo-spatial working memory), which differently interact with conscious detection (De Loof, Poppe, Cleeremans, Gevers, & Van Opstal, 2015). Mental load has also been demonstrated to affect conscious perception. For example, performing an arithmetic cognitive task along with a visual search task produces a decrease of correct responses and an increase of false alarms (Pérez-Moreno, Conchillo, & Recarte, 2011). The impairment in visual detection is greater as mental load increases (see also Recarte et al., 2008).

Nonetheless, the above-cited experiments focus either on mental load or on the executive process of working memory, while according to Posner and Petersen’s model of attention (S. E. Petersen & Posner, 2012; Posner & Petersen, 1990), the anterior executive network would be more related to interference control. In the present work, we explored whether interference control (a key mechanism of executive attention) would modulate conscious perception, as working memory does.

According to the dual mechanisms of control framework (Braver, 2012), interference control operates via 1) reactive control, which relies upon detection of interference to reactivate task goals; and 2) proactive control, involving sustained active maintenance of task goals. Reactive control suppresses the activation of task-irrelevant information in an online, trial-by-trial basis; whereas proactive control prepares the system, priming task-relevant processing pathways prior to stimulus-onset (De Pisapia & Braver, 2006). Reactive or proactive control mechanisms can be implemented depending on task characteristics. For example, in tasks with high proportion of congruent stimuli (e.g. 75% congruent trials and 25% incongruent trials), participants' expectancy for interference is low and therefore the most effective control strategy will be to reactivate control mechanisms when an incongruent stimulus appears. In contrast, low proportion congruent tasks (e.g. 25% congruent trials and 75% incongruent trials) induce a high expectancy for interference, making proactive control mechanisms more likely to be recruited (Braver, 2012; De Pisapia & Braver, 2006). Overall, the proactive strategy of control is thought to be more resource consuming. However, on a trial-by-trial basis, incongruent trials will elicit more interference under the reactive control mode than under the proactive control mode, due to the necessity of retrieving inactive goal representations (Braver, 2012; Braver, Reynolds, Donaldson, & Louis, 2003).

In the present research, we explored for the first time in the literature the interactions between interference control and conscious perception. We asked participants to perform a Stroop task along with a conscious detection task, in which participants had to mark the location of a near-threshold target. We analyzed perceptual sensitivity and response criterion to detect the near-threshold stimulus. In order to test the impact of reactive control on conscious perception, we made the proportion of congruent trials larger than the proportion of incongruent trials (75%-25%, respectively, Experiment 1). As a consequence, participants were more likely to recruit reactive control mechanisms when an incongruent stimulus appeared, due to the low expectancy of interference. Our hypothesis was that when facing an incongruent trial in a context of high proportion of congruent trials, the cost of transiently reactivating goal representations would impact conscious perception on that trial (Braver, 2012; Braver et al., 2003). We conducted another experiment (Experiment 2), in which the proportion of incongruent trials was larger than the proportion of congruent trials (75%-25%, respectively). As the implementation of proactive control is thought to involve a sustained maintenance of task-goals along the task, we did not expect any effects of this control mechanism in conscious perception.

Finally, we manipulated timing of control, by presenting the Stroop and conscious detection tasks either in a concurrent (dual task) or sequential procedure. This arrangement allowed us to explore whether interference control would affect conscious perception when presenting the near-threshold stimulus simultaneously with the conflict task or after conflict resolution. Previous evidence suggests that dual tasks involve attentional selection (Sigman & Dehaene, 2008; Tombu et al., 2011) engaging frontal areas common to the executive attention network (S. E. Petersen & Posner, 2012). One can expect then that dual tasks should reduce the availability of the executive attention system. Following this idea, we hypothesized that the interference effect would be greater in the concurrent or dual-task procedure, as compared to the sequential procedure.

According to the gateway hypothesis (Posner, 1994, 2012), which considers attention as an important pre-requisite of conscious perception, we expected to observe modulations of perceptual sensitivity and/or response criterion for incongruent trials relative to congruent trials. Following the dual mechanisms of control framework (Braver, 2012), this modulation should be greater in conditions of low interference expectancy (Experiment 1) as compared to conditions of high interference expectancy (Experiment 2), due to the recruitment of reactive control. The effect was expected to be larger under dual-task conditions, i.e. for the concurrent as compared to the sequential task (Sigman & Dehaene, 2008; Tombu et al., 2011). Finally, since detecting and correcting errors is also considered to activate the executive system (Norman & Shallice, 1986), we explored perceptual sensitivity and response bias after Stroop hits and errors, hypothesizing that error commission will impair conscious perception.

3.2. Experiment 1

3.2.1. Participants

Twenty-three healthy participants from the University of Granada took part in the experiment (3 males, mean age of 21.84 years, SD of 4.03). Data from 22 participants were included in the analyses, as one participant did not finish the experiment. Participants reported to have normal or corrected-to-normal visual acuity, normal color discrimination, no known neurological disorders, and spoke Spanish as their first language. The experiments were conducted in accordance with the ethical guidelines of the Department of Experimental Psychology, University of Granada. All subjects gave written informed consent in compliance with the ethical standards of the 1964 Declaration of Helsinki.

3.2.2. Apparatus and stimuli

E-prime software was used to control the presentation of stimuli, timing operations, and behavioral data collection (W Schneider, Eschman, & Zuccolotto, 2002). Experiments were conducted using a 24” screen Intel Computer running at 60Hz. Participants sat at approximately 57 cm from the monitor. Two black markers and a centered fixation point (a black plus sign, 0.5° × 0.5°) were displayed at the beginning of the trial, on a grey color background (49 cd/m^2). Each marker consisted of a black square outline (7.5° width × 6° height), placed 10° to either the left or the right side of the fixation point. Spanish words for blue (*azul*, 2.5° × 1°), green (*verde*, 3° × 1°), and yellow (*amarillo*, 4.5° × 1°) colors were presented 1° above fixation. Words were presented either in blue, green, or yellow ink, and could make a given trial either congruent (when word meaning and ink color matched) or incongruent (when word meaning and ink color differed). 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 0.3°), with a maximum and minimum Michelson within-stimulus contrast of 0.92 and 0.02, respectively.

3.2.3. Procedure

Participants were required to perform two consecutive tasks. First, they had to discriminate the word's ink color as fast and accurately as possible. Participants responded with their right hand, pressing a keyboard key for each given color (the color-key mapping was counterbalanced across participants, keys "b", "n", "m"). In this experiment, stimuli were congruent (the word meaning and ink color matched) on 75% of the trials, and incongruent (the word meaning and ink color did not match) on 25% of the trials. Then, participants performed a Gabor detection task, reporting if they had perceived its appearance. On this task, participants were asked to respond accurately, with no time pressure. They were asked to respond only when they were confident about their perception. The response was given by choosing one of two arrow-like stimuli (>>> or <<<), pointing to the two possible locations of the target: right and left sides of the screen (see Figure 10). The arrows were presented one above the other, with their position randomized in each trial. Participants were required to indicate the location of the Gabor with their left hand, pressing an upper keyboard key ("d") corresponding to the upper arrow, or a lower key ("c") corresponding to the bottom arrow.

This response procedure was employed in order to minimize response preparation and anticipations (Chica et al., 2011). Participants were asked to press the space bar whenever they had not perceived the Gabor stimulus.

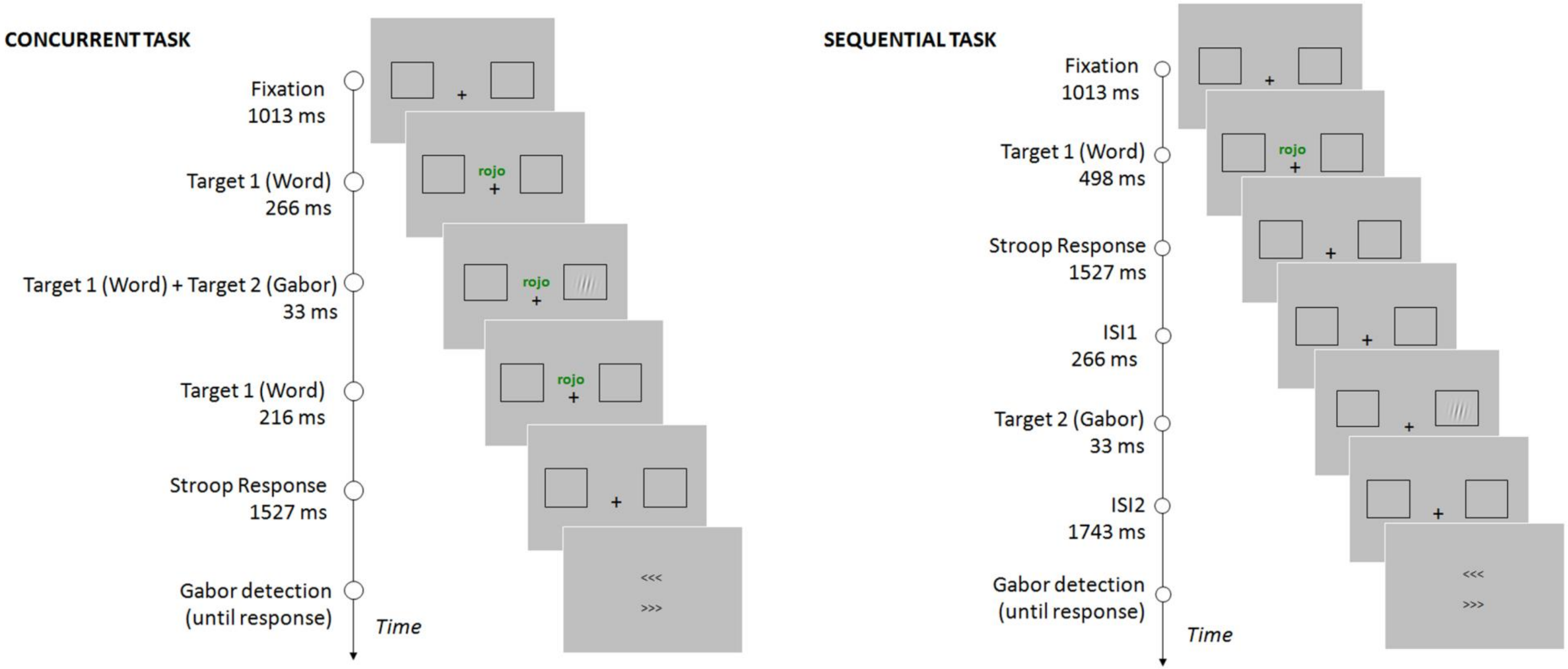


Figure 10. Timing and sequence of the stimuli on a given trial for the concurrent task (left) and the sequential task (right). In the concurrent task, the Gabor was presented while the word (Stroop stimulus) was still on the screen. Participants had to report the color of the ink in which the word was written, and then report the location of the Gabor using the arrows. In the sequential task, participants first responded to the word (Stroop stimulus), and the Gabor was presented after the response to the Stroop task was completed. The location of the Gabor was reported using the arrows.

Before the experimental trials, Gabor contrast was calibrated for each participant, in the absence of the Stroop stimulus. During titration, participants had to detect the Gabor and select its location. Titration began with a supra-threshold stimulus (Michelson contrast= 0.184), which contrast was manipulated depending on the mean percentage of seen targets every 16 trials. If the participant reported 63% or more targets during the last block of trials, Gabors at the immediately following lower contrast level (Michelson contrast minus 0.009) were used during the next block of trials; besides, if the percentage of seen targets was equal or lower than 38% during the last block of trials, the next block of trials presented Gabors at the immediately following higher contrast level (Michelson contrast plus 0.009). The titration procedure stopped when target contrast yielded a percentage of seen targets >38% and <63% for two consecutive blocks of 16 trials.

The experiment was conducted in two separate sessions, each containing titration, practice, and experimental trials. One of the sessions consisted of a concurrent task, while the other consisted of a sequential task (the order of the sessions was counterbalanced across participants). The difference between tasks was the timing of presentation of the stimuli (see Figure 10). The experiment consisted of a total of 720 experimental trials divided in two sessions (concurrent and sequential task). Within each session, 270 of the trials were congruent and 90 incongruent. The Gabor was presented in 80% of the trials and absent in 20% of the trials (catch trials). Each session started with 15 practice trials.

3.2.4. Results and Discussion

We firstly analyzed mean accuracy and reaction times (RTs) to respond to the Stroop task (see Table 1). In this experiment, 0.01% of the trials were considered anticipations (RTs faster than 150 ms) and eliminated from the RT analysis. Mean RT and accuracy data were submitted to two independent analyses of variance (ANOVA), with the within participants factors of congruency (congruent and incongruent trials) and task (concurrent and sequential).

Table 1. Mean RT and accuracy data for the Stroop task (with standard deviations in parentheses) for congruent and incongruent trials in Experiment 1 (high proportion congruent) and Experiment 2 (low proportion congruent).

			Mean RT, in ms	Mean proportion of correct responses
Experiment 1	Concurrent task	Congruent	682 (154)	.96 (.05)
		Incongruent	848 (205)	.88 (.06)
	Sequential task	Congruent	611 (149)	.94 (.06)
		Incongruent	789 (259)	.86 (.08)
Experiment 2	Concurrent task	Congruent	775 (211)	.93 (.06)
		Incongruent	821 (209)	.90 (.08)
	Sequential task	Congruent	663 (108)	.94 (.06)
		Incongruent	706 (110)	.91 (.08)

Then, we analyzed responses to the Gabor detection task to explore participants' conscious perception of the Gabor and its modulation by executive attention (congruent and incongruent trials). We analyzed participants' responses by using the signal detection theory, which provides a measure of perceptual sensitivity (d') and response criterion (c). Those indexes were calculated by computing *hits* or correct detections (when participants accurately determined the location of a presented Gabor), *misses* or trials in which the Gabor was presented but participants did not consciously reported it, *false alarms* (when participants consciously reported Gabors that were not presented), and *correct rejections* or trials in which the target was not presented and participants reported not having seen it. Trials in which participants incorrectly reported the location of a present Gabor were considered errors and removed from the analyses (1.64% of presented Gabors). Trials in which participants committed an error in the Stroop task were also excluded from the present data analyses (7.17% of the remaining trials). After eliminating Gabor detection errors and Stroop trial errors, a mean of 654 trials (SD=30) per participant were included in the analyses from Experiment 1.

Perceptual sensitivity (d’) and response criterion (c) were calculated with the following equations: $\mathrm{d'} = \mathrm{z(H)} - \mathrm{z(FA)}$; $\mathrm{c} = -0.5 * (\mathrm{z(H)} + \mathrm{z(FA)})$. H represents the hit rate, FA represents the false alarm rate, and z corresponds to z-scores, which were calculated using the inverse cumulative distribution function in Microsoft Excel 2011 (NORMSINV). Zero false alarm rates were corrected using the equation proposed by Snodgrass and Corwin (1988): $\mathrm{FA} = (\mathrm{FA} + 0.5)/(\mathrm{FA} + \mathrm{CR} + 1)$. For d’, larger values indicate an increased perceptual sensitivity (more hits and/or less false alarms). Concerning the response criterion index, smaller c values indicate a more liberal response criterion (more hits and/or more false alarms), while larger c values imply a more conservative criterion (less hits and/or less false alarms). Table 2 shows the mean proportion of hits and false alarms for each Stroop condition, task, and experiment.

Table 2. Mean proportion of hits and FA (with standard deviations in parentheses) for congruent and incongruent trials in Experiment 1 (high proportion congruent) and Experiment 2 (low proportion congruent), and for Stroop hits and Stroop errors in both experiments.

			Mean proportion of hits	Mean proportion of FA
Hits and FAs as a function of task and congruency				
Experiment 1	Concurrent task	Congruent trial	.60 (.16)	.06 (.07)
		Incongruent trial	.53 (.19)	.06 (.10)
	Sequential task	Congruent trial	.50 (.16)	.07 (.08)
		Incongruent trial	.51 (.19)	.07 (.11)
Experiment 2	Concurrent task	Congruent trial	.47 (.19)	.08 (.12)
		Incongruent trial	.46 (.16)	.06 (.08)
	Sequential task	Congruent trial	.41 (.18)	.06 (.12)
		Incongruent trial	.39 (.17)	.04 (.07)
Hits and FAs as a function of task and Stroop accuracy				
Experiment 1	Concurrent task	Stroop hit	.55 (.13)	.06 (.07)
		Stroop error	.42 (.20)	.08 (.23)
	Sequential task	Stroop hit	.54 (.16)	.07 (.09)
		Stroop error	.48 (.21)	.05 (.10)
Experiment 2	Concurrent task	Stroop hit	.47 (.17)	.06 (.08)
		Stroop error	.44 (.18)	.06 (.12)
	Sequential task	Stroop hit	.41 (.17)	.05 (.08)
		Stroop error	.25 (.20)	.08 (.21)

Mean d′ and c indexes were submitted to two repeated measures ANOVA with the within participants factors of congruency and task.

Finally, we analyzed mean d’ and c indexes to detect the Gabor as a function of Stroop accuracy. This analysis was meant to understand whether error commission could alter conscious perception of subsequently presented near-threshold stimuli. We performed two independent ANOVAs for mean d’ and c, with the within participants factors of Stroop response accuracy (Stroop hits and Stroop errors) and task (concurrent and sequential).

For each analysis, participants with mean scores above or below 3 standard deviations (SD) of their group mean were considered outliers and excluded from the analysis. For all analyses, post-hoc Fisher tests were used to further explore the interactions.

3.2.4.1. Stroop task

After checking for outliers, data from one participant were not included in the Stroop task accuracy analysis. No participants were excluded from the Stroop RT analysis.

When responding to the Stroop task, the expected congruency effect was observed: accuracy was higher for congruent than for incongruent Stroop trials, $F(1, 20) = 44.73$, $p < .001$, $\eta_p^2 = .69$, and RTs were shorter for congruent than for incongruent trials, $F(1, 21) = 66.16$, $p < .001$, $\eta_p^2 = .76$. None of the other main effects of interactions reached statistical significance (all *p*s > .14).

3.2.4.2. Gabor detection for congruent and incongruent Stroop trials

After checking for outliers, no participants were excluded from the mean d’ analysis. Data from one participant were not included in the mean c analysis.

The analysis of the mean d’ index did not show any significant main effect or interaction (all *p*s > .13), indicating that perceptual sensitivity was not modulated by the factors congruency or task (see Figure 11). For the c index, a main effect of congruency was found, $F(1, 20) = 8.61$, $p = .008$, $\eta_p^2 = .30$, with a more conservative response criterion to detect the Gabor for incongruent than congruent trials. Congruency did not interact with task, $F(1, 20) = 2.11$, $p = .16$, $\eta_p^2 = .10$, although post-hoc Fisher analyses revealed that the effect was statistically reliable for the concurrent task (*p* = . 012), and not for the sequential one (*p* = . 49) (see Figure 11). These results indicate that interference control elicited by the Stroop task modulates decisional stages of conscious processing, making participants' response criterion more conservative for incongruent than congruent trials.

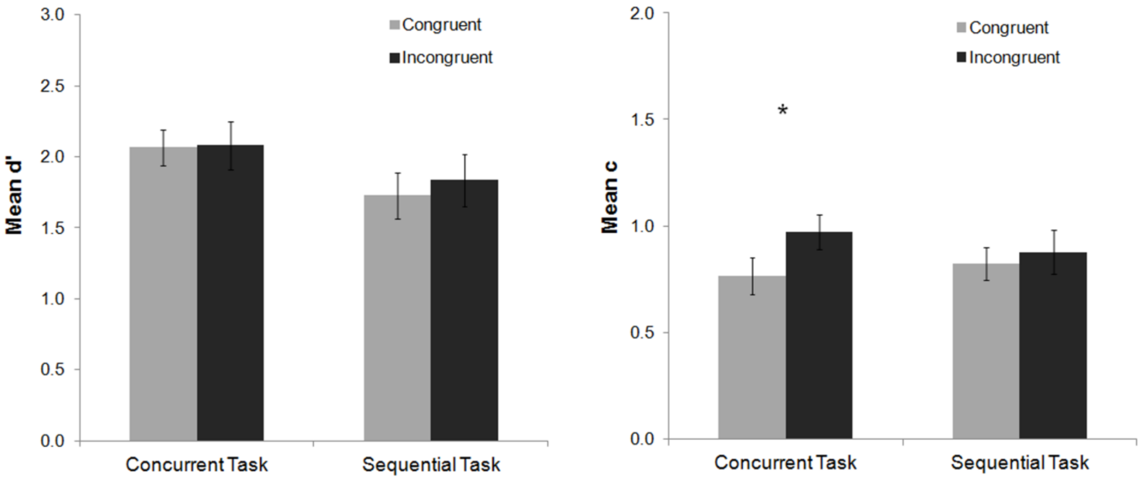


Figure 11. Mean d' and c indexes as a function of task and Stroop congruency in Experiment 1. No significant effects were observed on the analysis of the mean d' index (left panel). The right panel shows that participants maintained a more conservative response criterion for incongruent than congruent trials, especially on the concurrent task, although the interaction between task and congruency was not significant. Bars represent standard errors. Asterisks represent significant effects for the Fisher post-hoc comparisons (*p* < .05).

3.2.4.3. Gabor detection after error and hit Stroop trials

After checking for outliers, data from one participant were not included in the mean d' analysis nor in the mean c analysis of Stroop response accuracy.

For the mean d' analysis, there were no significant main effects or interactions (all *ps* > .25). The analysis of the mean c index showed a main effect of Stroop response accuracy, *F*(1, 20) = 20.30, *p* < .001, η_p^2 = .50, indicating a more conservative response criterion to detect the

Gabor after Stroop errors as compared to Stroop hits (see Figure 12). Post-hoc Fisher analyses revealed that this effect was statistically significant both for the sequential and the concurrent tasks (both *p*s < .001). Thus, committing an error in this experiment did not affect participants' perceptual sensitivity to detect the Gabor, but instead modulated decisional stages of processing related to response criterion.

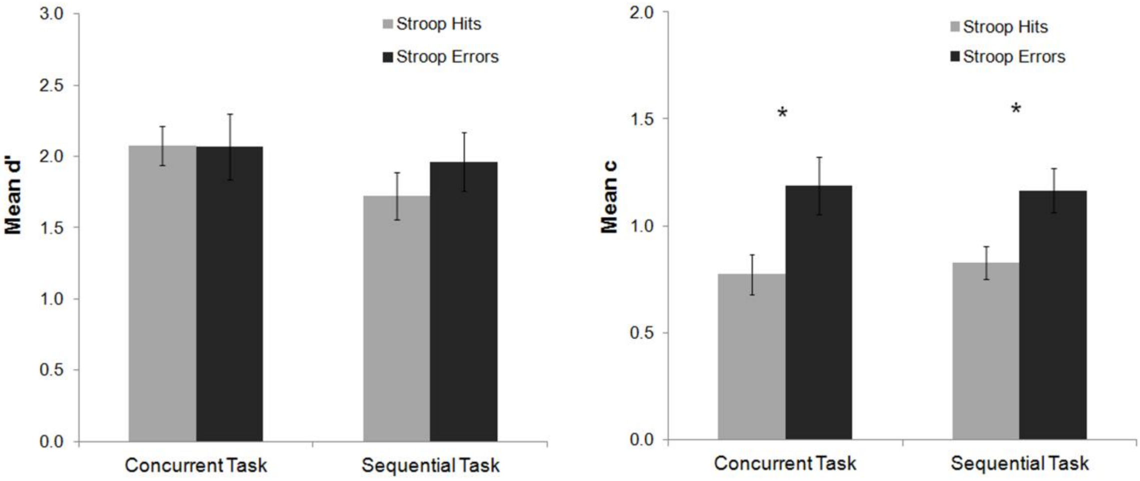


Figure 12. Mean d' and c indexes as a function of task and Stroop response accuracy in Experiment 1. No significant effects were observed on the analysis of the mean d' index (left panel). The right panel shows that response criterion to detect the Gabor was more conservative after an error on the Stroop task as compared to hit trials for both the concurrent and sequential tasks. Bars represent standard errors. Asterisks represent significant effects for the Fisher post-hoc comparisons (*p* < .05).

3.3. Experiment 2

A second experiment was conducted in order to explore whether results of Experiment 1 could be attributable to the proportion of congruent and incongruent stimuli, rather than to a pure congruency effect. In Experiment 2, we changed the frequency of congruent and incongruent trials in the Stroop task, making the proportion of incongruent stimuli larger than the proportion of congruent stimuli (75% and 25%, respectively). If the observed results were due to stimuli frequency rather than to executive control processes, the inverse patter of result should be observed in Experiment 2, in which incongruent trials were more frequent than congruent trials.

3.3.1. Participants

A different sample of twenty-three students (2 males, mean age of 20.50 years, SD of 1.66) from the University of Granada participated in the experiment.

3.3.2. Apparatus, stimuli, and procedure

Apparatus, stimuli, task, and procedures were the same as Experiment 1 except for the following: we switched the proportion of congruent and incongruent trials to 75% incongruent and 25% congruent trials.

3.3.3. Results and Discussion

3.3.3.1. Stroop task

After checking for outliers, data from one participant were excluded from the Stroop task accuracy analysis and from the Stroop RT analysis.

As in the previous experiment, the analyses of mean RTs and accuracy data demonstrated a main effect of congruency. Participants were faster, $F(1, 21) = 62.29$, $p < .001$, $\eta_p^2 = .75$, and more precise, $F(1, 21) = 9.95$, $p = .005$, $\eta_p^2 = .32$, for congruent than for incongruent trials. There was also a main effect of task on RTs, $F(1, 21) = 6.80$, $p = .016$, $\eta_p^2 = .24$, indicating faster RTs in the sequential task than in the concurrent task (see Table 1). The interaction between congruency and task was not significant ($F < 1$).

3.3.3.2. Gabor detection for congruent and incongruent Stroop trials

Trials in which participants incorrectly reported the location of a presented Gabor were considered errors and removed from the analyses (1.16% of presented Gabors of Experiment 2). Trials in which participants committed an error on the Stroop task were also excluded from data analyses (8.93% of the remaining trials). After eliminating Gabor detection errors and Stroop trial errors, a mean of 655 trials per participant (SD = 40) were included in the analyses of Experiment 2.

After checking for outliers, no participants were excluded from the mean d' analysis. Data from one participant were not included in the mean c analysis.

The ANOVA of the mean d' index did not show significant congruency or task effects (*p*s > .30), and no significant interaction ($F < 1$) (see Figure 13). For the mean c index, a main effect of task was found, $F(1, 21) = 8.05$, $p = .01$, $\eta_p^2 = .28$, while the main effect of congruency was not significant ($F = 1$). The congruency by task interaction for the mean c index was not significant either ($F < 1$).

