Attentional modulation of conscious perception

The role of the frontal lobe and its white matter connections

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Attentional modulations of conscious perception: The causal role of the frontal lobe and its white matter connections

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A mis abuelas, Rosario y Marita.

Mujeres inteligentes, valientes y revolucionarias.

The front page and the illustrations below the titles of the introductory chapters have been designed and drawn by Klara Hemmerich.

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La portada y las imágenes que acompañan al título de cada capítulo de la introducción han sido diseñadas y realizadas por Klara Hemmerich.

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ABSTRACTS

Abstract

At any given moment, we receive much more information that our cognitive system can consciously process. Therefore, a mechanism is necessary to select the information that is relevant for our goals or for survival, and to filter out the irrelevant one. Attention is proposed as one of these mechanisms, preparing the system to allocate processing resources, selecting relevant information –filtering out irrelevant distractors–, and allowing for the control of such processing resources. These heterogeneous functions of attention have led to the conception of attention as a system composed of three networks: alerting, spatial orienting, and executive control (Petersen & Posner, 2012). Some attentional systems have also demonstrated their influence over conscious perception by modulating perceptual sensitivity and/or by biasing responses. This has led to propose a thigh relationship between attention and conscious perception, and to the search of common neural substrates.

Attentional processes rely, to a great extent, in fronto-parietal networks (Fan et al., 2005). Meanwhile, some theories propose that conscious perception emerges when information is represented in a large-scale network of fronto-parietal regions (Dehaene et al., 2006). Although the involvement of parietal regions in conscious perception is widely accepted, there is an extensive debate about a causal involvement of the frontal lobe (Boly et al., 2017; Odegaard et al., 2017).

In this theoretical and empirical context, the main goal of the present doctoral thesis was to delineate the role of frontal regions, and long-range white matter tracts connecting them with other regions in the brain (i.e. the dorsal, middle, and ventral branches of the superior longitudinal fasciculus, SLF I, II, and

III), in the relationship between attention and conscious perception. Specifically, we explored the role of the executive control network, which in this context has been less explored. This network is involved in the voluntary control of processing in novel or complex situations. To accomplish this aim, two different studies were conducted:

- In the first study, we searched for common neural substrates of executive control and conscious perception, employing a design of functional magnetic resonance imaging (fMRI). Participants had to detect near-threshold Gabor stimuli, while resolving a Stroop task in which incongruent trials were infrequent.
- In the second study, we explored the causal involvement of a frontal region – the right SMA – in the interaction between executive control and conscious perception by using online transcranial magnetic stimulation (TMS). Additionally, a control (vertex stimulation) and an active condition (right frontal eye field [FEF] stimulation) were included. Participants performed a similar task that the one employed in the previous study.
- A common aim of both studies was to explore the involvement of the SLF I, II, and III in executive control modulations of conscious perception by using diffusion-weighted imaging (DWI) tractography.

Results of the fMRI study demonstrated an interaction between executive control and conscious perception in the functional coupling between some fronto-parietal regions, which were more strongly coupled for seen as compared to unseen reports, but only when trials were Stroop-congruent. Additionally, the microstructural properties of the left SLF II significantly correlated with the neural interaction between executive control and conscious perception. The follow up

TMS experiment demonstrated that two of such reported frontal regions, the right SMA and the right FEF, were causally involved in the interaction between executive control and conscious perception, but only when white matter properties of the right SLF III or a frontal association tract (i.e. the left frontal aslant tract) were taken into account. Participants with a greater integrity of the tracts were sheltered from the TMS modulation. This suggest, at least, partially shared frontal neural substrates for executive control and conscious perception.

In conclusion, this doctoral thesis provides new data for the understanding of how executive control interacts with conscious perception and about the neural mechanisms underlying these interactions. They support that the frontal lobe may be a common neural substrate for executive attention and conscious perception. They also emphasize the role of long-range white matter tracts, reinforcing models based on distributed networks. Finally, results highlight the importance of white matter in individual variability in cognitive measures and neuromodulation effects, in healthy participants.

Resumen / Abstract in Spanish

Constantemente, recibimos mucha más información de la que podemos procesar de forma consciente. Por tanto, es necesario disponer de un mecanismo que seleccione la información relevante para nuestros objetivos (por ejemplo, la supervivencia), filtrando la irrelevante. La atención se ha propuesto como uno estos mecanismos, ya que prepara al organismo, selecciona y filtra la información y controla los recursos de procesamiento. Esta heterogeneidad en las funciones de la atención ha llevado a proponer modelos donde esta se describe como un sistema compuesto por diferentes redes: alerta, orientación espacial y control ejecutivo (Petersen & Posner, 2012). Algunas de estas redes atencionales han demostrado afectar a la percepción consciente, modulando la sensibilidad perceptual o el criterio de respuesta. Esto ha llevado a proponer la existencia de una estrecha relación entre la atención y la percepción consciente, promoviendo la búsqueda de sustratos neurales comunes entre ambos procesos.

Los procesos atencionales involucran, en gran medida, regiones fronto-parietales (Fan et al., 2005). Por otra parte, algunas teorías proponen que la percepción consciente emerge cuando la información es representada en redes de largo alcance de regiones fronto-parietales (Dehaene et al., 2006). Sin embargo, aunque la implicación de las regiones parietales en la percepción consciente es ampliamente aceptada, en la actualidad existe un debate abierto sobre el papel del lóbulo frontal (Boly et al., 2017; Odegaard et al., 2017).

Dentro de este contexto teórico y empírico, el objetivo principal de la presente tesis fue estudiar el papel de las regiones frontales, y de los tractos de sustancia blanca que las conectan con otras regiones parietales (las ramas

dorsal, media y superior del fascículo longitudinal superior, SLF I, SLF II y SLF III), en la relación entre atención y consciencia. En concreto, se estudió el papel de la red de control ejecutivo, cuyas modulaciones de la percepción consciente han sido menos exploradas. La red de control ejecutivo se pone en funcionamiento en situaciones en que los esquemas de comportamiento aprendidos no son útiles, porque la situación es nueva, difícil o peligrosa. Para responder al objetivo de la tesis, se llevaron a cabo dos estudios:

- En el primer estudio, se utilizó un diseño de resonancia magnética funcional (fMRI) para explorar los sustratos neurales comunes al control ejecutivo y la percepción consciente. Para ello, se empleó una tarea en la que los participantes debían detectar la aparición de estímulos Gabor en el umbral de consciencia, mientras respondían a una tarea Stroop con ensayos incongruentes infrecuentes.
- En el segundo estudio, exploramos el papel causal de una región frontal (el área motora suplementaria derecha, SMA) en la interacción entre control ejecutivo y consciencia perceptual, empleando estimulación magnética transcraneal (TMS). Adicionalmente, se incluyó una condición control (la estimulación del vertex) y una condición activa (la estimulación del área ocular frontal derecha, FEF). En este estudio, los/as participantes llevaron a cabo una tarea similar a la utilizada en el estudio anterior.
- En ambos estudios, se exploró el papel del SLF I, II y III en las modulaciones que el control cognitivo produce sobre la consciencia perceptual, utilizando tractografía realizada sobre imágenes de difusión por resonancia magnética (DWI).

Los resultados del estudio de fMRI mostraron una interacción entre el control ejecutivo y la consciencia perceptual en la conectividad funcional de regiones fronto-parietales. Estas regiones estaban más coactivadas cuando el estímulo Gabor era percibido que cuando no lo era, pero solo durante los ensayos Stroop congruentes. Por otra parte, las propiedades microestructurales del SLF II del hemisferio izquierdo correlacionaron con la interacción neural entre el control ejecutivo y la consciencia. En el experimento de TMS, dos de esas regiones (el SMA y el FEF derechos) mostraron una implicación causal en la interacción entre el control ejecutivo y la percepción consciente, pero solo cuando la estructura del SLF III derecho o de un tracto de asociación frontal (el tracto oblicuo frontal izquierdo) fue tenida en cuenta en los análisis. Las personas que mostraron más integridad en estos fascículos, también demostraron menos efectos moduladores de la TMS. Los resultados de ambos estudios sugieren la existencia, al menos, de sustratos neurales parcialmente compartidos entre el control ejecutivo y la conciencia perceptual.

En conclusión, la presente tesis doctoral proporciona nuevos datos que nos ayudan a entender cómo el control ejecutivo interacciona con la consciencia, y los mecanismos neurales que soportan estas interacciones. Los resultados apoyan que el lóbulo frontal pueda ser una de las regiones donde se encuentren tales sustratos comunes. También destacan el papel que los fascículos de sustancia blanca de largo alcance pueden tener en la atención y la consciencia, lo que apoya aquellos modelos basados en redes distribuidas. Finalmente, los resultados sugieren la influencia de la sustancia blanca en la variabilidad individual en medias cognitivas y de neuromodulación, incluso en participantes sanos.

THEORETICAL AND EMPIRICAL BACKGROUD

Chapter 1. Consciousness: the far reaches of neuroscience

Consciousness is a unique, ineffable, and complex form of experience. However, it is also experienced by us as a simple and obvious phenomenon (Delacour, 1995). This duality may explain the elusive definition of the concept. In the first place, we have to distinguish among *levels* and *contents* of consciousness. The levels of consciousness refer to a continuum that naturally ranges between being awake and vigilant in one extreme, to the slow-wave sleep in the other extreme. It also comprises states following brain injury and other conditions, such as coma or anesthesia (for an insight on this literature, the reader can remit to Bayne et al., 2016; Boly et al., 2009; Laureys et al., 2004; Laureys & Schiff, 2012, among others).

The contents of consciousness refer to the subjective experience of a given content (which is known as *phenomenological consciousness*) that can sometimes be reported and become available for reasoning and – complex and/or controlled – action (which is known as *conscious access*). At present, there is a debate on the validity of a conceptual and/or empirical distinction between phenomenological and access consciousness. According to some authors (Block, 2007), our conscious experience is richer that the information we can report, because our cognitive resources are limited (that is, phenomenology “overflows” access). However, others argue that reportability (i.e. cognitive availability) cannot be dissociated from the subjective experience (Cohen & Dennett, 2011; Overgaard, 2018). Apart from the conceptual distinction, this debate has implications related to the experimental approach to study conscious perception (this question will be addressed deeper in section 1.3.2).

There are many types of conscious contents, such as those coming from different sensory modalities, but also from emotion, thinking, pain, and so forth. This work will focus on the study of perceptual conscious access in the visual domain. This sensory modality has often be chosen among others in the study of conscious perception, because humans’ visual experience is predominant and rich, and due to its experimental tradition and advantages (Crick & Koch, 1998).

1.1. The functional role of conscious perception

From an evolutionary point of view, visual consciousness may serve us to integrate and unify information to generate a single complex representation of the visual scene, and to make it available for a sufficient amount of time to produce the more appropriate response (in the motor, language or other domains). Having multiple and parallel processing subsystems may be disadvantageous if we do not integrate the information and filter the noise (Crick & Koch, 1998; Dehaene et al., 2017; Delacour, 1995).

However, an ample amount of processing can occur without conscious access (for instance, perceptual, motor, emotional or semantic processing), producing changes in brain activity and behavior (Dehaene et al., 2017; Dehaene

& Naccache, 2001). Processing that occurs below the conscious threshold is known as *subliminal.* This kind of processing occurs when the strength of stimulation is too weak and information cannot reach consciousness even if it is attended. Information can also be *preconscious* when the strength of stimulation is strong enough to reach consciousness if information is attended, but it may remain unconscious if it is not attended (Fig. 1.1.; Dehaene et al., 2006).

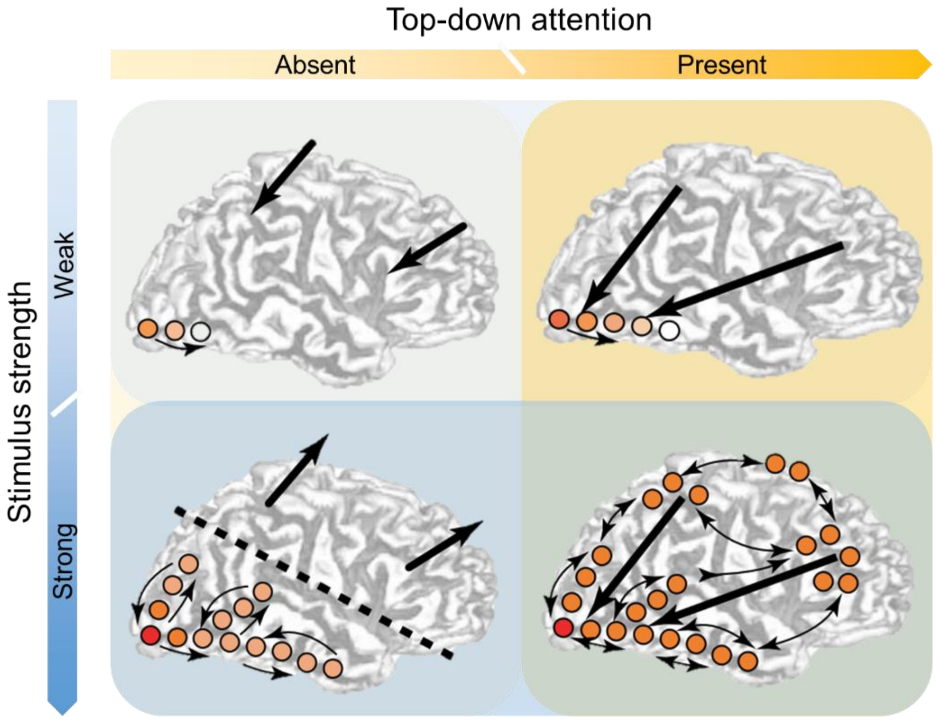

Figure 1.1. Schematic representation of the proposed brain states associated with subliminal, preconscious, and conscious processing, defined by stimulus strength (vertical axis) and top-down attention (horizontal axis). When stimulus strength is too weak, activation is restricted to early sensory regions, remaining weak and quickly dissipating, even if attended (subliminal processing). When stimulus strength is strong enough, activation is strong, durable, and can propagate to multiple specialized sensory-motor areas. However, if attention is away, activation does not spread to parieto-frontal areas (preconscious processing). If attention is directed to the stimulus, activation spreads to a fronto-parietal system, becoming available for being represented in working memory, and guiding intentional actions (conscious processing). Adapted with permission from Dehaene et al., 2006.

Widespread research has demonstrated the existence of subliminal perception. The most common evidence comes from studies showing that a visual subliminal stimulus can produce priming effects (i.e. facilitate the processing of an identical o related stimuli), even at abstract levels (e.g. semantic; Dehaene & Naccache, 2001; Dehaene, Naccache, et al., 1998; Dell'Acqua & Grainger, 1999). However, the existence of nonconscious processing at higher levels is not sustained by all authors (Kunde et al., 2005; for a review on the topic see Dehaene, 2008; Dehaene & Changeux, 2011; Kouider & Dehaene, 2007). Some studies have also demonstrated that subliminal stimulation induce comparable brain activations than consciously perceived stimuli (Kouider & Dehaene, 2007). However, they usually produce weaker and shorter lasting brain activations, and these activations are more restricted to sensory regions than those produced by consciously perceived stimuli (Rees & Lavie, 2001, but see Boly et al., 2017). Evidence from subliminal processing also comes from lesions studies, such as the *blindsight phenomenon*, in which, after lesions of the primary visual cortex, some forms of visual processing are spared in the absence of subjective conscious experience (other dissociations between performance and consciousness –implicit and explicit knowledge– can be found in other neuropsychological syndromes, such as prosopagnosia, apperceptive agnosia or achromatopsia, Köhler & Moscovitch, 1997; Weiskrantz, 1997).

Nonetheless, according to Dehaene & Naccache (2001), subliminal processing has important limitations as compared to conscious processing, which seems to be necessary for some important mental operations. Conscious processing allows the durable maintenance of an active representation in the absence of the stimulation that generates it, which becomes globally available to the organism. It also permits the inhibition of automatic processes or responses, and the generation of novel strategies and intentionally driven behavior. Conscious systems are also able to monitor and access information about themselves (internal state, confidence about choices, reflection about errors, perception of personal skills, etc.). The combination of a globally accessible representation of internal and external information confers special advantages to organisms: it improves the efficiency for information processing, and allows social information sharing (Dehaene et al., 2017).

1.2. Theoretical frameworks in the study of consciousness

Diverse *theories of consciousness* have been proposed, which explain and integrate empirical data in a different manner, and give rise to diverse predictions and questions. Some of them also suggest *models of consciousness*, that is, a description of the brain properties from which conscious experience emerges (Seth, 2007). This section does not pretend to be an exhaustive review of such theories but it intends to offer a broad perspective of the variety of approaches. According to Block (2009), those theories with a greater impact in neuroscience can be sort in different theoretical frameworks.

The *biological theories* claim that consciousness is a biological state of the brain, and point to different brain processes as the source. For example, some theories (Block, 2007; Lamme, 2003) suggest a fundamental role of recurrent neurons interactions within and between areas, through feedback and feedforward waves. According to that model, widespread recurrent interactions are necessary to give rise to access consciousness. Crick & Koch (2003) propose that consciousness emerges from those coalitions of neurons that are sustained in a given moment (the “successful” ones). As a last example, Zeki & Bartels

(1999) suggest that each of the processing nodes of our perceptual system creates its own “microconsciousness”, which can bind or influence each other creating an integrate percept.

There is a current debate about the so call *first-order* and *higher-order* theories of consciousness*. First-order theories* propose that conscious perception emerges from neural representations coming from early sensory activity (Block, 2007; Lamme, 2003; Tse et al., 2005; Zeki & Bartels, 1999). According to these theories, activations in association areas such as the parietal or the frontal cortex are not necessary for conscious perception. Contrary, the *higher-order thought theory* (Lau & Rosenthal, 2011) states that higher-order representations are necessary for consciousness. These are defined as a mental representation of experiencing some particular perceptual content, or being in a certain mental state. In other words, the conscious representation of a perceptual content emerges only if is accompanied by another mental state about the experience. However, this theory does not propose any link with a mechanistic or neural model, although such high-order representations are usually linked with frontal and parietal activity.

The *information integration theory* (Tononi, 2008) claims that the capacity of a system to discriminate between a vast number of possible alternatives (information) in an integrated manner is a necessary and sufficient condition for the emergence of a conscious experience. This model proposes a measure (represented by Φ) of the quantity of integrated and unified information that a system can generate. According to this theory, any system with such properties would be able to generate consciousness.

The *global workspace theory* was first proposed by Baars (1988) and then developed by Dehaene and Changeux, and their collaborators (Dehaene et al., 2006; Dehaene, Kerszberg, et al., 1998; Dehaene & Changeux, 2011; Dehaene & Naccache, 2001). This theory postulates that for a content to reach consciousness, brain activation supporting such representation needs to extend, propagate, and reverberate into a network of higher associative areas, highly interconnected by long-distance connections (bottom right diagram in Fig. 1.1.). The theory considers an organization on specialized and automatic modules of processing, where nonconscious processing would be supported by parallel operations through interconnected modules. However, some mental operations would require the combination of information from different sources in an integrated (non-modular) manner. This would be possible thanks to a distributed neural system – the workspace.

1.3. Experimental approaches to visual conscious perception

1.3.1. Generating conscious perception

In the study of conscious perception, a wide diversity of paradigms have been employed (Dehaene & Changeux, 2011; Kim & Blake, 2005), having in common the generation and comparison of conscious and nonconscious conditions, while keeping as constant as possible other elements (perceptual stimuli, participants’ responses, etc.). This *contrastive analysis* (Fig. 1.2.) is usually accompanied of measures of neural activity, allowing for the search of the *neuronal correlates of consciousness* (NCC), that is, the minimal set of neuronal processes that are necessary and sufficient for the conscious experience of a content to emerge (Crick & Koch, 2003).

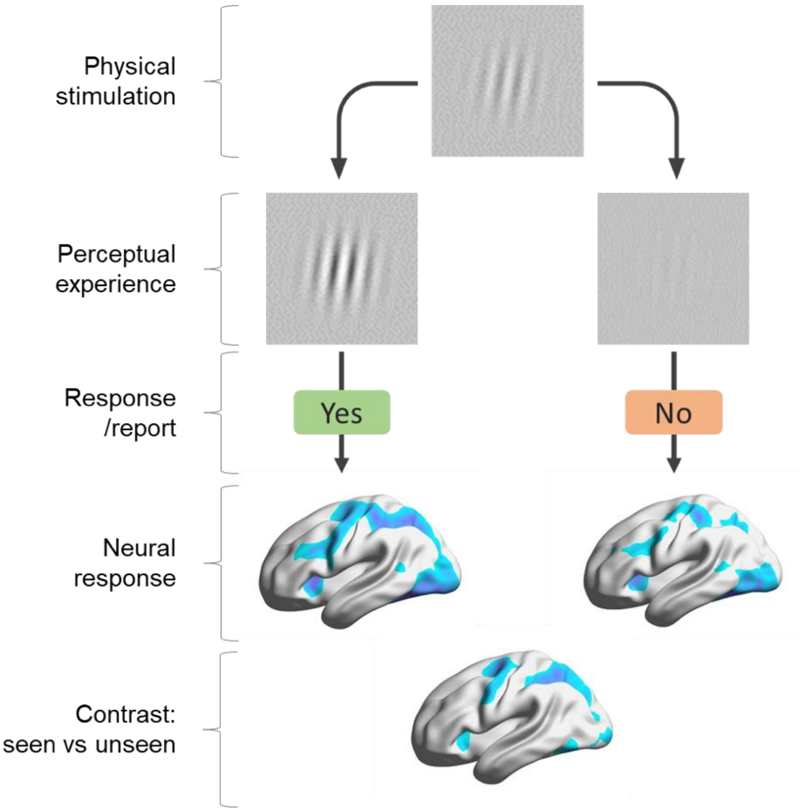

Figure 1.2. Representation of the contrastive analysis employed for the isolation of the neuronal correlates of consciousness (NCC). In the example, conscious perception of a Gabor stimulus in the threshold of consciousness is achieved, approximately, half of the times. Participants indicate when they see (“yes”) or do not see (“no”) the Gabor by pressing a key. Hemodynamic response in both conditions can be compared to isolate the NCC. Brain activations have been extracted from Martín-Signes, Paz-Alonso, et al., 2019 only with illustrative purposes.

Some paradigms have used a change in the stimulation to manipulate conscious access. For example, in *masking* procedures, a mask is presented in closed temporal and spatial proximity to the target (there are several masking procedures than can be revised in Breitmeyer & Ogmen, 2006). Other paradigms manipulate consciousness by presenting stimuli at the *threshold of consciousness* – but also over or below this threshold. To this end, the signal-to-noise ratio is manipulated (changing e.g. the contrast of the stimulus) until subjective perception of the stimuli reach the desired proportion (physical properties of the stimulus does not change but it is perceived only a percentage of the times).

Other paradigms have employed visual patterns with different perceptual interpretations, in which the representation accessing consciousness alternate in a natural way (Leopold & Logothetis, 1999). Some examples are *bistable figures* (ambiguity can lead to two distinct interpretations of the figure), *binocular rivalry* (the bistable perception is induced by the conflicting presentation of different visual patterns to each eye) or *continuous flash suppression* (the pattern presented in one eye is made non-conscious by the presentation of flashing shapes in the other eye).