In order to directly compare results from Experiment 1 and Experiment 2, we performed two 2-way ANOVAs (one for the concurrent and one for the sequential task). We observed that the congruency effect interacted with Experiment in the concurrent task, $F(1, 41) = 16.36$, $p < .001$, $\eta_p^2 = .29$, but not in the sequential task, $F < 1$. We also used Bayesian statistics, in which analyses are not biased against the null hypothesis, and we can establish evidence for the absence of an effect only on the observed data. Therefore, with the collected data, we can conclude if the alternative hypothesis is more probable than the null hypothesis or vice-versa. In Bayesian statistics a Bayesian Factor = 1 indicates no evidence in favor of either the null or the alternative (H1) hypothesis. Bayesian Factors < 1 indicate evidence in favor of the null hypothesis (in our case, comparable response criterion for congruent and incongruent trials), while Bayesian Factors > 1 indicate evidence in favor of the H1 hypothesis (in our case, a different response criterion for congruent and incongruent trials). Bayesian Factors > 10 are considered as strong evidence in favor of the H1 hypothesis, while Bayesian Factors >1 and <3 indicate anecdotal evidence for H1 (Jeffreys, 1961, cited by Jarosz and Wiley, 2014). A two-tailed repeated-measures Bayesian t-test was performed to compare response criterion on congruent and incongruent trials in the concurrent task in Experiments 1 and 2, with the default settings implemented in JASP 0.8.1.1 software (JASP Team, 2016, retrieved from https://jasp-stats.org/) [prior P(H0) = P(H1) = 0.50, Cauchy prior width = 0.707]. Results of the t-test performed in Experiment 1 demonstrated strong evidence in favor of the alternative hypothesis (BF_{10}=15.82). In contrast, the same analyses for the concurrent task in Experiment 2 demonstrated only anecdotal evidence in favor of the alternative hypothesis (BF_{10}=1.373).

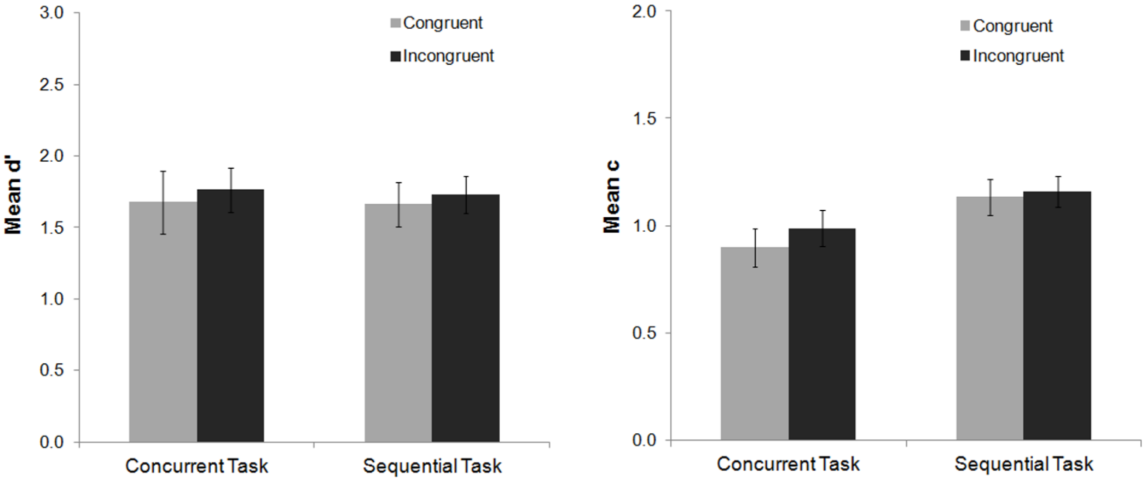


Figure 13. Mean d’ and c indexes as a function of task and Stroop congruency in Experiment 2. No main effects or interactions were found for the mean d’ index (left panel). For the mean c index (right panel) no congruency effects were found. A main effect of task was observed, but it did not interact with the congruency factor. Bars represent standard errors.

The results of these experiments demonstrate that the effect of congruency found in Experiment 1 for the mean c index was not due to differences on stimulus frequency alone. Low frequency congruent trials did not impact response criterion (Experiment 2) while low frequency incongruent trials did (Experiment 1). Therefore, participants' response criterion to detect the Gabor on incongruent trials as compared to congruent trials was not more conservative because these trials were less frequent than congruent trials, but because they were both incongruent and infrequent, a known condition to produce a reliable activation of the executive control system, intensifying the interference effect of the Stroop task (Lindsay & Jacoby, 1994). We can therefore conclude that our manipulation of executive attention by the Stroop congruency did not alter perceptual sensitivity, but modulated response criterion under conditions of high executive conflict (Experiment 1), and not merely due to stimuli exposure or stimulus frequency.

3.3.3.3. Gabor detection after error and hit Stroop trials

After checking for outliers, no participants were excluded from the mean d' analysis of Stroop response accuracy. One participant was not included in the analysis of the mean c index.

For the mean d' analysis, a main effect of task was observed, *F*(1, 22) = 5.18, *p* = .033, η_p^2 = .19, which was modulated by Stroop response accuracy, *F*(1, 22) = 13.82, *p* = .001, η_p^2 = .39. In the sequential task, participants' ability to detect the subsequent Gabor decreased after Stroop errors as compared to Stroop hits (Fisher post-hoc analysis, *p* < .001). This effect was non-significant for the concurrent task (Fisher post-hoc analysis, *p* = .29) (Figure 14). For the mean c analysis, the main effects of Stroop response accuracy and task were significant (*F*(1, 21) = 19.31, *p* < .001, η_p^2 = .48; *F*(1, 21) = 5.14, *p* = .034, η_p^2 = .20, respectively). The interaction between both factors was not significant ($F(1, 21) = 2.77$, $p = .11$, $\eta_p^2 = .12$). Overall, participants' response criterion was more conservative after Stroop errors as compared to Stroop hits (both for the concurrent and the sequential tasks, Fisher post-hoc analysis, both *p*s < .02), and for the sequential as compared with the concurrent task.

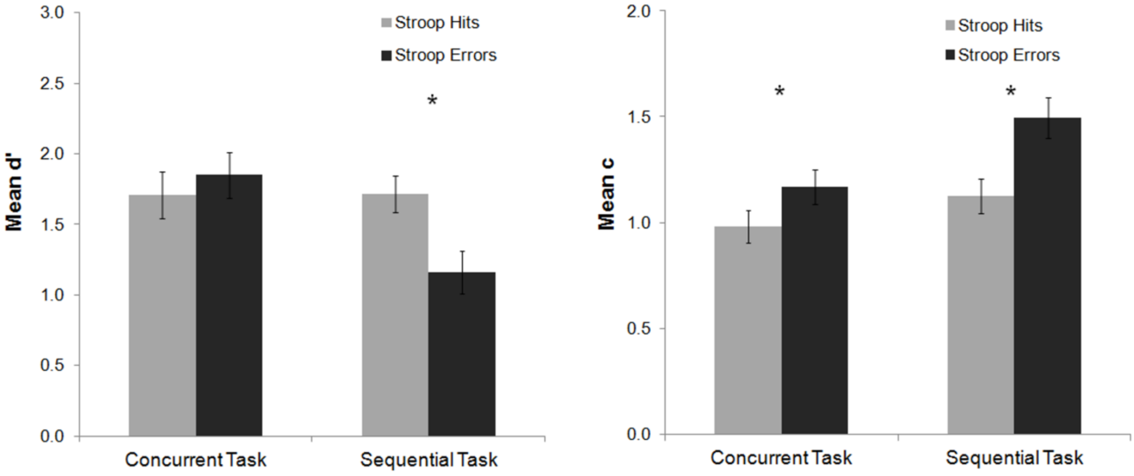


Figure 14. Mean d' and c indexes as a function of task and Stroop response accuracy in Experiment 2. For the d' index (left panel), committing an error in the Stroop task impaired participants' perceptual sensitivity to detect the subsequent Gabor in the sequential task. For the c index (right panel) response criterion to detect the Gabor was more conservative after an error on the Stroop task as compared to hit trials for both the concurrent and the sequential task. Bars represent standard errors. Asterisks represent the significant effects for the Fisher post-hoc comparisons ($p < .05$).

An unexpected result regarding error commission modulations on conscious perception was the lack of effects in perceptual sensitivity in Experiment 1 (high proportion congruent), as compared to Experiment 2 (low proportion congruent). A plausible explanation for this absence of effect in Experiment 1 could be the difference in Stroop error distribution among experiments. In order to explore whether errors were equally distributed among experiments, we performed an ANOVA of the percentage of Stroop errors for participants from the two experiments, with the within-subject factors of congruency and task, and experiment as a between-subject factor. The analysis revealed a significant interaction between congruency and experiment, $F(1, 43) = 14.23$, $p < .001$, $\eta_p^2 = .25$, indicating that in Experiment 1, participants committed more errors on incongruent Stroop trials compared to congruent trials, while errors in Experiment 2 were more equally distributed among congruent and incongruent trials. I.e., in Experiment 1, most errors were made on incongruent Stroop trials. In Experiment 2, by contrast, the congruency effect was reduced, making this experiment a better condition for observing error commission modulations on conscious perception with no contamination of the congruency factor. Committing an error on the Stroop task in Experiment 1 leaded to a more conservative response criterion to detect the near-threshold stimulus, as incongruent trials from that experiment made participants' response criterion more conservative. This suggests that the impact of error-commission in Experiment 1 could be masked by the congruency effect, and therefore error commission modulations could be more reliably observed in Experiment 2.

3.4. General Discussion

The present study explored for the first time the interactions between the anterior executive network of attention and conscious perception. In particular, we explored whether inference control would modulate perceptual sensitivity and response criterion to detect near-threshold information. Participants were asked to detect a near-threshold target while performing a classic Stroop task, in a high proportion congruent condition (eliciting reactive control) and in a low proportion congruent condition (eliciting proactive control). In agreement with the gateway hypothesis (Posner, 1994, 2012), if attention were a prerequisite for consciousness, the transient recruitment of non-active task goals under reactive control situations would affect conscious perception, either impairing perceptual sensitivity on incongruent as compared to congruent trials or modulating response criterion. We did not expect modulations of either perceptual sensitivity or response criterion in situations where proactive control was implemented. Moreover, modulations of perceptual sensitivity or response criterion were expected to be larger under dual-task conditions, i.e. for the concurrent as compared to the sequential task. Finally, we predicted that error commission in the Stroop task would impair perceptual sensitivity of the near-threshold stimulus for that given trial or modulate participants' response criterion in situations in which error commission occurred before the near-threshold stimulus presentation, i.e. in the sequential task. In the concurrent task, by contrast, we did not expect conscious access modulations produced by error commission, because when the Gabor appears, participants have not responded to the Stroop task yet.

As predicted, reactive control mechanisms (elicited under conditions of high proportion of congruent trials) impacted conscious perception, resulting in a more conservative response criterion to report the Gabor on incongruent as compared to congruent Stroop trials. This result could not be accounted for by solely stimulus frequency, as the effect was not observed in the low proportion congruent condition (Experiment 2) (for a review of proportion congruent effects, see Bugg and Crump, 2012).

It could be argued that our results could be explained by working memory load rather than interference control, because in the concurrent task participants had to maintain the response for the Gabor detection task after the Stroop response. Although it is true that working memory requirements are larger in the concurrent task than in the sequential task, working memory requirements are comparable for incongruent trials in both experiments, but these trials differ in their capacity to elicit reactive as compared to proactive control. Therefore, working memory load cannot solely explain the congruency effect reported in the response criterion index.

An alternative or maybe a complementary explanation to our data relates to mental load. Although the concept of mental load is difficult to define, some studies have demonstrated that performing an arithmetic cognitive task along with a visual search task impairs the latter (Pérez-Moreno et al., 2011), and that the higher the mental load of the cognitive task, the greater the impairment in the visual search task. This result is comparable to the congruency effect demonstrated in the present study, but some theoretical differences should be noted. While mental arithmetic tasks largely rely on working memory processes, even if they are not presented within the visual domain, the Stroop task is traditionally associated to interference control rather than to working memory (Miyake et al., 2000). Nonetheless, it is plausible that our results and those found by Pérez-Moreno et al. (2011) and Recarte et al. (2008) are different measures of the same phenomenon.

Finally, some authors could also argue that perceptual load, instead of mental load or interference control, could be mediating our results. In our study, both the Stroop stimuli and the Gabor stimuli were presented in the visual modality, increasing the perceptual load in the concurrent task as compared to the sequential task (Lavie, Beck, & Konstantinou, 2014). Although perceptual load is larger in the concurrent task than in the sequential task, it is comparable for congruent and incongruent trials. Following the same logic than above, the congruency effect observed in response criterion was only observed in Experiment 1 (with a larger proportion of congruent trials) and not in Experiment 2 (with a larger proportion of incongruent trials). Perceptual load is comparable for incongruent trials in both experiments, but these trials differ in their capacity to elicit reactive as compared to proactive control. Therefore, perceptual load cannot solely explain the congruency effect observed in the response criterion index.

This new body of research complements the literature on the relation between conscious perception and the different attention networks, broadening our knowledge about how interference control interacts with conscious processing. Particularly, our results support the idea that, as alertness and orienting, executive attention also modulates conscious perception. Importantly, this study confirms that the interference aspect of executive control – and not only working memory load (De Loof et al., 2015, 2013; Fougnie & Marois, 2007; Scalf et al., 2011) or mental load (Pérez-Moreno et al., 2011; Recarte et al., 2008)- affects conscious access of near-threshold information.

Previous research exploring the relation of alerting and orienting systems of attention and conscious perception had demonstrated modulations of perceptual sensitivity by both attentional systems (Botta et al., 2014; Chica et al., 2012a; Chica et al., 2016, 2011, 2010; Kusnir et al., 2011; Wyart and Tallon-Baudry, 2008). However, rather than modulating perceptual sensitivity to detect stimuli, interference control impacted participants' response criterion. These results fit recent literature using the attentional blink phenomenon and working memory encoding, demonstrating that the impairment of the second target detection in this paradigm is due to delayed rather than suppressed processing (Scalf et al., 2011; Vogel & Luck, 2002). Coherent with this idea, the reactivation of behaviorally relevant task goals after conflict detection (reactive control) impacts perceptual decision making rather than modulating perceptual sensitivity. In contrast, recruitment of proactive control, a more efficient strategy, could have actively maintained the representation of both the Stroop task and the conscious detection task goals, preparing the system in a manner that would prevent interference modulations of conscious perception. According to this idea, the interference control aspect of executive attention will influence conscious access in a similar way as working memory load does in inattentional blindness and attentional blink paradigms (Akyürek et al., 2007; Colzato et al., 2007).

Error detection and correction is considered another important function of the executive attentional system (Norman & Shallice, 1986). Moreover, error commission consistently affected the decision criterion to report the near-threshold target, making participants' criterion more conservative on errors as compared to hit Stroop trials. Contrary to our hypothesis, error commission modulated response criterion not only in the sequential task but also in the concurrent task. This result was unexpected, since in the concurrent task Gabors were presented before participants responded to the Stroop task. However, the Gabor detection response in the concurrent task was given after the Stroop response (and therefore, after Stroop hits or Stroop errors). Hence, it is plausible that participants made the perceptual decision about the Gabor after having responded to the Stroop task in both the concurrent and the sequential tasks. The effect of Stroop response accuracy in the concurrent task could reflect participants' reinterpretation of their conscious experience after committing an error in the Stroop task (i.e. during the inter-stimulus interval or the Gabor detection response time). Importantly, in the low proportion congruent condition (Experiment 2), committing an error in the sequential Stroop task not only impacted participants' decision criteria but also modulated perceptual sensitivity in the sequential task, impairing their ability to detect the target when it was presented after a Stroop error as compared to Stroop hits. One possible explanation for this effect could be that, similarly to the post-error slowing phenomenon (Rabbitt, 1966), the impairment to detect near-threshold stimuli after an error could be reflecting performance evaluation processes. In this case, participants would be engaged in apprehending the error-situation, preventing the conscious detection of the subsequent target (Danielmeier & Ullsperger, 2011), as shown by Buzzell et al. (2017). According to the gateway hypothesis, error commission could be preventing the attentional amplification of the near-threshold stimulus, necessary to conscious perception. However, other explanations are possible. For example, both errors on the Stroop task and changes in Gabor detection on a given trial might have been produced by general fluctuations in cognitive control (Esterman, Noonan, Rosenberg, &

Degutis, 2013; Leber, Turk-browne, & Chun, 2008). More research should be done to clarify this issue.

In conclusion, results from this study seem to support the gateway hypothesis on the relation between attention and consciousness (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Posner, 1994, 2012; Rees & Lavie, 2001). Given that our manipulations of interference control resulted in an impact on the conscious access of near-threshold stimuli, we can conclude that attention acts as a prerequisite for conscious processing, facilitating or preventing a given stimulus from accessing consciousness. However, other models such as the cumulative influence hypothesis (Tallon-Baudry, 2012) suggest independent contributions of attention and consciousness to a single process of perceptual decision-making. According to this hypothesis, attention and consciousness mechanisms separately influence participants' decision on the perception of a given stimulus. In this model, a decision variable accumulates consciousness-related neural activity, but also, attention-related neural activity. The cumulative influence hypothesis suggests that behavioral reports based on this decision variable could show an interaction between attention and consciousness, whereas neural variables could be separately related to attention and consciousness (Tallon-Baudry, 2012). Future lines of research should attempt to address whether behavioral changes in conscious perception observed in situations of interference control do reflect an actual interaction between attention and consciousness at a neural level.

Chapter 4: Neural Modulations of Executive Attention on Conscious Perception

The content of this chapter is currently under review as Colás, I., Capilla, A., Chica, A.B. The neural modulations of interference control over conscious perception.

4.1. Introduction

We can only report a small portion of the information reaching our senses. How is this information 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 & Naccache, 2001; Posner, 1994). Dehaene and colleagues (Dehaene et al., 2006; Dehaene, Sergent, & Changeux, 2003; Dehaene & Changeux, 2004; Dehaene & Naccache, 2001) suggest that the extent to which a certain stimulus gains access to conscious processing depends not only on the (bottom-up) stimulus strength but also on top-down attentional amplification. This idea follows the Global Neuronal Workspace model (Baars, 2002, 2005) 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 & Changeux, 2004). Other models also highlight the importance of attentional amplification for conscious perception (S. E. Petersen & Posner, 2012; Posner & 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, Gratton, Fabiani, & Beck, 2009; V. Wyart & Tallon-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 (S. E. Petersen & Posner, 2012; Posner & 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., 2012a; Chica et al., 2011; Kusnir et al., 2011; Petersen et al., 2017; Wyart and Tallon-Baudry, 2008). 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 insula (Chica, Paz-Alonso, Valero-Cabre, & Bartolomeo, 2013).

Although several studies have explored the modulations of executive control over conscious perception, most of them have mainly focused on manipulating working memory (Fougnie & Marois, 2007; Scalf et al., 2011) or mental load (Pérez-Moreno et al., 2011). For example, the magnitude of the attentional blink phenomenon (Shapiro, Arnell, & Raymon,

1997) can be modulated by active working memory load (Akyürek et al., 2007; Colzato et al., 2007). Working memory load also increases the subjective visibility threshold, modulating the impact of a prime stimulus on the response to the target (De Loof et al., 2013). Although the above-cited studies illustrate a behavioral relationship between the working memory aspect of executive control and conscious processing, there is reasonable evidence in the literature suggesting that executive control and conscious perception rely on common brain networks. Specifically, the prefrontal-parietal network has been identified as the “core correlate” of consciousness, due to its implication in conscious perception regardless of the content (Bor & Seth, 2012). This network has likewise been linked to working memory processes, executive control, and chunking (Abe et al., 2007; Bor, Duncan, Wiseman, & Owen, 2003; Erickson et al., 2007; Koechlin & Summerfield, 2007). Studies analyzing event-related potentials have confirmed this interaction between executive control processes and conscious perception. For example, Niedeggen et al. (2015) predicted conscious access in a distractor-induced blindness paradigm using the amplitude of a frontal negativity in event-related potentials (ERPs). In another study, Vogel and Luck (2002) found a complete suppression of the P3 component during the attentional blink, demonstrating that central processes such as working memory consolidation were postponed during the time interval between the two (to-be-detected) targets.

Working memory, however, is only one of the three core aspects of executive functions, which also include interference control and cognitive flexibility or set shifting (Diamond, 2013; Lehto et al., 2003; Miyake et al., 2000). The executive control network of attention refers to a system involved in the voluntary control of processing in novel or complex situations, when automatic responses are not sufficient for achieving a particular goal (Posner & Raichle, 1994). The interference control aspect of executive function enables us to attend selectively, focusing on some features or stimuli while suppressing attention to others.

Therefore, executive control appears to be equivalent to the interference component of the broader concept executive function (Diamond, 2013; S. E. Petersen & Posner, 2012). 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, Triviño, & Chica, 2017). However, to our knowledge, this relation between interference control and conscious perception has only been explored at the behavioral level, and therefore evidence is missing on the neural basis of this effect.

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 an essential role on the decisional stage of verbally reporting consciously perceived information. The information of attentional and perceptual systems will be analyzed in different and independent brain networks, but it will be integrated within the frontal lobe for decision-making (decision about reporting the stimulus presence or absence). Contrary, both the Global Neural Workspace model (Baars, 2002, 2005; Dehaene et al., 2006) and the gateway hypothesis (S. E. Petersen & 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 between interference control and conscious perception probably in frontal lobe regions.

Our aim was to explore whether the behavioral effect found in Colás et al. (2017) reflected a neural interaction between interference control processes and conscious perception, or whether interference control and conscious perception mechanisms separately influence behavior. For that purpose, 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 targets). 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% incongruent, a manipulation known to prompt reactive control (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver, 2012; De Pisapia & Braver, 2006). In the other session, 25% of the Stroop trials were congruent and 75% incongruent, increasing the recruitment of proactive control (Botvinick et al., 2001; Braver, 2012; De Pisapia & Braver, 2006). We analyzed the anterior N2 component locked to the appearance of the Stroop word, a component that has been related to conflict solving (Folstein & Van Petten, 2008; S J 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 expected this difference to be larger when participants had to implement reactive control (i.e. in the high proportion congruent session), because according to the dual mechanisms framework (Braver, 2012; De Pisapia & Braver, 2006), proactive control would be maintained across both congruent and incongruent trials in the low proportion congruent session. In addition, we conducted source-location analyses, and we expected the N2 component to be localized in the anterior cingulate cortex (V. Van Veen & 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 targets. 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 from 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.

4.2. Methods

4.2.1. Participants

Twenty-six students from the University of Granada (Spain) gave their signed informed consent to participate in the study in exchange for 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 in the behavioral analyses. For the ERP analyses, data from four more 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.

4.2.2. Apparatus and stimuli

E-prime software (Walter 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 85Hz. Participants sat at approximately 57 cm from the screen. Two black markers and a central fixation point (a black plus sign, 0.3° × 0.3°) were displayed at the beginning of each trial. The markers consisted of a black square outline (6° width × 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° × 0.5°), green (*verde*, 2° × 0.5°), and yellow (*amarillo*, 4 ° × 0.5°) 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 0.3°), with a maximum Michelson contrast of 0.92 and a minimum Michelson contrast of 0.02.

4.2.3. Procedure

Figure 15 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 the word onset. Participants could respond to the Stroop word from the moment it was displayed and for a maximum period of 2016 ms (word duration plus 1524 ms). After that, participants were required to respond to the Gabor detection task, with no time limit. An interstimulus interval of 2508 ms was set after the Gabor response, allowing participants to blink and prepare for the next trial.

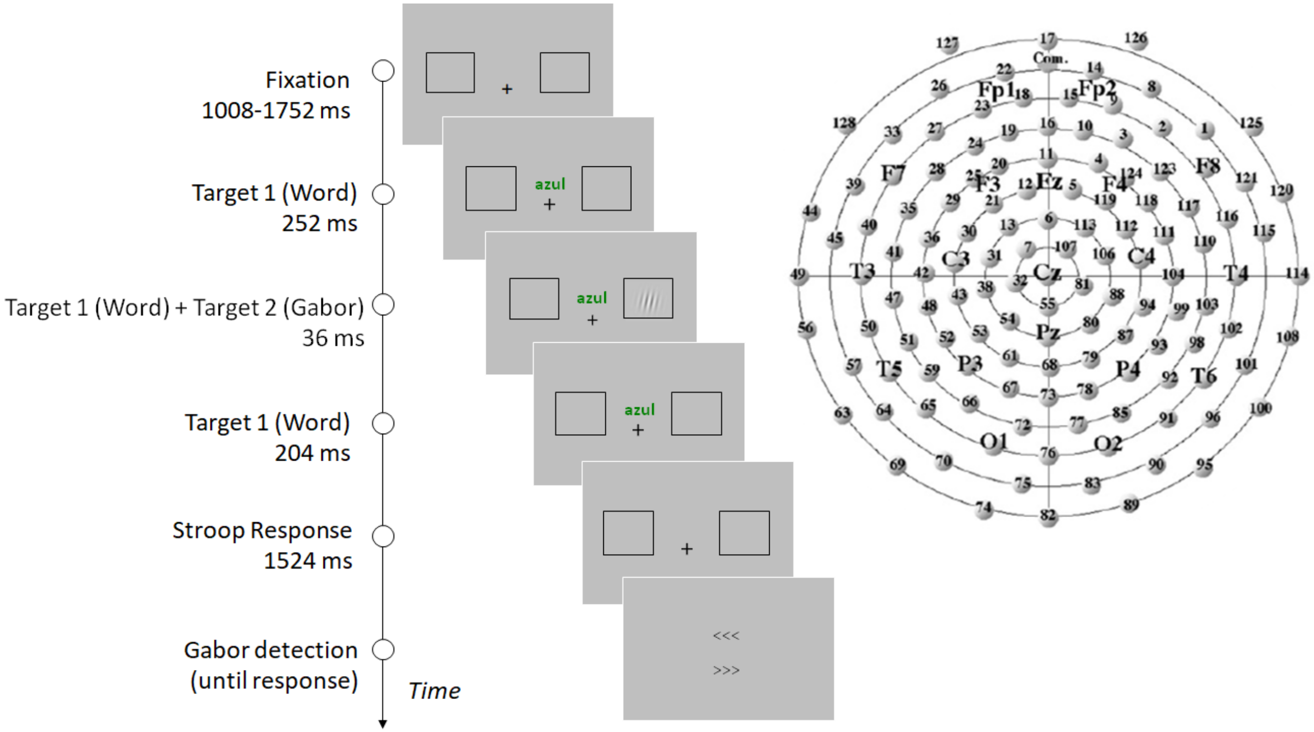


Figure 15. Timing and sequence of events in a given experimental trial (left). Electrode distribution around the scalp (right; the top of the figure represents the frontal area). Additional sites according to the 10–20 international system are shown for further reference.

Participants were required to perform two consecutive tasks. First, they had to discriminate the word's ink color as fast and accurately as possible. Participants responded with their right hand, pressing a keyboard key for each given color (the color-key mapping was counterbalanced across participants). In 12% of the trials, no word was presented and no response was required. Then, participants performed the Gabor detection task, reporting if they had perceived its appearance. They were asked to respond accurately and without time pressure, reporting the Gabor location only when they were confident about their perception. The response was given by choosing one of two arrow-like stimuli (>>> or <<<), pointing to the two possible locations of the target: right and left sides of the screen. The arrows were presented one above the other, with their position randomized in each trial. Participants indicated the location of the Gabor with their left hand, pressing an upper keyboard key corresponding to the upper arrow, or a lower key corresponding to the bottom arrow. This response procedure was employed in order to minimize response preparation and anticipations (Chica et al., 2011). Participants were asked to press the space bar whenever they had not perceived the stimulus. No Gabor was presented in 19% of the trials (catch trials).

Before the experimental trials, participants passed through a titration procedure, where the Gabor was calibrated for each participant in the absence of the Stroop stimulus. During titration, participants had to detect the Gabor and select its location. Titration began with a supra-threshold stimulus (Michelson contrast= 0.184), which contrast was manipulated based on the mean percentage of seen targets every 16 trials. If participants reported 63% or more targets during the last block of trials, Gabors at the immediately following lower contrast level (Michelson contrast minus 0.009) were used during the next block of trials; however, if the percentage of seen targets was equal or lower than 38% during the last block of trials, the next block of trials presented Gabors at the immediately following higher contrast level

(Michelson contrast plus 0.009). The titration procedure stopped when target contrast yielded a percentage of seen targets >38% and <63% for two consecutive blocks of 16 trials.

Participants completed two separate sessions, each containing titration, practice (15 trials), and experimental trials. In one of the sessions, congruent trials were more frequent than incongruent trials (75% congruent trials - 25% incongruent trials; high proportion congruent session), whereas in the other session, incongruent trials were more frequent than congruent trials (75% incongruent trials - 25% congruent trials; low proportion congruent session). The order of the sessions was counterbalanced across participants. The experiment consisted of a total of 1088 experimental trials (544 trials per session, divided into 4 experimental blocks of 136 trials). Therefore, a total of 360 congruent trials and 120 incongruent trials were presented in the high proportion congruent session (no Stroop word was presented in the remaining 64 trials). In the low proportion congruent session, the proportion of congruent and incongruent trials reversed, giving a total of 360 incongruent trials, 120 congruent trials, and 64 trials in which the word was not presented. Each session contained a total of 96 Gabor catch trials (trials in which the Stroop word was presented in absence of the Gabor stimulus). Participants were allowed to take a short break after every 68 trials. Additionally, after every 136 trials, the experimenter checked the impedance of the electrodes.

4.2.4. EEG signal recording and analysis

The analysis of the EEG signal at the sensor level was performed using the Net Station software package (https://egi.com/). After preprocessing the EEG signal, event-related potentials locked to the Stroop word were analyzed.

The source-level analysis was performed using the FieldTrip software package (Oostenveld et al., 2011; http://www.ru.nl/fcdonders/fieldtrip/) and in-house Matlab code. Its aim was to identify the neural generators underlying the N2 component modulations.

4.2.4.1. Sensor level analysis

EEG was recorded using a high-density 128-channel Geodesic Sensor Net (Tucker et al., 1994; see Figure 15). The head-coverage included sensors lateral to and below both eyes to monitor horizontal and vertical eye movements (HEOG and VEOG). Impedances for each channel were measured and kept below 50 KΩ before testing. All electrodes were referenced to the Cz electrode during the recording and were re-referenced to the average of all electrodes off-line. The EEG signal was acquired at a sampling rate of 250 Hz. It was band-pass filtered online between 0.1 and 100 Hz using an elliptic filter, and subsequently filtered offline by using a 0.3–30 Hz band-pass Butterworth filter. Epochs were segmented from 200 ms before the presentation of the Stroop word to 450 ms after its appearance. A 200 ms segment prior to the Stroop word presentation was used to calculate the baseline. Trials containing eye blinks or eye movements (electro-oculogram channel differences greater than 70 μV) or more than 20% of bad channels were rejected. Overall, a total of 22% of the trials were rejected due to artifacts or to anticipatory responses. Data from four participants were excluded because after applying artifact detection tools, less than 15 trials per condition remained. Word-related ERP analyses were performed over the following mean total of trials: for the high proportion congruent session, congruent-seen (137), congruent-unseen (94), incongruent-seen (40) and incongruent-unseen (29); for the low proportion congruent session, congruent-seen (44), congruent-unseen (35), incongruent-seen (125) and incongruent-unseen (109).

4.2.1.2. Source level analysis

The localization of brain sources was carried out by means of beamforming (Gross et al., 2001; B. D. Van Veen, van Drongelen, Yuchtman, & Suzuki, 1997). Source localization was performed on a standard MRI in MNI (Montreal Neurological Institute) space provided by the EEGLAB toolbox (https://sccn.ucsd.edu/eeglab/), which was segmented into 12-mm resolution voxels. The forward model was computed using a standard boundary element method (BEM) volume conduction model (Oostenveld, Stegeman, Praamstra, & Van Oosterom, 2003) and standard electrode positions. Lead fields were calculated for the 3 possible orientations of each voxel. We computed the spatial filter coefficients by means of linearly constrained minimum variance beamformer (LCMV; Van Veen et al., 1997). In order to obtain the filter coefficients, the single-trial covariance matrix was calculated for 444 ms segments corresponding to the time window after the Stroop word presentation, as well as 200 ms from the baseline period. Regularization (lambda parameter) was set to 10%, i.e. a unit matrix scaled to 10% of the mean across eigenvalues of the covariance matrix was added to it. Subsequently, each sensor-level trial was projected into each voxel of source-space through the spatial filter corresponding to the optimally oriented dipole. Source-level trials were averaged for the different conditions separately, thus obtaining the corresponding source-level ERPs. To avoid differences in amplitude due to voxels depth, source-level ERPs were all normalized as relative change with respect to the root mean square of the baseline activity for each voxel (Capilla, Belin, & Gross, 2013). Finally, we averaged the brain activation results across subjects and identified the voxels exhibiting absolute spatial maxima/minima in the time window of the ERP component of interest (i.e. N2 component).

4.3. Results

4.3.1. Behavioral results

Data from twenty-one participants were included in the behavioral analyses. Participants perceived an average of 54% of the trials (SD= 13%). The mean rate of false alarms was 4.1% (SD= 6.4%). Mean target contrast (averaged contrast levels used during the experiment for each participant) was not different in the high proportion congruent session and the low proportion congruent session, t(20)= -0.05, *p*=.95.

We firstly analyzed mean accuracy and reaction times (RTs) to respond to the Stroop task. We performed two independent analyses of variance (ANOVA), with the within participants factors of proportion congruency (high proportion congruent and low proportion congruent sessions), congruency (congruent and incongruent Stroop trials), and awareness (targets reported as "seen" or "unseen").

Second, we analyzed responses to the Gabor detection task to explore participants' conscious perception of the Gabor and its modulation by interference control. We analyzed participants' responses by using the signal detection theory, which provides a measure of perceptual sensitivity (d') and response criterion (beta). The indexes were calculated by computing participants' hits or correct detections (when participants accurately determined the location of a presented Gabor), misses or trials in which the Gabor was presented but participants did not consciously report it, false alarms (when participants consciously reported Gabors that were not presented), and correct rejections or trials in which the target was not presented and participants reported not having seen it. Trials in which participants incorrectly reported the location of a present Gabor were considered errors and removed from the analyses (1.83% of presented Gabors). Trials in which participants pressed any key before the presentation of the Gabor detection response display were considered anticipations and removed from the analyses (0.22% of presented Gabors). Trials in which participants committed an error in the Stroop task were also excluded from the Gabor detection task analyses (9.77% of the remaining trials). After eliminating Gabor detection errors and Stroop trial errors, a mean of 947 trials (SD=66) per participant were included in the analyses.

Perceptual sensitivity (d') and response criterion (beta) were calculated with the following equations: $\mathrm{d'} = \mathrm{z(H)} - \mathrm{z(FA)}$; $\beta = \mathrm{Yz(H)}/\mathrm{Yz(FA)}$. H represents the hit rate, FA represents the false alarm rate, and z corresponds to z-scores, which were calculated using the inverse cumulative distribution function in Microsoft Excel 2011 (NORMSINV). The Y-score corresponds to the normal distribution function in Microsoft Excel 2011. Zero false alarm rates were corrected using the equation proposed by Snodgrass and Corwin (1988): $\mathrm{FA} = (\mathrm{FA} + 0.5)/(\mathrm{FA} + \mathrm{CR} + 1)$. For d', larger values indicate an increased perceptual sensitivity (more hits and/or less false alarms). Beta = 1 indicates a non-biased criterion; the higher the beta value, the more conservative the criterion (fewer hits and/or fewer false alarms), and the smaller the beta value, the less conservative the criterion (more hits and/or more false alarms).

Mean d' and beta indexes were submitted to two repeated measures ANOVAs with the within participants factors of proportion congruency (high and low proportion congruent) and congruency (congruent and incongruent). For all analyses, post-hoc Fisher tests were used to further explore the interactions.

4.3.1.1. Stroop task

The analysis of the mean RTs demonstrated a main effect of congruency, $F(1, 20)=53.06$, $p<.001$, $\eta_p^2 =.73$, with shorter RTs for congruent than for incongruent trials (see Table 3). As expected, this congruency effect was modulated by proportion congruency, $F(1, 20)=34.43$, $p<.001$, $\eta_p^2 =.63$. Although the congruency effect was significant for both sessions (both *p*s < .001), the effect was larger in the high proportion congruent session as compared with the low proportion congruent session. None of the other main effects or interactions were significant (all *p*s >.10).

Table 3. Mean RTs (in ms) and accuracy, with standard errors in parenthesis, as a function of proportion congruency (high and low proportion congruent session), congruency (congruent and incongruent trial), and awareness (targets reported as “seen” or “unseen”).

	High proportion congruent 75% congruent – 25% incongruent				**Low proportion congruent 25% congruent – 75% incongruent**			
	Congruent trial		**Incongruent trial**		**Congruent trial**		**Incongruent trial**	
	Seen	**Unseen**	**Seen**	**Unseen**	**Seen**	**Unseen**	**Seen**	**Unseen**
Mean RT	649 (35)	639 (27)	768 (53)	771 (39)	617 (31)	619 (28)	663 (31)	663 (27)
Mean accuracy	.93 (.02)	.92 (.02)	.85 (.03)	.81 (03)	.93 (.02)	.89 (.02)	.89 (.02)	.87 (.02)

The analysis of the mean accuracy in the Stroop task demonstrated a main effect of congruency, $F(1, 20)=29.85$, $p<.001$, $\eta_p^2 =.60$, which significantly interacted with proportion congruency, $F(1, 20)=9.88$, $p=.005$, $\eta_p^2 =.33$. Participants were more accurate in congruent trials as compared with incongruent trials in the high proportion congruent session ($p<.001$). In the low proportion congruent session, the congruency effect did not reach significance (Fisher post-hoc test, $p=.07$). A main effect of awareness was also observed, $F(1, 20)=14.61$, $p=.001$, $\eta_p^2 =.42$, demonstrating that participants were more accurate in the Stroop task in trials where they also perceived the Gabor stimulus as compared with trials in which the Gabor was missed (see Table 3). None of the other main effects or interactions reached statistical significance (all *p*s >.10).

4.3.1.2. Gabor detection task

The interaction between proportion congruency and congruency was not significant for the d' index, *F*(1, 20)=2.56, *p*=.12, η_p^2 =.11, but it reached statistical significance for the beta index, *F*(1, 20)=9.14, *p*=.007, η_p^2 =.31. Response criterion was comparable for incongruent trials in the high and low proportion congruent sessions (*p*=.478), while a more conservative criterion was observed for congruent trials in the low proportion congruent session as compared with the high proportion congruent session (*p*<.001) (see Table 4). Within the low proportion congruent session, response criterion to detect the Gabor was more conservative for congruent trials as compared with incongruent trials (*p*=.014). The reversed pattern was observed in the high proportion congruent session, although it did not reach statistical significance (*p*=.131). No other main effects or interactions reached statistical significance (all *p*s >.08 for d', and all *p*s >.21 for beta).

Table 4. Mean percentage of hits, false alarms, d', and beta (with standard errors in parenthesis) as a function of proportion congruency (high and low proportion congruent session) and congruency (congruent and incongruent trial).

	High proportion congruent **75% congruent – 25% incongruent**		**Low proportion congruent** **25% congruent – 75% incongruent**	
	Congruent trial	**Incongruent trial**	**Congruent trial**	**Incongruent trial**
Mean hits	.57 (.03)	.56 (.03)	.55 (.03)	.53 (.03)
Mean FA	.05 (.02)	.06 (.02)	.03 (.02)	.03 (.01)
Mean d'	2.14 (.17)	2.13 (.20)	2.42 (.18)	2.18 (.16)
Mean beta	10.22 (1.75)	13.53 (2.34)	20.72 (2.02)	15.05 (2.34)

4.3.2. EEG results

Behavioral results for the seventeen participants used in the EEG analyses showed the same main effects and interactions as the results described above.

We analyzed the event-related potentials (ERPs) locked to the appearance of the Stroop word. Within each session (high proportion congruent and low proportion congruent), we set up 4 conditions based on congruency (congruent and incongruent Stroop trials) and awareness (targets reported as “seen” or “unseen”). Visual inspection of Stroop-related ERPs in both sessions revealed three main components (see Figure 16). We first observed a P1 component (peaking at 120 ms) in parieto-occipital electrodes. This component was followed by a left-lateralized parieto-occipital negativity, the N1 component (peaking at 190 ms). Finally, we observed a negative N2 component in left-lateralized frontal electrodes, peaking at 320 ms.

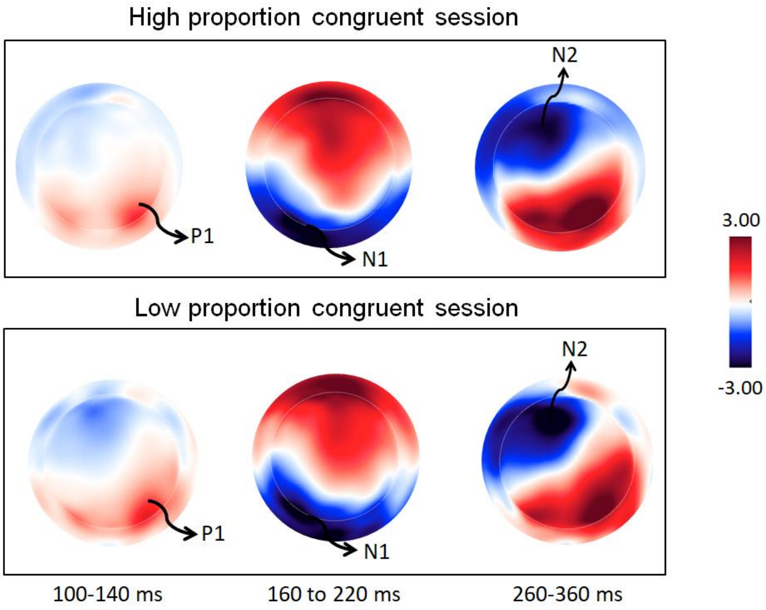


Figure 16. Topography maps for components P1, N1, and N2 for the high proportion congruent session (upper panel) and the low proportion congruent session (lower panel).

We calculated the mean amplitude of P1 (time window from 100 to 140 ms after the Stroop word onset), N1 (time window from 160 to 220 ms), and N2 (time window from 260 to 360 ms) for each participant in a sample of representative electrodes from the 10-20 electrode system (O1/O2, P3/P4, T5/T6, Pz, T3/T4, C3/C4, electrodes 21/25 representing F3 and electrodes 119/124 representing F4, electrodes 11/12/5 representing Fz, F7/F8) (see Chica et al., 2012). To determine the scalp location where each component was maximally elicited, we performed a one-way ANOVA for each component, with electrode as a factor. For all components, the main effect of electrode was significant (all *p*s < .05). The P1 component was larger in P3/P4 electrodes (M= .88 µ), followed by the Pz electrode (M= .34 µ). These two amplitudes were statistically different (post-hoc planned comparisons, *p* = .01), therefore, we only included electrodes P3 and P4 in the P1 analyses. The largest mean amplitude of the N1 component was observed in electrodes O1/O2 (M= −1.61 µ), followed by electrode T5 (M= −1.60 µ). These two amplitudes did not differ statistically (post-hoc planned comparisons, *p* = .99). The N2 component was larger in Fz electrode (M= -2.16 µ), followed by left-lateralized electrodes F3 (M= -2.03 µ) and F7 (M= -1.92 µ). These amplitudes did not differ statistically (Fisher post-hoc test, all *p*s > .64). T3 amplitude did not differ from the Fz, F7and F3 electrodes, but this electrode was not included in the analysis because the anterior N2 component (sensitive to the violation of expectations and conflict detection) has been associated to frontal and central electrodes rather than to temporal electrodes (Folstein & Van Petten, 2008; S J Luck, 2012).

4.3.2.1. Mean amplitude analyses

We analyzed the modulation of each component for each experimental condition by calculating its mean amplitude (20 ms before and 20 ms after the higher peak) at the electrodes where each component was maximally elicited (P3/P4 electrodes for the P1 component, electrodes O1/O2 and T5 for the N1 component, and electrodes F3, F7, and Fz for the N2 component).

The ANOVAs for the P1 and N1 components, with the factors of proportion congruency, congruency, and awareness, did not show any significant main effects or interactions (all *ps* > .10).

For the N2 ANOVA, a main effect of awareness was observed, $F(1,16)= 7.30$, $p = .016$, $\eta_p^2 = .31$. N2 was enhanced for seen as compared with unseen trials. This effect was mediated by an interaction between proportion congruency, congruency, and awareness, $F(1,16)= 11.17$, $p = .004$, $\eta_p^2 = .41$ (see Figure 17). In the high proportion congruent session, incongruent trials elicited a larger N2 for seen as compared with unseen trials (Fisher post-hoc test, $p=.04$). Although not significant, the effect reversed for congruent trials ($p=.13$). In the low proportion congruent session, by contrast, seen trials elicited an overall larger N2 component than unseen trials, although the effect was only significant for congruent trials ($p=.001$; $p=.35$ for incongruent trials).

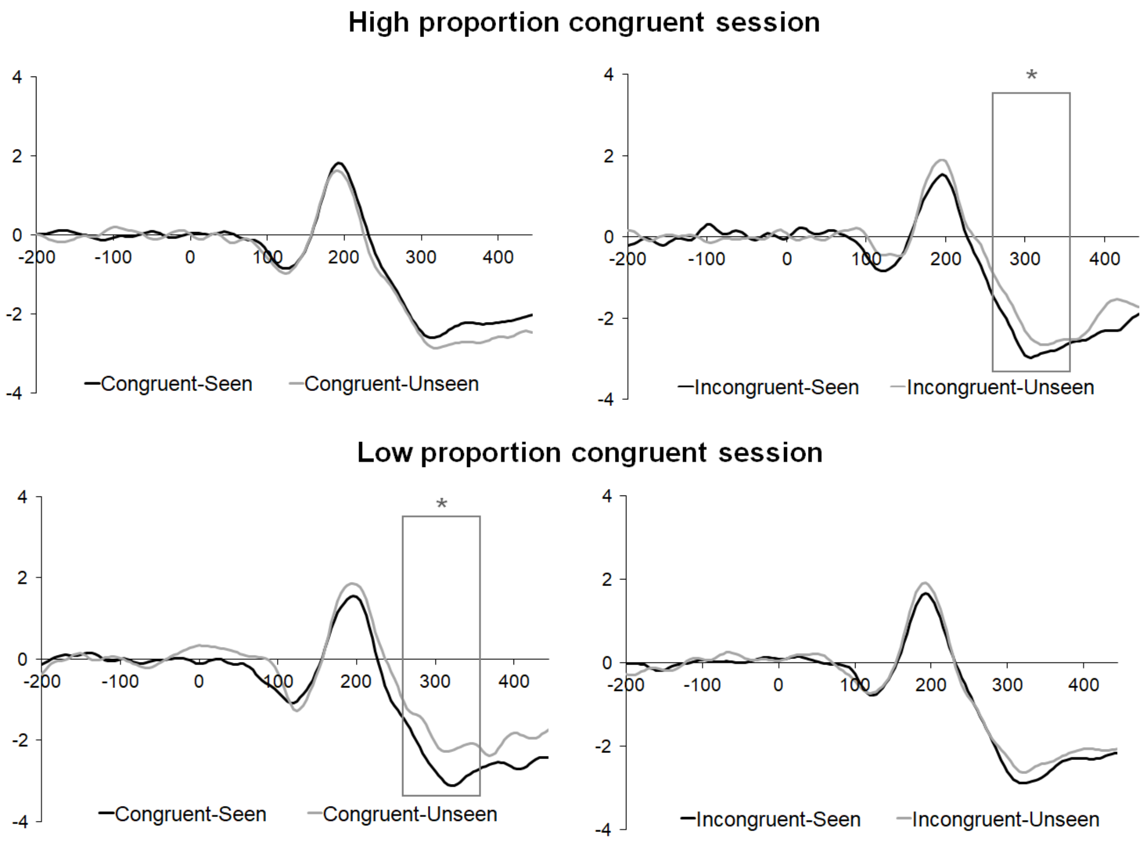


Figure 17. N2 component amplitude for electrodes F3, F7, and Fz as a function of congruency and awareness for the high proportion congruent session and the low proportion congruent session. The y-axis represents the amplitude of the wave (in µv). The x-axis represents time, with the value 0 corresponding to the onset of the Stroop word. In the high proportion congruent session, incongruent seen trials elicited a larger N2 amplitude as compared with incongruent unseen trials. In the low proportion congruent session, congruent seen trials elicited a larger N2 amplitude as compared with congruent unseen trials.

4.3.2.2. Source-location analyses

We first compared the neural sources underlying the N2 component for congruent and incongruent trials in the high proportion congruent and the low proportion congruent sessions (see Figure 18). Overall, the anterior cingulate cortex (ACC), which has been related to conflict detection and conflict monitoring (Botvinick et al., 2001; Botvinick, Cohen, & Carter, 2004; C S Carter, Botvinick, & Cohen, 1999), showed more activation on incongruent as compared to congruent Stroop trials. This difference appeared to be larger in the high proportion congruent session than in the low proportion congruent session, in agreement with the dual mechanisms of control framework (Braver, 2012; De Pisapia & Braver, 2006).

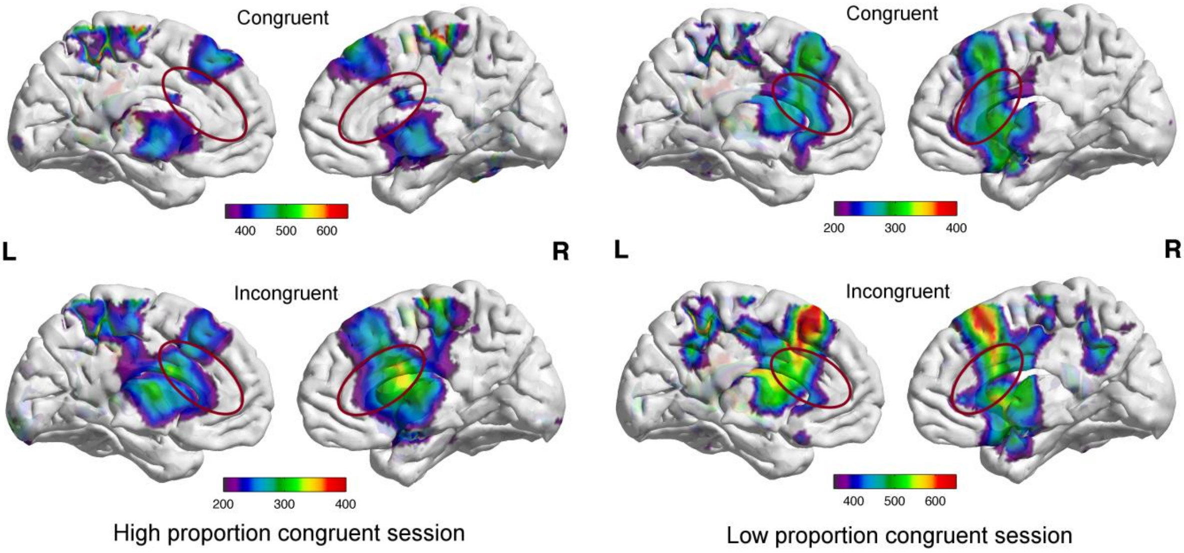


Figure 18. Medial view of the brain sources with maximum percent relative change in activation for the N2 component for congruent and incongruent trials from the high proportion congruent and the low proportion congruent sessions. The left panel shows the brain sources for the N2 component for the high proportion congruent session, whereas the right panel shows the brain sources for the low proportion congruent session. The upper panel shows the activation on congruent trials, whereas incongruent trials appear in the bottom panel.

We then compared the activation of the ACC as a function of awareness, congruency, and proportion congruency (see Figure 19). In the high proportion congruent session, the ACC was activated for incongruent-seen trials but not for incongruent-unseen trials. In the low proportion congruent session, the ACC was activated both for incongruent seen and unseen trials, maybe indicating the recruitment of proactive control strategies (Braver, 2012; De Pisapia & Braver, 2006). In the more frequent Stroop trials in each session (i.e. congruent trials from the high proportion congruent session, and incongruent trials from the low proportion congruent session), the ACC activation did not seem to differentiate between seen and unseen trials.