Finally, some paradigms manipulate attention to disrupt conscious access (the relation between attention and consciousness will be addressed in depth in the next chapter). Some classical examples are *inattentional blindness* (an unexpected visible object is undetected because attention is focused in another task; Mack & Rock, 1998) and *change blindness* (a failure in noticing a change in an object or scene, even when attention is not involved in another task; Simons & Levin, 1997). Some variants are the *attentional blink* and the *psychological refractory period,* in which the detection of one target is impaired or delayed, respectively, by the presentation of a previous target close in time (Pashler, 1994; Shapiro et al., 1997).

1.3.2. Measuring the "proper" conscious perception

The paradigms presented above require to distinguish when the participant is having or not a conscious perception. This can be made by employing objective or subjective measures (Boly et al., 2013; Seth et al., 2008).

Objective measures rely on the assumption that when consciously perceiving a stimulus, above chance performance is expected in a forced-choice direct task of stimulus perception (for example, detection, location, or classification). Increasingly, the study of conscious access relies on participants' subjective reports (Del Cul et al., 2007; Sergent & Dehaene, 2004). *Subjective measures* are based on the participant's introspection of their perceptual experience (e.g. ratings of stimulus visibility) or in their metacognitive ability to report their performance in a perceptual task (e.g. confidence judgements). A third type of measures, *post-decision wagering*, determines consciousness by asking participants to place an economic wager on their decisions in perceptual tasks (Persaud et al., 2007). These measures have benefited from the signal detection theory (SDT) to, respectively, measure stimulus discrimination/classification accuracy, or accuracy in a metacognitive/wagering task (Abdi, 2007).

More recently, *no-report paradigms* have been employed, in which the contents of consciousness are decoded from neural or physiological signals (Tsuchiya et al., 2015). For example, perceptual contents can be inferred from eye movements in a binocular rivalry task in which the alternating representations have opposing directions of motion (Kapoor et al., 2020). Also, multivariate techniques offer a new approach to decode conscious contents from signals proceeding from e.g. intracortical recordings, electroencephalography (EEG), or functional magnetic resonance imaging (fMRI) (Haynes, 2009; Kapoor et al., 2020). One remarkable advantage of these paradigms is that they can be used when reports are difficult to accomplish (e.g. babies, animals, or non-responsive patients).

Regardless of the measure, isolating the “true” mechanisms of conscious perception is the main challenge of an experimental approach to conscious perception. This is also fundamental in the search for the NCC. However, measures and paradigms can overestimate (i.e. include processes that are unconscious or that exceed conscious perception *per se*) or underestimate (i.e. omit processes that belong to the conscious experience) conscious perception. Indeed, the contrastive analysis described above has been criticized because it can confound the real NCC with processes that precede or follow conscious perception. Such processes (and the neural underlying mechanisms) may be necessary (a prerequisite), or a consequence of the conscious experience, but not sufficient to generate the conscious perception themselves (Aru et al., 2012).

Report-based paradigms can be contaminated by the inclusion of post-perceptual processes associated with the manipulation of the accessed representation, necessary to give the report. Further, if we consider that our phenomenological experience is richer than the information we can access and report, all measures that require participants’ reports would underestimate conscious perception. No-report paradigms offer a new approach to overpass such limitations (Tsuchiya et al., 2015). However, they also risk for the inclusion of nonconscious processes. Indeed, some authors argue that the distinction between access and experience is pointless, making it impossible to scientifically study conscious perception (Cohen & Dennett, 2011; Overgaard, 2018).

Overestimation of conscious perception can also occur for objective, as compared to subjective, measures. As mentioned before, some tasks can be performed better than chance under subliminal conditions, and thus, responses can be classified as conscious in the absence of perceptual experience

(Dehaene, 2011). Furthermore, as subjective measures rely on high-order processes, such as metacognition and introspection, there seem to be empirical consequences of the diverse types of reporting employed (Overgaard & Sandberg, 2012).

Despite the limitations of the experimental approach, and the conceptual and empirical open debates, the study of consciousness has been a fruitful field of research over the last years, with an expected astounding future (Boly et al., 2013; Seth, 2018).

Chapter 2. On the relation between attention and consciousness: from consensus to debate

If we think about our day-to-day experience, we can presume that attention has a determinant role in our conscious experience. For example, we are usually aware of stimuli that we attend to and, when our attention is away, we usually miss them. Also, as reviewed in Chapter 1, some of the paradigms in the study of conscious perception, manipulate attention to impair or reduce the conscious experience. Indeed, visual attention has a well-known role in the selection of information, and thus, attended items are processed faster, deeper, and better than others in the scene (Posner, 1994).

Since William James (1890) highlighted the link between attention and consciousness, there is a theoretical and experimental tradition in the study of their relationship. However, while some authors argue that attention and consciousness are tightly related (or even two sides of the same coin; De Brigard & Prinz, 2010; Posner, 1994; Prinz, 2010), others establish a conceptual, functional, and neural differentiation between them (Koch & Tsuchiya, 2007; Lamme, 2003; Tsuchiya & Koch, 2008). Although the relation is noticeable, the key question for many authors is if attention is necessary and sufficient to bring stimuli into consciousness. Therefore, the debate is condensed in three open questions that have been addressed extensively by focusing on the role of top-down/endogenous attention over conscious perception (for a review, see Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2008; Van Boxtel et al., 2010).

Attention without consciousness. Phenomena such as inattentional blindness, change blindness, or attentional blink suggest that when attention is away (because it is directed to other task or to other stimulus), conscious perception does not emerge (and objective performance is impaired). Also, patients with *spatial neglect*, a neurological condition that usually follows damage to the right hemisphere and its connections to the ipsilateral frontal lobe, show a reduced or a lack of attention to the contralesional side of space (Bartolomeo et al., 2012). They also show a lack of awareness to contralateral stimuli, failing to report and respond to events occurring in the neglected field. However, new evidence seems to question the assumption of the necessity of attention for conscious perception. Some investigations have proved attentional modulations of non-conscious stimuli, demonstrating that even when attended, some information does not reach consciousness (as it is the case for subliminal information). Priming and aftereffects produced by invisible stimuli can also be modulated by different types of attention. For example, the subliminal priming effect of a color masked disk over color discrimination of a target was enhanced when a cue signaled the location of appearance of the priming (Kentridge et al., 2008). Also, some invisible stimuli orient spatial attention both in healthy participants (e.g. human nudes; Jiang et al., 2006) and in patients (like the blindsight patient GY, who was faster and more accurate in detecting targets in his blind hemifield when it was cued; Kentridge et al., 1999). However, while this modulation has been shown for some types of attention (e.g. spatial, temporal, or feature-based), no modulations have been reported for other types of attention (e.g. object-based attention, Tapia et al., 2010). In sum, evidence suggests that although the lack of attention impairs conscious perception in many situations, attention is not sufficient for conscious processing to occur, as many times, attentional effects are observed for invisible stimuli. However, some authors have offered alternative explanations (e.g. saccadic eye movements to the cued region) that do not rule out the necessity of attention for conscious perception (see De Brigard & Prinz, 2010; Prinz, 2010).

Consciousness without attention. When a single object is presented without competition, it is usually consciously perceived independently of the attentional state (Reynolds & Chelazzi, 2004). However, in dual-task paradigms participants have to perform two different tasks at the same time (usually one occurring at the central fixation point and another one in the periphery). Performance is compared to that on a single-task condition. When attention is directed to a demanding central task, some peripheral tasks can be performed without slowing down their performance. This happens for the detection and discrimination of certain visual information (Braun & Julesz, 1998), the perception of the gist of a natural scene (Fei Fei et al., 2002), or the discrimination of face-gender (Reddy et al., 2004). Indeed, fMRI experiments show similar activations for areas participating in the peripheral task during dual and single task conditions (Reddy et al., 2007). However, performance of some other tasks (e.g. discrimination of color orientation or rotated letters) is affected when performing the dual task (Fei Fei et al., 2002; Reddy et al., 2007). This view has received criticism, pointing, among other claims, to the excessive training usually employed in these tasks, to the possibility that some residual attention is being directed to the peripheral task under dual task conditions, or that some tasks could be solved through unconscious processing (De Brigard & Prinz, 2010; Prinz, 2010, but see Matthews et al., 2018).

Opposite effects of attention and consciousness. As it was stated at the beginning of the chapter, commonly, attention and consciousness have positive (and similar) effects over performance and perceptual experience. However, although limited, there are some examples of paradoxical effects (decrease of performance with enhanced attention or conscious processing) or opposite effects of attention and consciousness manipulations. For example, Van Boxtel and collaboratos (2010) found that the duration of an afterimage (that is, an image that is perceived for a period of time after the original source – the adaptor stimulus – is moved away) increased when the adaptor was visible but decreased when attention was directed to it (although, recent investigations have challenged this results, Travis et al., 2017). Also, some indirect evidence comes from an investigation about unconscious thinking, which found that complex choices are better if taken after a period of “thinking without consciousness”, during which a little employment of attentional resources is better than having all attentional resources available for the choice (Dijksterhuis & Strick, 2016). The search for opposite effects of attention and conscious perception is crucial to conclude that both processes are independent, however, it still has a long way to go.

2.1. Models on the relationship between attention and conscious perception

The link between attention and conscious perception has been conceptualized in different models (Fig. 1.3.) (some of them are reviewed in Lamme, 2003; Tallon-Baudry, 2012).

Among the most influential, the classical *gateway model* (Cohen & Dennett, 2011; Dehaene & Naccache, 2001) proposes that attention selects and amplifies information. Attended items are the ones accessing conscious experience, preferentially gaining conscious report. According to this hypothesis, attention is necessary for conscious perception (although not sufficient, Dehaene et al., 2006). I.e., this model proposes that attention can make stimuli available for consciousness, although not all attended items might reach consciousness due to the lack of other pre-requisites (e.g. weak stimulation, lack of vigilance, excessive noise, etc.). An opposite conception, although less supported by empirical data (but see Hsu et al., 2011), is the *reverse dependence hypothesis*, which claims that conscious perception could influence the emerging attentional processes. In other words, the conscious or unconscious status of a stimuli could determine the type of attentional influences that can take place over it (Tallon-Baudry, 2012).

Catherine Tallon-Baudry elaborated the *cumulative influence model* (Tallon-Baudry, 2012), according to which attention and consciousness are independent processes, but both influence a decision stage that will lead (or not) to the stimulus' report. Additionally, the author proposes decision as an important component in any model of consciousness: participants' reports of conscious perception would depend on the accumulated evidence. Also, other authors

(Lamme, 2003) consider that many events can be part of our phenomenological conscious experience without attention, but attention is needed for reporting some of them (conscious access).

Nevertheless, there is general agreement in the definition of attention as a heterogeneous construct, and thus, some forms of attention may be dissociated from consciousness while others may not. In the next subsections I will review behavioral interactions found between the three attentional networks proposed by Posner and Petersen (1990) and visual conscious perception.

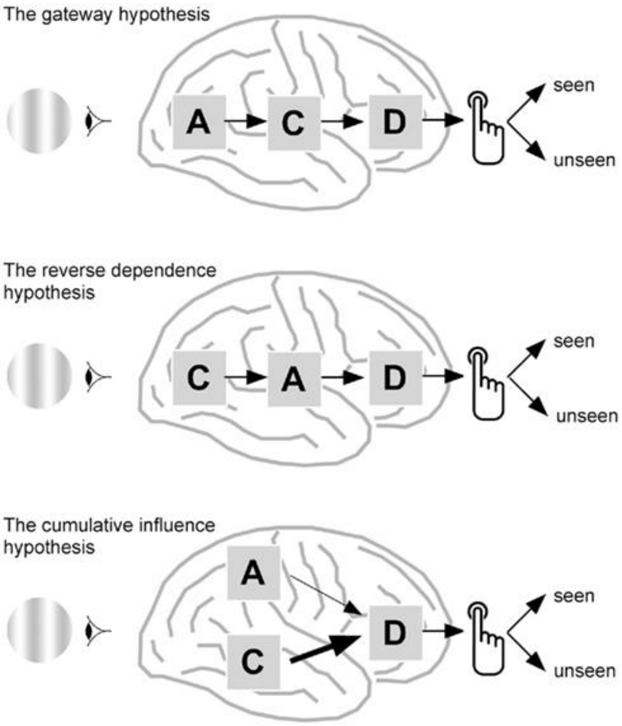

Figure 1.3. Models reflecting different options of how attention and conscious perception could be related. A, attention-related activity; C, consciousness-related activity; D, decisional process. Reprinted with permission from Tallon-Baudry, 2012.

2.1. The attention system, and its link to conscious perception

Similarly to the concept of consciousness, it seems that “everyone knows what attention is” (James, 1890), while also the opposite may be true: “no one knows what attention is” (Hommel et al., 2019). Despite the broad variety of definitions, many of them seem to concur in the conception of attention as a mechanism for the selection of information, given that we have a limited amount of processing resources. Posner and Petersen (1990) suggested that the human attentional system can be divided in three attentional networks, each of them representing a different set of attentional functions. These networks – namely alerting, orienting and executive control – are also anatomically separated from other cognitive systems, and supported by distinct neural networks (Fig. 1.4.) (Petersen & Posner, 2012; Posner & Petersen, 1990).

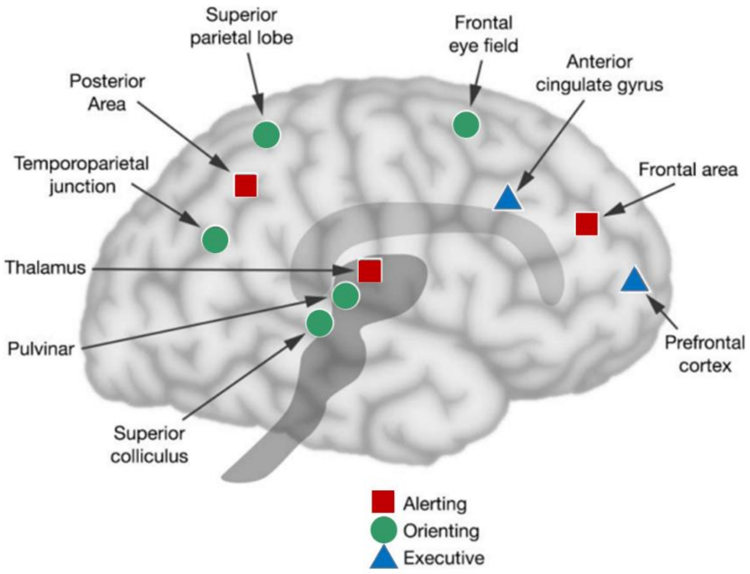

Figure 1.4. Original representation of the anatomy of the three attentional networks: alerting, orienting, and executive attention (a detailed and updated review of their neural substrates will be presented in chapter 3). Adapted with permission from Posner & Rothbart, 2007.

2.1.1. Phasic alerting

The *alerting network* is in charge of preparing and maintaining a state of vigilance, to process high priority signals faster and better, or to maintain an activity over time (Posner & Petersen, 1990; Sturm & Willmes, 2001). Therefore, the notion of alertness comprises both t*onic alertness,* which refers to a sustained state of vigilance, and *phasic alertness,* which refers to a transient increase in the preparation of the cognitive system, usually appearing after an external warning signal. During this work, I will solely focus in the second conception of alertness.

In phasic alertness paradigms, an alerting cue (in the same or a different sensory modality than the target) is presented before the target appears. Although the signal does not provide information about the location of appearance of the target (and it usually provides little temporal information), it speeds up responses in detection or discrimination tasks (compared to non-cue trials; Coull et al., 2001; Posner, 1978). To address the differences between phasic alertness and temporal orienting (i.e. the ability to voluntarily orient attention to a given point in time) the reader can see Weinbach & Henik (2012). Sometimes the decrease in reaction time (RT) produced by the alerting cues can be accompanied by an increase in errors (which is known as speed-accuracy trade-off; Posner, 1978), although it is not always de case (Cobos et al., 2019; Kusnir et al., 2011).

Initially, behavioral effects of phasic alertness were attributed to a reduction in the time for preparation and execution of motor responses (Posner, 1978; Sturm & Willmes, 2001). However, increasingly, it has been shown that phasic alertness affects early perceptual processes. For example, warning signals increase visual processing speed, and influence the spatial distribution of attentional resources (Botta et al., 2014; Chica, Thiebaut de Schotten, et al., 2012; Finke et al., 2012; Matthias et al., 2010; Petersen et al., 2017; Robertson et al., 1998; Wiegand et al., 2017).

Auditory phasic alerting also enhances conscious perception of near-threshold targets (targets that are only perceived in about 50% of the trials) in healthy participants by affecting early stages of perception, e.g. modulating perceptual sensitivity or lowering the threshold for conscious perception (Botta et al., 2014; Chica et al., 2016; Cobos et al., 2019; Kusnir et al., 2011; Martín-Signes, Pérez-Serrano, et al., 2019; Petersen et al., 2017). Furthermore, in neglect patients, the use of an alerting cue improves awareness deficits for left events (Robertson et al., 1998), which also temporally ameliorates after an alertness training (Thimm et al., 2006).

2.1.2. Spatial orienting

The *spatial orienting network* supports the ability to select information from a specific spatial location (Posner, 1980; Posner & Petersen, 1990). Although I will focus on the spatial component, orienting of attention can be also feature-based (e.g. orienting attention to a given color), or object-based (e.g. orienting attention to vertical lines). Spatial attention can be oriented to the location where a salient or relevant stimulus occurs. This *exogenous* or *bottom-up* orienting of attention is fast (reaching its peak at around 100 ms), although short lasting (Müller & Findlay, 1988; Muller & Rabbitt, 1989). But attention can also be allocated according to our plans, intentions, or task goals. This *endogenous* or *top-down* orienting of attention is slower than exogenous attention (reaching its peak at around 300 ms), although longer lasting (Müller & Findlay, 1988; Muller & Rabbitt, 1989). Furthermore, the attentional deployment to a specific location can occur *overtly* (i.e. accompanied by eye or head movements) or *covertly* (i.e. without any eye or head movement) (Posner, 1980).

Experimentally, the control of spatial attention has been investigated thought different paradigms. One of the most broadly employed is the Posner spatial cueing paradigm (Posner, 1980), in its distinct variants (for a review see Chica, Martín-Arévalo, et al., 2014). In the exogenous version, a spatially non-predictive peripheral cue (e.g. a small circle) appears in some of the trials in one of the possible locations. In the endogenous spatial version, a spatially predictive central symbolic cue (e.g. an arrow[1] or a colored stimulus) signals one of the possible locations where the target will likely appear. For both types of cues, trials are categorized as “valid” or “cued” when the target appears at the cued location, and “invalid” or “uncued” when the target appears at a different location. The allocation of attention at the cued location gives raise to the *facilitation effect*, which is demonstrated by shorter RT and/or greater accuracy for responding to the target in the valid compared to the invalid condition. However, there are crucial experimental variables that can substantially affect behavioral results; for example, at long cue-target intervals (longer than 300 ms), the effect of exogenous orienting can reverse, that is, valid cues produce longer RT than invalid cues (a phenomenon called *inhibition of return,* Posner et al., 1985).

The behavioral advantage provided by spatial cues has demonstrated to emerge from the modulation of several processes, probably combined at different time points during visual tasks. Spatial orienting improves discriminability (by

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[1] Although arrow cues have been extensively used in endogenous spatial orienting paradigms, overlearned symbolic cues with a spatial meaning (like arrows, or words such as “up” and “down”) have demonstrated to orient attention also in an exogenous or bottom-up manner (Hommel et al., 2001). Thus, investigations employing those stimuli as cues might produce mixed results due to the modulation of both forms of spatial orienting.

signal quality enhancement and external noise reduction), accelerates the speed of processing, and produces changes in decision criteria (Carrasco, 2006; Carrasco & McElree, 2001; Dosher & Lu, 2000; Pestilli & Carrasco, 2005). For example, both peripheral and central cues increase contrast sensitivity in a discrimination task of supra-threshold targets (Ling & Carrasco, 2006). However, by employing near-threshold targets, exogenous and endogenous spatial attention have demonstrated differential effects over conscious perception. Predictive and non-predictive peripheral cues (triggering exogenous spatial attention) increased the probability of conscious detection of near-threshold targets when they appeared in valid compared to invalid locations. However, predictive central cues (triggering endogenous spatial attention) were inefficient in the modulation of conscious perception of near-threshold targets (Botta et al., 2014; Chica et al., 2010; Chica, Lasaponara, et al., 2011). Although these data are in accordance with the idea of attention and conscious perception independency (Kentridge et al., 2008; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008), they may highlight the heterogeneity of the attention system, where some forms of attention (e.g. endogenous) are not crucial for the emergence of conscious perception.

2.1.3. Executive control

The *executive control network* is required in situations for which we do not have a learned schema of action, or it is not appropriate (Petersen & Posner, 2012). This usually happens when the situation is novel, difficult, dangerous, or changing, when it involves planning or decision making, or when it includes conflict or errors that have to be detected and solved (Norman & Shallice, 1986). In the literature, the terms executive control, cognitive control, or attentional control, are many times used as synonymous (however, I will employ the former designation during this work).

According to Posner & Digirolamo (1998), executive control is implemented in the situations above described, when executive functions are necessary. Many cognitive functions are under the umbrella of executive functions, and their specific components vary in the literature between models (Botvinick et al., 2001; Miller & Cohen, 2001; Miyake et al., 2000). Among those functions, some of the most important are: i) shifting between mental sets or tasks, ii) inhibition of prepotent and competing responses, iii) conflict detection, monitoring, and resolution, iv) planning and decision making, and v) working memory.

For many authors, this set of functions is closely bounded with consciousness (Dehaene & Naccache, 2001; Norman & Shallice, 1986). In fact, we have the intuition that those situations that require to modify our routine actions or to create new ones, require conscious control. However, this view is firmly debated and challenged by some evidence (Kunde et al., 2012; Mayr, 2004; van Gaal et al., 2012). In short, control (e.g. task preparation or response inhibition) can be triggered by subliminal explicit events, but implicit control originated by task environment or previous events (such as conflict frequency or conflict history) requires conscious processing (see Kunde et al., 2012).

Given its complexity, the experimental study of the executive control network has been carry out through diverse experimental tasks. Dual-tasks paradigms require the distribution of our limited resources among tasks concurrently performed, and thus, the control of such resources. As reviewed in

Chapter 1, execution of a central task can impair conscious perception for some tasks occurring at the periphery (while other tasks are unaffectedly performed, Matthews et al., 2018). However, on these paradigms, the isolation of executive processes is achieved by comparing single and dual-task conditions, therefore, many other factors (memory load, response selection and execution, etc.) differ between conditions. Others approaches have employed a unique task with different conditions varying in difficulty, where a greater deployment of the executive control network is expected. Some of these tasks will be reviewed below.

The effects of executive attention over conscious perception have been less studied than those of the alerting and orienting networks depicted above, with the exception of working memory. A close relationship between working memory and consciousness has been theoretically proposed (Baars, 1988; Ebbinghaus, 2013), and experimentally demonstrated. For example, in the attentional blink phenomenon, the failure to perceive the second stimulus is attributed to the encoding of the first stimulus in working memory (Ophir et al., 2020). Also, under situations of high working memory load (for example, by concurrently remembering a sequence of letters), the threshold for consciously detection a stimulus increases (De Loof et al., 2013, 2015). However, when information retained in visuospatial working memory shares perceptual characteristics with the to-be-detected stimuli (e.g. color), the threshold for conscious detection decreases (Gayet et al., 2013).