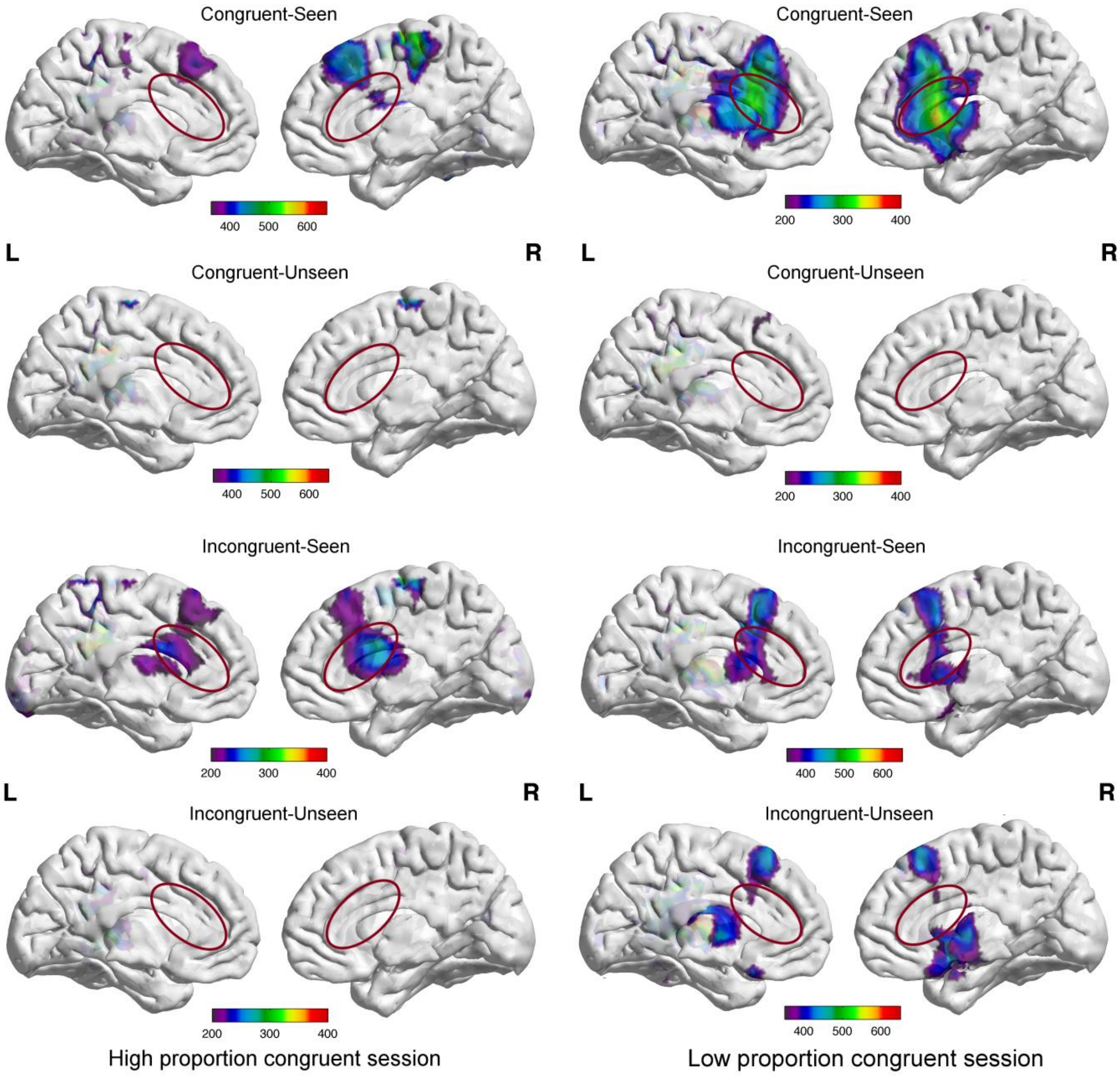


Figure 19. Medial view of the brain sources with maximum percent relative change in activation for the N2 component in the high proportion congruent session (left) and the low proportion congruent session (right) as a function of congruency and awareness.

4.4. Discussion

The present study addressed for the first time the neural mechanisms underlying the interference control modulation of conscious perception. We explored whether the behavioral interaction between interference control and conscious perception found in Colás et al. (2017) reflected a neural interaction in ERP components associated with conflict resolution (the anterior N2 component, Folstein and Van Petten, 2008; Luck, 2012), usually localized in fronto-central electrodes, and corresponding to neural activity in the ACC (V. Van Veen & Carter, 2002). The finding of this interaction is hypothesized by the attentional gateway hypothesis (S. E. Petersen & Posner, 2012; Posner, 1994), while the cumulative influence hypothesis (Tallon-Baudry, 2012) predicts that interference control and conscious perception mechanisms could be dissociated at the neural level.

The experimental paradigm employed allowed us to manipulate interference control as a mental task-set, prompting the recruitment of either reactive or proactive control mechanisms (in the high and low proportion congruent sessions, respectively) (Braver, 2012; De Pisapia & Braver, 2006). Moreover, the manipulation of congruent and incongruent Stroop trials allowed us to analyze the experienced trial-by-trial conflict. We registered participants' reports on the conscious perception of a near-threshold Gabor that was presented simultaneously to the Stroop stimulus, exploring the neural correlates of interference control and conscious perception through EEG recordings. If attention and conscious perception separately influenced decision-making concerning the perception of a stimulus, as proposed by the cumulative influence hypothesis (Tallon-Baudry, 2012), ERPs evoked by Stroop word would not differ between trials in which the near-threshold Gabor was consciously perceived as compared to non-consciously perceived trials. Conversely, if attention and conscious perception interacted at the neural level, as suggested by the gateway hypothesis (S. E. Petersen & Posner, 2012; Posner, 1994), we would expect to observe differences in the ERPs evoked by Stroop word for consciously perceived as compared to non-consciously perceived trials.

The ERP results demonstrated an effect of conscious perception in the generation of the N2 component, which is assumed to reflect the operation of a conflict detection system (S J Luck, 2012; Yeung, Botvinick, & Cohen, 2004). This component demonstrated an interaction between congruency and awareness that was modulated by proportion congruency. As expected, N2 was enhanced for incongruent-seen trials as compared to incongruent-unseen trials in the high proportion congruent session. This result seems to indicate that when exerting reactive control, the detection of conflict on a given trial is associated to the conscious perception of near-threshold stimuli. In the low proportion congruency session, N2 was overall enhanced for seen as compared to unseen trials, although the effect was only significant for congruent trials. These results suggest a modulation of the N2 component for seen as compared to unseen trials on infrequent Stroop trials from each session (incongruent Stroop trials from the high proportion congruent session and congruent Stroop trials from the low proportion congruent session). This observation is consistent with previous literature reporting that the N2 component is sensitive to the mismatch between an expectation and a stimulus (S J Luck, 2012). This expectation mismatch, which could easily be elicited by infrequent Stroop stimuli in our experimental paradigm, has also been observed to evoke ACC activity (J Downar, Crawley, Mikulis, & Davis, 2000; Kiehl, Laurens, Duty, Forster, & Liddle, 2001a, 2001b). Hence, conflict prompted by the presentation of infrequent Stroop stimuli was associated to a larger N2 component for consciously perceived as compared with non-perceived Gabors. As stated by Posner and Raichle (1994), the executive control network of attention refers to a system involved in the voluntary control of processing in novel or complex situations. Importantly, neural activity associated with this form of interference demonstrated to modulate the conscious perception of near-threshold stimuli.

Source localization analyses confirmed that the ACC was one of the most activated brain regions in the time window of the N2 component. When Stroop trials were infrequent and therefore unexpected (incongruent trials from the high proportion congruent session and congruent trials from the low proportion congruent session), the ACC activation was associated to perceived trials but not to non-perceived trials. The Global Workspace model posits the importance of frontal lobe regions in conscious perception (Baars, 2002, 2005; Dehaene et al., 2006), although evidence supporting their specific role is scarce. Our data add empirical evidence to the implication of frontal lobe functions in both interference control and conscious perception, supporting the predictions of the gateway hypothesis.

Unexpectedly, we did not observe a main effect of congruency in the N2 component. Source-location analyses, however, show that in the high proportion congruent session, ACC activation was restricted to incongruent Stroop trials, as compared to congruent trials within that session. Moreover, although the type of mechanism of control recruited (reactive vs proactive control) did not modulate the N2 wave by itself, ACC activity was elicited by both congruent and incongruent Stroop trials from the low proportion congruent session. This more generalized ACC activation in the low proportion congruent as compared with the high proportion congruent session may be indicative of the use of proactive control strategies, which are thought to be maintained previous to conflict-stimulus presentation (Braver, 2012; De Pisapia & Braver, 2006).

The neural modulations described in this study could account for the observed behavioral changes in response criterion due to conflict detection in Colás et al. (2017). Contrary to our expectations, however, the results from the present study did not completely replicate our previous findings. In the previous study, we observed response criterion modulations in situations where reactive control mechanisms were more likely to be recruited (high proportion congruent session). We did not find, nor expected, modulations of conscious perception in situations where proactive control was implemented, i.e. the low proportion congruent session. Data from the present study challenges our interpretation of the previous results, supposing that changes of response criterion were only observed in the high proportion congruent condition due to the higher amount of conflict that was triggered in incongruent trials from the high proportion congruent session, in opposition to incongruent trials from the low proportion congruent session (for a review of proportion congruent effects, see Bugg and Crump, 2012). Analyses of accuracy and RTs in the Stroop task suggest that the conflict effect in the high proportion congruent session was, in fact, greater than the conflict effect in the low proportion congruent session. However, in the present study, the conflict-related N2 component was modulated by conscious perception in both the high and low proportion congruent sessions, pointing to a more expectancy-related form of conflict.

Importantly, the experimental design used in the present study varied substantially from the previous one. Specifically, in the first study we manipulated proportion congruency between participants, as opposed to the present within-participants manipulation. That is, participants from the ERP study performed both the high proportion congruent and the low proportion congruent sessions in a counterbalanced order, whereas participants from the previous study carried out only one of the mentioned sessions. Moreover, in addition to this experiment in which the Gabor appeared concurrently to the Stroop stimulus, participants from the previous study also performed another less demanding session where the Gabor detection task and the Stroop task were presented in a sequential manner. Those differences could have influenced participants' preferences for reactive or proactive control mechanisms, confounding our findings by increasing individual differences in implementing different mechanisms of control (Braver, 2012; Gonthier, Macnamara, Chow, Conway, & Braver, 2016) or adopting different control strategies in each study. Moreover, the previous experiment did not control for intra-individual variability in the implementation of control strategies (due to affective-motivational factors or cognitive individual differences (Braver, 2012)), as it was conducted in a between-participants design. More research is needed to replicate those findings controlling for these sources of variability in order to address the necessary and sufficient conditions in which executive control impacts participants' response criterion in conscious detection tasks.

In summary, the results of the present experiment demonstrated that conscious perception is associated to an amplitude modulation of the N2 component. Therefore, the generation of a conflict-related potential, known to be implicated in situations of stimuli competition or expectations' mismatch, is also associated with conscious perception of near-threshold information. Note that this effect was only observed on infrequent Stroop trials (incongruent trials from the high proportion congruency session, and congruent trials from in the low proportion congruent session), suggesting that this conflict component differentiated between consciously perceived and non-perceived targets in situations in which interference control was elicited due to the presentation of unexpected stimuli. If, as proposed by the cumulative influence hypothesis (Tallon-Baudry, 2012), attention independently influenced participants' perceptual decision making, we would not have expected to find differences between consciously perceived and non-perceived trials in a component associated to the conflict detection system, neither that this effect was modulated by our manipulations of congruency and proportion congruency.

One could argue that those differences in N2 amplitude could be related to the consequences of conscious access, such as the phenomenological experience, working memory maintenance, or metacognitive processes about the perception of the stimulus. However, it is important to consider that this effect appeared 260-360ms after the presentation of the Stroop stimulus, not after the near-threshold stimulus presentation. A more plausible explanation, taking into account the timing of presentation of the stimuli, is that in situations of large conflict, greater N2 component amplitudes indicate a better preparation to detect and solve the conflict, allowing the top-down amplification of information giving rise to conscious perception. This interpretation is in line with the predictions of the gateway hypothesis and the Global Neuronal Workspace model, according to which executive attention modulates conscious perception through the top-down amplification of stimulus-evoked activity in sensory areas. Importantly, this relation is associated with a neural interaction between both mechanisms of the interference control subsystem of attention and conscious perception in the anterior N2 component, localized in the anterior cingulate cortex.

Chapter 5: Attention Deficits in Confabulations after Acquired Brain Injury

The content of this chapter is in preparation as Colás, I., Busquier, H., Chica, A.B., Triviño, M. Attention deficits as a consequence of acquired brain injury. Exploration of alertness, orienting and inhibition processes in confabulating patients.

5.1. Introduction

Confabulation is a type of memory distortion, which involves the production of statements or actions unintentionally incongruous to the subject’s past, present, and future situation (Dalla Barba, 1993). One of its defining characteristics is the lack of consciousness of the deficit (anosognosia), which leads confabulators to maintain these false memories and beliefs with no intention to deceive, and in spite of the evidence against them (DeLuca, 2000; M K Johnson, Hayes, D’Esposito, & Raye, 2000; Turner, Cipolotti, Yousry, & Shallice, 2008). Confabulations are commonly observed in patients with Alzheimer’s disease (La Corte, Serra, Attali, Boissé, & Dalla Barba, 2010), and have also been described in patients after acquired brain injuries, such as aneurysms in the anterior communicating artery (ACoA), hypoxia, stroke in the middle cerebral arteries, limbic encephalitis, head injury, brain tumours, or Wernicke–Korsakoff syndrome (for an example see Nahum et al., 2012). From a clinical perspective, confabulations can have a huge impact on daily living, as some confabulators require permanent supervision (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017).

Confabulating patients usually show memory impairments along with deficits in executive functions (Bajo, Fleminger, Metcalfe, & Kopelman, 2017; Ciaramelli & Ghetti, 2007; Ciaramelli, Ghetti, Frattarelli, & Làdavas, 2006; Lavie, 2005; Nahum, Bouzerda-Wahlen, Guggisberg, Ptak, & Schnider, 2012; Nahum, Ptak, Leemann, & Schnider, 2009; Turner, Cipolotti, Yousry, & Shallice, 2008, 2007). They tend to perform poorly on free recall and recognition tests, showing a failure to learn materials that have been presented repeatedly and a quick forget (M K Johnson, Hayes, D’Esposito, & Raye, 2000). Unlike amnesic patients, confabulators usually commit numerous false positives in recognition tasks and intrusions in free recall (Gilboa et al., 2006; Triviño, 2012). Concerning executive deficits, confabulating patients struggle to access the information in fluency tests (a Schnider, von Däniken, &

Gutbrod, 1996) and to inhibit verbal and motor responses (Fotopoulou, Conway, & Solms, 2007). The preservation of cognitive flexibility, working memory, or reasoning has also been called into question (Cunningham et al., 1997; M K Johnson, O'Connor, & Cantor, 1997); however, these functions do not seem to be consistently impaired among confabulators (Gilboa et al., 2006; McVittie, McKinlay, Della Sala, & Macpherson, 2013; A. Schnider, 2008). Besides the memory problem, attention seems to modulate the presence of confabulations, as demonstrated when divided attention has been manipulated (Ciaramelli et al., 2009; Cunningham et al., 1997), and when selective attention has been explored with visual search tasks (Ródenas, Lupiáñez, Arnedo, & Triviño, 2016). This evidence supports the claim that confabulation is not a pure memory deficit (Dalla Barba & La Corte, 2013), highlighting the importance of exploring the functioning of attentional networks in patients suffering from confabulation.

A current controversy exists about the brain structures whose malfunction is responsible for confabulations, as they can result from lesions located in more than 20 anterior and posterior brain areas (Dalla Barba & Boissé, 2010; Gilboa & Moscovitch, 2002). Usually, confabulations involve frontal lobe injury (Gilboa & Moscovitch, 2002), as well as structures from the anterior limbic system such as the genu of the internal capsule, the amygdala, the perirhinal cortex, and the medial hypothalamus (A. Schnider, 2003). Importantly, the anterior limbic system shares connections with the ventromedial prefrontal cortex and the posterior orbitofrontal cortex, areas that also elicit confabulations when injured (Gilboa et al., 2006). It is known that frontal lobe areas maintain reciprocal connections with the medial temporal lobes, so that both frontal and temporal lobes work together during encoding and remembering (Hirstein, 2005; Simons & Spiers, 2003). However, patients with medial temporal damage have also been found less likely to confabulate (Moscovitch & Melo, 1997; Schacter, Verfaellie, & Pradere, 1996). One explanation for this apparently contradictory data is the one given by Dalla Barba and colleagues (Dalla Barba & Boissé, 2010; Dalla Barba & La Corte, 2013), who suggest that lesions to the hippocampus lead to amnesia rather than to confabulations; whereas confabulations arise after damage to the temporoparietal cortex, the orbitofrontal cortex, or the thalamus as long as the hippocampus is at least partially preserved. Therefore, the anterior limbic system (aside from the hippocampus) and its connections to the prefrontal cortex could be crucial for the appearance of confabulations (Gilboa & Moscovitch, 2002; A. Schnider, 2003; Turner, Cipolotti, Yousry, & Shallice, 2008). Importantly, in the last decades, the study of cerebral functions has evolved from the observation of different brain areas to the study of neural networks and connection fibers, as it has been demonstrated that the same brain areas can be involved in various cognitive or emotional processes through the activation of specific neural circuits (Nyberg & McIntosh, 2001). Studies in this line have demonstrated that the cingulum and fornix tracts, two long-distance tracts from the limbic system (Catani, Dell'acqua, & Thiebaut de Schotten, 2013), are injured in patients with rupture of the anterior communicating artery aneurysm (ACoA), a pathology that often leads to confabulations (DeLuca, 2009; Hong et al., 2012). Taken together, this evidence suggest that, as proposed for certain types of amnesia (Aupée et al., 2001; Nahum et al., 2014; David M. Tucker, Roeltgen, Tully, Hartmann, & Boxell, 1988; Warrington & Weiskrantz, 1982), confabulation could be considered as a disconnection syndrome, probably affecting the main connections of the hippocampal-diencephalic and parahippocampal-retrosplenial network, such as the ventral cingulum, the fornix, and the mammillo-thalamic tract (see Catani et al., 2013, for a review of the limbic syndromes).

The study of the mechanisms underlying confabulation is crucial for the development of theoretical models, but it has also important practical implications in clinical neuropsychology. For a long time there has been no standardized rehabilitation program for reducing confabulations, as interventions have usually been tested in single-case reports

(Dayus & van den Broek, 2000; Del Grosso Destreri et al., 2002). Recently, Triviño et al. (2017) demonstrated the efficacy of an experimental memory treatment in reducing the frequency and number of confabulations in patients with acquired brain injury. The rehabilitation program also decreased perseverations, intrusions in free recall, and false positives in recognition in a sample of 20 confabulating patients. The treatment was expected to reduce confabulations through the improvement of selective attention during information encoding, monitoring processes during retrieval, and/or memory control processes after retrieval. The training of the above-mentioned processes would enhance awareness of the deficit and make confabulating patients increase the use of top-down processes of monitoring and verification. However, as the rehabilitation approach focused on three different mechanisms, it was not possible to know which one of them was associated with the reduction of confabulations. Nonetheless, the authors propose that the core impairment in confabulation could be related to selective attention or conflict detection mechanisms (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017).

Following Triviño's work (2017), in the present study we were interested in exploring the functionality and integrity of the three networks for attention (Petersen and Posner, 2012; Posner and Petersen, 1990) in confabulating patients. According to Posner and Petersen's model, attention can be divided into three distinct neural networks that are dissociable at the functional and anatomical levels. Alertness, spatial orienting, and executive functions are largely orchestrated by the frontal lobes, usually in coordination with parietal structures (Posner and Dehaene, 1994). Lesion studies, neuropsychological evidence, and functional magnetic resonance imaging (fMRI) studies have highlighted the role of the neurotransmitter Norepinephrine through projections of the Locus Coeruleus to the frontal and parietal lobes in alertness (Berger & Posner, 2000; for a review, see Aston-Jones and Cohen, 2005). The orienting of attention has been proposed to be implemented by two independent fronto-parietal subsystems: a dorsal network involved in the voluntary orienting of attention, and a ventral network involved in the re-orienting of attention to task-relevant stimuli (Corbetta and Shulman, 2002). The dorsal network includes brain areas from the dorsal frontal and parietal cortices, such as the frontal eye-fields, the superior parietal lobe, and the intraparietal sulcus, whereas the ventral stream is implemented in the temporoparietal junction and the ventral frontal cortex (Corbetta, Patel & Shulman, 2008). Coherent with fMRI evidence, recent tractography studies have demonstrated that the Superior Longitudinal Fascicule (SLF; connecting the parietal and frontal lobes thought three branches) has been largely implicated in the spatial orienting of attention, as its disconnection on the right hemisphere is related to spatial attentional deficits in neglect (Bartolomeo, Thiebaut De Schotten, & Doricchi, 2007; Thiebaut de Schotten et al., 2014). Recent research has also observed a correlation between the integrity of the left branch of the SLF with alertness in healthy controls (Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2017). Less is known about the implication of this fascicule in executive attention, or in the appearance of confabulations. On the other hand, studies analyzing grey matter and white matter microstructure have related executive control network of attention to the prefrontal cortex and, more specifically, to the anterior cingulate cortex and the cingulum bundles (Jin Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Metzler-Baddeley et al., 2012; Yeung, Botvinick, & Cohen, 2004).

In the present study, we used three experimental tasks to assess alertness, spatial orienting, and executive control in a group of confabulating patients. We divided the attention network test (Jin Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Jin Fan, McCandliss, Sommer, Raz, & Posner, 2002) into three separated tasks in order to simplify stimulus presentation and responses, as confabulating patients tend to have deficits in verbal and behavioral inhibition (Fotopoulou, Conway, & Solms, 2007). The alerting task used an auditory stimulus (on 50% of the trials) that was not predictive of the location of the target or the time interval in which it will be presented. The orienting task used a peripheral cue that attracted spatial attention either exogenously or endogenously. In different blocks of trials, we manipulated the predictability of the cue. It was not predictive of the future location of the target in one of the blocks, and it was predictive of the future location of the target in the other block of trials. In both the alerting and orienting tasks, participants had to discriminate an X/O stimulus presented in the left or right visual field by pressing either a left or a right situated key. This allowed us to measure a Simon-type conflict, as confabulating patients tend to be faster and more accurate when the response location matched the stimulus location as compared to conditions in which the response location did not match the stimulus location (Ródenas et al., 2015). Finally, we presented participants with a Go-NoGo task to measure executive control. In different blocks of trials we manipulated the proportion of Go stimuli hypothesizing that the condition with a high proportion of Go stimuli would require more executive control (response inhibition) when a NoGo stimulus was presented. From the multiple aspects of executive control, we chose to measure the motor inhibition component through a Go-NoGo task because previous studies from our lab had already explored stimulus-stimulus interference, stimulus-response interference, and inhibition of distractors (Ródenas et al., 2015).

We compared confabulators performance in the three experimental tasks with a lesion control group and a control group of healthy participants. Participants from the lesion control group were patients with acquired brain injury involving similar areas to the confabulating patients, but who did not show confabulations. We tried to match the three groups in age, years of education, and gender. If, as suggested by Triviño and colleagues, the core deficits involved in confabulations are related to selective attention and conflict detection processes (Triviño et al., 2017), we should expect larger impairments in the spatial orienting (Ródenas et al., 2016) and executive control tasks (Cunningham et al., 1997; Fotopoulou et al., 2007; M K

Johnson, O’Connor, & Cantor, 1997; a Schnider, von Däniken, & Gutbrod, 1996) in confabulating patients as compared to the two control groups.

We also acquired participants’ structural magnetic resonance images (T1 and DWI sequences) to explore the brain structures damaged in confabulating patients and the white matter tracts associated with attention deficits in those patients. We focused our analysis on the integrity of SLF, because the ventral branch of this fascicule (the so-called SLF III) has been largely implicated in the spatial orienting of attention (both in brain-damaged patients suffering neglect (Bartolomeo et al., 2007b) and in healthy controls (Thiebaut de Schotten et al., 2011), and in phasic alerting (Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2017). Less is known about the implication of the SLF in executive attention, although we could expect a correlation between executive attention and the dorsal branch of the SLF (the so-called SLF I), which is related to top-down attentional control. In addition, we expected that executive attention indexes would correlate with the microstructure of the anterior cingulum bundle. However, the analyses of the integrity of the anterior portion of the cingulum are still in progress and therefore are not included in this chapter.

5.2. Methods

5.2.1. Participants

62 participants (17 healthy controls, 22 lesion controls, and 23 confabulating patients) volunteered to take part in this experiment (35 males; mean age 61 years, SD = 13). All participants gave their written informed consent to participate in this study, in accordance with the Declaration of Helsinki (World Medical Organization, 1996). The study was approved the local ethical committees of the “Virgen de las Nieves” Hospital and the University of Granada.

The group of confabulating patients consisted of patients presenting confabulations (assessed through the Spanish adaptation of the Dalla Barba Provoked Confabulation Interview; see Llorente, 2008) as a consequence of acquired brain injury, whereas the lesion control group included patients with acquired brain injury (with similar etiology and lesion location as confabulating patients) in the absence of confabulations. Exclusion criteria for both clinical groups were: inability to maintain a vigilant state, language comprehension and/or production deficits, acute confusional state, or a history of psychiatric illness. Healthy control participants should present neither history of neurological or psychiatric conditions nor findings on their magnetic resonance images. All participants had a normal or corrected-to-normal vision, as well as normal hearing capacities. Brain lesions overlap for each group of patients can be seen in Figure 20. Most patients had right-hemisphere lesions, affecting the frontal lobes (superior and middle orbitofrontal cortices, and regions of the superior, middle, and inferior frontal gyri), the right post-central gyrus in the parietal lobe, the right insular cortex and operculum, the right putamen, and regions of the right inferior and middle temporal gyri.