Recently, inhibition and conflict control components have been investigated in relation with conscious perception, by employing one of the token interference tasks, the Stroop task (Stroop, 1935). In this task, color words are presented, written in different colors, and the participant's task is to name or discriminate the color of the word, inhibiting the preponderant response of reading. In congruent trials, the word meaning coincides with the word color (for example, the word "blue" written in blue). In incongruent trials, the word meaning and the word color do not match (for example, the word "blue" written in yellow). Evidence of the conflict is demonstrated by slower and/or less accurate responses for incongruent compared to congruent trials. When this task (presented at fixation) has been combined with a detection task of near-threshold visual stimuli presented in the periphery, response criterion was more conservative to detect the stimuli for incongruent compared to congruent trials (Colás et al., 2017). Also, when analyzing event related potentials with EEG recordings, the anterior N2 evoked-potential (usually associated with conflict resolution) was enhanced for seen compared to unseen incongruent Stroop trials (Colás et al., 2018). These results suggest that when executive control is elicited in conflict situations, conscious perception is altered by the modulation of decision stages of processing.

Chapter 3. Neural substrates: from theory to matter

In the two previous chapters, I have delineated theoretical and conceptual frameworks in the study of conscious perception and the attention system, and importantly, in the relation between them. Also, I have reviewed how these processes affect our experience and behavior, by themselves and interacting with each other. This third and last chapter of the introduction will adopt a neuroscientific point of view to examine the neural processes that subtend attention and conscious perception. This approach is important not only because it offers a better understanding of how, where, and when attention and conscious perception operate (Crick & Koch, 1990), but it also takes a fundamental role outlining the nature of the relation between them. In addition, a deep knowledge of the NCC and attention is fundamental from a clinical and rehabilitation perspective.

3.1. Neural correlates of consciousness

Models of conscious perception try to respond to one of the critical questions in the field: the NCC, that is, the specific neural processes underlying a perceptual content and thus, considered sufficient to generate it. The NCC can be searched in specific regions or networks, or in types of neural activity. The study of the electrophysiological signals and mechanisms is a compelling approach to the NCC. Some of them (e.g. late event-related potentials, synchrony, or complexity measures) have been proposed as markers of consciousness. However, this approach is beyond the scope of this work (for an insight on this literature, the reader can remit to e.g. Melloni et al., 2007; Northoff & Lamme, 2020; Railo et al., 2011). Leaving aside the theoretical model, empirical data from healthy participants and patients provide convergent but conflicting evidence too. The same happens when different neuroimaging or neurostimulation methodologies are employed as neural correlational or causal measures. Just as it seems to happen in other areas of study of consciousness, the NCC is a debated question. However, there is a general agreement in the requirement of an integrated, distributed, and interdependent interaction of brain regions and networks for consciousness to occur. Nevertheless, the specific brain regions where this takes place are questioned (for a recent and extensive review on the topic see Northoff & Lamme, 2020).

3.1.1. Early and higher visual areas

The first cortical area responsive to visual stimulation is the primary visual cortex (V1), whose neurons respond to simple features (e.g. orientation). As manifested in blindsight patients, V1 seems to be necessary for a normal visual experience (Weiskrantz, 1997). Although it is usually sustained that V1 is not sufficient for conscious perception, its direct or indirect role in consciousness is a matter of debate (Crick & Koch, 1995; Silvanto, 2014). Many other regions of the extrastriate cortex, along the ventral visual pathway, contribute to conscious perception of specific contents (e.g. V4 for color or fusiform gyrus for face perception). Lesions of such nodes can cause consciousness alterations of the corresponding perceptual representations (e.g. achromatopsia or prosopagnosia, following the anterior examples). Also, their stimulation can induce phosphenes (i.e. short light flashes) or disrupt such percepts (Rees et al., 2002).

According to some theorists, activity in occipito-temporo-parietal areas (also named as a posterior cortical "hot zone", Boly et al., 2017; Koch et al., 2016) is sufficient for conscious perception. Although the initial interest in the search for the NCC was directed to fronto-parietal regions (Crick & Koch, 1998), no-report paradigms have revealed a limited or null involvement of anterior (e.g. prefrontal) regions in conscious perception (Koch et al., 2016; Tsuchiya et al., 2015). Under the assumption that such paradigms avoid the contamination of NCC with other processes recruited in "report" paradigms, it has been argued that posterior regions are the proper-NCC, while anterior areas are only involved in succeeding cognitive processes such as reporting, working memory manipulations, response preparation, etc. (however, see Odegaard et al., 2017; Safavi et al., 2014 for alternative interpretations).

3.1.2. The "prefrontal" debate

It has been widely suggested that, although conscious contents are distributed in different early and higher sensory regions and networks, and thus, they are necessary for conscious experience, they are not sufficient without the activity of the prefrontal lobe (Del Cul et al., 2009; Lau & Rosenthal, 2011) and its connections with the parietal lobe (Bor & Seth, 2012; Dehaene & Changeux, 2011; Dehaene & Naccache, 2001; Laureys & Schiff, 2012; Rees & Lavie, 2001).

Evidence supporting this view comes from fMRI studies employing the contrastive approach (Dehaene & Changeux, 2011; Rees et al., 2002). For example, using a change blindness paradigm, frontal and parietal regions were activated during conscious detection of a change in the scene, while little activity outside the ventral pathway was evoked by undetected changes (Rees & Lavie, 2001). Lesion studies involving prefrontal (Colás et al., 2019; Del Cul et al., 2009; Odegaard et al., 2017) or fronto-parietal damage (e.g. patients with spatial neglect, Bartolomeo et al., 2007) demonstrate that conscious perception can be affected even with intact early and higher visual areas (Rees, 2001). Meanwhile, stimulation studies (some of them review in Dehaene & Changeux, 2011), support a causal role of these areas in conscious processing. Finally, intracellular recordings and, more recently, multivariate fMRI techniques, have shown that some perceptual contents are represented in the prefrontal cortex (Kapoor et al., 2020; Panagiotaropoulos et al., 2012; Wang et al., 2013).

As introduced in the previous section, the implication of prefrontal and fronto-parietal regions in conscious perception has been recently questioned, giving rise to an open debate (Boly et al., 2017; Odegaard et al., 2017; Safavi et al., 2014). In any case, it is accepted that no unique brain area is necessary for conscious perception, whereas localizing NCC still has a long way to go (Sandberg et al., 2016).

3.1.3. The role of white matter in conscious perception

As predicted by some theories (e.g. the global workspace theory, Dehaene & Changeux, 2011), conscious perception requires a long-distance cortical network, primarily allowing the communication between perceptual and higher associative areas. Advances in diffusion-weighted imaging (DWI) have permitted to identify, in living humans, tracts composed by long association fibers (Fig. 1.5.), especially running between fronto-parietal regions, whose integrity may be necessary for conscious perception (Catani & Thiebaut de Schotten, 2008). One of the main fronto-parietal pathways is the *superior longitudinal fasciculus* (SLF). It has been divided in three different branches: a dorsal branch (SLF I), connecting the superior parietal lobe and the dorsal and medial parts of the frontal lobe; a middle branch (SLF II) connecting the angular gyrus and the posterior regions of the superior and middle frontal gyrus; and a ventral branch (SLF III), connecting the supramarginal gyrus and the inferior frontal gyrus (Nakajima et al., 2020; Rojkova et al., 2016; Thiebaut de Schotten et al., 2011). Other ventral associative tracts, which also deserve to be introduced, are the *inferior fronto-occipital fasciculus* (IFOF), connecting the inferior and medial occipital lobe and the orbital and polar frontal lobe, and the *inferior longitudinal fasciculus* (ILF), connecting occipital and posterior temporal regions and anterior temporal regions (Forkel, Thiebaut de Schotten, Kawadler, et al., 2014; Rojkova et al., 2016; Wakana et al., 2004).

Much of the evidence for the involvement of such white-matter tracts in conscious perception comes from lesion studies. In spatial neglect, the disconnection of the right hemisphere and the ipsilateral frontal lobe, plays a fundamental role in the occurrence and severity of this condition. Some studies have reported that spatial neglect symptoms are related with the SLF, the IFOF, and the ILF (Bartolomeo et al., 2007; Ciaraffa et al., 2013; Doricchi et al., 2008; Lunven & Bartolomeo, 2017). Other conditions characterized by white matter injury also exhibit impairments in conscious perception. For example, a masking study with patients with multiple sclerosis showed that they required a longer target-mask period to achieve conscious access of masked stimuli (masking threshold), and this effect was related to damage of the right dorsolateral prefrontal white matter and the right IFOF (Reuter et al., 2009). A similar result was recently found in patients with psychosis (Berkovitch et al., 2021), identifying an association between masking threshold and the integrity of long-range (e.g. IFOF) and interhemispheric tracts. Also, patients with prefrontal lesions exhibited a negative correlation between the contrast needed to perceive near-threshold Gabors and the integrity of the right SLF III (Colás et al., 2019). In healthy participants, individual differences in bistable perception (e.g. percept duration) were correlated with microstructural properties (i.e. fractional anisotropy) of the SLF (Kanai et al., 2010). The evidence reviewed above highlights the importance of structural connectivity within a broad fronto-parietal network in conscious access.

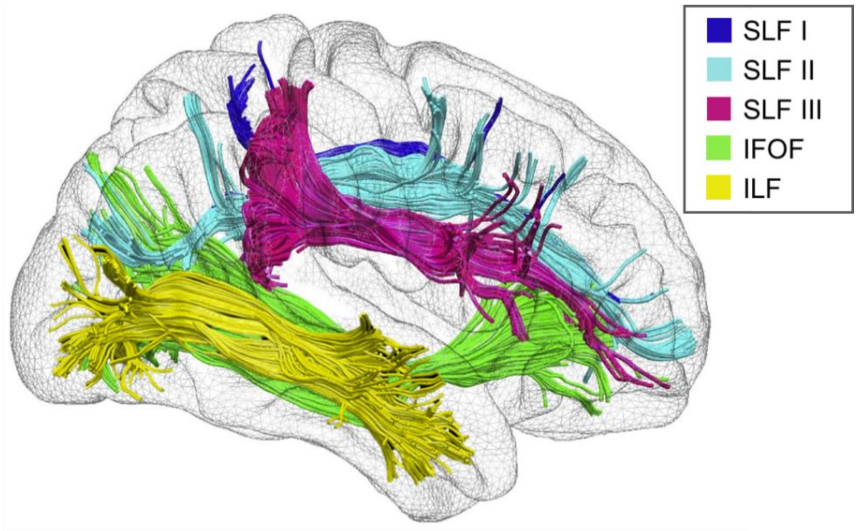

Figure 1.5. Some of the human associative white matter pathways, delineated by DWI tractography in the right hemisphere. IFL, inferior longitudinal fasciculus; IFOF, inferior fronto-occipital fasciculus; SLF I, dorsal superior longitudinal fasciculus; SLF II, middle superior longitudinal fasciculus; SLF III, ventral superior longitudinal fasciculus. Adapted with permission from Bartolomeo & Malkinson, 2019.

3.2. Shared neural correlates for attention and conscious perception

As it has been reviewed along these chapters, attention and conscious perception are interconnected processes from a theoretical and empirical perspective. However, this intuitive view can be revised from a neural perspective. As proposed by Tallon-Baudry (2012), if attention and conscious perception are intrinsically related, shared neural substrates are expected. However, if they constitute separated processes, they should also rely on separated neural bases. The next few pages briefly cover what is known about the neural bases of the attentional systems (i.e. phasic alerting, spatial orienting, and executive control), and their common neural mechanisms with conscious perception.

3.2.1. Phasic alerting

Sturm & Willmes (2001) suggested the existence of a right hemisphere *anterior alerting system* involved in both, tonic and phasic alerting. This system comprises a network of midbrain and thalamic areas, as well as frontal (anterior cingulate cortex [ACC] and dorsolateral prefrontal cortex) and inferior parietal areas (Clemens et al., 2011; Sturm et al., 1999; Sturm & Willmes, 2001). In addition, tasks including warning signals (and thus, entailing phasic alerting) activate left fronto-parietal areas, such as the supplementary motor area (SMA), and the inferior and superior parietal lobe (Fan et al., 2005; Yanaka et al., 2010). There is also evidence of the contribution of the locus coeruleus–norepinephrine system to warning-signal effects (Coull et al., 2001; Marrocco & Davidson, 1998). It has been suggested that the ACC could send and receive signals from and to, the locus coeruleus (probably mediated by the thalamus), serving as a connection between brain-stem activation (for maintaining alertness) and cortical areas for information processing (Sturm & Willmes, 2001; Yanaka et al., 2010).

An fMRI study from our lab explored the interaction between phasic alerting and conscious perception, by focusing on the auditory warning signal period, and its influence to the succeeding emergence of conscious perception of a near-threshold Gabor (Chica et al., 2016). Results demonstrated that many of the areas usually linked with phasic alerting (for example, caudate, ACC, and SMA), were more activated when the target was later perceived, especially when the warning signal was absent. In other words, the activation of such alerting related areas when the alerting tone was not present, may facilitate conscious perception. This interaction effect for the ACC, thalamus, and caudate was found at the moment of cue appearance, and about 2 seconds later in the SMA. This late activation could be priming motor selection and response, as a consequence of the activation of the anterior alerting system (see also Yanaka et al., 2010). Additionally, functional connectivity analyses revealed an essential role of the coupling between caudate and ACC for conscious perception. The strength coupling was comparable high for all trials with warning signals (regardless of whether the target was later perceived or not), but it was larger for consciously seen targets (as compared to unseen targets) when the warning signal was absent.

In a follow up study from our lab (Martín-Signes, Pérez-Serrano, et al., 2019), we proved the causal involvement of the SMA in the interaction between phasic alerting and conscious perception by using a similar task. We hypothesized that the inhibition of the SMA might alter the benefit of the alerting cue over conscious perception. To this aim, we use offline repetitive TMS (rTMS) over the SMA, and included a sham condition (in which the coil was placed in the same area while a recording of the original TMS sound was reproduced, but no pulses were applied) and an active condition (the left inferior parietal lobe, IPL). Results showed that the facilitation effect of phasic alertness over conscious perception was reduced after rTMS over the SMA (due to an increase of the percentage of seen Gabors when the warning signal was absent), as compared with the pre-stimulation session, and with the sham stimulation condition. Additionally, a negative correlation between the TMS effect and the microstructure of the right SLF III was found. rTMS over the left IPL produced no modulations, demonstrating a region-specific effect. These results highlight the causal implication of a frontal region, the SMA, in the relationship between phasic alertness and conscious perception.

3.2.2. Spatial orienting

Corbetta & Shulman (2002) proposed the existence of two attentional systems, sustained by separated networks of brain areas: a *dorsal fronto-parietal system*, including the bilateral superior parietal lobe, the intraparietal sulcus, and the frontal eye field (FEF), and a *ventral fronto-parietal system*, including the bilateral temporoparietal junction, and the middle and inferior frontal gyri, primarily of the right hemisphere (Corbetta et al., 2008). The dorsal network is involved in top-down (goal-directed) orientation of attention and selection of appropriate responses, while the ventral network mediates detection and shifts of attention to relevant, salient or unexpected stimuli (Corbetta & Shulman, 2002; Vossel et al., 2014). These fronto-parietal regions interact with the visual processing that occurs in early areas (e.g. by the amplification of target-related neural signals), constituting a mechanism for the selection of relevant information

(Cosman et al., 2018; Marshall et al., 2015; Reynolds & Chelazzi, 2004; Schafer & Moore, 2011; Silvanto et al., 2006). The observed overlap between fronto-parietal regions involved in attentional control and those that correlate with visual perception (see section 3.1.2.), has led some authors to propose a tight relation between attention and conscious perception (Rees & Lavie, 2001), although there are alternative views (Koch & Tsuchiya, 2007; Tsubomi et al., 2012; Wyart & Tallon-Baudry, 2008).

An fMRI study from our lab explored the interaction between exogenous spatial orienting and conscious perception, by focusing on the neural correlates of the attentional orienting period, and their influence to the succeeding emergence of visual conscious perception (Chica et al., 2013). According to the results, some key nodes of the dorsal fronto-parietal network (e.g. FEF) were more activated or functionally coupled when a spatial cue was presented at the same location that the subsequent target (valid trials), and this target was later perceived. On the contrary, when the spatial cue appeared at the opposite location that the subsequent target (invalid trials), the activation/coupling of these nodes was lower when the target was later perceived. Also, a component of the ventral network, the supramarginal gyrus, was more activated during invalid trials (which require reorienting of attention), when the target was later perceived (see also Webb et al., 2016). The authors demonstrated that the neural interactions between spatial attention and conscious perception occurred in nodes of the spatial orienting network (and not in early or higher visual areas), demonstrating that this attentional system is important for selecting which information will be consciously perceived and accessed (Chica et al., 2013; Chica, Valero-Cabré, et al., 2014).

However, the neural correlates of endogenous spatial orienting seem to show little overlap with those of conscious perception (in accordance with the behavioral dissociations often found, e.g. Koch & Tsuchiya, 2007). For example, in an fMRI study utilizing a paradigm with central orienting cues and near-threshold Gabors, only activity in the thalamus was increased for seen as compared to unseen targets on invalid trials but not on valid trials (Chica et al., 2016). However, no occipital or fronto-parietal regions usually involved in endogenous orienting, correlated with participants’ conscious reports. Similar results have been found exploring electrophysiological markers using EEG or magnetoencephalography (Chica, Botta, et al., 2012; Wyart & Tallon-Baudry, 2008).

3.2.3. Executive control

Early studies (Macdonald et al., 2000; Posner & Petersen, 1990) have related executive control processes with activity in prefrontal regions, emphasizing the role of areas such as the ACC and the dorsolateral prefrontal cortex (dlPFC). The conflict monitoring theory proposes a role of the ACC in conflict evaluation and monitoring, while the dlPFC is more related to flexible readjustments of behavior related to cognitive control (Botvinick et al., 2001; Macdonald et al., 2000). Miller & Cohen (2001) pointed to the prefrontal cortex as a key region for executive control, stemming from its wide connections, from and to, many brain systems, and its capacity for maintaining representations of goals and actions. Later proposals extended the number of regions or networks involved in executive control. For example, Cole & Schneider (2007) suggested a tightly coupled set of regions, that would form a cognitive control network, including the previously mentioned ACC and dlPFC, the SMA, anterior insula, premotor cortex, posterior parietal cortex, and inferior frontal junction. Some other models (Dosenbach et al., 2008; Petersen & Posner, 2012) propose the existence of two separate executive control networks. On the one hand, a *fronto-parietal network* (with a distinct identity from the orienting network), that includes lateral frontal and parietal regions, initiates and adjusts attentional control in a trial-by-trial manner. On the other hand, a *cingulo-opercular network*, including the medial frontal cortex, the ACC, and the thalamus, maintains set-task across time and adjusts control after errors. Dosenbach and collaborator (2008) additionally proposed a set of cerebellar regions involved in error processing, which would send and receive error information from and to both executive networks. Other models have suggested an antagonist (Bressler & Menon, 2010) or integrated role (Cocchi et al., 2013) of the *default mode network* in executive control. New approaches conceptualize executive control as an emergent property of multiple interacting nodes in the brain, in which any of those elements can exert control and also be controlled (Zink et al., 2021). In contrast with hierarchical views, where brain regions or networks exert control over basic processes, a network conceptualization puts the focus in the communication between nodes.

The above mentioned regions and networks, largely overlap with the prefrontal and fronto-parietal brain areas suggested by some models of conscious perception, which link both, conscious perception and executive control, to a global workspace (Dehaene, Kerszberg, et al., 1998; Dehaene & Changeux, 2011). A study from our group, examined this hypothesis by employing a task in which participants had to detect a near-threshold Gabor and perform a concurrent Stroop task, while EEG data was recorded (Colás et al., 2018). As mentioned in Chapter 2, executive control comprises a broad set of functions, therefore, this study was focused in the inhibitory control subcomponent. Results showed that the N2 component, usually linked to conflict detection, was larger for trials in which conflict was present (incongruent Stroop trials) as compared to no conflict trials (congruent Stroop trials), but only when the target was later perceived. This result may reflect that when there is a better preparation for conflict detection and control execution (reflected by larger N2 amplitudes), a conscious report of the subsequent target is more likely to occur. Source localization analysis also showed that N2 was related to activity of the ACC, which exhibited a similar pattern of results. These findings are in agreement with others before, indicating that the ACC participates in a distributed conscious control network (Dehaene et al., 2003).

3.2.4. The role of white matter in attention and conscious perception

Structural connectivity sustaining attentional networks has been widely examined (e.g. Ge et al., 2013; Luna et al., 2021; Niogi, 2010). Among candidate white matter tracts, long-range fronto-parietal tracts (primarily the SLF) have received a great interest given their anatomical association with different attentional subsystems. Indeed, it has been suggested that the SLF I overlaps with the dorsal fronto-parietal system, while the ventral system overlapps with the SLF III. The SLF II could represent a communication path between dorsal and ventral systems (Thiebaut de Schotten et al., 2011). As stated before in this work, evidence from neglect patients suggests a reliable role of the SLF in spatial orienting (Bartolomeo et al., 2007; Ciaraffa et al., 2013; Doricchi et al., 2008; Lunven & Bartolomeo, 2017), also confirmed by data from healthy population (Carretié et al., 2012; Thiebaut de Schotten et al., 2011). The executive control network has also been related with the SLF in healthy population (Crespi et al., 2018; Sasson et al., 2012, 2013; Smolker et al., 2018) and in several conditions showing executive impairments (Chiang et al., 2015, 2016; Makris et al., 2008; Muir et al., 2015; Oh et al., 2018; Sui & Rajapakse, 2018; Wu et al., 2020). Finally, the alerting system has been associated with the cerebello-thalamic tract, the internal capsule, the dorsolateral prefrontal-caudate tract, and the corpus callosum (Ge et al., 2013; Luna et al., 2021; Niogi, 2010), while only some evidence has related sustained attention with the SLF (Klarborg et al., 2013, but see below).

Research examining possible shared neural substrates for conscious perception and attention in fronto-parietal white matter is very limited. One study from our group (Chica et al., 2018) employed previous fMRI-DWI data (Chica et al., 2013, 2016) to explore the influence of the SLF III microstructure over the functional interactions previously observed between exogenous orienting and phasic alerting with conscious perception in fronto-parietal regions. Results showed that reduced integrity of the left SLF III was associated with a larger functional interaction between exogenous orienting and conscious perception in the left FEF. In addition, increased integrity of the left SLF III predicted larger functional interactions between phasic alerting and conscious perception in the left ACC.

More recently, the right SLF III was related to the interaction between phasic alerting and conscious perception, explored while stimulating the SMA with rTMS (Martín-Signes, Pérez-Serrano, et al., 2019). Interestingly, participants with lower mean HMOA (hindrance modulated orientational anisotropy; a measure of the microstructural organization of white matter) of this tract were the ones showing greater TMS modulation of the alerting effect. Specially, the microstructure of the right SLF III was significantly correlated with the rTMS effect in the no-tone condition. This results suggest that a good integrity of this fasciculus, connecting inferior parietal and frontal regions, could protect from the rTMS effects, especially in the absence of alerting cues (see Chapter 6 of this thesis for similar results). Although still scarce, these outcomes offer a new and intriguing approach to the study of the common neural mechanisms for attention and conscious perception. They also suggest that individual variability in behavioral or neuromodulation effects could be related to particular differences in white matter structure.