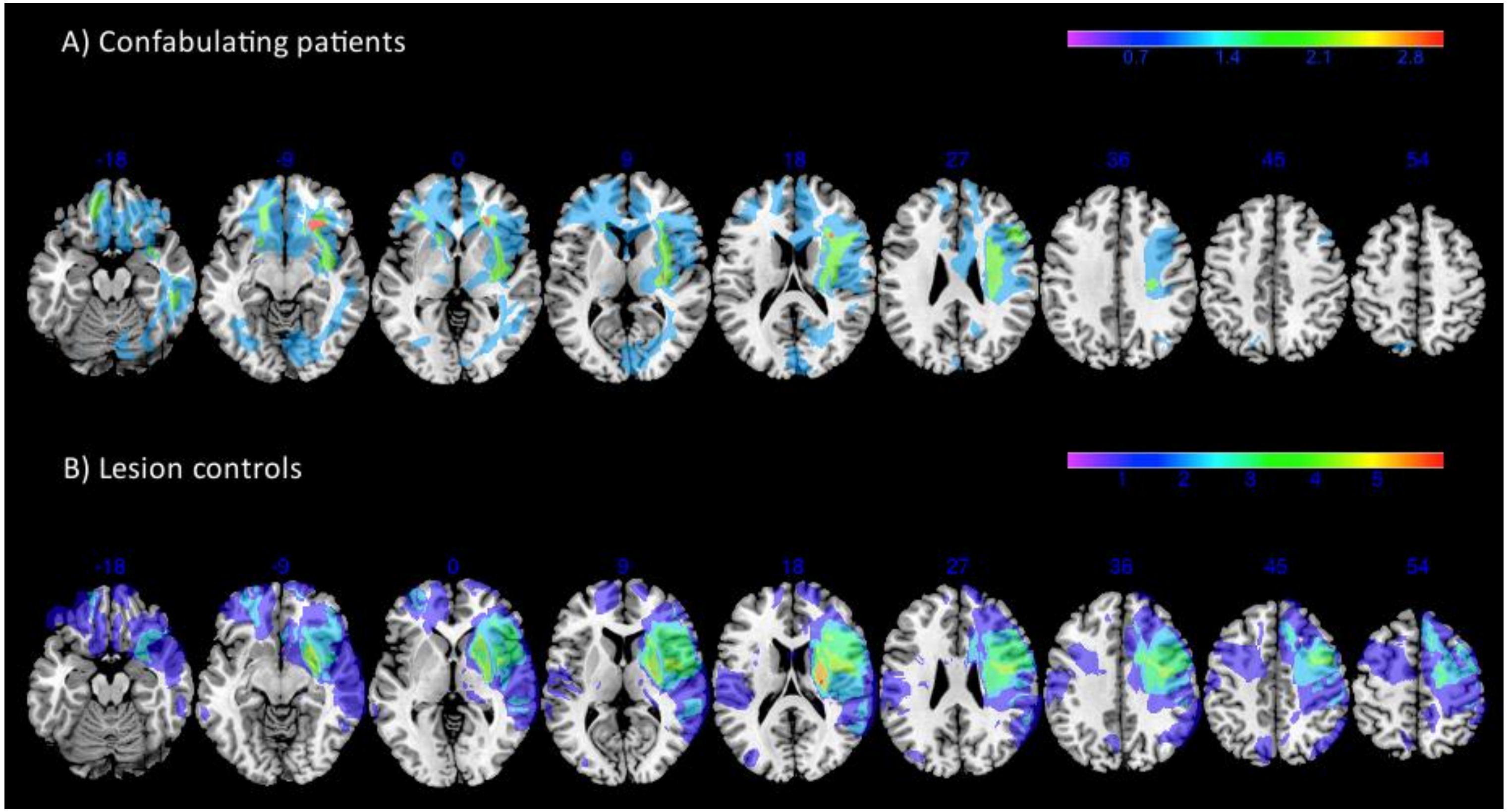


Figure 20. Overlapping of the lesions of patients from the confabulating group (A) (N=10) and from the lesion control group (B) (N=20). Warmer colors indicate a greater amount of patients showing lesions in those brain regions (maximum overlap: 3 patients in the confabulating group, and 6 patients in the lesion control group). Images are shown in neurological view (right hemisphere on the right side).

Table 5 shows the mean age, mean years of education, the total N of the three groups of the study, as well as the time since lesion and etiology of the lesion for the groups of lesion controls and confabulating patients.

Table 5. Demographical and clinical characteristics of the three groups of participants. The first three columns show the total sample of each group (with gender in parenthesis), mean age, and years of education (with SD in parenthesis). The last two columns show the months since lesion (with SD in parenthesis) and lesion etiology (with the number of patients in parenthesis) for the two clinical groups.

	N (62)	Age	Years of education	Months since lesion	Etiology of the lesion (N)
Healthy controls	17 (7 males)	62 (3.1)	11 (1.1)	-	-
Lesion controls	22 (14 males)	58 (7.7)	12 (0.9)	10 (2.4)	Vascular (13) Tumor resection (5) Traumatic (3) Subdural hematoma (1)
Confabulating patients	23 (14 males)	63 (2.7)	9 (0.9)	5 (1.7)	Vascular (15) Traumatic (4) Korsakoff syndrome (3) Hydrocephalus (1)

Participants underwent a comprehensive neuropsychological assessment including the evaluation of attention, perception, memory, language, and executive processes, in addition to assessment of confabulations. In the present work we report performance of healthy controls, lesion controls, and confabulating patients on tests measuring confabulations, memory, attention, and executive functions (see Table 6 on Results section), which are the cognitive processes that have been typically affected in confabulating patients, and thus, the cognitive processes of interest in the present study.

5.2.2. Experimental tasks

5.2.2.1. Alertness task

Apparatus and stimuli. E-prime software (Schneider, Eschman & Zuccolotto, 2002) was employed for task programming, stimulus presentation, and data collection. An HD Packard Bell 16’7” monitor was used. Participants sat at approximately 57” from the computer screen, and wore stereo headphones throughout the whole task. Visual stimuli were presented in white color against a black color background. A centered fixation point (0.5° x 0.5°) and two lateral markers (4.5° width x 3° height) appeared on the screen, with a distance of 5.5° between the markers and the fixation point (as measured from the center of the markers to the fixation point). Targets consisted of two white letters, an “X” and an “O” (0.7° x 0.6° each) that appeared within the lateral markers. In 50% of the trials, an alerting cue (500 Hz, 85 decibels) was presented. Timing and sequence of the stimuli are shown in Figure 21.

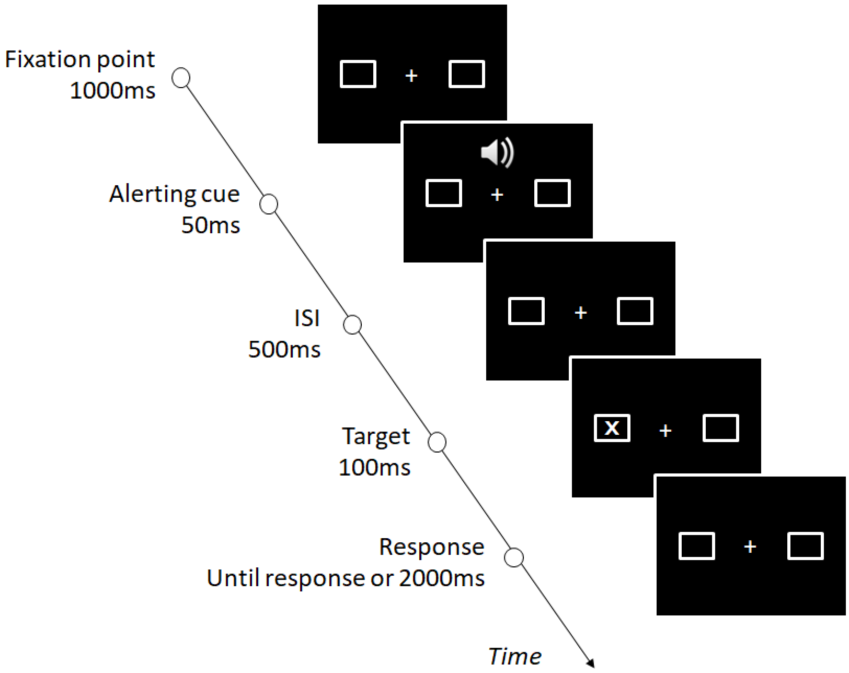


Figure 21. Timing and sequence of stimuli in the alertness task on a given trial.

Procedure. The experimental task was administered individually to each participant in a quiet and dimly illuminated room. Participants were asked to put their right index finger on the right mouse button and their left index finger on the left mouse button. Participants with left-side hemiplegia used their right hand but different fingers for both the left and right mouse buttons. Participants had to perform a discrimination task (see Figure 21), clicking one of the mouse buttons in response to the presentation of target "X", and the other mouse button whenever target "O" was presented (response button was counterbalanced across participants), regardless of the location of the stimuli. They were instructed to respond as fast and accurate as possible. Participants were not given any particular instructions concerning the alerting cue, except that they had to wear earphones because in some versions of the experiment a sound was presented. Participants completed 20 practice trials with feedback (to correct responses, incorrect responses, and no responses) before performing the experimental block, which consisted of 80 experimental trials with no feedback. Participants were allowed to take a short break after every 30 trials.

5.2.2.2. Orienting task

Apparatus and stimuli. Apparatus in this task was the same as in the alertness task, except that no earphones were used in the orienting task, as no auditory stimuli were presented. The experimental task was modified in order to assess spatial orienting instead of phasic alerting (see Figure 22). The fixation point, the two lateral markers, and the targets were the same as in the alertness task. In addition, before target appearance, a peripheral cue (white circle, 0.9° x 0.7°) appeared on the screen (0.3° x 0.1° distance from the lateral markers). The peripheral cue could appear above the marker in which the target will later appear, making that trial valid, or above the opposite marker, making that trial invalid.

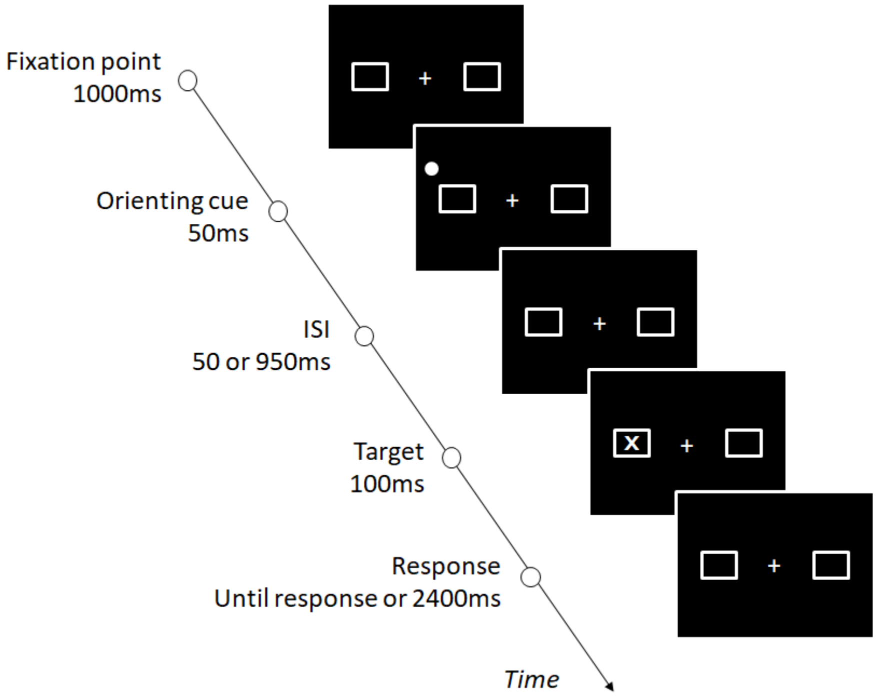


Figure 22. Timing and sequence of stimuli in the orienting task on a given valid trial.

Procedure. Instructions and procedure were similar to those in the alertness task. Participants were told to respond to the target and to not respond to the peripheral cue. The experiment consisted of 20 practice trials with feedback (to correct responses, incorrect responses, and no responses) and two experimental blocks without feedback. The first experimental block had 120 trials, in which 50% of the trials were valid and 50% were invalid trials (60 valid and 60 invalid trials). Therefore, in this block the peripheral cue was non-predictive of the target location. The second experimental block had 200 trials, where 70% of the trials were valid, and 30% of the trials were invalid (140 valid trials and 60 invalid trials). Therefore, in this block the peripheral cue was predictive of the target's location. Participants were allowed to take a short break after every 40 trials. The two experimental blocks were always presented in this sequence (see Bartolomeo et al., 2007; López-Ramón et al., 2011), and participants were encouraged to make a longer pause between blocks.

5.2.2.3. Go-NoGo task

Apparatus and stimuli. Apparatus in the Go-NoGo task was the same as in alertness and orienting tasks. In this task, a white central marker (4.5° x 3°) was presented in the center of the screen, on a black color background. Targets consisted of two numbers ("0" or "8", 0.7° x 0.6° each) that appeared inside the marker. Counterbalanced across participants, one of the numbers was assigned to the Go stimulus and the other number to the NoGo stimulus. Timing and sequence of the stimuli are shown in Figure 23.

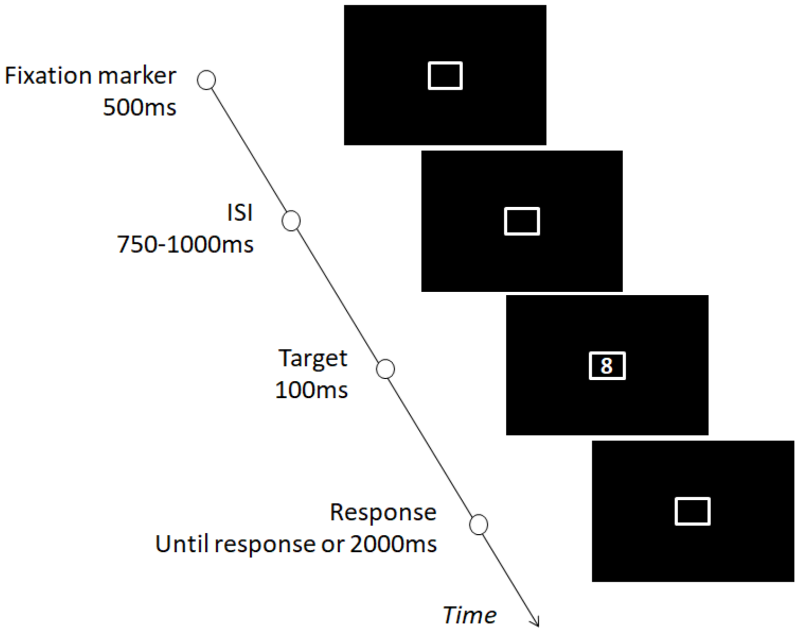


Figure 23. Timing and sequence of stimuli in the Go-NoGo task, on a given trial.

Procedure. Participants were instructed to press the left or right button of the mouse when the Go stimulus was presented and to withhold the response when the NoGo stimulus was presented. Response button and Go/No-Go targets were counterbalanced across participants. There were 10 practice trials with feedback (to correct responses, incorrect responses, and no responses to the Go stimulus) and two experimental blocks (100 trials) without feedback. In one of the blocks, the amount of Go and No-Go targets were equal (50 Go trials and 50 No-Go trials). In the other block, 80% were Go targets, whereas 20% were No-Go targets. Participants were allowed to take a short break after every 40 trials. The order of presentation of the experimental blocks was counterbalanced across participants, and participants were encouraged to make a longer pause between them.

5.2.3. Structural imaging acquisition and lesion delimitation

Brain MRI 3D T1 scans were acquired on a Siemens 3 Tesla TRIO TIM system with a 32-channel head coil for signal reception (echo time of 4.18 ms, repetition time of 2300 ms; acquisition matrix = 256 × 256; voxel resolution = 1 × 1 × 1 mm; slice thickness = 1 mm; 50% inter-slice gap; flip angle = 9°; 176 volumes acquired). T2 images were also acquired for lesion delimitation purposes. Lesions were assessed by an expert radiologist (HB) and by a neuropsychologist (IC), trained to read brain scans. First, lesion extent was determined for each patient by manually drawing the lesion borders directly onto the original 3D T1 MRI, by using the MRIcro software (Rorden and Brett, 2000, www.mricro.com). Then, the 3D brain scans and lesion volumes were normalized to the standard Montreal Neurological Institute (MNI) brain template in Statistical Parametric Mapping-8 (http://www.fil.ion.ucl.ac.uk/spm) running under Matlab 7.14, (http://www.mathworks.com). In order to reduce lesion-induced registration errors, spatial normalization was performed excluding the voxels contained in the lesion mask, thereby preventing the damaged areas from biasing the transformation (Brett, Leff, Rorden, & Ashburner, 2001; Volle et al., 2008). After normalization, the brain lesion was manually segmented, and its borders were redefined in the normalized brain. Finally, MRIcron software (Rorden & Brett, 2000) was used to estimate the lesion volume.

5.2.4. Diffusion-weighted imaging acquisition and preprocessing

We used a fully optimized acquisition sequence for the tractography of diffusion-weighted imaging (DWI), which provided isotropic (2 × 2 × 2 mm) resolution and coverage of the whole head with a posterior-anterior phase of acquisition. A total of 70 near-axial slices were acquired on a Siemens 3 Tesla TRIO TIM system equipped with a 32-channel head coil. We used an echo time (TE) of 88 msec and a repetition time (TR) of 8400 msec. At each slice location, 6 images were acquired with no diffusion gradient applied. Additionally, 60 diffusion-weighted images were acquired, in which gradient directions were uniformly distributed on the hemisphere with electrostatic repulsion. The diffusion weighting was equal to a b-value of 1500 s/mm^2. Finally, at each slice, diffusion-weighted data were simultaneously registered and corrected for subject motion and geometrical distortion adjusting the gradient accordingly (ExploreDTI, http://www.exploredti.com; see Leemans and Jones, 2009).

Damped Richardson Lucy Spherical Deconvolution (Dell’Acqua et al., 2010) was computed to estimate multiple orientations in voxels containing different populations of crossing fibers (Alexander, 2005; Anderson, 2005; Tournier, Calamante, Gadian, & Connelly, 2004). Algorithm parameters were chosen as previously described (Dell’Acqua, Simmons, Williams, & Catani, 2013). A fixed-fiber response corresponding to a shape factor of $\alpha = 2 \times 10–3$ mm^2/s was chosen (Dell’Acqua et al., 2013). Whole brain tractography was performed selecting every brain voxel with at least one fiber orientation as a seed voxel. From these voxels, and for each fiber orientation, streamlines were propagated using Euler integration with a step size of 1 mm (as described in Dell’Acqua et al., 2013). When entering a region with crossing white matter bundles, the algorithm followed the orientation vector of least curvature (as described in Schmahmann and Pandya, 2007). Streamlines were halted when a voxel without fiber orientation was reached or when the curvature between two steps exceeded a threshold of 45°. Spherical deconvolution, fiber orientation vector estimations, and tractography were performed using Startrack (http://www.natbrainlab.co.uk).

In order to facilitate the tractography dissection, regions of interest (ROI) for the three branches of the SLF were defined on the CS-MNI template calculated above, based on the guidelines provided in previous reports (see Catani and Thiebaut de Schotten, 2008; Rojkova et al., 2015). For each participant, the CS Map was registered to the CS-MNI152 template using ANTs.

Tract-specific measures of tract microstructural organization (i.e. mean Hindrance Modulated Orientational Anisotropy or HMOA for the whole tract, Dell'Acqua et al., 2013) were extracted from each dissected tract. HMOA provides information about the microstructural diffusion properties of distinct fiber orientations and therefore specific to the orientation of the reconstructed tracts and more accurate than classical fractional anisotropy measures, which decreases when fibers cross due to local partial volume effect. White matter correlates were studied by using a track-wise statistical approach that takes into consideration how different voxels are associated along the same white matter pathway (Thiebaut de Schotten et al., 2014).

5.2.5. Statistical Analysis

5.2.5.1. Participants

We carried out a Kruskal-Wallis ANOVA to assess whether the three groups differed on age or years of education, and a Mann-Whitney U test to check whether lesion controls and confabulators differed on months since the lesion onset.

5.2.5.2. Experimental tasks

We analyzed the mean accuracy for the alertness and orienting tasks. We did not analyze RTs in these two tasks because the large number of errors in the two clinical groups precluded the analysis of correct RTs. In the Go-NoGo task, we analyzed the percentage of hits (correct responses to the Go stimulus), the percentage of commissions (responses to the No-Go stimulus), and RTs to the Go stimulus. For each task, we run a repeated measures ANOVA for each dependent variable, with group as a between participants factor. Fisher post-hoc analyses were used to further explore interactions. We also explored whether significant interactions could be explained by the level of education or by the time since lesion conducting two additional ANOVAs with those variables as covariates. Simon congruency was included as an independent variable in the analyses of the alertness and orienting tasks, as this effect was clearly impacting participants' mean accuracy in those tasks.

5.2.5.3. Study of the grey matter

A t-test for independent samples was conducted in order to explore differences in lesion volume between the lesion control group and the group of confabulating patients. In order to study the anatomical correlates of alertness, spatial orienting and inhibition in our clinical samples, voxel-based symptom lesion mapping (VLSM) was performed. This technique consists of a voxel-by-voxel regression with one or more continuous measures (Bates et al., 2003), derived from the behavioral performance of the two groups of patients. For the VLSM, only significant voxels at $p < .05$ were considered (non-corrected for multiple comparisons). We used the nonparametric Brunner–Munzel test with 1000 permutations threshold (Inoue, Madhyastha, Rudrauf, Mehta, & Grabowski, 2014; Medina, Kimberg, Chatterjee, & Coslett, 2010), which corrects for the number of independent comparisons in a volume, without making assumptions about the spatial structure of the data (Kimberg, Coslett, & Schwartz, 2007). Lesion volume was added as a regressor in the VLSM analyses. Data from 30 participants from the lesion control and confabulating patients groups were included in the VLSM analyses (brain scans from the three Korsakoff patients could not be included in the analyses as they did not show any focal lesions in the MRI scans, and the rest of the patients presented contraindications for magnetic resonance imaging).

5.2.5.4. Study of the white matter

We assessed the lateralization of the three branches of the SLF in each group of participants, conducting t-test for single means on the HMOA lateralization index for each SLF branch (SLF I, SLF II and SLF III). Lateralization indexes were computed with the equation proposed by Zhao et al. (2016)[1], by which positive values indicate a right lateralization and negative values indicate a left lateralization. Finally, Pearson product-moment correlation coefficients were computed to assess the relationship between the integrity of the SLF of the three groups of participants and their behavioral performance on the experimental tasks and an index of confabulation from the neuropsychological tests. We employed Bonferroni's correction to correct for multiple comparisons; we performed 48 correlations in total (8 indexes by 6 SLF branches), and therefore results were considered significant when the *p*-value was inferior to 0.001 (the result of dividing alfa -0.05- between the number of comparisons). Partial correlations including lesion volume as a covariate were used for the two groups of patients to control for the effect of this variable in the observed correlations. For the diffusion-weighted imaging analyses, data from 45 participants were included (the rest of the participants presented contraindications for magnetic resonance imaging).

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[1] (HMOA right - HMOA left) / (HMOA right + HMOA left)

5.3. Results

5.3.1. Participants

The Kruskal-Wallis ANOVAs with age and years of education as dependent variables and group as a between participants factor demonstrated that there were no differences in age for the three groups of participants, $\chi^2(2, N= 62)= 3.77$, $p = .15$; however, there were significant differences in the years of education of the three groups, $\chi^2(2, N= 62)= 8.17$, $p = .02$. The level of education of confabulating patients was statistically lower than the level of education of lesion controls ($p = .03$). The Mann-Whitney U test for the number of months passed since the lesion until the assessment procedure showed significant differences between both clinical groups, $Z= 2.34$, $p = .02$. In order to account for these differences between the groups, years of education and months since lesion will be used as covariates in the analyses to control for the effect of both variables.

Table 6 shows the performance of confabulating patients in different neuropsychological tests measuring confabulations, memory, attention, and executive functions[2]. For data description purposes, we considered matched healthy controls' scores as non-impaired performance, and described both clinical groups' scores in relation to healthy controls' mean scores and SDs in each test. Confabulating patients presented an impaired performance in all neuropsychological tests measuring confabulations. They showed confabulations in the Dalla Barba Interview and in the Complex Rey Figure recall. They also showed a large number of intrusions in free recall and false positives in recognition, as measured by the Spanish version of the California Verbal Learning Test (Test de Aprendizaje Verbal España-Complutense, TAVEC). In addition, an impairment of short-term and long-term

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[2] The neuropsychological assessment also included perception and language tests; however, healthy controls, lesion controls and confabulating patients did not show impairments in these cognitive functions.

memory was observed in confabulators, when measured both in free and cued recall. Importantly, confabulating patients presented deficits in attention tests, especially in selective attention, alternating attention, and inhibition. Finally, they showed a poor performance but did not have impairments in executive functions, such as abstraction (measured with the Similarities subtest), working memory (Digit Span), and verbal fluency.

Table 6. Healthy controls, lesion controls, and confabulators' performance on neuropsychological tests measuring confabulations, attention, memory, and executive functions. Asterisks signal impaired performance.

COGNITIVE FUNCTION	TEST / PUNCTUATION	Healthy controls	Lesion controls	Confabulating patients
CONFABULATION	Dalla Barba Interview (errors)	0.19 (0.40)	1.55 (1.37)*	23.33 (9. 06)**
	Intrusions in free recall (TAVEC[1])	2.41 (2.27)	5.05 (5.77)	17.25 (18.02)**
	False positives in recognition (TAVEC)	1.35 (1.37)	2.45 (3.62)	15.85 (7.18)**
	Rey's Complex Figure[1] (confabulations)	0.00 (0.00)[†]	0.09 (0.29)*	0.85 (0.37)**
SUSTAINED ATTENTION	Auditory 'A' Test (Omissions/ Commissions)	0.18 (0.39)/ 0.18 (0.39)	0.26 (0.62)/ 0.09 (0.29)	0.50 (0.86)/ 0.41 (1.50)
SELECTIVE ATTENTION	Picture Completion (WAIS-IV)	11.36 (2.65)	9.65 (3.76)	3.71 (2.15)**
ALTERNATING ATTENTION	Color Trail B[2] (errors)	1.00 (2.33)	1.00 (1.84)	6.00 (8.20)
	Color Trail B (time in seconds)	112 (32)	224 (151)**	321 (134)**
INHIBITION	Inhibition Index (5 Digits Test)[1]	20.31 (8.40)	23.78 (22.70)	59.75 (67.02)**
MEMORY	Short-term free recall (TAVEC)	9.82 (3.21)	8.77 (4.02)	1.60 (1.50)*
	Short-term cued recall (TAVEC)	11.88 (2.87)	9.86 (3.72)	2.90 (2.49)**
	Long-term free recall (TAVEC)	11.00 (3.16)	8.91 (4.24)	1.70 (1.49)*
	Long-term cued recall (TAVEC)	11.76 (3.11)	9.91 (3.78)	2.75 (1.86)*
EXECUTIVE FUNCTION	Similarities (WAIS-IV)	13.06 (3.59)	11.78 (4.00)	6.38 (3.57)
	Digit Span (WAIS-III)	12.31 (2.60)	10.78 (3.13)	7.60 (2.11)
	Verbal Fluency (letter F)	8.69 (5.69)	9.57 (5.95)	3.55 (2.81)
	Verbal Fluency (animals)	17.38 (5.45)	17.57 (5.41)	8.27 (3.31)

[1] The attention deficits in one confabulating patient made these tests inapplicable to that patient.

[2] The attention deficits in one lesion control and nine confabulating patients made this test inapplicable to those patients.

Asterisks represent impaired performance in the clinical groups (* = scores 2SD below the mean score of matched healthy controls; ** = scores 3 or more SD below the mean score of matched healthy controls).

[†] In this test, scores >0 were considered impaired, and lesion controls' mean score and SD were used to assess confabulating patients' performance.