MOTIVATION AND AIMS

Chapter 4. Motivation, research aims and significance

4.1. Motivation

The broad picture described in the introduction of this work offers a variety of open questions, as well as a wide range of approaches to answer them. From an empirical, theoretical, but also daily perspective, we can presume that attention and conscious perception are tightly related processes. Given the heterogeneity of attention, modulations produced by different attentional networks over conscious perception have been explored separately. In this context, phasic alerting and exogenous orienting have demonstrated to enhance conscious perception (Chica, Lasaponara, et al., 2011; Kusnir et al., 2011; Martín-Signes, Pérez-Serrano, et al., 2019; Robertson et al., 1998), while endogenous orienting has shown weak or null effects (Koch & Tsuchiya, 2007). However, the role of executive control remains underexplored, and results are less consistent (Colás et al., 2017, 2018). At the neural level, alerting, orienting, and executive control processes rely, to a great extent, in different frontal and parietal cortical regions, and long-range white matter tracts connecting such areas (Fan et al., 2005; Ge et al., 2013). Meanwhile, some theories propose that conscious perception emerges when information is represented in a large-scale network of fronto-parietal regions (Dehaene et al., 2006). Although the involvement of parietal regions is widely accepted, mainly due to the causal evidence coming from patients with neglect, there is an extensive debate about a causal involvement of the frontal lobe in conscious access (Boly et al., 2017; Odegaard et al., 2017). The relationship between conscious perception and attentional processes has also been addressed by the search of common or distinct neural bases (Nani et al., 2019; Tallon-Baudry, 2012). The brain mechanisms supporting the interaction between spatial orienting and conscious perception have been explored with correlational and causal methodologies, demonstrating a role of fronto-parietal regions in attention and conscious perception (Chica et al., 2010, 2013; Chica, Valero-Cabré, et al., 2014). Similarly, there is correlational evidence of the role of certain fronto-striatal regions in phasic alerting and conscious perception (Chica et al., 2016), and causal evidence of the involvement of, at least, a frontal region (the SMA; Martín-Signes, Pérez-Serrano, et al., 2019). In the last place, there is evidence of an association between amplitude enhancement of an electrophysiological component related to conflict detection (the N2 component, source-localized in the ACC), and conscious perception (Colás et al., 2018). However, the low spatial resolution of the EEG does not permit to stablish a strong demonstration of a role of frontal regions in the interaction between executive control and conscious perception.

4.2. Research aims

The main goal of this doctoral thesis is to delineate the role of frontal regions, and fronto-parietal white matter tracts, in the relation between attention and conscious perception. Specifically, we focused in the executive control subcomponent of attention, given that its behavioral and neural relation with conscious perception has been underexplored. To accomplish this aim, two studies were conducted. Each of them tried to respond to a general question and other specific ones, that hopefully will shed light on the common picture[2].

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[2] Note that the two chapters that compose the experimental series section consist of a research article that has been published in an indexed journal. Therefore, there might be certain overlap in the introduction and discussion of the different chapters, and with the introduction and general discussion of this doctoral thesis.

Chapter 5: *Are there neural common substrates for executive control and conscious perception?*

The first objective of this study was to replicate and better outline the behavioral effects of the executive control network (manipulated through a Stoop task) over the conscious perception of near-threshold Gabor stimuli. Previous studies from our lab found that Stroop conflict did not modulate perceptual sensitivity but response criterion to detect near-threshold Gabor stimuli (Colás et al., 2017). A second objective was to determine the neural mechanisms supporting the interaction between executive control (its inhibitory component) and conscious perception, by employing a correlational methodology, such as fMRI. To the best of our knowledge, this question has been only addressed before exploring common electrophysiological markers with EEG (Colás et al., 2018). fMRI has a better spatial resolution, enabling the search for those brain areas where common neural mechanisms could occur. The third objective was to explore the involvement of long-range fronto-parietal white matter tracts, through the delineation of the 3 branches of the SLF with DWI tractography. We correlated their microstructural properties with behavioral and blood-oxygen-level dependent (BOLD) effects.

Chapter 6: *Is the frontal lobe casually involved in the interaction between executive control and conscious perception?*

Based on the results of the previous study (chapter 5), in which Stroop conflict did not modulate neither response criterion nor perceptual sensitivity, the first aim of this study was to test if perceptual stages of conscious processing could be modulated if incongruent Stroop trials (compared to congruent trials) generated a greater conflict. Therefore, the behavioral paradigm used in the former study (a Stroop task concurrent with a detection task of near-threshold Gabor stimuli) was slightly modified and tested. The second objective of this work was to prove the causal involvement of a frontal region in the interaction between executive control and conscious perception, by employing a causal methodology, such as TMS. The SMA was selected as a target because its functional connectivity with the superior parietal lobe demonstrated a significant interaction between executive attention and conscious perception (functional connectivity was increased for consciously perceived as compared to non-consciously perceived targets, but only for congruent trials). Additionally, two active control conditions were included: vertex and right FEF stimulation (a frontal region for which, based on the previous study, no interaction effects were expected). The last objective of this study was to explore the involvement of the 3 branches of the SLF with DWI tractography. We correlated their microstructural properties with behavioral and TMS effects.

4.3. Statement of significance

Attention has been commonly conceived as a gate or spotlight that selects information for further processing or conscious access (Dehaene et al., 2006), but there are other conceptualizations. For example, attention and conscious perception can be seen as separate mechanisms that feed a decisional variable (Tallon-Baudry, 2012). A greater understanding of how attention can modulate conscious perception may offer a better perspective of the nature of their relation. In this context, the present doctoral thesis explored the modulations of the executive control network (its inhibitory component) over conscious perception, extending the scarce previous research on its role (Colás et al., 2017, 2018).

Besides, the comprehension of the neural mechanisms supporting the interaction between attention and conscious perception is fundamental to characterize them as a separate, or conversely, a tight entity (Tallon-Baudry, 2012). This doctoral thesis explores the common neural mechanisms for executive control and conscious perception, and focused in the causal role of frontal areas in executive control interactions with conscious perception. One of the more intriguing questions in neuroscience is the search for the NCC, and the existing open debate about the implication of frontal regions in conscious perception (Boly et al., 2017; Odegaard et al., 2017) makes it an even more exciting challenge. This doctoral thesis modestly aims at adding some evidence about a frontal implication in conscious perception.

Finally, the development of DWI constitutes a new tool to explore the role of white matter structure in healthy people. The involvement of long-range white mater tracts, connecting frontal and parietal regions, in attention and conscious perception is proposed by some theories (Dehaene & Naccache, 2001). This doctoral thesis explores the involvement of the different branches of the SLF in the relation between executive control and conscious perception.

In sum, this doctoral thesis aims at adding some evidence, at the behavioral and neural level, about the relation between attention and conscious perception. This may increase our knowledge about which theories or models better explain data, and may allow to generate new integrated ones. This doctoral thesis also aims at exploring the causal involvement of frontal cortical regions, as well as the role of fronto-parietal white matter tracts, in different cognitive processes. This may increase our understanding of the functioning of the brain. At this stage, this doctoral thesis constitutes basic research, which is fundamental for the development of science. In the future, we expect that this present and future research, lead us to a better comprehension of those conditions that are accompanied by attention or consciousness deficits, and importantly, to a more efficient and adequate treatment strategies.

EXPERIMENTAL SERIES

Chapter 5. Are there neural common substrates for executive control and conscious perception?

The content of this chapter has been published in Martín-Signes, M., Paz-Alonso, P. M., & Chica, A. B. (2019). Connectivity of frontoparietal regions reveals executive attention and consciousness interactions. *Cerebral Cortex*, *29*(11), 4539-4550.

5.1. Abstract

The executive control network is involved in the voluntary control of novel and complex situations. Solving conflict situations or detecting errors have demonstrated to impair conscious perception of near-threshold stimuli. The aim of this study was to explore the neural mechanisms underlying executive control and its interaction with conscious perception using functional magnetic resonance imaging and diffusion-weighted imaging. To this end, we used a dual-task paradigm involving Stroop and conscious detection tasks with near-threshold stimuli. A set of prefrontal and frontoparietal regions were more strongly engaged for incongruent than congruent trials while a distributed set of frontoparietal regions showed stronger activation for consciously than nonconsciously perceived trials. Functional connectivity analysis revealed an interaction between executive control and conscious perception in frontal and parietal nodes. The microstructural properties of the middle branch of the superior longitudinal fasciculus were associated with neural measures of the interaction between executive control and consciousness. These results demonstrate that conscious perception and executive control share neural resources in frontoparietal networks, as proposed by some influential models.

5.2. Introduction

In our daily life, we are able to perform a wide set of tasks without deliberate attention or awareness. However, a different sort of actions appear to require attentional resources (Norman & Shallice, 1986). Executive control operates when our acting schemas are ineffective, impossible, or insufficient to lead with a specific situation, such as those that involve planning, novelty, error or conflict detection/resolution (Diamond, 2013; Posner & Digirolamo, 1998). The executive control network is one of the three main attentional networks proposed by Petersen and Posner, together with alerting and spatial orienting (Petersen & Posner, 2012; Posner & Petersen, 1990).

Attentional processes either boost conscious perception when aligned to the target or the relevant dimensions, or impair consciousness when attention is away, as demonstrated in many previous observations (Shapiro et al., 1997; Simons & Levin, 1997; Solomon, 2004) . Based on this evidence, some theories propose that attention is a gateway for conscious perception (Chica & Bartolomeo, 2012; Dehaene et al., 2006; Dehaene & Naccache, 2001; Posner, 1994). According to these proposals, research examining the effects of alerting and spatial orienting attentional networks over conscious perception has revealed that these attentional subsystems can interact with consciousness differently (Botta et al., 2014; Chica, Botta, et al., 2012; Chica, Lasaponara, et al., 2011; Koch & Tsuchiya, 2007; Kusnir et al., 2011; Petersen et al., 2017; Wyart & Tallon-Baudry, 2008). Nevertheless, the role of the executive network on conscious processing remains under-explored. Recently, Colás and collaborators used a dual-task paradigm combining a detection task of near-threshold stimuli with a Stroop task. Results revealed a modulation of decision criteria to detect the near-threshold stimuli when they were presented concurrently with the Stroop task, which was reflected in the modulation of the N2 potential and associated with the activation of the anterior cingulate cortex (ACC) (Colás et al., 2017, 2018). Furthemore, in dual-task situations, in which executive control is also required, conscious perception can be delayed or impaired (Meyer & Kieras, 1997; Pashler, 1994; Shapiro et al., 1997). These results suggest that executive control elicited by conflict situations influences perception or decision stages of conscious processing through the involvement of frontal regions on both conflict monitoring/resolution (Egner & Hirsch, 2005; Fan et al., 2005; Szameitat et al., 2002) and conscious perception (Lau & Rosenthal, 2011; Rees et al., 2002; Rounis et al., 2010).

Early studies on the neural underpinnings of executive control associated Stroop effects with the functioning of frontal regions, such as the dorsolateral prefrontal cortex (dlPFC) and the ACC (Egner & Hirsch, 2005; Fan et al., 2005; Macdonald et al., 2000; Milham et al., 2001; Miller & Cohen, 2001; Nee et al., 2007; Pardo et al., 1990). According to the conflict monitoring theory, these two frontal structures have complementary roles: while the ACC evaluates and monitors the presence of conflict, the dlPFC implements cognitive control (Botvinick et al., 2001; Macdonald et al., 2000; Nee et al., 2007). In addition to the ACC and dlPFC, there is agreement on the implication of a wider set of regions in executive control processes, including the dorsal premotor cortex, supplementary motor area (SMA), inferior frontal junction, anterior insula, and posterior parietal cortex (Cocchi et al., 2013; Cole & Schneider, 2007). Dosenbach and collaborators proposed that this set of regions is organized into two distinct networks: the *fronto-parietal* and the *cingulo-opercular* networks. The former network would exert a rapid-active control using feedback information to affect processing of the succeeding item, while the latter might constitute a set-maintenance system that integrates the received information to exert proactive control (Dosenbach et al., 2008). Other models propose a central role to the cingulo-opercular network in switching from the default mode network to the frontoparietal control network (Bressler & Menon, 2010).

Anatomically, parietal and frontal cortical regions are structurally connected by the superior longitudinal fasciculus (SLF), a fiber tract organized in three parallel longitudinal branches: dorsal (i.e. SLF I), middle (i.e. SLF II), and ventral (i.e. SLF III) (Rojkova et al., 2016; Thiebaut de Schotten et al., 2011). Previous research evidence has linked white matter microstructure of the SLF II and III with exogenous and endogenous spatial orienting in healthy populations (Carretié et al., 2012; Thiebaut de Schotten et al., 2011) and in patients with signs of spatial neglect (Bourgeois et al., 2015; Ciaraffa et al., 2013; Doricchi et al., 2008; Thiebaut De Schotten et al., 2014; Vallar et al., 2014). Sustained attention has been linked with the microstructural properties of the right SLF in typically developing children (Klarborg et al., 2013) and in individuals with attention-deficit/hyperactivity disorder (Chiang et al., 2015; Konrad et al., 2010; Wolfers et al., 2015). Recently, the neural interaction between conscious perception and different attentional subsystems (phasic alerting and exogenous orienting) has been related to the microstructure of the SLF III (Chica et al., 2018; Martín-Signes, Pérez-Serrano, et al., 2019).

In the present study, we investigated the neural bases of the interaction between executive control and consciousness using functional magnetic resonance imaging (fMRI) and diffusion-weighted imaging (DWI) tractography. In the scanner, participants performed a Stroop task concurrently with a conscious detection task of near-threshold Gabor stimuli (see also Colás et al., 2017, 2018). Behaviorally, we expected to observe impaired Gabor detection for incongruent trials as compared to congruent trials (Colás et al., 2017). At the neural level, we expected to observe a distributed frontoparietal network more strongly engaged for consciously seen as compared with unseen Gabors. In addition, frontal regions, such as the ACC, the dlPFC, or the insula, should be more engaged during incongruent trials, in which executive control strategies are required, as compared with congruent trials. If executive control modulates conscious perception, then brain activations associated with executive control should be related to subsequent conscious reports. We expected to find neural interactions between conscious perception and executive control in the activation of the above-mentioned frontoparietal regions or in the functional connectivity among them. Finally, using DWI tractography, we explored to what extent the microstructural properties of the different branches of the SLF were associated with behavioral and functional correlates of executive control and its interaction with consciousness.

5.3. Methods

5.3.1. Participants

A sample of 20 right-handed volunteers (11 females, mean age 25.70 years, standard deviation [SD] = 3.34) took part in the study. Participants were inexperienced with the task and reported to have a normal or corrected-to-normal vision, normal color-discrimination, and Spanish as their native language. Participants had no neurological or psychiatric conditions and followed all the safety requirements to undergo MRI studies. They signed an informed consent form to participate in the experiment, and received a monetary compensation for their time and effort (10 €/hour). The study was reviewed and approved by the Ethics Committee of the University of Granada, and was carried out in compliance with the recommendations of the Helsinki Declaration.

5.3.2. Apparatus and stimuli

E-prime software was used to control the presentation of stimuli, timing operations, and behavioral data collection (Schneider et al., 2002). Images were presented in a screen (NNL, 32'', 1024 × 768, 60 Hz) located at the back of the scanner and viewed with a mirror mounted on the head coil. Two markers (3º height x 5.3º width) and a central fixation point (0.4º x 0.4º) were displayed against a gray background at the beginning of the trial. Each marker consisted of a black square outline, placed 4.5º to the left and right of the fixation point. Spanish words for blue ("azul", 0.4º height x 1.6º width), green ("verde", 0.4º height x 2º width) and yellow ("amarillo", 0.4º height x 3º width) colors were presented 0.6º above the fixation point. Words were displayed either in blue, green, or yellow ink (Figure 5.1.). Trials were sorted as congruent when the word meaning and the ink color matched, and as incongruent when the word meaning and the ink color were different. The target was a Gabor stimulus that could appear inside the lateral boxes. Matlab 8.1 (http://www.mathworks.com) was used to create 100 Gabor stimuli (4 cycles/deg spatial frequency, 1.8º in diameter, SD of 0.1°), with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively. Target contrast was manipulated before the experimental task in order to adjust the percentage of consciously perceived targets to ~50% (see Procedure).

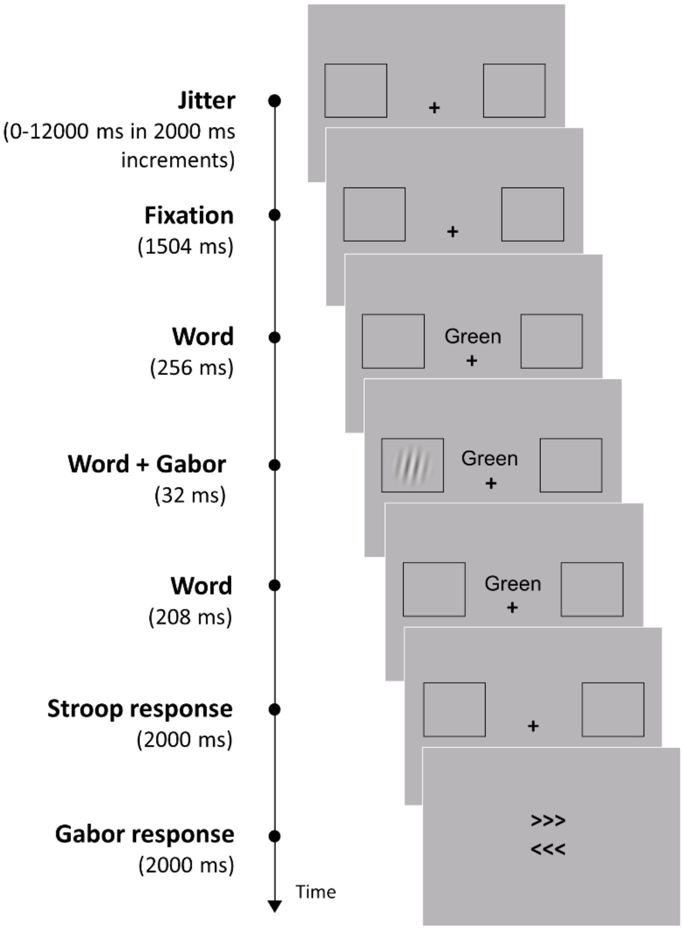

Figure 5.1. Sequence and timing of events in a trial of the experimental task. Words were displayed either in blue, green, or yellow ink. The example shows a trial with the Gabor present.

5.3.3. Procedure

The timing and sequence of the events presented in a trial are depicted in Figure 5.1. In each trial, participants were presented with a color word and a Gabor stimulus (although 25% of the trials were catch trials, in which the Gabor was not presented). 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 to this task with the index, middle, and ring finger of their right hand (color-key mapping counterbalanced across participants) using a 6-horizontally aligned-button fiber-optic box. Second, participants had to report if they consciously detected the appearance of the Gabor. They were asked to respond as accurately as possible and only when they were confident about their perception. The response was given by choosing one of the two arrow-like stimuli (>>> or <<<) pointing to the two possible locations of the target appearance (right or left box). The arrows were presented one above the other, with their position randomized in each trial. Participants were required to indicate the location of the target, with the left hand, using a 6-aligned-button fiber-optic box positioned vertically. They used the ring finger to press an upper key (corresponding to the upper arrow), and the middle finger to press a lower key (corresponding to the bottom arrow). This was done to avoid response preparation before the subjective response was executed. If they had not perceived the Gabor, participants were asked to use the index finger to press a third key. Participants were explicitly instructed to fixate the central plus sign throughout all the experiment.

In the scanner, but before the experimental trials, Gabor contrast was titrated for each participant to ensure that the percentage of seen targets would be ~50% in both sessions. Titration began with a supra-threshold stimulus (Michelson contrast = 0.184), whose contrast was manipulated in successive blocks depending on the mean percentage of seen targets after every 8 trials. After each block, if participants reported seeing 63% or more targets, 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%, the next block of trials used 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 ranging between ≥38% and ≤63% for two consecutive blocks of trials.

The experiment consisted of two sessions with 5 functional scans each. Each functional scan lasted for approximately 8 minutes. Across both sessions, participants encountered a total of 600 trials. Congruent and incongruent trials were presented in a pseudorandomized order during scanning. Incongruent trials accounted for 20% of the experimental trials. The Gabor was present on 75% of the trials, and absent on the remaining 25% of the trials (catch trials). The jitter fixation and the order of trial types within each scan was determined with an optimal sequencing program (i.e., Optseq2), designed to maximize the efficiency of recovery of the Blood-Oxygen-Level Dependent (BOLD) response (Dale, 1999; http://surfer.nmr.mgh.harvard.edu/optseq/). The jitter fixation periods were interleaved with the experimental trials as determined by the optimization program.

5.3.4. MRI data acquisition

Functional and structural images were collected on a 3-T Siemens Trio MRI scanner at the Mind, Brain, and Behavior Research Center (CIMCYC, University of Granada), using a 32-channel whole-head coil. Functional images were acquired using a gradient-echo echo-planar pulse sequence [Repetition Time (TR) = 2000 ms, Echo Time (TE) = 25 ms, 35 interleaved 3.4-mm cubic axial slices, no inter-slice gap, flip angle = 75°, Field of View (FOV) = 220 mm, 345 volumes per run]. Prior to each functional scan, several volumes were discarded to allow for saturation of the signal. High-resolution T1-weighted anatomical images (TR = 2530 ms, TE = 3.5 ms, flip angle = 7º, slice thickness = 1 mm, FOV = 256 mm) were also collected.

Additionally, a total of 70 near-axial slices were acquired using a sequence fully optimized for tractography of DWI providing isotropic 2-mm resolution and coverage of the whole head with a posterior-anterior phase of acquisition (TR = 8400 ms and TE = 88 ms). At each slice location, 6 images were acquired with no diffusion gradient applied and 60 diffusion-weighted images in which gradient directions were uniformly distributed in space. The diffusion weighting was equal to a b-value of 1500 s mm^2.

5.3.4. fMRI data analysis

SPM8 (Welcome Department of Cognitive Neurology, London) was used to conduct standard preprocessing routines and analyses. Images were corrected for differences in timing of slice acquisition and were realigned to the first volume by means of rigid-body transformation. Then, functional images were spatially smoothed using a 4-mm full width at half-maximum (FWHM) isotropic Gaussian kernel. Next, motion parameters obtained from realignment were used to inform a volume repair procedure (ArtRepair; Stanford Psychiatric Neuroimaging Laboratory) that identified bad volumes on the basis of within-scan movement and signal fluctuations, and then corrected bad signal values via interpolation. A volume-by-volume correction with a 1.5 mm threshold was applied, which did not correct more than 12% of the total volumes in any participant. After volume repair, structural and functional volumes were coregistered and spatially normalized to T1 and echo-planar imaging templates, respectively. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm cubic voxels. Templates were based on the MNI305 stereotaxic space. Then, functional volumes were spatially smoothed with a 7-mm FWHM isotropic Gaussian kernel.