5.3.2. Experimental tasks

5.3.2.1. Alertness task

We ran an ANOVA on the mean accuracy, with Simon congruency (congruent or incongruent) and alertness cue (present or absent) as factors (see Table 7). Group (healthy controls, lesion controls, and confabulating patients) was introduced in the analysis as a between participants factor. From the 62 participants of the study, two participants did not complete the alertness task, and data from six additional participants (three lesion controls and three confabulating patients) were excluded from the analyses as they showed signs of neglect in the neuropsychological assessment. Therefore, data from 54 participants were included in the accuracy analyses from the alertness task (number of trials per condition; M= 20, SD= 3).

Table 7. Mean accuracy (standard error in parenthesis) as a function of group, Simon congruency, and alertness cue.

Group	Simon congruent		Simon incongruent	
	Cue absent	Cue present	Cue absent	Cue present
Healthy controls	.87 (.06)	.90 (.05)	.84 (.07)	.80 (.07)
Lesion controls	.81 (.06)	.86 (.05)	.77 (.06)	.76 (.07)
Confabulating patients	.61 (.06)	.66 (.05)	.40 (.06)	.48 (.06)

A main effect of group was observed, $F(2,51)= 10.41$, $p < .001$, $\eta_p^2 = .29$; healthy controls and lesion controls performed better than confabulating patients (both *p*s < .001). The main effect of Simon congruency was also significant, $F(1,51)= 13.43$, $p = .001$, $\eta_p^2 = .21$, indicating higher accuracy on congruent Simon trials as compared with incongruent Simon trials. This effect did not interact with the group factor, $F(2,51)= 1.89$, $p = .16$, $\eta_p^2 = .07$. The alertness cue effect, $F(1,51)= 6.68$, $p = .01$, $\eta_p^2 = .12$, interacted with the group factor, $F(2,51)= 4.31$, $p = .02$, $\eta_p^2 = .14$, indicating that the alertness cue effect on accuracy was only observed for confabulating patients ($p < .001$) whereas healthy controls and lesion controls did not show the effect (both *ps* > .22) (see Figure 24)[3]. No other main effects or interactions reached statistical significance (all *ps* > .06).

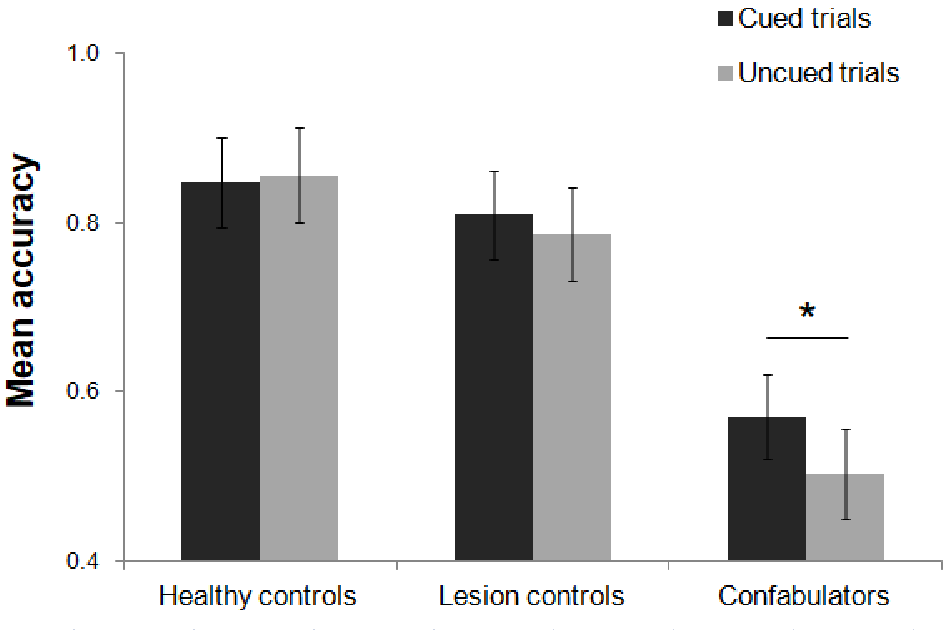

Figure 24. Alertness cue by group interaction in accuracy responses for the alertness task. Bars represent standard errors. Asterisks indicate statistically significant Fisher post-hoc comparisons.

In summary, confabulating patients showed lower accuracy than both healthy and lesion control groups. The expected Simon congruency effect was observed in the three groups. In contrast, the alertness cue effect was only observed in the group of confabulating patients, while it was not observed in healthy controls and lesion controls (although healthy controls did show the effect on RTs). Two further ANOVAs with years of education and time since lesion as covariates demonstrated that differences in the alertness cue effect between the three groups could not be accounted for by group dissimilarities in those variables. The alertness cue by years of education interaction and the alertness cue by time since lesion interaction were far from significance (both *ps* > .53).

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[3] An ANOVA on the mean RT for correct responses demonstrated that healthy controls showed the expected alertness effect on RTs (main effect, $p = .04$).

5.3.2.2. Orienting task

We conducted a repeated measures ANOVA on the mean accuracy, with Simon congruency (congruent or incongruent), predictability (non-predictive or predictive experimental block), SOA (short or long), and validity (valid or invalid) as factors (see Table 8). Group (healthy controls, frontal patients, and confabulating patients) was introduced in the analysis as a between participants factor. From the 62 participants of the study, three participants did not complete the orienting task, and data from six additional participants were excluded from the analyses as they showed signs of neglect syndrome in the neuropsychological assessment (three lesion controls and three confabulating patients). Therefore, data from 53 participants were included in the accuracy analyses (number of trials per condition; M= 20, SD= 13).

Table 8. Mean accuracy (standard error in parenthesis) as a function of group, Simon congruency, experimental block, SOA, and validity.

Group	Simon congruent								Simon incongruent							
	Non-predictive block				Predictive block				Non-predictive block				Predictive block			
	Short SOA		Long SOA		Short SOA		Long SOA		Short SOA		Long SOA		Short SOA		Long SOA	
	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid	Invalid	Valid
Healthy controls	.84 (.06)	.92 (.05)	.84 (.06)	.87 (.05)	.85 (.06)	.90 (.04)	.88 (.05)	.90 (.04)	.73 (.07)	.82 (.06)	.76 (.07)	.80 (.07)	.86 (.06)	.87 (.06)	.86 (.06)	.87 (.06)
Frontal patients	.75 (.06)	.81 (.05)	.80 (.06)	.79 (.04)	.77 (.05)	.83 (.04)	.76 (.05)	.86 (.04)	.71 (.07)	.75 (.06)	.75 (.06)	.73 (.06)	.74 (.05)	.77 (.06)	.77 (.06)	.79 (.06)
Confabulating patients	.55 (.06)	.64 (.05)	.60 (.06)	.58 (.05)	.55 (.06)	.66 (.04)	.59 (.05)	.68 (.04)	.42 (.07)	.43 (.07)	.44 (.07)	.44 (.07)	.35 (.06)	.47 (.06)	.42 (.06)	.49 (.06)

Results demonstrated a main effect of group, $F(2,50)= 12.57$, $p < .001$, $\eta_p^2 = .33$. Healthy controls and lesion controls performed better than confabulating patients (both *p*s < .001). We found a main effect of Simon congruency, $F(1,50)= 21.35$, $p < .001$, $\eta_p^2 = .30$, that interacted with group, $F(2,50)= 4.50$, $p = .02$, $\eta_p^2 = 15$. The Simon congruency effect was not significant for healthy controls and lesion controls (both *ps* > .12)[4], but it was statistically significant for confabulating patients ($p < .001$). The expected main effects of validity, $F(1,50)= 13.83$, $p < .001$, $\eta_p^2 = .22$, and predictability, $F(1,50)= 6.87$, $p = .01$, $\eta_p^2 = .12$, were observed. Responses were more accurate on valid as compared with invalid trials, and on the predictive as compared to the non-predictive block. An interaction between validity and SOA was found, $F(1,50)= 5.60$, $p = .02$, $\eta_p^2 = .10$, that was marginally mediated by predictability, $F(1,50)= 3.99$, $p = .05$, $\eta_p^2 = .07$. This marginal three-way interaction reflected the classic effects of validity, previously reported in the literature (Chica, Martín-arévalo, Botta, & Lupiá, 2014). In the non-predictive block, accuracy on valid trials was enhanced as compared to invalid trials (facilitation) at short SOAs ($p < .001$) but not at long SOAs ($p = .90$). In the predictive block, facilitation was observed both at short and long SOAs (both *p*s < .001). The three way interaction between validity, predictability, and SOA was not modulated by the group factor ($F < 1$). However, the interaction between validity, predictability, and group factor was significant, $F(2,50)= 4.76$, $p = .01$, $\eta_p^2 = .16$ (Figure 25). Planned comparisons demonstrated that the interaction between validity and predictability was different for the healthy control group as compared to both the lesion control group ($p = .06$, marginally significant) and confabulating patients ($p = .003$). Both clinical groups presented larger validity effects for the predictive as compared to the non-predictive cue block, which was not the case for the healthy control group[5]. No other main effects or interactions reached statistical significance (all *p*s > .07).

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[4] An ANOVA on the mean RTs for correct responses demonstrated that the group of healthy controls showed a Simon congruency effect on RTs (main effect, $p = .04$).

[5] The ANOVA on the mean RTs for correct responses demonstrated that this was not the case either for the RT dependent variable. The validity x predictability interaction was not significant for the healthy control group (Post-hoc planned comparisons, $p = .66$).

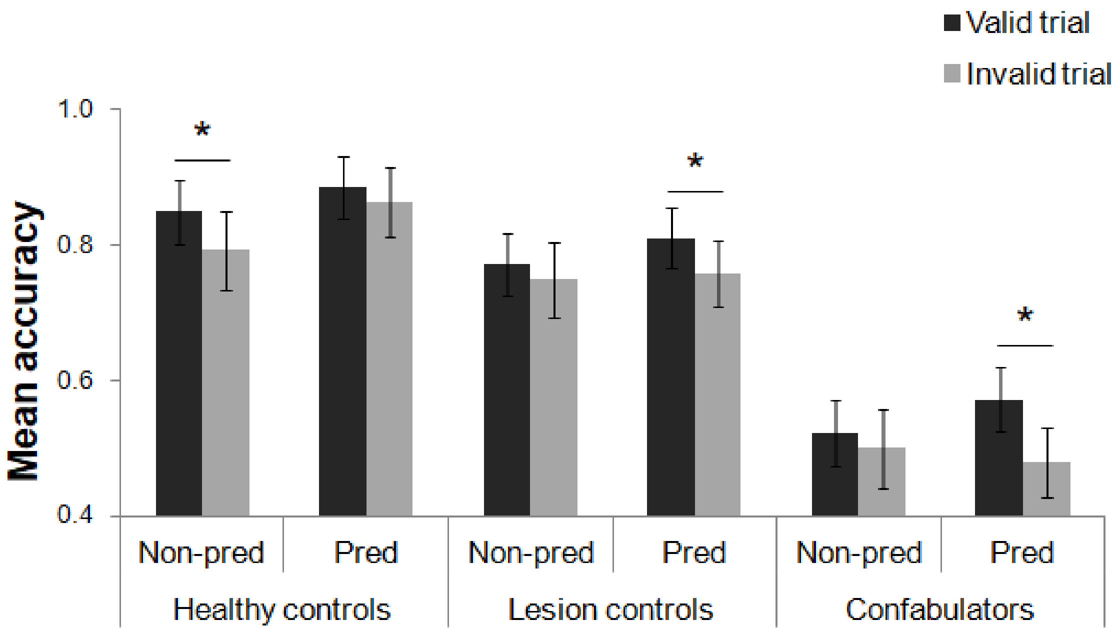

Figure 25. Validity x predictability x group interaction in accuracy responses for the orienting task. Bars represent standard errors. Asterisks indicate statistically significant Fisher post-hoc comparisons.

To summarize, as in the alertness task, confabulating patients showed lower accuracy as compared with healthy controls and lesion controls in the orienting task. The expected interaction between validity, experimental block, and SOA was marginally significant, and was not modulated by the group factor. The three groups equally benefited from the classic effects of validity, SOA, and predictability: valid trials elicited facilitation at short SOAs in the non-predictive block, and at both short and long SOAs in the predictive block. Both groups of patients showed greater validity effects on the predictive block as compared to the non-predictive block. Two additional ANOVAs with years of education and time since lesion as covariates demonstrated that this effect could not be accounted for by group dissimilarities in those variables. The validity by predictability interaction was not modulated by years of education, nor by time since lesion (both *ps* > .44). Finally, confabulating patients showed a Simon congruency effect on accuracy, whereas for healthy controls this effect was only observed on RTs. Again, complementary ANOVAs demonstrated no modulation of the covariates on the Simon congruency effect (both *p*s > .10).

5.3.2.3. Go-NoGo task

We ran three repeated measures ANOVAs to analyze the percentage of hits or correct responses to the Go stimulus, the percentage of commissions or responses to the No-Go stimulus, and RTs to the Go stimulus. Experimental block (50% Go - 50% No-Go block or 80% Go - 20% No-Go block) was considered as an intra-participant factor, and group (healthy controls, frontal patients, and confabulating patients) as a between participants factor (see Table 9). Data from patients with signs of neglect were not eliminated from these analyses because stimuli were not lateralized. Therefore, data from 62 participants were included in the analyses (number of trials per condition; M= 50, SD= 21).

Table 9. Mean percentage of hits, commissions, and RTs (standard error in parenthesis) as a function of group and experimental block.

Group	Hits		Commissions		RTs	
	50-50%	80-20%	50-50%	80-20%	50-50%	80-20%
Healthy controls	.98 (.05)	.99 (.04)	.05 (.03)	.11 (.04)	448 (57)	441 (44)
Frontal patients	.89 (.04)	.90 (.04)	.07 (.03)	.14 (.03)	544 (50)	513 (39)
Confabulating patients	.72 (.04)	.74 (.04)	.12 (.03)	.20 (.03)	815 (49)	729 (38)

The ANOVA for the mean percentage of hits showed a main effect of group, *F*(2,59)= 10.79, $p < .001$, $\eta_p^2 = .27$. Healthy controls and lesion controls made more hits than confabulating patients (both *p*s < .003). No other main effects or interactions reached statistical significance (all *p*s > .26).

The ANOVA for the mean percentage of commissions revealed a main effect of experimental block, *F*(1,59)= 20.75, $p < .001$, $\eta_p^2 = .26$, revealing that more commissions were observed in the experimental block with 80% Go and 20% No-Go trials as compared with the block with 50% Go and 50% No-Go trials. This effect was not mediated by the group factor ($F < 1$). No other main effects or interactions reached statistical significance (all *p*s > .31).

Finally, the mean RT ANOVA showed a main effect of group, *F*(2,59)= 14.22, $p < .001$, $\eta_p^2 = .33$, indicating larger RTs in the group of confabulating patients as compared with healthy controls and frontal patients (both *p*s < .001). The main effect of experimental block also reached statistical significance, *F*(1,59)= 11.69, $p < .001$, $\eta_p^2 = .17$, as did the interaction between experimental block and group factor, *F*(2,59)= 3.84, $p = .03$, $\eta_p^2 = .12$. While healthy controls and lesion controls did not show RTs differences between experimental blocks ($p = .79$ and $p = .12$, respectively), confabulating patients were faster in the block with 80% Go and 20% No-Go trials as compared with the block with 50% Go and 50% No-Go trials ($p < .001$) (see Figure 26).

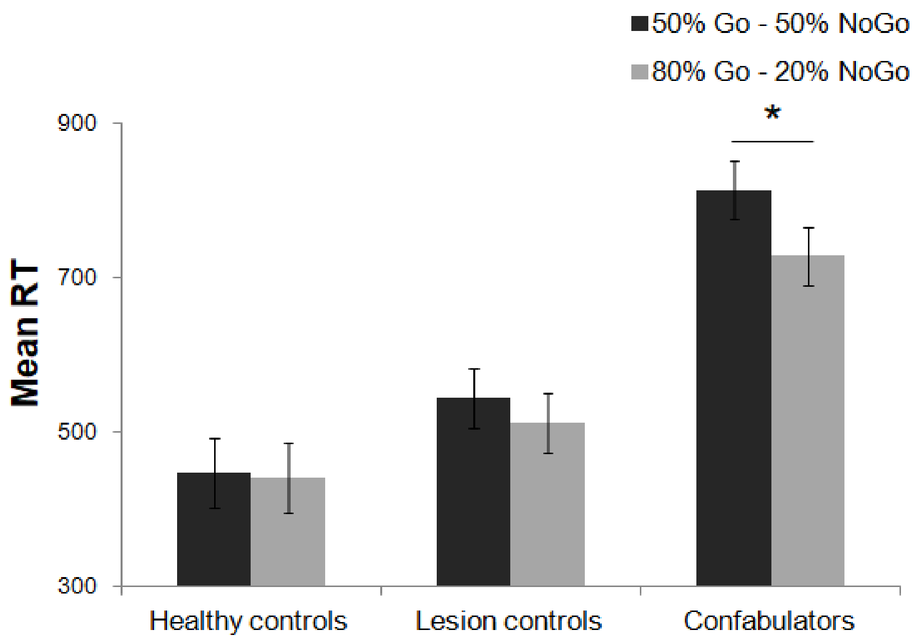

Figure 26. Group by experimental block interaction in RTs. Bars represent standard errors. Asterisks indicate statistically significant Fisher post-hoc comparisons.

In sum, confabulating patients made fewer hits and presented larger RTs than both healthy controls and lesion controls, while the three groups of participants presented more commissions in the experimental block with a higher proportion of Go trials as compared with the experimental block with the same amount of Go and No-Go trials. Interestingly, confabulating patients responded faster in the block with 80% Go and 20% No-Go trials as compared with the block with 50% Go and 50% No-Go trials, while healthy controls and lesion controls did not show RT differences across experimental blocks. Two further ANOVAs demonstrated that this experimental block by group interaction could not be accounted for by the differences on years of education or time since lesion (both *ps* > .69).

5.3.3. Study of the grey matter

In order to assess the lesional basis of the above-described behavioral differences between confabulating patients and lesion controls in the experimental tasks, we calculated one index for each observed effect:

- For the alerting task: mean accuracy on non-cued trials minus mean accuracy on cued trials.
- For the orienting task: mean accuracy on invalid trials in the predictive block minus mean accuracy on valid trials in the predictive block. Although in this task the Simon congruency effect was also influenced by the group factor, we did not include this index to avoid increasing the number of comparisons.
- For the Go-NoGo task: RTs in the block with 80% of Go trials minus RTs in the block with 50% of Go trials.

We performed VLSM analyses on the main accuracy for each task as well as on those indexes (seven behavioral measures in total, as accuracy in the Go-NoGo task was measured by both hits and commissions). In addition, we conducted another VLSM analysis on the total score of confabulations in the Dalla Barba Interview, to explore the lesional basis of this measure of confabulations in our sample of patients.

A t-test for independent samples demonstrated no significant differences in lesion volume between the two groups of patients, $t(27)= 0.27$, $p = .79$. However, as this variable could have modulated patients' performance on the experimental tasks regardless of the lesion location, it was included as a regressor in the VLSM analyses. VLSM revealed a significant implication of the right anterior insula (MNI coordinates, x=38, y=-8, z=7) and the right putamen (MNI coordinates, x=21, y=8, z=6) for the alertness cueing effect (see Figure 27).

These regions were therefore associated with the patients' alertness cueing effect (a better performance in the task on cued trials from the alertness task as compared with uncued trials). VLSM analyses also revealed a significant implication of the anterior right insula (MNI coordinates, x=34, y=17, z=15; and x=42, y=3, z=2), the right frontal operculum (MNI coordinates, x=45, y=-1, z=14), the right superior orbitofrontal gyrus (MNI coordinates, x=23, y=21, z=-13), the orbital and opercular regions of the right inferior frontal gyrus (rIFG) (MNI coordinates, x=36, y=36, z=-2; and x=38, y=19, z=16, respectively), and the right precentral gyrus in the posterior frontal lobe (MNI coordinates, x=44, y=-3, z=31) with the number of hits in the Go-NoGo task (see Figure 27). These regions were therefore associated with the patients' accuracy on Go trials. The analysis for the number of commissions in the Go-NoGo task revealed the implication of the triangularis part in the rIFG (MNI coordinates, x=32, y=22, z=25), and of the white matter of the inferior frontal gyrus (MNI coordinates, x=26, y=11, z=25) (see Figure 27). Results for the analyses of the behavioral indexes of the mean accuracy of the alertness and orienting task, for the validity index in the predictive block, for the mean RTs in the Go-NoGo task and for the number of confabulations in the Dalla Barba Interview did not yield significant results.

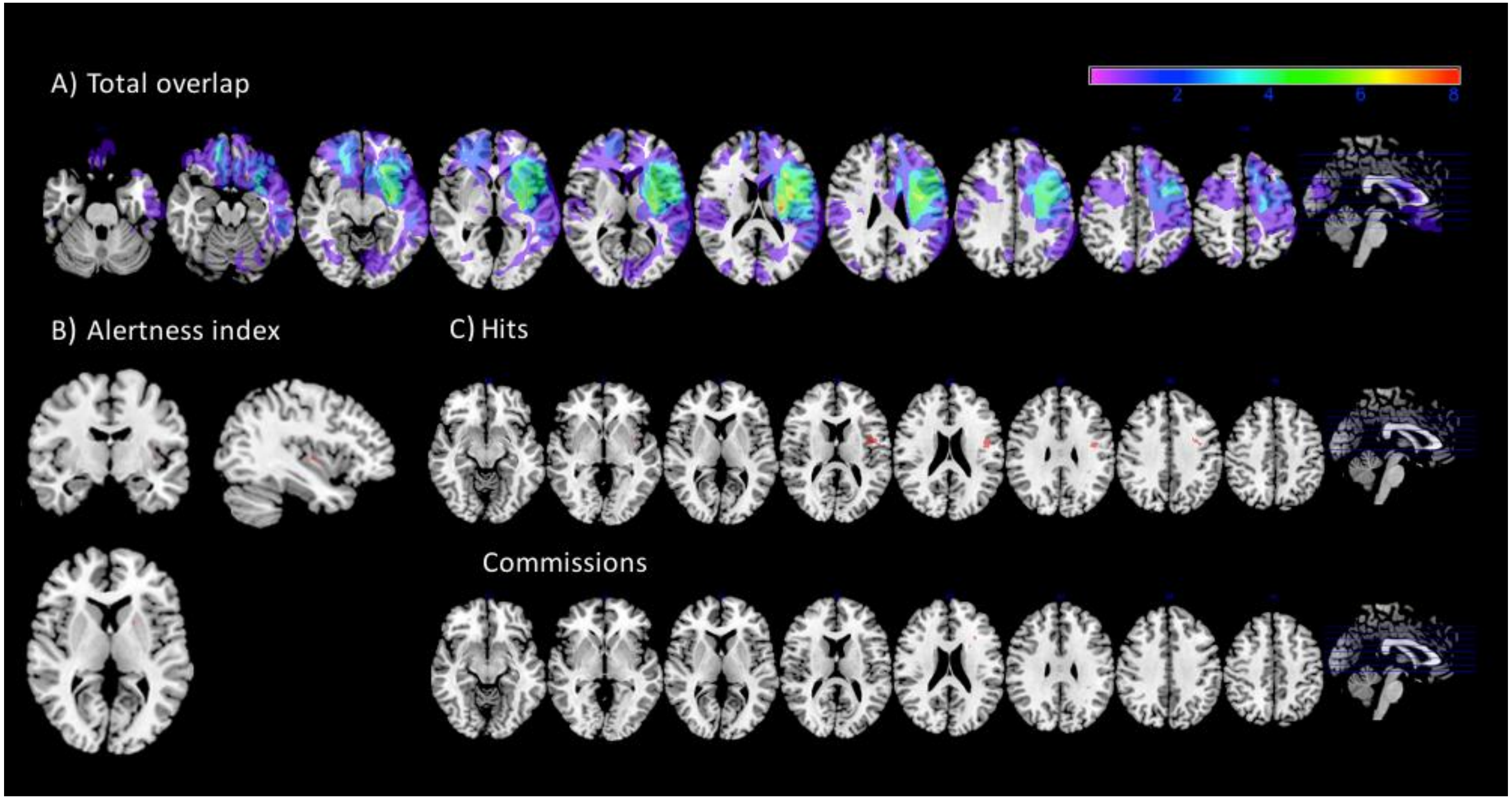

Figure 27. A) Lesion distribution in all patients, on which voxel-based lesion-symptom mapping analyses were performed. The maximum overlap (8 patients) was in the putamen, the insula, and subcortical white matter, in a location consistent with the trajectory of the ventral branch of the frontoparietal superior longitudinal fascicule (SLF III). B) VLSM results for the alertness cueing effect. C) VLSM results for hits and commissions in the Go-NoGo task. Images are shown in neurological convention (right hemisphere on the right side).

5.3.4. Study of the white matter

5.3.4.1. SLF anisotropy and lateralization

T-tests for single means analyses were run in order to assess the lateralization of the three branches of the SLF in each group of participants. For the healthy control group, the t-test showed that both SLF II and SLF III branches had a right lateralization in anisotropy, $t(12)= 2.66$, $p = .02$ and $t(12)= 4.45$, $p < .001$, respectively. SLF I lateralization index, by contrast, was not different from zero, $t(12)= .02$, $p = .98$, demonstrating that the fascicule was not lateralized. For the lesion controls and confabulating patients groups, none of the single means t-tests reached statistical significance (all *ps* > .37), indicating no anisotropy lateralization of any of the three branches of the SLF in our samples of patients (see Figure 28).