Finally, a 128 s high-pass filter was used to eliminate contamination from slow drift of signals.

Statistical analyses were performed on individual participants' data using the general linear model (GLM). fMRI time series data were modeled by a series of events convolved with a canonical hemodynamic response function (HRF). Three phases of each fMRI trial were modeled separately (stimuli presentation, Stroop response, and Gabor response). The model was created to examine the neural changes restricted to the stimuli presentation period and was used in whole-brain contrast, regions-of-interest (ROIs), and functional connectivity analysis. Congruent and incongruent trials were sorted as seen or unseen in agreement to participants' responses. Accordingly, this model included regressors for the conditions: congruent seen, congruent unseen, incongruent seen, and incongruent unseen. Catch trials, errors, Stroop response and Gabor response periods, were modeled separately and excluded from the main analysis. All coordinates along the manuscript are reported in Montreal Neurological Institute (MNI) atlas space (Cocosco et al., 1997).

Contrast images, computed on a participant-by-participant basis were submitted to group analysis. At the group level, whole-brain contrasts between conditions were computed by performing one-sample t-tests on these images, treating participants as a random effect. Whole-brain maps involving all participants were thresholded at $q < 0.05$ (false discovery rate [FDR] correction voxel wise) for target present versus jitter fixation (i.e., null events) contrast. ROI analyses were performed with the MARSBAR toolbox for use with SPM8 (Brett et al., 2002). ROIs consisted of significantly active voxels identified from the Target present > Null whole-brain functional contrast ($q < 0.05$, voxel-wise FDR corrected) across all participants within a specific MARSBAR anatomical ROIs. A set of ROIs (the center of mass and the volume in mm^3 are indicated between parentheses) were built, including frontal: left ACC (-8, 21, 29; 416 mm^3), right ACC (10, 24, 26; 552 mm^3), left frontal eye field (FEF; -24, 10, 49; 560 mm^3), right FEF (36, -1, 52; 552 mm^3), left inferior frontal gyrus (IFG; -39, 24, 19; 5088 mm^3), right IFG (41, 24, 18; 4512 mm^3), left insula (-32, 19, 4; 4608 mm^3), right insula (36, 21, 1; 3416 mm^3), left middle frontal gyrus (MFG; -33, 32, 25, 1976 mm^3), right MFG (37, 34, 23; 1416 mm^3), left SMA (-6, 3, 54; 7048 mm^3), right SMA (8, 9, 54; 4128 mm^3); and parietal regions: left inferior parietal lobe (IPL; -36, -46, 45; 6592 mm^3), right IPL (32, -51, 48; 1240 mm^3), left superior parietal lobe (SPL; -23, -61, 49; 4080 mm^3), and right SPL (26, -59, 53; 1512 mm^3). For each ROI, we performed a repeated-measures analysis of variance (ANOVA) on the parameter estimates values, with the factors congruency and awareness.

Finally, we assessed functional connectivity via the beta series correlation method (Rissman et al., 2004) implemented in SPM8 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (beta values) were sorted according to the study conditions of interest (congruency: incongruent/congruent, and awareness: seen/unseen) to produce a condition-specific beta series for each voxel. Two different functional connectivity analyses were performed: (1) pairwise connectivity between the regions showing the main effect of congruency (i.e., bilateral IFG, left MFG, bilateral SMA, left FEF, left IPL, and bilateral SPL). Although the congruency effect was marginal for the left ACC ($F = 3.86$, $MSE = 8.84$, $p= 0.06$, $\eta^2_p = 0.17$), we added this region to the pairwise functional connectivity analysis given its relevance in executive control (Macdonald et al., 2000; Milham et al., 2001; Nee et al., 2007; Pardo et al., 1990); and (2) whole-brain functional connectivity with the left ACC as the seed region.

First, using pairwise functional connectivity analyses we calculated beta-series correlation values for each pair of ROIs, condition, and participant. As indicated, these correlation values were obtained including all the trials in our fMRI experimental design assigned to each of the conditions. To identify significant coupling strength between ROIs in each condition of interest these beta-series correlation values were averaged and 2-tailed tests were used to determine the statistical significance of these r values correcting for multiple comparisons ($q < 0.05$, FDR). Then, to examine interactions in pairwise functional connectivity between these ROIs, due to the fact that correlation coefficients are inherently restricted to range from − 1 to + 1, an archyperbolic tangent transform was applied to these beta series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution (Fisher, 1921). These Fisher’s z normally distributed values were then submitted to repeated-measures ANOVAs with the factors Congruency and Awareness. Statistically significant interactions were followed by Tukey post hoc analyses to examine the effects determining these interactions.

Second, for whole-brain functional connectivity analysis, the beta series associated with the left ACC were correlated with voxels across the entire brain to produce beta-correlation images. Contrasts between beta-correlation images were also subjected to an archyperbolic tangent transform to allow for statistical inference based on temporally coupled fluctuations with this region. Congruent seen > Null, Congruent unseen > Null, Incongruent seen > Null, and Incongruent unseen > Null t-tests were performed on the resulting subject contrast images to produce group correlation contrast maps with a threshold of $q < 0.05$ (voxel-wise FDR corrected).

Statistical analyses were performed with STATISTICA 8.0 (StatSoft, Inc., 2007) and JASP 0.9.0.1 (JASP Team, 2018) softwares. Data and codes related to this article can be accessed on https://www.bcbl.eu/Datasharing/CerebCor2018-MartinSignes-PazAlonso-Chica/.

5.3.5. DWI tractography analysis

In 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).

Individual dissections of the tracts were carried out with the software TrackVis (R. Wang et al., 2007). The three branches of the SLF (on the left and the right hemisphere) were isolated using a multiple region of interest approach. Three frontal ROIs around the white matter of the superior, middle and inferior frontal gyri and a ROI around the white matter of the parietal lobe were delineated. A no-part ROI in the temporal white matter was used to exclude streamlines of the arcuate fasciculus projecting to the temporal lobe (Rojkova et al., 2016; Thiebaut de Schotten et al., 2011). A new index employed as a surrogate for tract microstructural organization (i.e., mean Hindrance Modulated Orientational Anisotropy, HMOA; Dell'Acqua et al. 2013) was extracted from each dissected tract on the left and right hemisphere.

Subsequently, we conducted Pearson correlations analysis using Z scores. Given the low number of subjects for these correlational analyses (N = 19), a Bayesian approach was taken in addition to the Null Hypothesis Significance Testing in order to examine the probability of the data given the alternative hypothesis (H1) relative to the null hypothesis (H0) (i.e., Bayes factor (BF)10 < 1/3 evidence favor H0; BF10 > 3 evidence favor H1; 1/3 < BF10 < 3 indicates data insensitivity) (Dienes & Mclatchie, 2018). The mean HMOA of the left and right SLF I, II and III was correlated with the congruency effect over the percentage of seen targets (percentage of seen targets for congruent minus incongruent condition). We also calculated an interaction index for the functional connectivity data of the three pairs of regions showing the interaction effect (left ACC and left IFG, left FEF and left IPL, and right SMA and right SPL). This index was calculated over the beta values, according to the following formula: beta values for seen minus unseen trials for the congruent minus incongruent condition.

5.3.6. Behavioral data analysis

Stroop reaction times (RTs) shorter than 150 ms were considered outliers and were eliminated from the analysis (0.59% of the trials, SD = 0.54). Anticipatory responses were also excluded (0.21% of the trials, SD = 0.05). False alarms (FA; trials in which participants consciously reported a Gabor that was not presented) accounted for only 4.9% (SD = 6.86) of the catch trials and were excluded from the analyses. Errors localizing a consciously seen Gabor (3.2% of the trials, SD = 0.17) were also excluded.

We analyzed mean accuracy and RT for the Stroop task and the percentage of seen targets for the Gabor detection task by means of a repeated-measured ANOVAs with the within-participant factor of Congruency (congruent/incongruent). We also analyzed participants’ responses to the Gabor detection task by using the signal detection theory (SDT, Abdi, 2007). We computed a nonparametric index of perceptual sensitivity (A′) and response criterion (β″) to detect the Gabor by using the following equations:

$$A' = 0.5 + \frac{(\text{Hit-FA})*(1+\text{Hit-FA})}{4*\text{Hit}*(1\text{-FA})};$$

$$\beta'' = \frac{\text{Hit}*(1-\text{Hit})-\text{FA}*(1-\text{FA})}{\text{Hit}*(1-\text{Hit})+\text{FA}*(1-\text{FA})}$$

A′ values usually range between 0.5 (the signal cannot be distinguished from noise) to 1 (perfect performance). For β″, values close to 1 indicate a conservative criterion while values close to −1 indicate a nonconservative criterion (Stanislaw & Todorov, 1999). These indices were also submitted to 2 repeated-measures ANOVAs with the within-participant factor of congruency.

5.4. Results

5.4.1. Behavioral results

For the Stroop task, we observed the expected Congruency effect. Mean accuracy was significantly higher for congruent compared to incongruent trials, F(1, 19) = 19.15, MSE = 0.0001, $p < 0.001$, $\eta^2_p = 0.50$, and RTs were also significantly shorter for congruent compared to incongruent trials, F(1, 19) = 54.20, MSE = 1941, $p < 0.001$, $\eta^2_p = 0.74$.

For the Gabor detection task, the percentage of seen targets was marginally larger for the congruent compared to the incongruent condition, F(1, 19) = 4.10, MSE = 0.001, $p = 0.057$, $\eta^2_p = 0.18$. When the analysis was repeated including the RT for incongruent trials minus RT for congruent trials as a covariate, the main effect of congruency on the percentage of seen targets reached statistical significance, F(1, 19) = 4.46, MSE = 0.001, $p = 0.049$, $\eta^2_p =$

0.20, demonstrating that the congruency effect on the percentage of seen targets was larger for those participants with larger congruency effects on RT.

SDT analyses revealed that Congruency did not influence either perceptual sensitivity (A′) or response criterion (β″) to detect the Gabor (all Ps ≥ 0.22). However, Congruency modulated the proportion of seen Gabors (see above) but not the proportion of FA (repeated-measures ANOVA comparing FA on congruent and incongruent conditions, F(1, 19) = 0.13, MSE = 0.009, P = 0.723, η2 p = 0.007). Table 5.1. shows the mean and the SD of the analyzed measures for congruent and incongruent trials.

Table 5.1. Behavioral data for the Gabor detection task and for the Stroop task for congruent and incongruent trials.

	Congruent		**Incongruent**	
	Mean	*SD*	*Mean*	*SD*
Seen trials (%)	54	16	52	17
FA (%)	4.98	6.61	4.80	7.26
A’	0.85	0.06	0.85	0.07
β’’	0.73	0.29	0.76	0.31
Stroop accuracy (%)	98	4.12	97	4.07
Stroop RT (ms)	1091	169	1194	135

FA, false alarms; RT, reaction times; SD, standard deviation.

5.4.2. fMRI results

The whole-brain contrast Target present > Null revealed the regions that demonstrated larger BOLD responses when the Gabor was presented as compared with fixation. Increased activations were found bilaterally in the cingulate cortex, FEF, inferior and middle frontal gyri, superior and inferior parietal lobe, SMA, insula, inferior and middle temporal gyri, occipital lobe, and subcortical regions such as the thalamus, caudate, putamen, and globus pallidus (Fig. 5.2. and Table 5.2.).

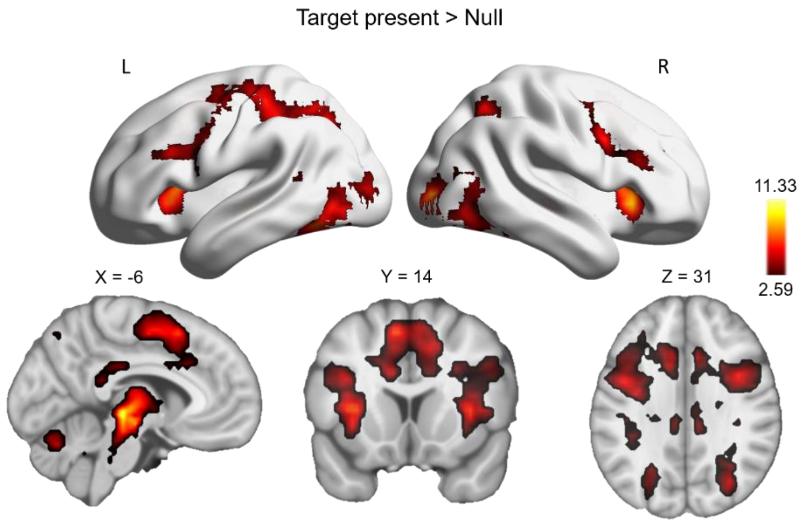

Figure 5.2. Brain renderings and sections showing activations for Target present > Null whole-brain contrast ($q < 0.05$, voxel-wise FDR corrected). The color bar denotes t-values.

Table 5.2. Brain activations obtained in the whole-brain contrast Target present > Null.

Brain area	**MNI (x, y, z)**			**z-score**	**Voxels**
Frontal					
L Insula	-33	17	7	5.11	165
R Insula	33	23	-2	5.56	117
L SMA	-6	14	52	4.81	262
R SMA	6	11	55	4.65	152
L IFG	-33	17	10	4.78	180
R IFG	36	26	7	4.98	162
L FEF	-24	10	49	4.76	21
R FEF	36	-1	52	4.17	21
L MFG	-30	38	16	3.66	74
L ACC	-9	23	28	3.49	6
R ACC	9	20	28	3.40	23
Parietal					
L IPL	-30	-49	46	5.08	232
R IPL	30	-55	49	4.37	47
L SPL	-27	-58	49	4.84	157
R SPL	27	-58	49	4.17	57
Occipital					
L IO	-39	-58	-11	5.78	174
R IO	39	-64	-11	6.13	154
L MO	-39	-79	-2	5.79	431

R MO	36	-88	4	5.36	267
L SO	-21	-67	37	3.70	32
R SO	27	-76	22	4.07	60
Subcortical					
L Thalamus	-6	25	-2	5.67	195
R Thalamus	9	-10	4	4.68	111
L Globus pallidus	-15	-1	-2	4.98	19
R Globus pallidus	15	2	-2	3.80	11

ACC, anterior cingulate cortex; FEF, frontal eye field; IFG, inferior frontal gyrus; IO, inferior occipital; IPL, inferior parietal lobe; L, left; MFG, middle frontal gyrus; MO, middle occipital; R, right; SMA, supplementary motor area; SO, superior occipital; SPL, superior parietal lobe.

Parameter estimate ROI analyses were conducted for those areas previously related to conscious perception or executive control (see Methods; Dehaene & Changeux, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Dosenbach et al., 2008). The analysis revealed a group of regions showing a statistically significant main effect of Congruency, with higher activations for incongruent than congruent trials. These regions included the bilateral IFG, left MFG, bilateral SMA, left FEF, left IPL, bilateral SPL, and (marginally) the left ACC. Another set of regions showed a statistically significant main effect of Awareness, with greater activations for seen than unseen trials. These regions included the left SMA, the bilateral FEF, the bilateral insula, the bilateral IPL, and the bilateral IPL (Table 5.3.).The right ACC and the right MFG were also analyzed and did not show any significant effect (all other ps ≥ 0.154). No interaction between Congruency and Awareness was found in any of the regions here examined (all ps ≥ 0.153).

Table 5.3. ROIs showing significant main effects of awareness and congruency in the parameter estimate analysis.

Brain area	F	MSE	p	η^2_p
Main effect of Congruency				
L IFG	44.24	2.14	> 0.001	0.70
R IFG	5.87	2.15	0.026	0.25
L IPL	16.66	3.55	0.001	0.47
L SPL	15.10	3.90	0.001	0.44
R SPL	12.05	3.15	0.003	0.40
L SMA	13.16	3.09	0.002	0.42
R SMA	9.87	2.70	0.005	0.34
L MFG	7.85	2.46	0.011	0.29
L FEF	7.43	2.11	0.013	0.28
L ACC	3.86	8.84	0.064	0.17
Main effect of Awareness				
L FEF	52.10	5.21	> 0.001	0.73
R FEF	10.89	9.47	0.004	0.38
L IPL	32.17	3.86	> 0.001	0.63
R IPL	8.98	9.91	0.008	0.33
L SPL	29.86	3.35	> 0.001	0.61
R SPL	13.29	6.43	0.002	0.43
L Insula	6.95	10.32	0.016	0.27
R Insula	4.81	12.04	0.041	0.20
L SMA	5.48	7.86	0.031	0.23

ACC, anterior cingulate cortex; FEF, frontal eye field; IFG, inferior frontal gyrus; IO, inferior occipital; IPL, inferior parietal lobe; L, left; MFG, middle frontal gyrus; MO, middle occipital; R, right; SMA, supplementary motor area; SO, superior occipital; SPL, superior parietal lobe.

We then conducted pairwise functional connectivity analyses including the regions showing the Congruency effect in the previous ROIs analyses. To explore if these areas showed significant coupling strength within each of the main 4 conditions of interest (i.e., congruent seen, congruent unseen, incongruent seen, incongruent unseen) pairwise beta-series correlation values were averaged per condition and two-tailed tests were used to determine the statistical significance of these *r* values. This analysis revealed a strong frontal connectivity together with frontoparietal connectivity during the congruent seen condition. However, in the other 3 conditions, the connectivity within frontal regions seemed to be reduced and the frontoparietal connectivity was scarce or non-existent. Figure 5.3. shows the pairs of nodes that revealed significant functional coupling per each of the main conditions in our fMRI experimental design.

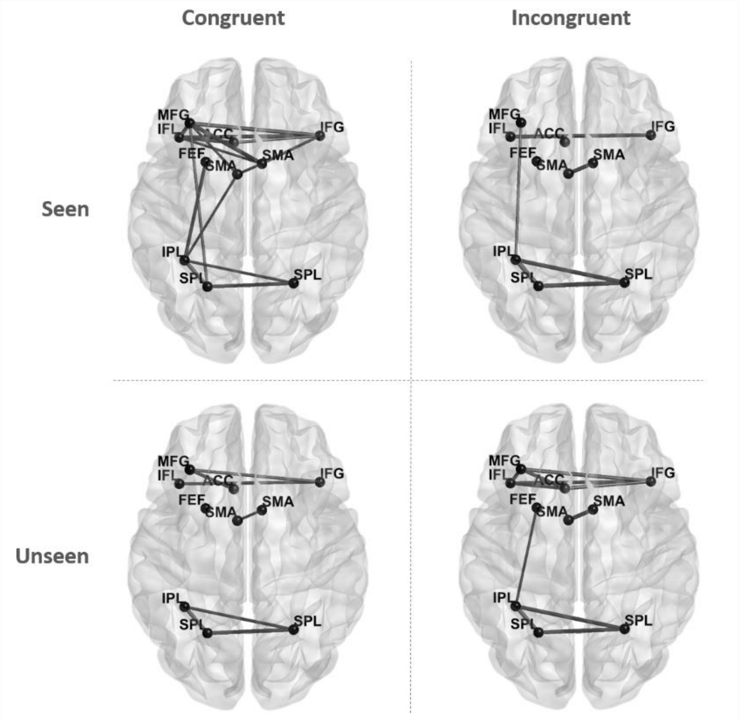

Figure 5.3. Pairwise functional connectivity between ROIs showing the congruency main effect for each condition of interest. Edges denotes significant coupling (*r*-values) among ROIs ($q < 0.05$, FDR corrected). ACC, anterior cingulate cortex; FEF, frontal eye field; IFG, inferior frontal gyrus; IPL, inferior parietal lobe; MFG, middle frontal gyrus; SMA, supplementary motor area; SPL, superior parietal lobe.

Then, to specifically examine interactions between Congruency and Awareness in pairwise functional connectivity, we conducted repeated-measures ANOVAs for these pairs of regions using normalized mean Z-transformed values (see Methods). Three pairs of regions showed a significant interaction between Congruency and Awareness in their functional connectivity: the left IFG and the left ACC, F = 8.50, MSE = 1.64, p= 0.011, η^2_p = 0.38, the left FEF and the left

IPL, F = 7.67, MSE = 1.55, p= 0.014, η^2_p = 0.32, and the right SMA and the right SPL, F = 5.03, MSE = 2.56, p= 0.041, η^2_p = 0.25. In the congruent condition, these three pairs of regions showed stronger functional connectivity for seen compared to unseen trials. However, in the incongruent condition, the pairwise functional connectivity was not significantly different in any of the three pairs of regions for seen as compared with unseen trials (all ps ≥ 0.121) (Fig. 5.4.).

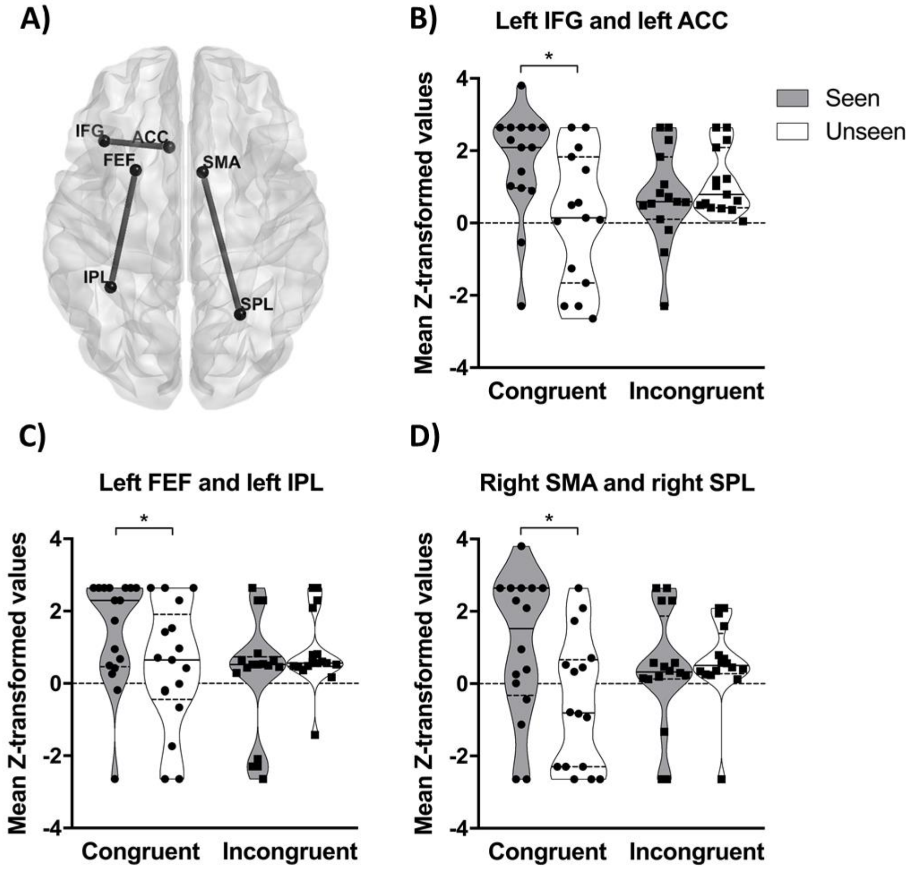

Figure 5.4. (**A**) Graphical representation of the three pairs of regions demonstrating a significant interaction between Congruency and Awareness in their pairwise functional connectivity. (**B-D**) Violin plots of the distribution of the mean Z-transformed values for the congruent (●) and incongruent (■) conditions and seen and unseen trials. The plots show the median (indicated by the solid horizontal lines) and quartiles (indicated by the dashed horizontal lines). Asterisks represent statistically significant T-tests.