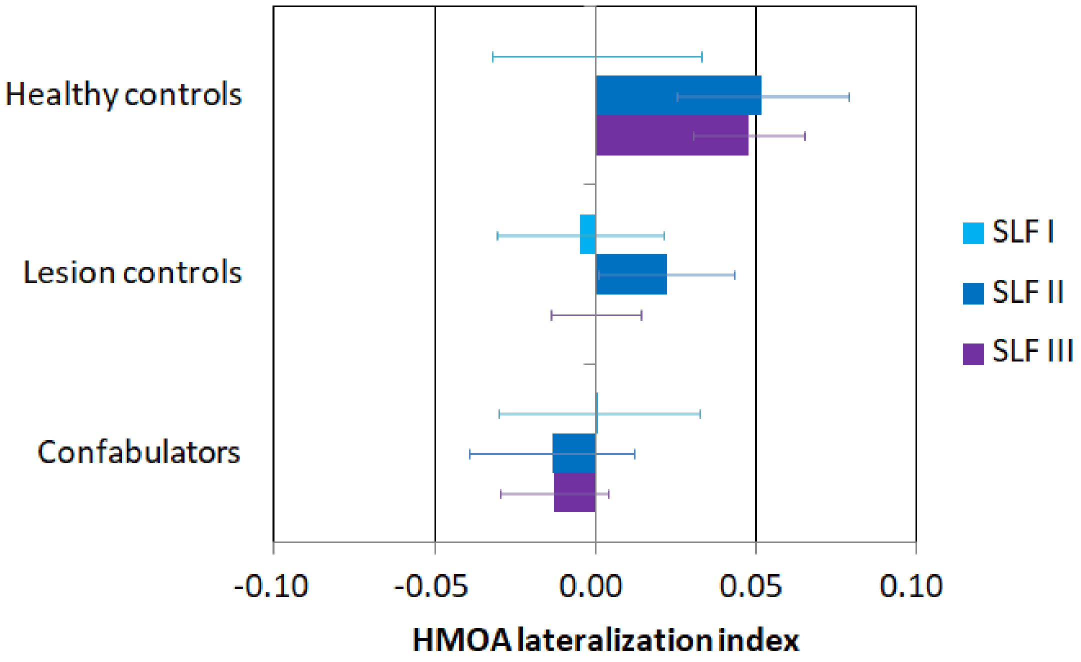

Figure 28. Lateralization of the mean HMOA of the three branches of the SLF in healthy controls, lesion controls, and confabulating patients. Bars represent standard errors. Healthy controls showed a right lateralization of SLF II and SLF III, while this lateralization was not observed in lesion controls or confabulating patients.

5.3.4.2. Behavioral indexes and their relation to SLF anisotropy

We explored the correlation of the same indexes tested in VLSM analyses (mean accuracy in the alertness and orienting tasks, the alertness index for the alertness task, the validity index in the predictive block for the orienting task, mean hits and commissions and the RT index for the Go-NoGo task, and scores in the Dalla Barba Interview) with the three branches of the SLF in both hemispheres. Thus, for each behavioral index (eight in total) six different comparisons were made. After applying Bonferroni correction for multiple comparisons only p-values < .001 are considered statistically significant.

In the alertness task, mean accuracy tended to correlate with integrity of the left SLF II, $r(41) = .42$, $p = .006$, and with integrity of the right SLF II and SLF III ($r(41) = .44$, $p = .003$ and $r(41) = .47$, $p = .002$, respectively). However, these correlations did not survive Bonferroni correction (all ps > .001). The alertness cueing index also showed a tendency to correlate with integrity of the right SLF III, $r(41) = .43$, $p = .005$, however, the correlation did not survive Bonferroni correction.

In the orienting task, mean accuracy correlated with integrity of the right SLF II, $r(42) = .49$, $p < .001$, and of the right SLF III, $r(42) = .55$, $p < .001$ (see Figure 29). The correlation with the right SLF I, $r(42) = .32$, $p = .035$, did not survive Bonferroni correction. We wondered if the correlation of the mean accuracy in the orienting task and the right SLF II and SLF III would be significant also in the two groups of patients, and if so, if it would be mediated by their lesion volume. We therefore conducted these two correlations including only participants from the two groups of brain-damaged patients, and we observed that they remained significant (both rs > .43, ps < .017). Moreover, the correlations remained significant (right SLF III, $r(26) = .40$, $p < .045$) or marginally significant (right SLF II, $r(26) = .37$, $p < .060$) when lesion volume was added as a covariate. The validity index in the predictive block tended to correlate with the integrity of the right SLF III, *r*(42) = .31, *p* = .04, however, this correlation did not survive the Bonferroni correction.

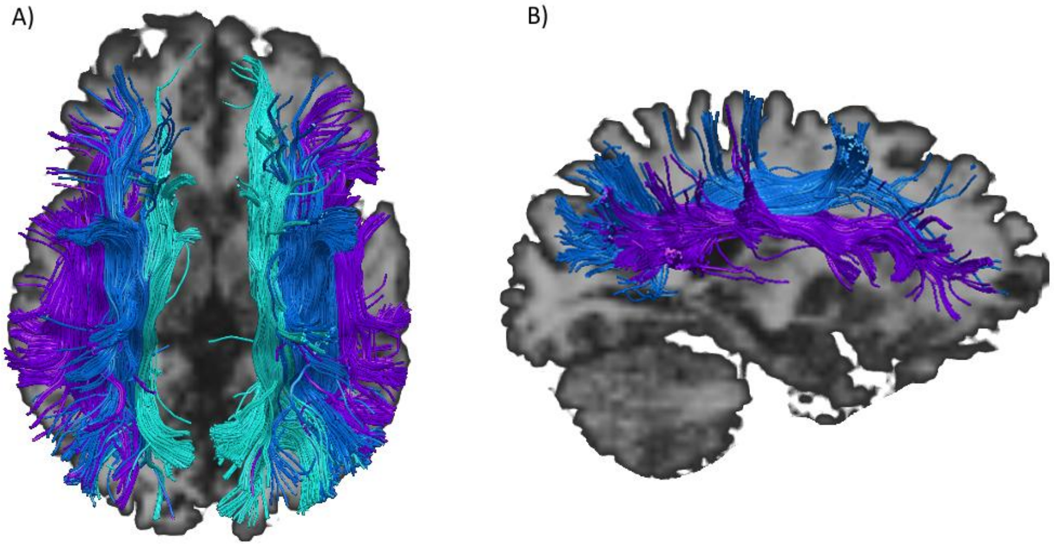

Figure 29. A) Axial superior view of the three branches of the SLF in left and right hemispheres of a given participant. B) Sagittal view of the right SLF II and SLF III of a given participant. A higher integrity of those branches of the SLF was related to a better performance in the orienting task in our study.

In the Go-NoGo task, the mean proportion of hits correlated with integrity of the right SLF II, *r*(43) = .51, *p* < .001, and the right SLF III, *r*(43) = .63, *p* < .001. The correlation with the right SLF I, *r*(43) = .33, *p* = .029, did not survive the Bonferroni correction. The analysis was repeated for the right SLF II and SLF III including only participants with brain damage, and the correlations remained significant (both *r*s > .48, *p*s < .006). However, these correlations were not significant when lesion volume was added as a covariate (both *r*s < .28, *p*s > .16). This indicates that these correlations could be mediated by lesion volume and might not be so much related to the integrity of the fasciculi themselves. The mean proportion of commissions did not significantly correlate with the integrity of any SLF branches (all *r*s < .23, *p*s > .13).

Mean RTs tended to correlate with the integrity of the right SLF III, *r*(43) = .37, *p* = .014, but this correlation did not survive the Bonferroni correction.

Finally, we correlated the total score in the Dalla Barba Interview, a neuropsychological test measuring confabulations, with the integrity of the three branches of the SLF of the left and right hemispheres. The Dalla Barba Interview score tended to correlate with integrity of the left SLF I and SLF II (both *r*s(41) = .36, both *p*s = .02), and with integrity of the right SLF I and SLF II (*r*(41) = .37, *p* = .02, and *r*(41) = .46, *p* = .002, respectively). However, these correlations did not survive the Bonferroni correction for multiple comparisons.

In sum, white matter results demonstrated that integrity of right SLF II and right SLF III correlated with participants' accuracy in the orienting task (the correlation with the right SLF III did not survive Bonferroni correction). The number of hits in the Go-NoGo task also seemed to correlate with the integrity of the right SLF II and right SLF III (the correlation with the right SLF I did not survive Bonferroni correction), although partial correlations demonstrated that this relationship was mediated by lesion volume. The correlations of the mean accuracy in the alertness task and integrity of the left SLF I, and right SLF II and SLF III, and of the validity index in the predictive block from the orienting task and the right SLF III, did not survive the Bonferroni correction for multiple comparisons. This was also the case for the correlation between the RT index in the Go-NoGo task and the integrity of the right SLF III, and for the correlation between the number of confabulations measured with the Dalla Barba Interview and the integrity of bilateral SLF I and SLF II.

5.4. Discussion

This work contributes to a better comprehension of the impaired cognitive processes in confabulation as well as its neural basis. We employ experimental tasks that can help to disentangle attentional deficits associated to confabulation, providing fine evidence about the neuropsychological profile of confabulating patients. We predicted that confabulating patients would present specific impairments on the functioning of the attention networks, which might be an important factor for confabulation to appear. As previously reported, our group of confabulating patients presented brain damage mainly in the frontal lobe (specifically in the inferior frontal cortex and the orbitofrontal cortex), the insula and in subcortical structures such as the putamen. They presented brain damage mostly in the right hemisphere, which is also consistent with the increased frequency of confabulations, paramnesic misidentification, and anosognosia in these patients (A. Schnider, 2008; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017; Venneri & Shanks, 2004). Homologous lesions in the left hemisphere are instead associated with severe language disorders (Berwick, Friederici, Chomsky, & Bolhuis, 2013). The neuropsychological assessment confirmed that confabulating patients and lesion controls showed confabulations in the Dalla Barba Interview and Rey's Figure test, and that confabulating patients also confabulated in verbal free recall and recognition, whereas healthy controls and lesion controls did not.

The aim of the present study was to explore the attentional deficits in confabulating patients using three different computerized tasks that measured phasic alertness, endogenous and exogenous spatial orienting, and executive control through a Go-NoGo task. The alertness and spatial orienting tasks presented lateralized stimuli requiring a lateralized shape discrimination response, therefore allowing measuring another form of conflict, the Simon effect. Behavioral results demonstrated that confabulating patients presented an important amount of errors for incongruent Simon trials. In general, their accuracy was lower than the accuracy in both the lesion control group and the healthy controls, and this effect was in part driven by the Simon congruency effect. The stimulus-response conflict measured in the Simon effect impaired confabulating patients' performance in the lateralized discrimination tasks. We also characterized the profile of response disinhibition in confabulation with the results of the Go-NoGo task. When the tendency to response was increased in the 80%Go – 20%NoGo block (as compared to the 50%Go – 50%NoGo block) confabulating patients demonstrated a benefit in RTs that was not present in the other groups of participants. Furthermore, neuropsychological assessment in our study revealed disinhibition in the group of confabulating patients, as demonstrated by the number of intrusions and false positives in memory tests. Confabulators also presented problems to inhibit dominant responses (as demonstrated by their inhibition scores in the 5 Digit Test), and to shift the attentional focus (as judged by their scores in the Color Trail B). This is consistent with previous results demonstrating executive attentional impairments associated to confabulation (Cunningham et al., 1997; Fotopoulou, Conway, & Solms, 2007; Ródenas, Rodríguez-Bailón, Funes, Lupiáñez, & Triviño, 2015). This response disinhibition might contribute to the presence of confabulation, in which responses are provided with no monitoring of the information (Gilboa et al., 2006; M K Johnson, Hayes, D'Esposito, & Raye, 2000; Moscovitch & Melo, 1997).

Confabulating patients also demonstrated increased alerting effects in the alertness task as compared to the two control groups. This result might also be related to their inability to inhibit distractors, using attentional signals that are not at all related to the relevant target (the alerting cue was not predictive of the location, moment of presentation, or identity of the target). It is important to notice that although the use of alerting signals was beneficial in this task (accuracy to respond to the discrimination task increased when the signal was presented as compared to no alerting signal conditions), many studies have demonstrated that alerting signals sometimes shorten RT but at the expense of accuracy (Jin Fan et al., 2009; Posner, 1994). Therefore, the increased use of alerting signals in confabulating patients might or not be beneficial for the patients depending on the task at hand. Confabulating patients could have presented a similar trade-off on the Auditory “A” test (measuring sustained attention), as they not only made omission errors, which could indicate a lower vigilant state, but also commission errors, which could point towards an inefficient usage of phasic alertness.

Concerning the orienting task, confabulating patients showed the traditional validity, predictability, and SOA effects, as they did lesion controls and healthy controls. However, both groups of patients had larger validity effects on the predictive block as compared to the non-predictive block, suggesting a larger dependence on exogenous cues as compared to healthy controls. This pattern of results seems similar to the increased alertness effect, and it could reflect a performance characterized by a higher reliance on external (alertness/orienting) cues due to a low sustained attention capacity. In fact, this high sensitivity to irrelevant stimuli, added to an impaired inhibition, could be mediating confabulating patients’ performance in the Picture Completion test, where instead of making omissions (not finding the target) they select irrelevant stimuli and have troubles inhibiting them.

The analysis of the grey matter showed that, as previously reported in the literature, the anterior insula and the anterior putamen have an important role in distractibility or task engagement (Langner & Eickhoff, 2013). Consistent with this evidence, damage to the right anterior insula and the right anterior putamen in our lesion controls and confabulating patients was associated to an increased use of the alertness cue. The right insula has also been related to sustained attention (Thakral & Slotnick, 2009). Moreover, the insula is anatomically and functionally connected to the anterior and middle cingulate cortex (Augustine, 1996;

Medford & Critchley, 2010; Taylor, Seminowicz, & Davis, 2009), a crucial structure for cognitive control and conflict resolution (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Jin Fan, Fossella, Sommer, Wu, & Posner, 2003). These two regions are proposed to constitute an insular–midcingulate network, involved in switching between central executive and default mode networks, which presumably mediate states of task engagement versus disengagement (Sridharan, Levitin, & Menon, 2008). Our data are coherent with previous literature pointing out to the role of the anterior right insula (as part of the insular-midcingulate network) on task engagement, as patients with lesions involving this region became more vulnerable to the alertness cue, which in our case was not relevant for target-processing.

Grey matter analyses also showed an implication of certain frontal regions of the right hemisphere, such as the orbitofrontal cortex and the opercular inferior frontal cortex, on the number of hits in the Go-NoGo task. This result fits the literature proposing that the right inferior frontal cortex (rIFC) implements attentional monitoring and attentional detection (Chatham et al., 2012; Sharp et al., 2010; Stuss & Alexander, 2007), as patients from our study with lesions involving this region led to a reduced response to Go targets in the Go-NoGo task. Damage to the rIFG was also related to the number of commissions in the Go-NoGo task, which reflects the ability to inhibit motor responses. This result fits previous fMRI studies demonstrating rIFG activation in stop-signal paradigms (Sharp et al., 2010), and some control models postulating that the rIFC exerts inhibitory control (Aron, Robbins, & Poldrack, 2004, 2014). Thus, this region could be mediating response inhibition to the No-Go stimulus in our sample of patients.

Concerning white matter pathways, the lesions of our two groups of patients mostly affected the trajectory of the right SLF. This was demonstrated by the analyses on the lateralization of the three SLF branches in each group. Whereas healthy controls showed the expected right lateralization of the SLF II and SLF III (Thiebaut de Schotten et al., 2011), this lateralization was not observed in lesion controls and confabulating patients, suggesting that the integrity of the right SLF II and SLF III in those patients was diminished due to their brain lesions (Zhao, Thiebaut de Schotten, Altarelli, Dubois, & Ramus, 2016).

Moreover, the analysis of the white matter provided important information about the brain networks underlying the functioning of the three attentional networks. Consistent with previous data (Thiebaut de Schotten et al., 2014) and with some theoretical models about spatial orienting (Thiebaut de Schotten et al., 2011), accuracy in the orienting task correlated with the integrity of the SLF II and SLF III in the right hemisphere. This is consistent with previous results demonstrating the importance of the right hemisphere in spatial orienting, especially in left unilateral neglect (Chica et al., 2012b), as lesions to the right parietal lobe and its connections to the ipsilateral frontal cortex are usually associated to important impairments of spatial orienting (Corbetta & Shulman, 2011). Even though the integrity of these branches of the SLF correlated with the accuracy in the orienting task, we did not observe impairments on patients' performance in the spatial orienting task, probably because patients' lesions involved mostly the frontal lobe, with preservation of parietal regions. These results are only partially consistent with Corbetta and Shulman's attentional model (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) proposing that the spatial orienting of attention (whether endogenous or exogenous) is implemented in a bilateral fronto-parietal network, while a right-lateralized ventral fronto-parietal network is related to the re-orienting of attention to task-relevant events. Data from neglect patients (Bartolomeo, Thiebaut De Schotten, & Doricchi, 2007; Lunven et al., 2015; Thiebaut de Schotten et al., 2014) demonstrate the importance of the right hemisphere for the orienting of attention, and the present set of data highlight the importance of right hemisphere white matter connections between the frontal and the parietal lobes.

We also observed a correlation between the integrity of the right SLF II and SLF III with the number of hits in the Go-NoGo task, although partial correlations demonstrated that these correlations were mediated by lesion volume. Therefore, executive control functions measured with the Go-NoGo task are not consistently related to the integrity of any of the branches of the SLF. This executive function might instead be related to the integrity of other frontal fascicules such as the cingulum (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Jin Fan, Fossella, Sommer, Wu, & Posner, 2003). We are currently dissecting this fascicule in our sample of participants to prove this hypothesis.

We also explored whether the functionality of cortical areas and their connections was related to confabulations, as measured by the Dalla Barba Interview. Although the correlations between the bilateral SLF I and SLF II and the score in the Dalla Barba Interview did not survive the correction for multiple comparisons, a relation between the integrity of the SLF and the number of confabulations would suggest a correlation between attentional circuits of the brain and confabulation, as this fascicule does not connect to structures from the limbic system. More research should be done in order to further explore this hypothesis. Alternatively, this relationship between the presence of confabulations and the integrity of white matter tracts could be observed in the cingulum bundle, which has projections from the amygdala, uncus, and parahippocampal gyrus to sub-genual areas of the frontal lobe (Crosby, Humphrey, & Lauer, 1962; Nieuwenhuys, Voogd, & van Huijzen, 2008). Next steps in the present study include testing the hypothesis that the integrity of the anterior bundle of the cingulum will correlate with participants' performance in executive attention measures, as suggested by previous studies (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Jin Fan, Fossella, Sommer, Wu, & Posner, 2003). Moreover, in light of the monitoring theories about confabulation, we intend to explore the relationship between this executive control bundle and neuropsychological measures of confabulation. Those analyses could contribute to identify the cognitive processes and neural networks responsible for confabulations after brain damage.

Chapter 6: General discussion

6.1. Summary of the empirical evidence presented in this thesis

The main aim of the thesis was to explore the role of frontal lobe structures in the control of attention. We examined this issue through two different series of studies, each one responding to a specific theoretical question. First, we investigated the functional and neural relationship between the executive control aspect of attention, a mechanism known to mainly rely on frontal networks and structures, and the conscious perception of visual stimuli. The two behavioral experiments from Chapter 2 revealed an impact of the interference control aspect of executive control on conscious perception. Specifically, participants adopted a more conservative response criterion to detect near-threshold stimuli on trials prompting a larger amount of interference control, such as when facing incongruent and infrequent Stroop stimuli (as compared to congruent and frequent stimuli), and when participants committed an error (as compared to a hit) in the Stroop task. This effect on the response criterion was associated with the implementation of reactive mechanisms of control. In contrast, in experimental conditions thought to prompt the recruitment of proactive control, committing a Stroop error in the sequential task led to a decreased perceptual sensitivity to detect subsequently presented near-threshold stimuli.

In order to explore whether this behavioral interaction was due to neural modulations of executive control processes on visual conscious perception, we conducted a similar experiment using high-density EEG (Chapter 3). We found that the conscious detection of the near-threshold stimulus was associated with an amplitude enhancement of the anterior N2 component to the presentation of the Stroop stimulus, assumed to reflect the operation of a conflict detection system (Luck, 2012; Yeung et al., 2004), on trials eliciting larger interference (incongruent and infrequent trials in the high proportion congruent session, and congruent and infrequent trials in the low proportion congruent session). Source-location analyses confirmed that changes in N2 component amplitude were likely produced by activation of the anterior cingulate cortex (ACC), a key brain area for cognitive control (Botvinick, Cohen, & Carter, 2004; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; S. E. Petersen & Posner, 2012). This conscious perception modulation depended on both congruency and proportion congruency, with an enhanced N2 for incongruent-seen trials as compared to incongruent-unseen trials in the high proportion congruent session, and an enhanced N2 for congruent-seen trials as compared to congruent-unseen trials in the low proportion congruent session. Therefore, the modulation of the N2 component for consciously perceived as compared to non-perceived trials seems to be more related to the interference generated by a mismatch between an expectation and a stimulus (as the effect was observed only on infrequent Stroop trials from each session), rather than to the interference produced by incongruent Stroop stimuli. In sum, data from the study presented in Chapter 3 showed frontal lobe modulations of neural activity associated with expectancy-related interference on visual conscious perception of near-threshold stimuli.

Results from this first line of research (Chapters 2 and 3) add empirical evidence to the existence of a tight relationship between attention and consciousness, and demonstrate that the recruitment of attentional control impacts conscious perception of near-threshold stimuli both at the behavioral and the neural level. This evidence is coherent with previous studies showing conscious perception modulations caused by working memory (Colzato, Spapé, Pannebakker, & Hommel, 2007; De Loof, Poppe, Cleeremans, Gevers, & Van Opstal, 2015; Fougnie & Marois, 2007), which constitutes one of the three aspects of the executive functions (Diamond, 2013; Miyake et al., 2000), and might also reflect the operation of the executive control network of attention.

The second line of research addressed the implication of the frontal lobes in attention and consciousness with a different approach. In this study, instead of manipulating attention and measuring consciousness (experimental studies in Chapter 2), and the neural activity associated to both processes (experiment in Chapter 3), we measured attention in a clinical population known to have deficits in consciousness and damage to the orbitofrontal cortex: patients showing the confabulating syndrome as a consequence of an acquired brain injury. The main aim of this line of research (Chapter 4) was to test the functionality and integrity of the three attentional networks in the confabulating syndrome after acquired brain injury, as compared with non-confabulating brain-damaged patients and a group of healthy controls. Confabulating patients' mean accuracy in the experimental tasks measuring attention was lower than other groups' mean accuracy, and they demonstrated executive control impairments as measured by the Simon congruency effect and by their performance in the Go-NoGo task (in addition to low scores in neuropsychological tests measuring executive functions). Concerning alertness, confabulating patients demonstrated increased alerting effects to the cue as compared both to lesion control patients and to healthy controls, showing a benefit in the alertness task of our study but also pointing to a difficulty to inhibit distractors, as the alertness cue was non-predictive of the location or identity of the target. On the other hand, confabulating patients showed no particular deficits in the spatial orienting task, although both confabulators' and lesion control patients' performance in the orienting task seemed to rely on spatial cues more than healthy controls' performance.

Brain damage in our sample of confabulating patients involved the frontal lobe (mainly the inferior frontal cortex and the orbitofrontal cortex), the right insula, and subcortical structures such as the putamen. The analysis of the grey matter revealed an implication of the right anterior insula in the use of the alertness cue in our sample of patients, as patients with lesions involving this region showed an increased alertness effect. The right insula is thought to play a role in sustained attention, and to mediate states of task engagement and task disengagement through its connections with the anterior and middle cingulate cortex (Augustine, 1996; Medford & Critchley, 2010; Sridharan, Levitin, & Menon, 2008; Taylor, Seminowicz, & Davis, 2009; Thakral & Slotnick, 2009). Grey matter analysis also showed an implication of the orbitofrontal cortex and the opercular inferior frontal cortex on the number of hits in the Go-NoGo task. Patients with lesions involving this region showed fewer responses to Go targets. In addition, the right inferior frontal cortex (rIFC) was related to the number of commissions in the Go-NoGo task, as our sample of patients with brain damage to that region demonstrated more responses to NoGo targets. This inability to inhibit motor responses in patients with right inferior frontal damage is coherent with previous literature highlighting the role of the rIFC in inhibitory control (Aron, Robbins, & Poldrack, 2014; Sharp et al., 2010). Moreover, some authors have also proposed that the rIFC is involved in attentional monitoring and attentional detection (Chatham et al., 2012; Sharp et al., 2010; Stuss & Alexander, 2007), which could also explain why damage to the right inferior frontal cortex was associated to fewer responses to Go targets and more responses to NoGo targets.

Lesions of our sample of patients mostly affected the white matter pathways of the middle and ventral branches of the right superior longitudinal fascicule (right SLF II and right SLF III, respectively). In addition, the integrity of the two fascicule positively correlated with the mean accuracy only in the orienting task (with a greater integrity of SLF II and SLF III in the right hemisphere associated to a higher accuracy in the orienting task). This result is consistent with previous studies demonstrating the role of the right hemisphere in spatial orienting, especially in left unilateral neglect (Chica, Thiebaut de Schotten, et al., 2012), as lesions to the right parietal lobe and its connections to the right frontal cortex are usually associated to important impairments of spatial orienting (Corbetta & Shulman, 2011).

In this study, we demonstrated confabulating patients' executive control deficits as measured by experimental tasks. This result is coherent with previous literature demonstrating an alteration of executive functions in confabulating patients (Fotopoulou, Conway, & Solms, 2007; M K Johnson, O'Connor, & Cantor, 1997; a Schnider, von Däniken, & Gutbrod, 1996), as executive functions encloses the executive control network of attention (Diamond, 2013). Moreover, we found that, in our sample of patients, right inferior frontal damage was responsible for an impaired performance in the Go-NoGo task, including the failure to respond to Go targets, and the inability to inhibit responses to NoGo targets. In addition, we explored the integrity of the SLF in our sample of patients, a fasciculus that has been associated to spatial orienting and phasic alertness (Chica, Thiebaut de Schotten, et al., 2012; Chica, Thiebaut de Schotten, Bartolomeo, & Paz-Alonso, 2017; Corbetta & Shulman, 2011; Thiebaut de Schotten et al., 2014), and observed that, coherent to previous literature, the integrity of the right SLF II and SLF III was related to participants' general performance in the spatial orienting task.

In the next paragraphs, I will further discuss the findings of the three studies presented in this thesis and their possible interpretations. I will also point to the implication and limitations of our studies, and describe future research directions.

6.2. The heterogeneous nature of cognitive control: evidence for different types of conflict

In the first line of research (Chapters 2 and 3), we manipulated the amount of interference elicited by the experimental task in each experimental session or trial. On one hand, we presented congruent and incongruent Stroop stimuli either within a high proportion congruent context or within a low proportion congruent context. According to the dual mechanisms framework of control (Braver, 2012), a high proportion congruent situation is likely to elicit reactive control mechanisms, whereas a low proportion congruent situation more likely prompts proactive control mechanisms. In addition, we manipulated the timing of presentation of the Stroop stimulus and the near-threshold stimulus, hypothesizing that interference would be higher when both stimuli were presented concurrently as compared to when the Stroop stimulus and the near-threshold stimulus were presented in a sequential manner. This hypothesis was based on dual-tasks literature proposing higher conflict in dual as compared with simple tasks, due to the serial processing aspect of a central decision-related processing stage (Sigman and Dehaene, 2008; Tombu et al., 2011).

A challenging observation regarding interference control in experiments from Chapters 2 and 3 is the variable output (in terms of mean accuracy and RTs, or the N2 component) of our manipulation of interference, either through the concurrent vs. sequential task manipulation or through the manipulation of congruency and proportion congruency variables. For example, the manipulation of the timing of presentation of the Stroop and near-threshold stimuli (concurrent vs. sequential) only seemed to have an impact in participants' response to the Stroop task in the low proportion congruent experiment (Experiment 2 in Chapter 2), where, as predicted, participants were faster to Stroop stimuli in the sequential task as compared to the concurrent task. However, this manipulation did not have any impact (as measured by mean accuracy and RTs in the Stroop task) in the high proportion congruent experiment (Experiment 1 in Chapter 2).

Regarding congruency and proportion congruency manipulations, participants' mean accuracy and RTs to the Stroop task indicated that more interference was elicited (participants responded slower and less accurately) on incongruent trials as compared with congruent trials through the three experiments presented in Chapters 2 and 3. Moreover, all the studies showed that participants' congruency effect (reflected by both mean accuracy and RTs measures) in the high proportion congruent situation was larger as compared with their congruency effect in the low proportion congruent situation. This is consistent with studies manipulating reactive and proactive strategies of control (West & Bailey, 2012), and suggests that our manipulation of proportion congruency was successful in eliciting reactive control mechanisms (in high proportion congruent situations) and proactive control mechanisms (in low proportion congruent situations).

However, we did not find the expected modulation of the N2 component due to interference control (Chapter 3): the amplitude of this event-related component showed no differences on incongruent as compared to congruent trials, neither in the high proportion congruent session nor in the low proportion congruent session. Moreover, when performing source-location analyses, both congruent and incongruent Stroop stimuli seemed to involve activation of the anterior cingulate cortex (ACC). This apparently inconsistent result is however coherent with previous studies using neuroimaging techniques which showed that both congruent and incongruent Stroop trials trigger higher ACC activations than neutral trials (Bench et al., 1993; Cameron S. Carter, Mintun, & Cohen, 1995). Therefore, the observed activation of the conflict-related ACC on congruent Stroop stimuli in our experiment could explain the contradiction between our behavioral and ERP results. In fact, recent studies have attempted to solve this contradiction by proposing that trials in the Stroop task reflect two different types of interference: information conflict and task conflict (Kalanthroff, Goldfarb, Usher, & Henik, 2013). Information conflict in the Stroop task refers to the mismatch between the word meaning and the word's ink color, whereas task conflict would concern the relevant identification of the color and the irrelevant but automatic reading process. Kalanthroff and colleagues argue that task conflict may arise in situations in which the proactive top-down control mechanism is diminished, making stimuli trigger a reactive response of the associated task demands (Kalanthroff et al., 2013). Studies from their research group have demonstrated that the implementation of reactive control strategies (in situations where the proportion of neutral non-word stimuli —e.g. XXXX— is higher than the proportion of word stimuli) elicit task conflict even in the absence of incongruent trials along the task (Goldfarb & Henik, 2007; Kalanthroff et al., 2013). This evidence suggests that under reactive control strategies (or, in the authors' words, "when proactive control is likely to be less active"), the conflict between the relevant task and the irrelevant task triggered by the association with a stimulus is elicited automatically, without the need of incongruent stimulation.

A potential concern of the results of our study, therefore, is that many different forms of conflict could be mediating individuals' behavioral and neural performance. In addition to our manipulation of interference through the timing of stimulus presentation and the manipulation of proportion congruency, stimulus and task conflict may be shaping our results. In that case, the variability of responses could be reflecting several control processes. In fact, in agreement with Norman and Shallice's model of attention (1986), we had already anticipated that task difficulty, novelty detection, and error-commission, were sources of conflict. However, the modulations of such different types of conflict might complicate the interpretation of the results. One possible solution to this confounding factor would be to try to replicate our experiments using the same experimental designs that have been reported in previous studies eliciting reactive and proactive control. In fact, a common approach to measure both reactive and proactive control in tasks eliciting conflict is to present cues (along with non-cued trials) informing about the type of stimulus (congruent or incongruent) that is going to appear next. In this kind of paradigms, participants can proactively confront incongruent trials following a cue, but they have to rely on reactive control mechanisms to respond to a non-cued incongruent stimulus (Goldfarb & Henik, 2007; Gonthier, Macnamara, Chow, Conway, & Braver, 2016; Kalanthroff et al., 2013).

It would be interesting to apply this cueing manipulation to our paradigm, in addition to the proportion congruency manipulation, in order to assess participants’ control strategies on a trial-by-trial basis. Hence, the replication of our findings with this kind of paradigms would allow us to disentangle which forms of conflict impact conscious perception. Future studies should attempt to replicate this effect using paradigms in which stimulus and task conflict are well dissociated, and in which reactive and proactive mechanisms of control can be assessed on a trial-by-trial basis (Gonthier et al., 2016; Kalanthroff et al., 2013).

6.3. The complex relationship of executive control aspect of attention and conscious perception

Our first line of research (Chapters 2 and 3) revealed that the executive control aspect of attention can modulate visual conscious perception, and that this behavioral interaction is supported by frontal mechanisms. Furthermore, it also suggests that this relationship between interference control and conscious perception is more fragile or more difficult to capture than the relationship between conscious perception and other attentional processes, such as exogenous orienting or phasic alerting (Botta et al., 2014; Chica et al., 2012b; Chica et al., 2016, 2010; Kusnir et al., 2011).

We employed high-density EEG in order to capture the neural modulations of interference control and conscious perception, and we found an enhanced amplitude of the N2 component for consciously perceived as compared to non-perceived near-threshold targets. This N2 modulation of conscious perception was observed on incongruent trials in the high proportion congruent session, suggesting a congruency-related interference modulation of conscious perception at the neural level, corresponding to the behavioral influence of this congruency-related interference on the decision criterion to respond to near-threshold stimuli in Experiment 1 from Chapter 2. In addition, in the high-density EEG experiment (Chapter 3) this consciousness modulation of the N2 component was also observed in the low proportion congruent session, with an enhancement of the N2 amplitude in congruent seen as compared to congruent unseen trials. Moreover, behavioral results from the high-density EEG experiment demonstrated that participants maintained a more conservative response criterion to the near-threshold stimulus on congruent as compared with incongruent trials from the low proportion congruent session. This combination of behavioral and neural results suggest a modulation of expectancy-related interference of the perceptual-decision aspect of conscious perception, due to the recruitment of frontal areas, likely involving the anterior cingulate cortex (ACC), on both interference detection and the decisional stage of conscious perception. Interestingly, growing literature suggests that expectation plays an important role in visual cognition, and that this influence might have been mistakenly attributed to attention (see Summerfield and Egner, 2009). Thus, future studies on the relationship between attention and conscious perception processes should attempt to address the role of expectancy in visual perception.

A potential limitation in the high-density EEG study (presented in Chapter 3) is that our N2 component occurs after the onset of the near-threshold stimulus, and therefore one might be concerned about the idea that the consciousness modulation of the conflict-related N2 component could be due to different potentials evoked by the presentation of the to-be-detected target. However, it is important to note that perceptual characteristics of the visual scene were identical on consciously perceived as compared to unconsciously perceived trials, because in both cases the near-threshold target was presented. Furthermore, source-location analyses revealed that the N2 component was associated to the activation of a series of frontal regions, critically involving the conflict-related anterior cingulate cortex (ACC) (Botvinick, Cohen, & Carter, 2004; Yeung, Botvinick, & Cohen, 2004).

Finally, it is important to note that the experiments of this thesis do not imply causal effects of executive control over conscious processes, but rather an association between the executive network of attention and conscious perception. The methodology employed in this thesis does not permit us to infer causality out of this complex relationship between attention and consciousness. Current studies in our laboratory using transcranial magnetic stimulation (TMS) technique are trying to disentangle whether this complex relationship reflects causal interaction, rather than just the implication of shared frontal structures in both executive control and conscious perception processes. For instance, in a recent TMS study from our research group, Martín-Signes and colleagues (in press) demonstrated that repetitive transcranial magnetic stimulation (rTMS) over the Supplementary Motor Area (SMA) –a frontal structure involved in the fronto-striatal network that mediates phasic alertness and conscious perception– reduced the alertness effect over conscious perception. Therefore, they concluded that the SMA has a causal implication in the phasic alertness modulation on conscious perception. Nevertheless, the studies presented in the first line of research of this thesis (Chapters 2 and 3) greatly contribute to our theoretical understanding of the nature of the relationship between executive control aspect of attention and conscious perception of visual stimuli, both at the behavioral and neural levels. Furthermore, they address a previously unexplored issue, filling the conceptual gaps in the study of how different networks of attention relate to visual conscious perception.

6.3. Attention deficits in confabulating patients: new insights and future directions

Our second line of research (study presented in Chapter 4) addresses for the first time the functionality and integrity of the three attention networks (S. E. Petersen & Posner, 2012) in a sample of confabulating patients after acquired brain injury, as compared with a group of non-confabulating brain-damaged patients (lesion controls) and a group of healthy controls.

Confabulations have been reported after brain lesions in more than 20 anterior and posterior brain areas (Dalla Barba & La Corte, 2013), albeit it seems that crucial damaged regions include the orbitofrontal cortex (more specifically, the ventromedial prefrontal cortex) and its connections with the limbic system (Gilboa & Moscovitch, 2017; A. Schnider, Nahum, & Ptak, 2017; Zald & Andreotti, 2010). Brain lesions in our group of confabulating patients involved, but were not limited to, frontal lobe regions such as the orbitofrontal cortex and the inferior frontal cortex, the right insula, and subcortical structures such as the putamen.

The neuropsychological profile of our sample of confabulating patients matched previous literature showing deficits in both memory processes and executive functions, and therefore supported the dual-deficit hypothesis of confabulations (Kapur & Coughlan, 1980; Kopelman, 1987; Stuss, Alexander, Lieberman, & Levine, 1978). Confabulating patients' performance in memory tests was characterized by a pattern of impaired free recall and cued recall both at short-term and long-term memory adding a high amount of intrusions affecting both verbal and visual memory tests (TAVEC and Rey Osterrieth's Complex Figure). They also showed a high rate of false positives in recognition in verbal memory (TAVEC). Compared to healthy controls, confabulators performance on semantic fluency (Verbal Fluency test – animals), abstract reasoning (Similarities WAIS-IV subtest), and verbal working memory (Digit Span WAIS-III subtest) was in the limit of being considered impaired performance. In addition, their scores in inhibition and alternating attention (Color Trail Test and 5 Digits Test), which also involve the executive control network of attention, were largely impaired. Interestingly, confabulating patients demonstrated a severe impairment of selective attention (Picture Completion WAIS-IV subtest) and a low —but, compared to our sample of healthy controls, not affected— performance on sustained attention (Auditory 'A' Test).

Our analysis of the grey matter showed no relationship between the number of confabulations committed in the Dalla Barba Provoked Confabulation Interview and the damaged cortico-subcortical areas in our sample of patients. Concerning the white matter analyses, the number of confabulations in the Dalla Barba Provoked Confabulation Interview showed a tendency to correlate with the integrity of the dorsal and middle branches of the bilateral superior longitudinal fascicule (SLFs I and II) –one of our tracts of interest due to its relation with attention performance (Thiebaut de Schotten et al., 2011)–, albeit this correlation did not survive statistical Bonferroni correction. The lack of positive results in the grey matter analysis was not unexpected, and points to the fact that confabulations could be more related to damage to white matter pathways connecting cortico-subcortical areas, rather than to damage to those areas themselves. However, these results should be interpreted with caution, due to the limited overlap observed in our sample of confabulating patients, and the little variability of lesion controls on their Dalla Barba Interview scores. The lack of a significant correlation between the SLF integrity and confabulations in the Dalla Barba Interview showed that the functionality of this attention-related white matter tract is not related to the syndrome of confabulations. However, based on the anatomy and function of the bundles of the anterior cingulate gyrus —a brain hub mostly involved in the executive control of attention (Botvinick et al., 2004), whose fibers connect limbic areas with sub-genual frontal regions (Crosby, Humphrey, & Lauer, 1962; Nieuwenhuys, Voogd, & van Huijzen, 2008)—, and given the pattern of executive dysfunction that confabulators exhibited both in previous literature and in our study, this white matter branch seems more likely to have a role in confabulation syndrome.

Confabulating patients' performance through the experimental tasks assessing the three attention networks confirmed that those patients had impairments in the executive control function of attention. Specifically, they showed a larger Simon congruency effect that was not observed in lesion controls or healthy controls, suggesting a higher conflict-sensitivity in confabulators' behavior. In addition, the number of responses to Go targets in the Go-NoGo task was significantly lower in the group of confabulating patients as compared with both lesion controls and healthy controls. Moreover, only the group of confabulating patients showed differences in RTs to Go targets when the frequency of Go and No-Go targets was manipulated between experimental blocks. Concretely, confabulators' RTs were faster on the block with 80% Go and 20% No-Go trials as compared to the block with 50% Go and 50% No-Go trials. This pattern of results in the Go-NoGo task (few responses to Go targets and faster RTs in the experimental block with a higher proportion of Go trials) seems to reveal a sustained attention deficit, by which confabulating patients missed more Go targets regardless of the experimental condition; and in greater disinhibition difficulties, reflected in faster RTs and a higher number of commissions (responses to NoGo targets) in the block with 80% Go – 20% NoGo trials. This evidence is coherent with previous literature showing sustained attention deficits (Cunningham et al., 1997; Del Grosso Destreri et al., 2002) and impaired inhibition capacity (Fotopoulou et al., 2007) in confabulating patients. Furthermore, this pattern of disinhibition in the Go-NoGo task (faster RTs in the block with 80% Go – 20% NoGo trials) was associated to lesions to the right inferior frontal cortex (rIFC), confirming that damage to that frontal region plays an important role in executive processes (Aron et al., 2014; Singh-Curry & Husain, 2009), and shedding light on the intimate relationship between confabulations, damage to specific areas in the frontal lobe (such as the rIFC), and executive dysfunction.

In the alertness task, confabulators benefited from the alertness cue, showing higher mean accuracy on cued as compared with uncued trials, whereas this effect was not observed in lesion controls or in healthy controls. An interpretation of this result is that confabulating patients showed no impairments in the alertness task, and that they showed the typical RT alertness effect in the mean accuracy dependent variable instead. Alternatively, confabulating patients' performance on this task could be reflecting an impaired sustained attention that would be overcome on cued trials. Consistent with this interpretation, damage to the right anterior insula and the right anterior portion of the putamen in our sample of patients was associated to an increased use of the alertness cue. The anterior insula and anterior putamen have been associated with sustained attention (Langner & Eickhoff, 2013; Thakral & Slotnick, 2009). In addition, the insula constitutes an insular-midcingulate network, involved in switching between central executive and default mode networks and therefore reflecting task engagement or disengagement (Sridharan et al., 2008). Therefore, it is plausible that our sample of confabulating patients had an important deficit in sustained attention, and that they largely depended on cued trials in the alertness task (as compared to lesion controls and healthy controls) due to their tendency to task-disengagement. Moreover, a low number of hits in the Go-NoGo task was associated to damage to the frontal operculum in the right hemisphere, consistent with the existence of a deficit in sustained attention in patients with injury to the insula/operculum (Sridharan et al., 2008), which would be associated with fewer responses to Go targets in the Go-NoGo task.

Confabulating patients showed a normal general pattern of results in the orienting network of attention, as they (as well as lesion controls and healthy controls) demonstrated the classic effects of validity, SOA, and predictability. Nonetheless, both lesion controls and confabulating patients showed a validity effect in the predictive block's accuracy, whereas healthy controls' validity effect was observed in the non-predictive block instead. A plausible interpretation of this pattern of results is that our groups of lesion controls and confabulating patients' performance in the orienting task relied more on the peripheral cues as compared to healthy controls' performance. Furthermore, lesions in our sample of patients mostly affected the right middle and ventral branches of the superior longitudinal fascicule (right SLF II and SLF III, respectively), which partially overlap with the ventral network of attention (Corbetta, Patel,

& Shulman, 2008; Thiebaut de Schotten et al., 2011), known to be involved in the reorienting of attention. Therefore, patients in our study could have difficulties in reorienting attention on invalid trials, which were less frequent than valid trials in the predictive block, but equally frequent as valid trials in the non-predictive block. Moreover, participants' mean accuracy in the orienting task correlated with the integrity of those white matter tracts, supporting the existence of a subtle dysfunction in lesion controls and confabulating patients in the reorienting of attention.

Previous literature assessing cognitive functions in confabulating patients had described both memory and executive deficits (Kapur & Coughlan, 1980; Kopelman, 1987; Stuss, Alexander, Lieberman, & Levine, 1978). In this thesis, we experimentally assessed for the first time the functionality and integrity of the three attention networks in this clinical population. In addition to a memory and executive dysfunction, revealed by neuropsychological tests, we observed a pattern of deficits in attention processes, including problems in sustained attention, the reorienting of attention, and executive control (interference and inhibition). This evidence suggests that, additionally to the cognitive impairments affecting memory processes and executive functions, confabulators show deficits in the three networks of attention.

As we noted in the Introduction, recent studies demonstrated that attention can modulate the presence of confabulations, suggesting that an impairment of attention processes might have a key role in the production of confabulations (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997; Ródenas, Lupiáñez, Arnedo, & Triviño, 2016; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017). Some theoretical models on confabulations, such as monitoring theories (Gilboa et al., 2006; M K Johnson, Hayes, D'Esposito, & Raye, 2000), propose that confabulations can arise as a consequence of a failure in either early memory processes (e.g. encoding or retrieval), or late processes of monitoring and verification of the retrieved information. As reviewed in the Introduction, the treatment for reducing confabulations proposed by Triviño and colleagues (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017) intervened in selective attention during encoding, monitoring during retrieval, and memory control after retrieval. The authors found that after the treatment, confabulating patients not only reduced their confabulations but also tended to improve in selective attention and planning as measured with neuropsychological tests. The reduction of confabulations after neuropsychological treatment was also associated to an improvement of patients' performance in a visual search task (Ródenas, Lupiáñez, Arnedo, & Triviño, 2016). However, memory scores remained the same when comparing pre and post-treatment scores, with the exception of the number of intrusions in recall and false positives in recognition. This is consistent with a case report study showing an improvement of a patient's executive function deficits after the spontaneous reduction of his tendency to confabulate (Kapur & Coughlan, 1980), and with other studies showing the stability of memory deficits in spite of the reduction of confabulations as the natural course of the syndrome (M K Johnson, Hayes, D'Esposito, & Raye, 2000). More importantly, the evidence presented by Triviño and colleagues suggests that confabulations may be associated to impaired attentional processes, such as selective attention or early conflict detection (Triviño, Ródenas, Lupiáñez, & Arnedo, 2017). Our research adds more evidence favoring this interpretation, and contributes to disentangle the particular attention functions affected in confabulating patients. These functions appear to involve specific mechanisms of the three networks of attention, as our sample of confabulating patients showed deficits in sustained attention, the reorienting of attention, and inhibition. Future steps in our line of research involve assessing the attention networks functionality and integrity in those patients after undergoing the behavioral treatment designed by Triviño and colleagues (2017), in order to test whether these impairments in attention ameliorate together with the reduction of confabulations.

Our group of confabulating patients developed the confabulation syndrome as a consequence of lesions from diverse etiologies (including vascular, traumatic, Korsakoff syndrome, and hydrocephalus), that is, the group of confabulators was not homogeneous regarding the etiology of the acquired brain damage. However, previous studies have observed no systematic differences in the ratios of confabulation in confabulating patients with lesions resulting from diverse etiologies (Cunningham et al., 1997), nor in the type of confabulations (Nahum, Bouzerda-Wahlen, Guggisberg, Ptak, & Schnider, 2012). Moreover, Triviño and colleagues' treatment for reducing confabulations has shown its efficiency regardless of the lesions etiology and volume. In fact, these authors rehabilitated a new sample of 24 confabulators (Triviño et al., in preparation), including confabulating patients as a consequence of a rupture of an aneurysm in the anterior communicating artery, strokes in the right middle cerebral artery, Korsakoff syndrome, and traumatic brain injury. They demonstrated a successful reduction of confabulations in their entire sample of patients, pointing to the homogeneous nature of confabulations, even when they are originated by a variability of brain lesions and etiologies. In future studies, it would be interesting to test this rehabilitation program in patients with confabulations resulting from dementia or cognitive impairment.

On the other hand, it has been proposed that different subtypes of confabulation would result from different mechanisms (Schnider et al., 1996; Nahum, et al., 2012). Being that the case, grouping all confabulating patients regardless of the content of their confabulations could bring together qualitatively different confabulation types and even obscure subtle cognitive differences between confabulators. As we described in the Introduction section, an important differentiation refers to the content of confabulations, as they can be classified into mnestic (confabulations related personal past memories or future plans) and non-mnestic (paramnesia, Capgras syndrome, Fregoli syndrome, and pseudohallucinations) confabulations (A. Schnider, 2008). Following Schnider's observation on the content of confabulations (2008), although mnestic and non-mnestic confabulations usually co-occur, they can be dissociated, suggesting different neural basis and cognitive mechanisms underlying them. A reasonable hypothesis is that those differences in confabulations are supported by damage to distinct brain networks. In fact, Dalla Barba and La Corte (2013) have proposed that confabulations involving plausible or semantically appropriate content arise after lesions of the thalamus and/or the orbitofrontal cortex, and their connections to the hippocampus, whereas implausible or semantically anomalous confabulations are related to lesions in temporo-parietal association areas and their projections to the hippocampus. It would be interesting to test in future studies whether mnestic and non-mnestic confabulations also rely on different brain networks.

This second line of research addressed some of the still controversial aspects in the literature of confabulations. On one hand, it deepened our knowledge regarding the cognitive profile of confabulating patients, helping to complete the picture of their impaired and preserved functions. Furthermore, our study assessed confabulating patients' attention processes through experimental tasks, which usually are more sensitive to cognitive impairments than traditional neuropsychological tests. Our results revealed mild impairments in sustained attention and the reorienting of attention in confabulating patients, whereas the greater deficits in this population corresponded to the executive control network of attention (Simon interference and Go-NoGo inhibition). Finally, we presented preliminary neuro-imaging data revealing the implication of the right inferior frontal cortex, the orbitofrontal cortex, the right anterior insula and the right putamen in the inhibition and sustained attention deficits in our sample of patients, whereas the performance in the orienting task was related to the integrity of the middle and ventral branches of the superior longitudinal fascicule in the right hemisphere (right SLF II and SLF III, respectively).

6.4. General conclusion

The first research line of this thesis examined for the first time the behavioral and neural interactions between interference control aspect of the executive control attention network (elicited by a classic Stroop task) and the visual conscious perception of near-threshold stimuli. Results from the first experimental series showed a modulation of the decision criterion to respond to the near-threshold stimulus on incongruent as compared to congruent Stroop trials. This effect was associated to the transient recruitment of reactive control, as incongruent trials were also infrequent (high proportion congruent condition), and participants were more likely to adopt reactive control strategies (Braver, 2012). We hypothesized that the impact of interference control on decision stages of conscious processing was due to the implication of shared frontal regions in both conflict detection and conscious perception. To test this hypothesis, we conducted a second experimental series in which we employed high-density EEG in order to look at the neural bases of this behavioral interaction. In this study, the finding of an interference control modulation on the response criterion to the near-threshold stimulus was replicated, although in this experiment it was associated with proactive strategies of control, as it was observed on congruent and infrequent trials (low proportion congruent condition). Results of the event-related potentials (ERPs) analyses in this experiment showed a modulation of the conflict-related N2 component to the Stroop stimulus (S J Luck, 2012; Yeung, Botvinick, & Cohen, 2004) by the conscious perception of the near-threshold stimulus. This modulation was only observed on incongruent and infrequent trials in the high proportion congruent session (when reactive control mechanisms are recruited) and on congruent and infrequent trials in the low proportion congruent session (thought to recruit proactive control mechanisms), suggesting that, in addition to interference-related conflict, the N2 component and its modulation also reflected expectancy-related conflict (S J Luck, 2012; Yeung et al., 2004). The source-location analyses confirmed that, as expected, the N2 component was associated with activation of the anterior cingulate cortex. Therefore, the combination of behavioral and electroencephalography results from this line of research suggests a modulation of interference-related and expectancy-related conflict on the perceptual-decision aspect of conscious perception, due to the recruitment of frontal areas, likely involving the anterior cingulate cortex, on both conflict detection and the decisional stage of conscious perception.

The second line of research of the present thesis explored attention processes and their neural substrates in the syndrome of confabulations after acquired brain injury, which is characterized by the unintentional (and unconscious) production of false memories (Dalla Barba, 1993). For the first time in the literature, we assessed confabulating patients' performance in three experimental tasks measuring the three attention networks (S. E. Petersen & Posner, 2012) and we explored the association between patients' performance on those tasks with grey matter and white matter damage. When compared with lesion controls (matched non-confabulating patients) and healthy controls, confabulators showed an impairment of the executive network of attention, characterized both by a higher Simon interference effect and disinhibition in a Go-NoGo task. Coherent to previous studies, this disinhibition pattern was related to damage to the right inferior frontal cortex (Aron, Robbins, & Poldrack, 2014). In addition, confabulating patients showed a greater alertness task, which was associated with damage to the right anterior insula and putamen, structures related to sustained attention and task engagement-disengagement (Sridharan, Levitin, & Menon, 2008;

Thakral & Slotnick, 2009). This data suggest that patients with lesions in the right anterior insula and putamen had deficits in sustained attention, and therefore greatly depended on phasic alertness cues to detect the subsequent target. Moreover, confabulating patients and lesion controls relied more on exogenous cues in the spatial orienting task than healthy controls, probably due to deficits in the ventral network of the reorienting of attention (Corbetta, Patel, & Shulman, 2008). In fact, lesions in our sample of patients mostly affected white matter pathways related to the ventral network of attention in the right hemisphere: the middle and ventral branches of the superior longitudinal fascicule (Thiebaut de Schotten et al., 2011). Coherent with previous studies in left unilateral neglect, the integrity of those white matter tracts positively correlated with our participants' performance in the spatial orienting task (Bartolomeo, Thiebaut De Schotten, & Doricchi, 2007). Results from the neuropsychological assessment in our study are coherent with previous literature showing both memory and executive deficits in confabulating patients (Fischer et al., 1995; Stuss et al., 1978); however, we focused on further examining the attention deficits associated with confabulations after acquired brain damage. Our research supports recent findings highlighting the role of attention mechanisms in the production of confabulations (Ciaramelli, Ghetti, & Borsotti, 2009; Cunningham et al., 1997; Ródenas, Lupiáñez, Arnedo, & Triviño, 2016; Triviño, Ródenas, Lupiáñez, & Arnedo, 2017), and disentangles the attentional mechanisms impaired in the syndrome of confabulations.

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