Finally, due to the critical role of the ACC in executive control, we conducted whole-brain functional connectivity analysis using a seed placed in the left ACC region for each of the 4 conditions of interest in our experimental design. As it can be observed in Figure 5.5., during the unseen conditions, there was a significant functional coupling for the left ACC mainly with midline and lateral frontal regions. This connectivity was especially observed in the incongruent unseen condition. However, the functional coupling of the left ACC for the seen conditions was scarce or inexistent.

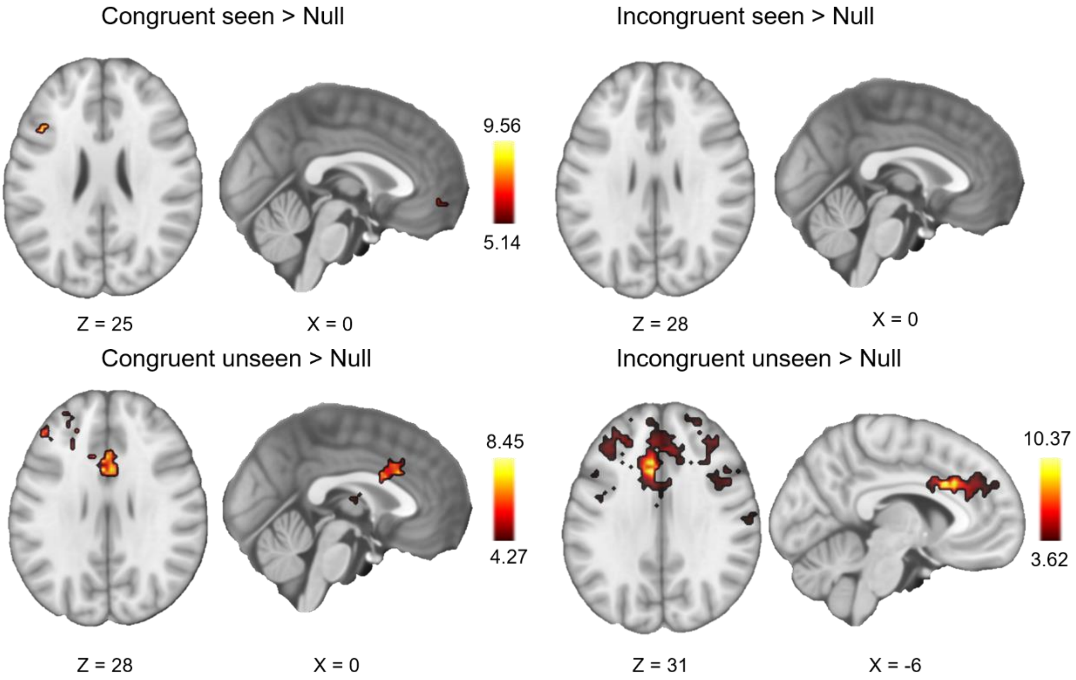

Figure 5.5. Brain regions showing whole-brain functional connectivity using the left ACC as a seed for the 4 conditions of interest vs Null ($q < 0.05$, voxel-wise FDR corrected). The color bar denotes t-values.

5.4.3. DWI tractography results

We found a significant positive correlation between the HMOA of the left SLF II and the congruency effect over the functional connectivity between the left IFG-left ACC, r = 0.676, p = 0.008, BF_{10} = 8.08, and the right SMA-right SPL, r = 0.655, p = 0.008, BF_{10} = 7.83. Higher HMOA of the left SLF II was associated with a larger congruency effect over the functional connectivity of these two pairs of frontoparietal regions (Figure 5.6.). Additionally, we found a significant positive correlation between the HMOA of the left SLF I and the congruency effect over the percentage of seen targets, $r = 0.465$, $p = 0.045$, $BF_{10} = 1.86$. BF analyses revealed that while the evidence in favor of the alternative hypothesis for the correlation between the behavioral congruency effect and the left SLF I HMOA resulted to be anecdotal, the evidence for the correlations between the pairwise functional connectivity and the left SLF II HMOA was substantial (Jarosz & Wiley, 2014).

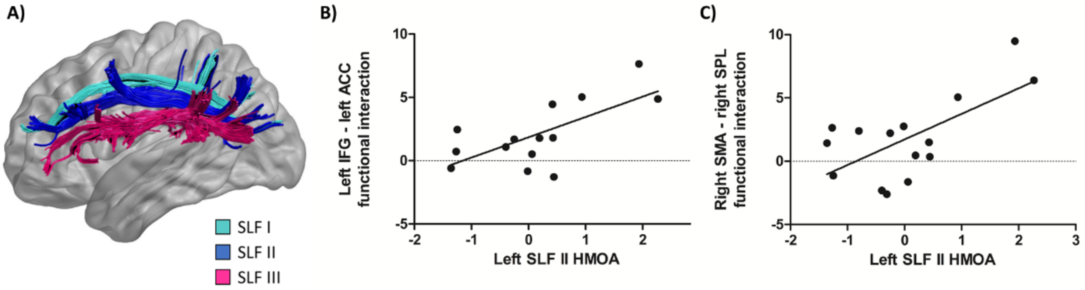

Figure 5.6. (**A**) Example of a virtual in vivo dissection of the SLF I (light blue), II (dark blue), and III (pink) of the left hemisphere using deterministic tractography. Pearson correlations between the mean HMOA of the left SLF II and the interaction in functional connectivity of (**B**) the left IFG and the left ACC, and (**C**) the right SMA and the right SPL. Normalized data by Z score transformation. The black line represents the best fit of the data.

5.5. Discussion

Conscious perception is impaired under situations of high conflict requiring activation of the executive control system (Colás et al., 2017; Meyer & Kieras, 1997). The present study aimed at examining this interaction between executive control and consciousness at the neural level with a methodology allowing a good spatial resolution. To this end, we used an event-related fMRI design while manipulating executive control with a Stroop task in which congruent and incongruent stimuli were presented concurrently with near-threshold Gabor stimuli.

At the behavioral level, the Stroop task induced a reliable interference effect with longer RT and lower accuracy for the incongruent compared to the congruent condition. Executive control also affected the conscious perception of the near-threshold Gabor, as fewer targets were perceived for the incongruent than the congruent condition, especially for those participants demonstrating larger RT effects on the Stroop task.

In dual-task paradigms, the conscious access of the second of two targets can be delayed in time (a phenomenon called the psychological refractory period, Pashler, 1994) or it can even fail (like in the attentional blink phenomenon, Shapiro et al., 1997). According to the *delayed conscious perception hypothesis*, response selection of one task can block the conscious awareness of another stimulus presented concurrently or within a short interval. This is hypothesized to occur because conscious access and response selection are serial processes which cannot occur in parallel (Marti et al., 2012; Pashler, 1994; Sigman & Dehaene, 2008). In our paradigm, we did not analyze RT to the conscious detection task as the response was given by the participants without time pressure. However, as in the attentional blink phenomenon, the conscious access of the Gabor stimulus may have been impaired in the incongruent Stroop trials as conflict detection and resolution on these trials require more time before selecting the response.

The present fMRI results showed that a group of frontal and parietal regions demonstrated larger BOLD responses for the incongruent than the congruent condition. Another group of frontoparietal regions demonstrated larger BOLD responses for seen than unseen Gabors. These results are in agreement with previous literature on cognitive control (Cocchi et al., 2013; Cole & Schneider, 2007), and with some influential models proposing the importance of a distributed frontoparietal network for conscious perception (Dehaene et al., 2006; Dehaene & Naccache, 2001).

Nevertheless, we did not find an interaction between executive control and consciousness in the ROI analysis for any of the frontoparietal regions here examined. Previous research manipulating spatial orienting and alerting while measuring conscious perception of near-threshold stimuli have demonstrated reliable interactions in frontoparietal (for spatial orienting, Chica et al., 2013) and frontostriatal (for alerting, Chica et al., 2016) regions. If the results were focused exclusively on ROI analyses, one could have concluded that executive attention and conscious perception exert their effects through independent brain networks. This result would have supported the *cumulative influence hypothesis* proposed by Tallon-Baudry (2012), according to which attention and conscious perception independently feed a decision-making mechanism implemented in the frontal lobe. This hypothesis predicts that attention and consciousness rely on distinct neural mechanisms, and therefore both processes should not interact at the neural level. Consistently, previous results have demonstrated that at least some attentional subsystems, such as endogenous attentional orienting, can be dissociated at the neural level from conscious perception (Chica, Botta, et al., 2012; Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008).

However, after exploring functional connectivity, we did find an interaction between executive control and consciousness in the functional coupling of three frontoparietal pairs of regions: left IFG-left ACC, left FEF-left IPL, and right SMA-right SPL. Importantly, these pairs of regions were more strongly coactivated when the Gabor was consciously seen than when it was not consciously seen for congruent Stroop trials, while the coactivation of these regions was similar for seen and unseen targets on incongruent Stroop trials. One interpretation of these results is that frontoparietal connectivity is important for consciousness in situations of low conflict (i.e., congruent conditions), but when conflict is experienced (i.e., incongruent conditions), frontoparietal connectivity is not associated with conscious perception. An alternative possibility is that this frontoparietal connectivity is important for the conscious perception of near-threshold targets (as shown in Chica et al. 2013). Thus, in conditions where conflict is experienced (i.e., incongruent trials), parts of these networks could be recruited to solve the conflict, and be thus unavailable to sustain conscious perception, hence the absence of normal frontoparietal correlation[3].

Our data are consistent with models such as the gateway hypothesis or the global neural workspace, which postulate that attention modulates conscious perception either by increasing perceptual gain or biasing decision mechanisms (De Lange et al., 2011; Reynolds & Chelazzi, 2004). The manipulation of executive control with the Stroop task involves conflict detection and resolution, cognitive processes in which frontal lobe structures such as the ACC and the dlPFC are crucial (Egner & Hirsch, 2005; Macdonald et al., 2000; Milham et al., 2001; Nee et al., 2007; Pardo et al., 1990). This system would share neural

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[3] We would like to thank an anonymous reviewer for this suggestion.

resources with conscious perception, and therefore an interaction between executive attention and conscious perception was expected in frontal regions.

Due to the critical role of the ACC for conflict evaluation and monitoring, we also explored functional connectivity with a seed placed in this region. We found a functional coupling between the left ACC and other frontal regions for the incongruent unseen condition, which was reduced or inexistent in the other three conditions. This enhanced functional connectivity between the left ACC and frontal regions was observed in the condition with a higher amount of conflict: incongruent Stroop trials in which the Gabor was missed.

Neuroimaging studies examining divided attention and the attentional blink phenomenon have linked these processes with the functioning of a frontoparietal network, with a critical role of left frontal areas (Fagioli & Macaluso, 2009; Salo et al., 2017; Yaple & Vakhrushev, 2018). Damage in the frontal lobes is also associated with impairments in temporal selection of visual stimuli and divided attention (Correani & Humphreys, 2011; Godefroy & Rousseaux, 1996). Studies in dual-tasks examining the neural mechanism of the psychological refractory period point out to a large parietofrontal network, with a critical role of the lateral prefrontal cortex (Schubert & Szameitat, 2003; Sigman & Dehaene, 2008; Strobach et al., 2018; Szameitat et al., 2002). Therefore, being able to concurrently solve the Stroop task and to consciously detect the appearance of the Gabor may require the activity of frontal areas and their connection with parietal regions.

A further aim of this work was to explore the role of white matter fibers connecting the parietal and the frontal lobes in the interaction between executive attention and conscious perception. Recent work has linked the microstructure of the ventral branch of the SLF with diverse behavioral and neural measures related to the interaction between alerting and orienting attentional mechanisms with conscious perception. The microstructure of the ventral branch of the left SLF predicted the neural interactions (measured with fMRI) observed between alerting and orienting attentional mechanisms and conscious perception (Chica et al., 2018). Moreover, the microstructure of the ventral branch of the right SLF also modulated the effect caused by transcranial magnetic stimulation (TMS) over the SMA in a conscious perception task preceded by an alerting signal. In this case, the more increased the HMOA of the right SLF III, the more reduced the TMS effects (Martín-Signes, Pérez-Serrano, et al., 2019). In this study, we correlated behavioral and neural effects of the executive attentional modulations over conscious perception with the microstructure of the dorsal, middle, and ventral branches of the SLF. We found a positive correlation between the HMOA of the left SLF II and the functional connectivity measures of the interaction between executive control and perceptual consciousness.

Although research linking white matter microstructure and behavioral or functional data is still scarce, this investigation contributes to the knowledge of the functional role of the different branches of the SLF in attentional mechanisms (Parlatini et al., 2017). While the ventral branch seems to be involved in bottom-up processes (such us alerting and orienting), the more dorsal branches (i.e. SLF II and maybe SLF I) seem to be involved in top-down processes (such as executive control). Regarding patients, one study has linked the white matter volume of the SLF with impairments in executive control measures (Blanc et al., 2012) while another study found structural white matter abnormalities, including the SLF, in attention-deficit/hyperactivity disorder (Makris et al., 2008); however, these studies did not distinguish between the different branches of the SLF. However, we reckon that due to the sample size of the study, this correlational analysis should be considered merely exploratory, and conclusions drawn with caution.

To conclude, our data support the gateway theory about the relationship between attention and consciousness (Dehaene et al., 2006; Dehaene & Naccache, 2001; Posner, 1994). Executive control modulated the conscious perception of near-threshold stimuli, which, at the neural level, was reflected in the functional connectivity of frontoparietal regions. DWI analysis highlighted the role of the middle branch of the SLF in the interaction between executive control and consciousness. This study demonstrates the importance of taking into account functional and structural connectivity measures for a more complete understanding of the neural mechanisms supporting executive attention and consciousness interactions.

5.6. Acknowledgments

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Chapter 6. Is the frontal lobe casually involved in the interaction between executive control and conscious perception?

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6.1. Abstract

The executive control network is involved in novel situations or those in which prepotent responses need to be overridden. Previous studies have demonstrated that when control is exerted, conscious perception is impaired, and this effect is related to the functional connectivity of fronto-parietal regions. In the present study, we explored the causal involvement of one of the nodes of this fronto-parietal network (the right Supplementary Motor Area, SMA) in the interaction between executive control and conscious perception. Participants performed a dual task in which they responded to a Stroop task while detecting the presence/absence of a near-threshold Gabor stimulus. Concurrently, transcranial magnetic stimulation (TMS) was applied over the right SMA or a control site (vertex; Experiment 1). As a further control, the right Frontal Eye Field (FEF) was stimulated in Experiment 2. Diffusion-weighted imaging (DWI) tractography was used to isolate the three branches of the superior longitudinal fasciculus (SLF I, II and III), and the frontal aslant tract (FAT), and to explore if TMS effects were related to their micro- and macrostructural characteristics. Results demonstrated reduced perceptual sensitivity on incongruent as compared to congruent Stroop trials. A causal role of the right SMA on the

modulation of perceptual sensitivity by executive control was only demonstrated when the microstructure of the right SLF III or the left FAT were taken into account. The volume of the right SLF III was also related to the modulation of response criterion by executive control when the right FEF was stimulated. These results add evidence in favor of shared neural correlates for attention and conscious perception in fronto-parietal regions and highlight the role of white matter in TMS effects.

6.2. Introduction

Steadily a big amount of information is reaching our senses, creating a complex, changing, and highly-demanding environment. However, our processing capacities to deal with it are limited. It has been proposed that consciousness may have a role in reducing the noise and increasing the integration of information (Delacour, 1995). Attention is also known to play a key role in the selection of information, especially in crowded environments (Dehaene & Changeux, 2011; Posner, 1994). Following Posner and Petersen's taxonomy of attention (Petersen & Posner, 2012; Posner & Petersen, 1990), the executive control network is one of the three main attentional networks, together with the alerting and orienting networks. Executive control is implemented when situations involve novelty, planning, conflict detection/resolution, and error detection/correction (Norman & Shallice, 1986).

Many authors believe that attention and consciousness are closely related processes, although the nature of such relation is still under debate (Cohen & Dennett, 2011; Dehaene et al., 2006; Tallon-Baudry, 2012). At the behavioral level, different forms of attention have shown to interact with conscious perception (Chica et al., 2010; Kusnir et al., 2011; Petersen et al., 2017). In particular, executive control modulates conscious perception (Martín-Signes, Paz-Alonso, et al., 2019), most likely influencing decision stages of processing (Colás et al., 2017, 2018). Exploring the neural mechanisms involved in attention and consciousness might provide clues on the nature of their relation. Namely, if attention and consciousness are related processes, shared or partially shared neural correlates are expected (Tallon-Baudry, 2012).

The frontal cortex (together with parietal regions) is crucial for cognitive control (Cocchi et al., 2013; Cole & Schneider, 2007; Diamond, 2013; Macdonald et al., 2000) and, according with some theories, also for conscious perception. The global workspace theory (GWT) postulates that distributed large-scale brain networks linking higher visual areas to frontal and parietal cortex are essential for conscious perception (Dehaene et al., 2006; Dehaene, Kerszberg, et al., 1998; Dehaene & Naccache, 2001; Del Cul et al., 2009; Rees et al., 2002). However, the implication of the frontal regions (and the fronto-parietal network) in conscious perception is in the center of a current debate (Boly et al., 2017; Bor & Seth, 2012; Odegaard et al., 2017), with some authors arguing that frontal regions are only involved in the processes that emerge after conscious access (e.g. the reporting of the perceptual content or its cognitive manipulation; Tallon-Baudry, 2012).

If both systems (i.e. executive control and conscious perception) share neural resources, an interaction between both processes would be expected in frontal regions. A recent study (Martín-Signes, Paz-Alonso, et al., 2019) demonstrated an interaction between executive control and consciousness in the functional connectivity between a set of fronto-parietal regions (including left inferior frontal gyrus –IFG, left anterior cingulate cortex –ACC, left frontal eye field –FEF, left inferior parietal lobe –IPL, right supplementary motor area –SMA, and right superior parietal lobe –SPL). In this functional magnetic resonance imaging (fMRI) study, participants resolved a Stroop task presented at fixation while trying to detect near-threshold Gabor patches presented in the periphery. fMRI data demonstrated that functional connectivity increased between the left IFG-ACC, the left FEF-IPL, and the right SMA-SPL, for congruent trials when near-threshold Gabors were reported as compared to non-reported Gabors. No differences in functional connectivity between these regions were observed on incongruent trials.

According to theories such as the GWT, not only functional connectivity is important for conscious perception. Structural connectivity within the fronto-parietal network may be also key for conscious access. The superior longitudinal fasciculus (SLF) is an extensive longitudinal white matter tract connecting the frontal and parietal lobes. It has been divided in three different branches: SLF I, SLF II and SLF III, labeled from dorsal to ventral. The SLF I extends between the superior parietal lobe and the dorsal and medial parts of the frontal lobe; the SLF II connects the angular gyrus and the posterior regions of the superior and middle frontal gyrus; the SLF III extends between the supramarginal gyrus and the inferior frontal gyrus (Nakajima et al., 2020; Rojkova et al., 2016; Thiebaut de Schotten et al., 2011). The SLF has been linked to different attentional functions, including spatial orienting, sustained attention, and executive control in the healthy population (Carretié et al., 2012; Klarborg et al., 2013; Sasson et al., 2012, 2013; Thiebaut de Schotten et al., 2011) and in different neurological conditions related with attention or awareness deficits (for example, spatial neglect, Doricchi et al., 2008; Thiebaut De Schotten et al., 2014; and attention-deficit/hyperactivity disorder, Chiang et al., 2015, 2016; Wolfers et al., 2015). Newly, the microstructure of the right SLF III has been associated with the perceptual contrast needed to perceive near-threshold targets in patients with prefrontal damage (Colás et al., 2019). The neural interaction between conscious perception and different attentional subsystems has also been related to the microstructure of the SLF (Chica et al., 2018; Martín-Signes, Paz-Alonso, et al., 2019; Martín-Signes, Pérez-Serrano, et al., 2019).

The aim of this study was to explore the causal role of a frontal region in the interaction between executive control and conscious perception by using transcranial magnetic stimulation (TMS). To this aim, participants performed a Stroop task (to manipulate executive control, Stroop, 1935) concurrent with a detection task of near-threshold Gabor stimuli (see Colás et al., 2017). Based on previous correlational fMRI findings (Martín-Signes, Paz-Alonso, et al., 2019), the right SMA was selected as a target region (Experiment 1) because its functional connectivity with the right SPL demonstrated an interaction between executive control and conscious perception. The SMA has been traditionally linked to the motor control domain (Brass, 2002; Luppino et al., 1993), however, especially the anterior part, is also linked to cognitive control functions (Miller & Cohen, 2001; Nachev et al., 2008). The right FEF was selected as an active control region (Experiment 2), because this region was related to conscious perception but not to the interaction between executive control and conscious perception. Based on previous observations demonstrating the role of the SLF in conscious perception, executive control, and the interaction between both processes (and its implication in other attentional systems), we also explored the role of the three branches of the SLF in the TMS effects over the expected behavioral interaction (as done before, Martín-Signes, Pérez-Serrano, et al., 2019).

If our results show a causal role of the right SMA in the interaction between executive control and consciousness, this would add evidence in favor of shared neural correlates for executive control and conscious perception (Tallon-Baudry, 2012). The implication of a frontal region (i.e. the SMA) and its relation with the microstructural properties of SLF (a fronto-parietal tract) would constitute new evidence for the involvement of the fronto-parietal network in conscious perception.

6.3. Experiment 1: right SMA versus Vertex

6.3.1. Methods

6.3.1.1. Participants

G*power (Faul et al., 2007) was used to calculate sample size based on the effect size of a previously observed interaction between alerting and TMS region in a similar experiment (Martín-Signes, Pérez-Serrano, et al., 2019; η^2p = 0.38). We calculated sample size for a F test (interaction between Congruency and TMS region, $\alpha = 0.05$; Power = 0.95). A sample of 24 participants was required. Therefore, 24 right-handed volunteers (12 females, mean age 24 years, standard deviation [SD] = 3.60) took part in the study.

Participants were unexperienced with the task and reported to have normal or corrected-to-normal vision, normal-color discrimination, and Spanish as their native language. Participants had no neurological or psychiatric conditions and followed all the safety requirements to undergo MRI and TMS studies (Rossi et al., 2012). They signed an informed consent to participate in the experiment and received a monetary compensation for their time and effort (10 Euros/hour). The study was reviewed and approved by the Ethical Committee of the University of Granada and was carried out according to the recommendations of Helsinki Declaration.

6.3.1.2. Apparatus and stimuli

The paradigm and procedure was an adaptation of the one employed in Martín-Signes et al., 2018. E-prime software was used to control the presentation of stimuli, timing operations, and behavioral data collection (Schneider et al., 2002). Images were presented in a computer screen (Benq T903, 19’’ wide, 1280x1024, 60 Hz) while participants where sited at an approximate distance of 77 cm. Two markers (3° height × 5.3° width) and a central fixation point (0.4° × 0.4°) were displayed against a gray background at the beginning of the trial. Each marker consisted of a black square outline, placed 4.5° to the left and right of the fixation point. Spanish words for blue (“azul”, 0.4° height × 1.6° width), green (“verde”, 0.4° height × 2° width), red (“rojo”, 0.4° height × 1.6° width), and yellow (“amarillo”, 0.4° height × 3° width) colors were presented 0.6° above the fixation point (Fig. 6.1. A). Words were colored either in blue, green, red, or yellow. Trials were sorted as congruent when the word meaning and the word color matched, and as incongruent when the word meaning and the word color were different. Response latencies to the Stroop task were collected using an ATR 20 microphone with low impedance connected to a Serial Response Box (Psychology Software Tools, Schneider, 1995).

The target was a Gabor stimulus that could appear inside of one of the lateral boxes. Matlab 8.1 (http://www.mathworks.com) was used to create 100 Gabor stimuli (4 cycles/deg spatial frequency, 1.8° in diameter, SD of 0.1°), with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively. Gabor contrast was manipulated before the experimental task in order to adjust the percentage of consciously perceived targets to ~50% (see Procedure).

6.3.1.3. Procedure

The timing and sequence of the events presented in a trial are depicted in Fig. 6.1. A. In each trial, participants were presented with a color word and a Gabor stimulus (except for catch trials, in which the Gabor was not presented).

Participants were required to perform two consecutive tasks. First, they had to discriminate the color of the word as fast and accurately as possible. Participants responded to this task orally and response latencies (i.e. reaction times, RTs) were collected through the microphone. For the computation of the accuracy, the experimenter recorded the participant's responses using four keys of the keyboard ("1" for yellow, "2" for red, "4" for blue and, "5" for green). Second, participants had to report if they consciously detected the appearance of the Gabor. They were asked to respond as accurately as possible and only when they were confident about their perception. The response was given by choosing one of the two arrow-like stimuli (>>> or <<<) pointing to the two possible locations of target appearance (right or left box). The arrows were presented one above the other, with their position randomized in each trial. Participants were required to indicate the location of the target, with the right hand. They had to press an upper key ("K"), corresponding to the upper arrow or a lower key ("M") corresponding to the bottom arrow. If they had not perceived the Gabor, they were asked to press the space bar. Participants were explicitly instructed to fixate the central plus sign throughout all the experiment.

Each participant performed two experimental blocks, one for the right SMA stimulation and one for the control TMS site (vertex, see Fig. 6.1. B). The order of the SMA and vertex blocks was counterbalanced between participants. Each block consisted in 240 trials (accounting for a total of 480 trials for the experiment). The proportion of Congruent-Incongruent Stroop trials was 70-30%, respectively. The Gabor was present on 66% of the trials, and absent on the remaining 34% of the trials (catch trials).

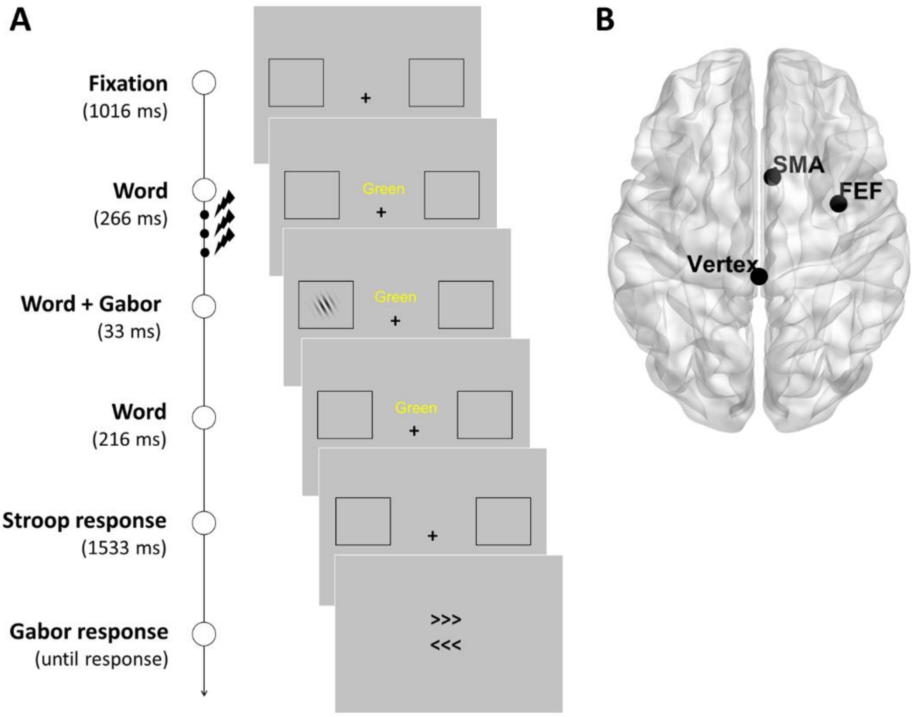

Figure 6.1. (**A**) Representation of the sequence of events on a given trial. The image shows a Stroop incongruent trial with a Gabor present on the left location. Thunderbolt symbols indicate the burst of TMS pulses. (**B**) Representation of the TMS sites for Experiment 1 (right supplementary motor area, SMA), Experiment 2 (right frontal eye field, FEF), and the control TMS site for both experiments (vertex) in an axial brain view.

6.3.1.4. MRI data acquisition

Structural images were collected on a 3-T Siemens Trio MRI scanner at the Mind, Brain, and Behavior Research Center (CIMCYC, University of Granada), using a 32 channel whole-head coil. High-resolution T1-weighted anatomical images (Repetition Time [TR] = 2530 ms, Echo Time [TE] = 3.5 ms, flip angle = 7°, slice thickness = 1mm, field of view = 256mm) were collected. Additionally, a total of 70 near-axial slices were acquired using a sequence fully optimized for tractography of diffusion-weighted imaging (DWI) providing isotropic 2-mm resolution and coverage of the whole head with a posterior–anterior phase of acquisition (TR = 8400 ms and TE = 88 ms). At each slice location, 6 images were acquired with no diffusion gradient applied and 60 diffusion-weighted images in which gradient directions were uniformly distributed in space. The diffusion weighting was equal to a b-value of 1500 s/mm^2.

6.3.1.5. TMS procedure

TMS was delivered by means of a biphasic repetitive stimulator (Super Rapid 2, Magstim, Whitland UK) and a 70-mm figure-of-eight coil (Magstim, Whitland UK) positioned at ~45° respect to the scalp. The TMS coil was controlled by a robotic arm (TMS Robot, Axilum Robotics) and a TMS neuronavigation system (Brainsight, Rogue Systems, Montreal, Canada) with the capacity to estimate and track in real time the relative position, orientation, and tilting of the coil on the sectional and 3D reconstruction of the participant's MRI. The TMS robot guaranties the accurate stimulation of a given brain region during the experiment, by automatically adjusting its position if a movement larger than 5 mm was detected.

On each trial, a burst of three TMS pulses were applied at 40 Hz simultaneously to the presentation of the Stroop word and with a total duration of 56 ms. As previously done elsewhere (Bourgeois et al., 2013; Chica, Bartolomeo, et al., 2011), we attempted to use a fixed TMS intensity of 80% of the maximum stimulator output (MSO). This intensity was adjusted for each participant to avoid discomfort, and face or hand muscular movements. The mean applied TMS intensity was 69% of MSO (SD = 7.35). For each participant, the same TMS intensity was used for the right SMA and the vertex stimulation. The right motor threshold (MT) was determined for each participant at the beginning of the experiment (see Martín-Arévalo et al., 2019 for a detailed explanation of the procedure). The mean right MT was 65% of MSO.

Scalp coordinates for the stimulation sites were located by using the native space of each participant's T1. The TMS stimulation site was the right SMA (Montreal Neurological Institute [MNI] coordinates: x = 6, y = 11, z = 55), which was extracted from a previous fMRI study (Martín-Signes, Paz-Alonso, et al., 2019) (see Fig. 6.1. B). We checked the exact location of the stimulated region in each participant’s brain: for 12 participants the coordinates overlapped with the pre-SMA, for 8 participants with the SMA-proper, and for 4 participants the coordinates landed in between both regions. Given the slight variability in the location of the coordinates in each participant’s brain, and the spatial resolution of TMS (Jahanshahi & Rothwell, 2000), we can conclude that the SMA complex (i.e. pre-SMA and SMA-proper) was stimulated. From now on, we will refer to it as the SMA for the sake of simplicity. The control stimulation site was the vertex (MNI coordinates: x = 0, y = −34, z = 78; Martín-Arévalo et al., 2019), which was not expected to induce any specific behavioral effects (Jung et al., 2016).

6.3.1.6. DWI tractography analysis

In each slice, DWI data were simultaneously registered and corrected for subject motion, and eddy current and echo planar imaging distortions, adjusting the gradient accordingly (ExploreDTI, Irfanoglu et al., 2012; Leemans et al., 2009; Leemans & Jones, 2009). Spherical deconvolution was then performed employing the damped Richardson–Lucy deconvolution algorithm (Dell’Acqua et al., 2010) with the Software StarTrack (http://www.natbrainlab.com). Algorithm parameters were $\alpha = 2$, algorithm iteration = 400, and $\eta = 0.06$ and $v = 8$ as regularization terms (Dell’Acqua et al., 2013). Whole-brain deterministic tractography was performed using a modified Euler tractography algorithm (angle threshold = 45º, absolute hindrance modulated [HMOA] threshold = 0.1, and relative threshold = 10%).

Individual dissections of the tracts were carried out with the software TrackVis (Wang et al., 2007). The 3 branches of the SLF (on the left and the right hemispheres) were isolated using a multiple region of interest (ROI) approach. Three frontal ROIs around the white matter of the superior, middle and inferior frontal gyri and a ROI around the white matter of the parietal lobe were delineated. Streamlines of the arcuate fasciculus projecting to the temporal lobe were excluded by drawing a no-part ROI in the temporal white matter. Cingulate fibers were distinguished from the SLF I by delineating the frontal ROI above the cingulate sulcus (See Rojkova et al., 2016; Thiebaut de Schotten et al., 2011 for a detailed explanation of the method). The HMOA, an index employed as a surrogate for tract microstructural organization (Dell'Acqua et al., 2013), was extracted from each dissected tract. The mean HMOA is defined as the absolute amplitude of each lobe of the fiber orientation distribution and considered highly sensitive to axonal myelination, fiber diameter, and axonal density. Also, following the suggestion of a reviewer, two measures of the macroscopic properties of the tracts (i.e. volume and number of tracks) were extracted.

6.3.1.7. Behavioral data analysis

Mean accuracy and RTs for the Stroop task were analyzed by means of two repeated-measured analysis of variance (ANOVA) with the factors of Region (SMA and vertex) and Congruency (congruent and incongruent). Stroop RTs shorter than 350 ms (10.41%[4] of the trials, SD = 0.17) and errors in the Stroop task (1.13% of the trials, SD = 0.01) were eliminated from the RTs analysis. Additionally, 5 participants were excluded from the RTs analysis[5]. Stroop task analyses included only Gabor present trials. Errors localizing a consciously seen Gabor (1.12% of the trials, SD = 0.01) were excluded from all the analysis.

We analyzed participants' responses to the conscious detection task using the signal detection theory (SDT, Abdi, 2007). We computed the mean percentage of seen targets when the Gabor was present (hits), and when the Gabor was absent (false alarms; FA). Non-parametrical indices of perceptual sensitivity (A') and response criterion (Beta'') were computed.

$$A' = 0.5 + \frac{(\text{Hits} - \text{FAs}) * (1 + \text{Hits} - \text{FAs})}{4 * \text{Hits} * (1 - \text{FAs})};$$

$$\text{Beta}'' = \frac{\text{Hits} * (1 - \text{Hits}) - \text{FAs} * (1 - \text{FAs})}{\text{Hits} * (1 - \text{Hits}) + \text{FAs} * (1 - \text{FAs})}$$

A' values usually range between 0.5 (the signal cannot be distinguished from the noise) and 1 (perfect performance). For Beta", values close to 1 indicate a conservative criterion, whereas values close to −1 indicate a non-conservative criterion (Stanislaw & Todorov, 1999). SDT analyses included only correct response Stroop trials. SDT indices were submitted to two repeated-measures

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[4] This relatively high percentage of RTs under 350 ms was caused by an interference of the TMS sound with the microphone. During the trial, the microphone was opened after the TMS pulses were applied to capture the participant´s response. However, in some of the trials, the sound of the TMS pulses reverberated for a longer time and thus, interfered with the recording of the microphone. This problem affected the first 13 participants but it was solved for the rest of the sample.

[5] Participants with >30% of the trials affected by the interference of the TMS sound (see footnote 1) were excluded for the RTs analysis.

ANOVAs with the factors of Region (SMA and vertex) and Congruency (congruent and incongruent).

We were interested in exploring the role of the three branches of the SLF in the TMS effects over the interaction between executive control and conscious perception. We performed two multiple linear regression with the forward method, to predict the interaction effects on A' and Beta''. As predictors, we used the mean HMOA of the right and left SLF I, II and III. To calculate the interaction indices, we subtracted the congruent minus incongruent condition for SMA stimulation minus the congruent minus incongruent condition for vertex stimulation. In the index, the larger the value, the larger the TMS effect over the congruency effect. One participant was excluded from the linear regression analysis of Beta'' index due to an outlier value (>3 SD from the mean).

6.3.2. Results

For the Stroop task, the expected Congruency effect was observed. Mean accuracy was significantly higher for congruent compared with incongruent trials, $F(1, 23) = 39.23$, $MSE = 0.0005$, $p < 0.001$, $\eta^2p = 0.63$, and RTs were also shorter for congruent compared with incongruent trials, $F(1, 18) = 36.16$, $MSE = 5019$, $p < 0.001$, $\eta^2p = 0.67$ (Figure 6.2. C-D). No effects of Region or interactions were found (all ps > 0.425).

For the Gabor detection task (Fig. 6.2. A–B), perceptual sensitivity was enhanced for congruent compared with incongruent trials, $F(1, 23) = 6.65$, $MSE = 0.0003$, $p = 0.017$, $\eta^2p = 0.22$). However, no effects of Region or interactions were found (all ps > 0.344). Moreover, no significant results were observed when response criterion (Beta'') was analyzed (all ps > 0.121).

The results of the regression analysis ($F(1,22) = 5.826$, $p = 0.025$, $R^2 = 0.209$) showed that the right SLF III was a significant predictor for the TMS effects over perceptual sensitivity (A' index), $\beta = -0.458$, $p = 0.025$. Similarly ($F(1,21) = 5.799$, $p=0.025$, $R^2 = 0.216$), the right SLF III was also a significant predictor for the TMS effects over response criterion (Beta'' index), $\beta = -0.465$, $p = 0.025$. This suggests that participants with lower mean HMOA of the right SLF III had larger TMS effects both in A' and Beta'' indices (see Fig. 6.3. A–B).

We then replicated the repeated-measures ANOVAs for A' and Beta'' including the significant predictor as a covariate (i.e. the mean HMOA of the right SLF III). When doing so for the A' analysis, the interaction between Region and Congruency reached significance, $F(1, 22) = 6.20$, MSE = 0.0001, $p = 0.021$, $\eta^2p = 0.22$, and this interaction depended on the mean HMOA of the right SLF III, $F(1, 22) = 5.83$, MSE = 0.0001, $p = 0.025$, $\eta^2p = 0.21$. TMS over the SMA (as compared with the vertex condition) impaired conscious perception for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the right SLF III (Fig. 6.3. C–D). For Beta'', the interactions between Region and Congruency, and between Region x Congruency x right SLF III did not reach significance ($F(1, 22) = 4.04$, MSE = 0.059, $p = 0.057$, $\eta^2p = 0.15$, and $F(1, 22) = 4.21$, MSE = 0.059, $p = 0.052$, $\eta^2p = 0.16$, respectively).

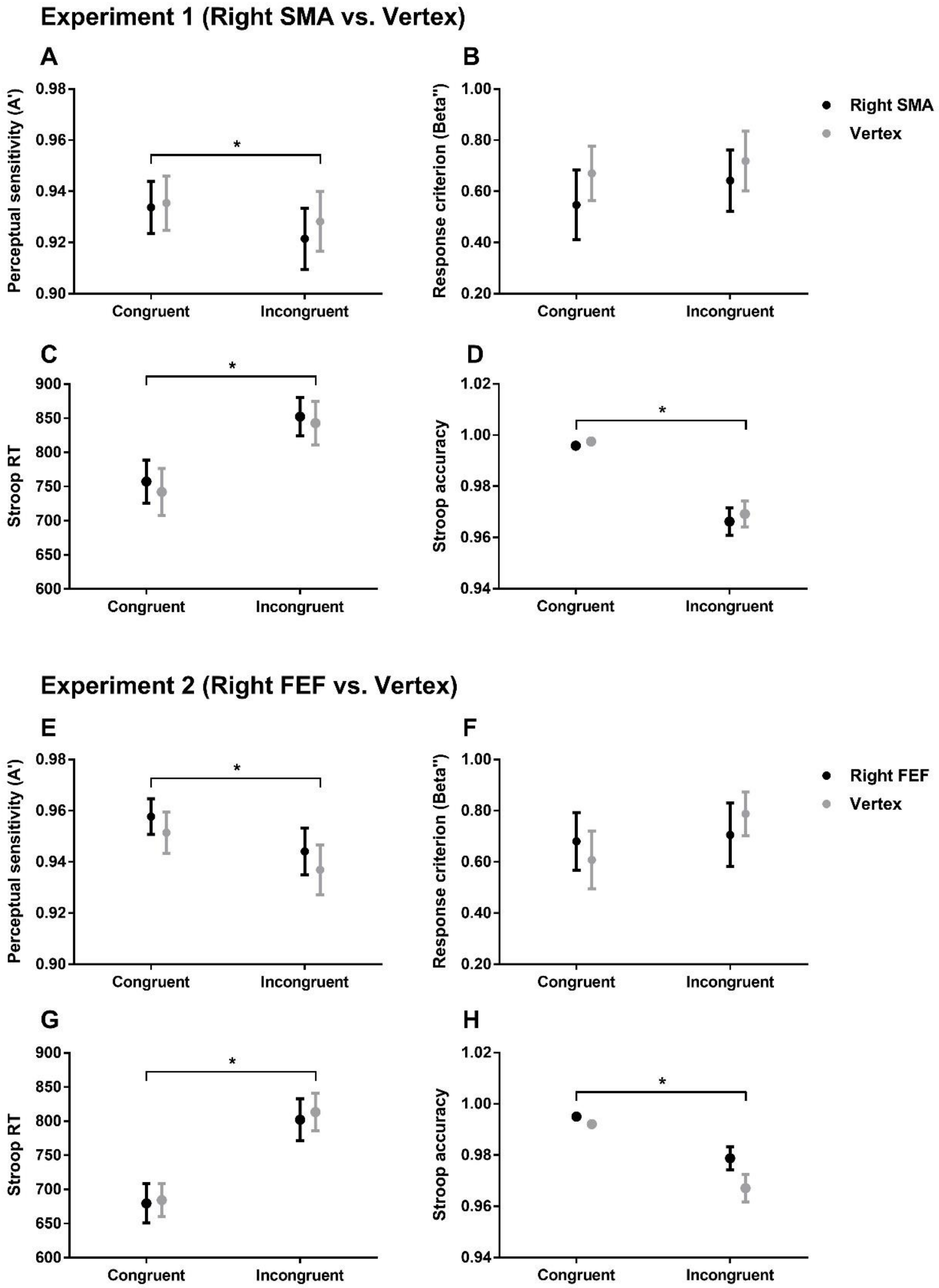

Figure 6.2. Congruency effect for (**A, E**) perceptual sensitivity, (**B**, **F**) response criterion, (**C**, **G**) Stroop reaction time (RT, in ms), and (**D**, **H**) Stroop accuracy for Experiments 1 and 2. Errors bars represent standard errors of the mean. Asterisks represent significant Congruency main effects.

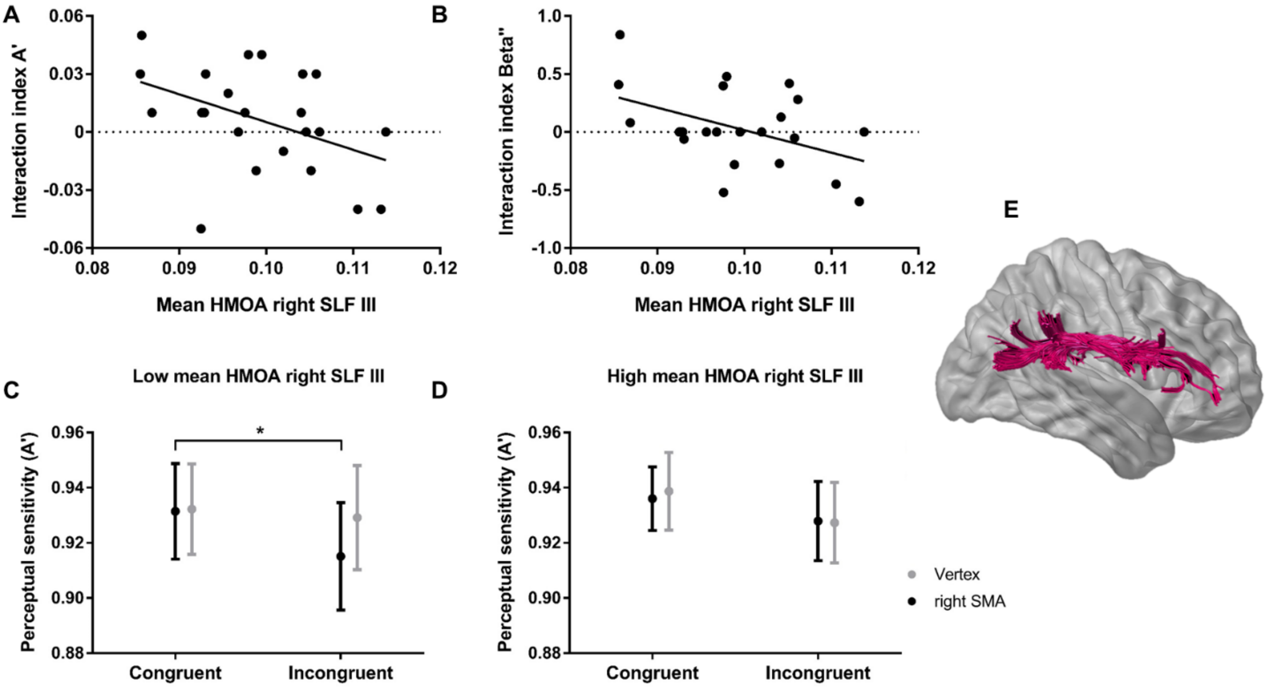

Figure 6.3. (**A**, **B**) Correlation between the mean HMOA of the right SLF III and the SMA-TMS effect (Experiment 1) for perceptual sensitivity and response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 1, Region and Congruency interaction for perceptual sensitivity for participants with a mean HMOA of the right SLF III under the median (low mean HMOA) and over the median (high mean HMOA). Errors bars represent standard errors. Asterisk represent a significant comparison between congruent and incongruent condition when the right SMA was stimulated, t = 3.66, p = 0.004. (**E**) Representation of a virtual in vivo dissection of the SLF III of the right hemisphere using deterministic tractography.

6.3.2.1. Post hoc DWI tractography analysis

Additional dissections. Following the suggestion of a reviewer, the frontal aslant tract (FAT) and the SPL-SMA complex of the SLF I were delineated and included in the DWI tractography analysis. In order to test the relation between the new tracts and behavioral and TMS effects, we followed the same pipeline that was employed for the SLF analysis (see Methods).

FAT is a recently defined tract that runs from the medial part of the superior frontal lobe (i.e. pre-SMA, SMA-proper, and ACC) to the posterior IFG (Catani et al., 2012; Thiebaut de Schotten et al., 2012). Thus, it connects the targeted area with the terminations of the SLF III. This tract might be important for language, speech, and executive control (Dick et al., 2019). The left and right FAT were delineated by using a multiple ROI approach (Fig. 6.4. E; Catani et al., 2012). A 6 cm-sphere ROI was placed in the SMA complex, and a 5 cm-sphere ROI was placed in the triangularis and opercularis parts of the IFG. We performed two regression analyses with the interaction index for A' and Beta'' using the mean HMOA of the left and right FAT as predictors. The results of the regression analysis ($F(1,22) = 5.44$, $p = 0.029$, $R^2 = 0.198$, and $F(1,21) = 5.201$, $p = 0.033$, $R^2 = 0.199$, respectively) showed that the left FAT was a significant predictor for the TMS effects over perceptual sensitivity (A' index), $\beta = -0.445$, $p = 0.029$, and response criterion (Beta''), $\beta = -0.446$, $p = 0.033$ (See ¡. 6.4A-B). When including the mean HMOA of the left FAT as a covariate for the repeated-measures ANOVA for A' and Beta'', the interaction between Region and Congruency reached significance only for A', $F(1, 22) =5.82$, $MSE = 0.0001$, $p = 0.025$, $\eta^2p = 0.21$, and this interaction depended on the mean HMOA of the left FAT, $F(1, 22) = 5.44$, $MSE = 0.0001$, $p = 0.029$, $\eta^2p = 0.20$. TMS over the SMA (as compared with the vertex condition) impaired conscious perception for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the left FAT (Fig. 6.4. C–D).

The SLF I connects the superior parietal lobe with the anterior cingulate cortex, by passing thought the SMA complex (Bozkurt et al., 2016, 2017; Jang & Hong, 2012). We delineated this SPL-SMA segment of the right and left SLF I by using a multiple ROI approach. We employed a parietal ROI (see dissection of the SLF) and a 6 cm-sphere over the SMA complex. We then performed two regression analyses with the interaction index for A' and Beta'' using the mean

HMOA of the left and right SPL-SMA complex. The results of the regression analysis (F(1,19) = 4.62, p = 0.045, R^2 = 0.196) showed that the mean HMOA of the right SPL-SMA complex was a significant predictor for the TMS effects over response criterion (Beta'' index), β = -0.442, p = 0.045. But, when including this predictor as a covariate for the repeated measures ANOVA for Beta'', no significant interactions between region and congruency were found (all ps > 0.206).

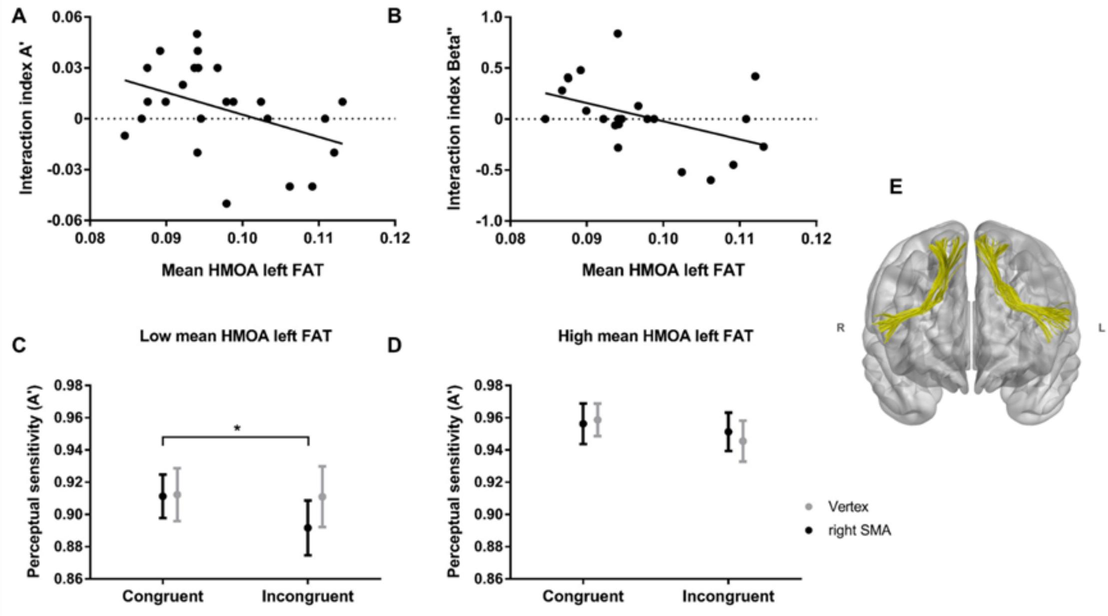

Figure 6.4. (**A**, **B**) Correlation between the mean HMOA of the left FAT and the SMA-TMS effect (Experiment 1) for perceptual sensitivity and response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 1, Region and Congruency interaction for perceptual sensitivity for participants with a mean HMOA of the left FAT under the median (low mean HMOA) and over the median (high mean HMOA). Errors bars represent standard errors. Asterisk represent a significant comparison between congruent and incongruent condition when the right SMA was stimulated, t = 2.29, p = 0.043. (**E**) Representation of a virtual in vivo dissection of the right and left FAT using deterministic tractography.

Analysis of the macroscopic properties. Following an identical pipeline to the microscopic analysis (i.e. mean HMOA), we analyzed the relation between the volume of all dissected tracts and the TMS effects over the behavioral measures (A’ and Beta’’ indices). Although the number of tracks was also extracted, it was not analyzed here. We refer to the available data of this work for further analysis (https://osf.io/g8ue5/?view_only=b54ba6ec57b54810b92a220f402da6e8).

The results of the regression analysis for the SLF (F(1,21) = 5.03, p = 0.036, R^2 = 0.193) showed that the volume of the left SLF I was a significant predictor for the TMS effects over response criterion (Beta’’ index), β = -0.440, p = 0.036. But, when including this predictor as a covariate for the repeated measures ANOVA for Beta’’, no significant interactions between region and congruency were found (all ps > 0.463). No other significant models were found for any of the tracts for any of the behavioral measures (all ps > 0.073).

6.4. Experiment 2: right FEF versus Vertex

6.4.1. Methods

6.4.1.1. Participants

24 right-handed volunteers (12 females, mean age 23 years, SD = 2.87) took part in the study.

6.4.1.2. Apparatus and stimuli, procedure and analysis

These were identical to Experiment 1 with the exception of the TMS target (Fig. 6.1. B). The TMS stimulation sites were the right FEF (MNI coordinates: x = 36, y = −1, z = 53), which was extracted from a previous fMRI study (Martín-Signes, Paz-Alonso, et al., 2019), and the vertex. The mean TMS intensity applied was 60% of MSO (SD = 6.95). The mean right MT was 66% of the MSO. Stroop RTs shorter than 350 ms accounted for 0.60% of the trials (SD = 0.01). Errors in the Stroop task constituted 1.21% of the trials (SD = 0.01) and errors localizing a consciously seen Gabor 1.30% of the trials (SD = 0.03). DWI data from two participants could not be collected (N = 22).

6.4.2. Results

For the Stroop task, mean accuracy was also significantly higher for congruent compared with incongruent trials, F(1, 23) = 22.33, MSE = 0.0005, $p < 0.001$, $\eta^2p = 0.49$, and RTs were shorter for congruent compared with incongruent trials, F(1, 23) = 140.85, MSE = 2691, $p < 0.001$, $\eta^2p = 0.86$ (see Fig. 6.2. G-H). We also found an effect of Region for mean accuracy, F(1, 23) = 6.31, MSE = 0.0002, p = 0.019, $\eta^2p = 0.22$, with better performance when TMS was applied over the right FEF as compared to the vertex condition. No other effects or interactions were found (all ps > 0.174).

For the Gabor detection task, we found a significant Congruency effect over perceptual sensitivity (A’), F(1, 23) = 12.04, MSE = 0.0004, p = 0.002, $\eta^2p = 0.34$, with better performance for congruent than incongruent trials. No significant effects over response criterion (Beta’’) were found (all ps > 0.225, see Fig. 6.2. E-F).

The linear regression analysis including the mean HMOA of the right and left SLF I, II and III as predictors, revealed no significant models to predict the TMS effect for neither of the two dependent variables tested (i.e. behavioral indices of A’ and Beta’’). To confirm that the TMS effects found in Experiment 1 were region-specific, we replicated the repeated-measures ANOVAs for A’ and Beta’’ including the mean HMOA of the right SLF III as a covariate. Results showed that the interaction between Region and Congruency was still not significant neither for A’ nor for Beta’’ (all ps > 0.605). We also conducted Pearson correlations between the mean HMOA of the right SLF III and the interaction index for A' and Beta''. No significant correlations were found between the variables (all ps > 0.747).

6.4.2.1. Post hoc DWI tractography analysis.

Additional dissections. As done for Experiment 1, left and right FAT and SPL-SMA complex of the SLF I were incorporated to the DWI tractography analysis. The linear regression analyses revealed no significant models to predict the TMS effects for neither of the two dependent variables tested (i.e. behavioral indices of A' and Beta'') for any of the tracts (all ps > 0.129).

Analyses of the macroscopic properties. As done for Experiment 1, volume of the dissected tracts was incorporated to the DWI tractography analysis. The results of the regression analysis for the SLF ($F(1,18) = 8.69$, $p = 0.003$, $R^2 = 0.521$) showed that the volume of the right SLF I and III were significant predictors for the TMS effects over response criterion (Beta'' index), $\beta = 0.376$, $p = 0.047$ and $\beta = -0.667$, $p = 0.002$, respectively (Fig. 6.5. A-B). When including the volume of the right SLF III as a covariate for the repeated-measures ANOVA for Beta'', the interaction between Region and Congruency reached significance, $F(1, 17) =11.71$, $MSE = 0.095$, $p = 0.003$, $\eta^2p = 0.41$, and this interaction depended on the volume of the right SLF III, $F(1, 17) = 10.49$, $MSE = 0.095$, $p = 0.005$, $\eta^2p = 0.38$. TMS over the right FEF (as compared with the vertex condition) was associated to a more liberal response criterion for incongruent Stroop trials. However, this effect was mainly observed in participants with low integrity values of the left FAT (see Figure 6.5. C-D). No significant interactions between Region and Congruency were found when the right SLF I was included as a covariate (all ps > 0.712). No other significant models were found for other tracts in any of the behavioral measures (all ps > 0.236).

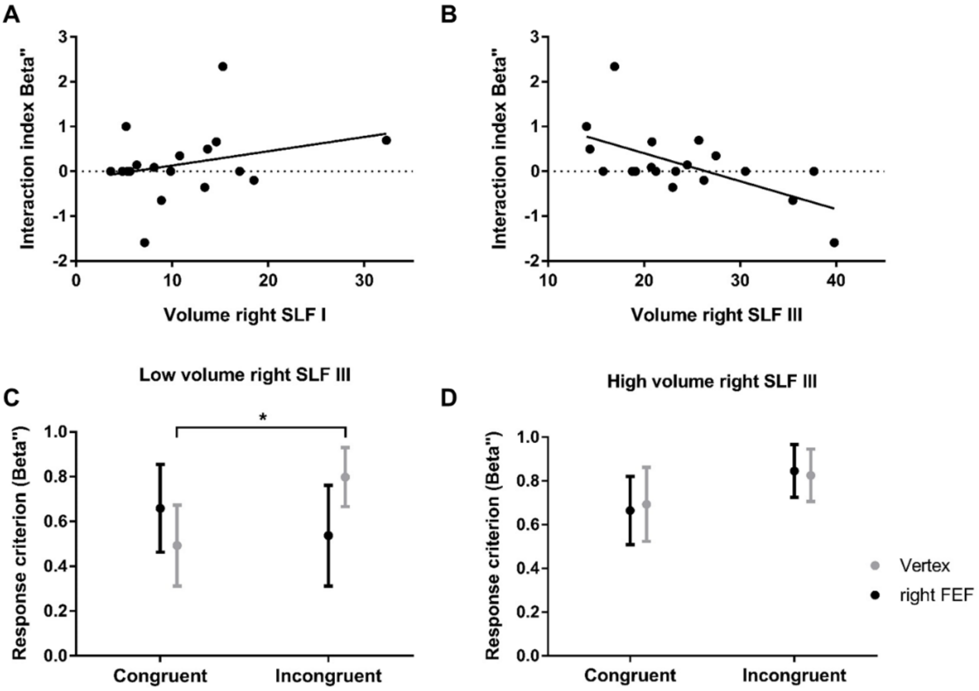

Figure 6.5. (**A, B**) Correlation between the volume (in ml) of the right SLF I and SLF III, and the FEF-TMS effect (Experiment 2) for response criterion. The black line represents the best fit of the data. (**C**, **D**) For experiment 2, Region and Congruency interaction for response criterion for participants with a volume of the right SLF III under the median (low volume) and over the median (high volume). Errors bars represent standard errors.

6.5. Discussion

The aim of this work was to explore the involvement of a frontal region, the right SMA, in the interaction between executive control and conscious perception by using TMS, a methodology that allows establishing causal relations by temporally modulating the state of the brain. In a dual task, executive control was manipulated with a Stroop task in which congruent and incongruent trials were presented at the same time that a near-threshold Gabor stimulus had to be detected. This work aims to contribute to the current debate about the nature of the relation between conscious perception and attention, by exploring the executive control network, which in this context has been much less studied than other attentional networks. Also, this work aims to contribute to the debate about the involvement of the frontal regions and the fronto-parietal network in conscious perception. The right SMA (Experiment 1) and the right FEF (Experiment 2) were stimulated by using online TMS. Also, the implication of fronto-parietal white matter was explored thought the delineation of the three branches of the SLF. Complementarily to the preliminary hypothesis, the involvement of white-matter tracts connecting the targeted region (i.e. the SMA) with other relevant regions was explored through the delineation of the FAT and the SPL-SMA complex of the SLF I. A white matter macroscopic property of the tracts (i.e. volume) was also examined.

Behaviorally, in both Experiment 1 and 2, perceptual sensitivity to detect the near-threshold Gabor was significantly reduced for incongruent compared to congruent Stroop trials. However, no effects of executive control over decision criteria were found. In previous studies using a similar paradigm, executive control elicited by the Stroop task influenced participants' response criterion (Colás et al., 2017, 2018) or the percentage of seen targets (Martín-Signes, Paz-Alonso, et al., 2019) but not perceptual sensitivity. One difference between the present experiment and the ones listed above is the response modality employed for the Stroop task, which changed from a manual to a vocal-response. It has been well stablished that vocal-response interference excess manual-response interference (MacLeod, 1991; White, 1969). It has also been demonstrated that the size of the stimulus set can affect the evoked interference as exact stimulus repetition can produce priming effects (Hommel, 1998; Mayr et al., 2003). In the present experiment, we expanded the stimulus set by using four different word colors (compared with the three-color set used previously). The changes introduced in the paradigm (a vocal-response and a bigger set size) might have induced a greater interference effect that might account for the different results found. It is possible that a greater involvement of executive control mechanisms in the incongruent compared with the congruent trials is needed in order to modulate perceptual sensitivity to detect near-threshold stimuli.

In Experiment 1, TMS was applied over the right SMA or a control stimulation site (vertex) concurrently with the dual task. Previous fMRI work (Martín-Signes, Paz-Alonso, et al., 2019) demonstrated that functional connectivity increased between the right SMA-SPL for congruent trials when near-threshold Gabors were reported as compared to non-reported Gabors. No differences in functional connectivity between these regions were observed on incongruent trials. Therefore, the TMS modulation of the SMA compared to the vertex condition was expected to produce differential effects over conscious perception depending on the executive control condition (i.e. congruent or incongruent). However, we did not find any SMA-TMS effects when exploring the contribution of executive control over perceptual sensitivity or response criterion.

A further aim of this work was to explore the contribution of long-range white matter tracts connecting the parietal and the frontal lobes in conscious access and its relation with executive control. Some studies have linked the microstructure of the SLF with different measures of the executive functions in healthy population (Crespi et al., 2018; Sasson et al., 2012, 2013; Smolker et al., 2018) and with executive dysfunctions in several conditions (Chiang et al., 2016; Makris et al., 2008; Muir et al., 2015; Oh et al., 2018; Sui & Rajapakse, 2018; Wu et al., 2020). Some other studies have found a relation between the microstructure of the SLF and conscious perception or consciousness disorders (Bourgeois et al., 2015; Colás et al., 2019; Matthews et al., 2011, 2012). However, literature exploring the contribution of the different dorsal-to-ventral branches of the SLF to executive control or conscious perception (or its interaction) is scarce (but see Colás et al., 2019; Quentin et al., 2015; Wu et al., 2020).

In addition, previous work has shown that neural interactions between different attentional networks and conscious perception are modulated by the microstructure of the SLF. Using fMRI measures of the neural interaction between both processes, reduced integrity of the left SLF III was associated with a greater neural interaction between spatial orienting and conscious perception; while increased integrity of the left SLF III was associated with a greater neural interaction between phasic alerting and conscious perception (Chica et al., 2018). Moreover, reduced integrity of the left SLF II was associated with a greater neural interaction between executive control and conscious perception (Martín-Signes, Paz-Alonso, et al., 2019).

In accord, we performed linear regression analyses including the microstructure of the three branches of the SLF for the right and left hemispheres as predictors of the TMS modulation of the executive control and conscious perception interaction, reflected in perceptual sensitivity and response criterion. For Experiment 1, the results of the linear regression showed that the right SLF III was a significant predictor for the TMS effect on perceptual sensitivity (A’) and response criterion (Beta’’). When the microstructure of the right SLF III was included as a covariate in the ANOVA, results indicated that the TMS over the

SMA reduced perceptual sensitivity (A’) only for the incongruent Stroop condition. As previously shown (Martín-Signes, Pérez-Serrano, et al., 2019), participants with lower HMOA were the ones showing larger TMS effects. There is evidence in the literature that the SLF III participates in executive control and conscious perception and thus, it may be that a good integrity of this long-range fronto-parietal tract prevents from the disruption caused by the SMA stimulation and, only for participants with lower integrity of the tract, behavioral effects are observed.

Some studies have demonstrated a modulation of the stimulation-induced interference in the behavior, produced by the microstructural properties in the white matter tracts connecting the targeted region and other key regions in the involved circuits (Barredo et al., 2019; Brodie et al., 2014; Quentin et al., 2013, 2015; Rodríguez-Herreros et al., 2015). In our study, only the SLF I innervates the SMA, while the SLF II and III do not (Vergani et al., 2014). However, the SLF III connects (among other structures) the inferior frontal gyrus (IFG), which participates in cognitive control and is well connected with the SMA through the FAT (Nakajima et al., 2020; Vergani et al., 2014). Thus, it is also plausible that a well-connected SMA-IFG by the SLF III prevents from the disruptive effects of TMS over the SMA. Indeed, the microstructure of the left FAT was a significant predictor for the SMA-TMS effects over perceptual sensitivity and response criterion. In line with the results obtained for the SLF III, participants with lower integrity of this tract showed greater TMS effects over perceptual sensitivity. As mentioned, the FAT originates in the SMA complex and terminates in the IFG, which is also the termination of the SLF III. Although the definition of this tract is recent (Catani et al., 2012), it has been proposed a role on control, planning and coordination of motor programs and the inhibition of competing motor plans. Some level of hemispheric specialization has been found, with a left FAT particularly involved in speech actions and a right FAT more related with inhibitory control, especially in the visuo-spatial domain (Dick et al., 2019). Although an involvement of the right FAT was expected because of the hemispheric location of the stimulated SMA and the right SLF III association found, the verbal nature of the Stroop task employed could account for the observed results. Also, the microstructure of the right SPL-SMA complex of the SLF I was a significant predictor for the SMA-TMS effects over response criterion. This result is in agreement with a previous study in which functional connectivity between the right SMA and the right SPL reflected an interaction between executive control and conscious perception (Martín-Signes, Paz-Alonso, et al., 2019). Nevertheless, due to the post hoc nature of these analysis, they should be interpreted with caution.

In Experiment 2, the right FEF was selected as an active control region to demonstrate that the TMS effects found over the right SMA were region specific. In a previous study (Martín-Signes, Paz-Alonso, et al., 2019), larger blood oxygenation level-dependent (BOLD) responses were found for seen than unseen trials on the right FEF, and thus, an effect was expected for conscious perception but not for executive control or for the interaction between both processes. Nevertheless, we did not find a TMS effect over consciousness (neither a modulation related to the microstructure of the SLF). This result is in agreement with theories arguing that consciousness is a distributed process and does not rely in a specific region (Dehaene & Changeux, 2011) and thus, the modulation of one particular region may not be enough to impair conscious perception. Conversely, a main TMS effect over executive control was found, as TMS over the right FEF increased Stroop accuracy compared with the vertex condition. Although this result was unexpected, there are examples in the literature showing a role of FEF in attentional control (Cosman et al., 2018; Muggleton et al., 2003) and inhibitory control (Muggleton et al., 2010; Xu et al., 2007), both processes presumably involved in resolving the Stroop task.

The post hoc exploration of the macroscopic properties of the tracts showed that TMS over the right FEF modulated response criterion on incongruent trials when the volume of the right SLF III was taken into account. The convergence of results over this tract in Experiment 1 and 2, and in previous work (Colás et al., 2019; Martín-Signes, Pérez-Serrano, et al., 2019), suggest a role of the right SLF III on conscious perception and its relation with some attentional processes, such as executive control, and phasic alerting. Nevertheless, further investigation is needed to better understand the relation between micro- and macroscopic properties of the tracts and behavioral or TMS-related variables.

Although interesting, the findings of this work need to be understood in the context of some limitations, some of them intrinsic to many TMS designs. One important point is that the SMA complex is a medial structure and the TMS pulse might not reach deeper layers. It is plausible that the partially null results of this work (when white matter properties are not taken into account in the analyses) are due to a difficulty on the stimulation of the SMA. Also, the TMS targets for this investigation were situated over the right hemisphere. Although DWI data were extracted from tract from both hemispheres, further investigation from left targets and networks is needed. Finally, correlations between DWI tractography and behavioral measures were explored with a limited number of participants. Also, post hoc examinations increased the number of comparisons. Further studies with larger samples and *a priori* hypothesis would allow to confirm the findings.

To conclude, the results of this work can be summarized in some key contributions. They support the behavioral interaction between executive control and conscious perception, showing that a greater interference is needed to observe a modulation of perceptual sensitivity. However, although the investigation of the neural interactions between executive control and conscious perception has produced positive results (Colás et al., 2018; Martín-Signes, Paz-Alonso, et al., 2019 and the present study), it seems to be less robust than the interaction found between consciousness and other attentional systems (namely spatial attention, Chica et al., 2010, 2013; Chica, Valero-Cabré, et al., 2014; Rees & Lavie, 2001, and alerting, Chica et al., 2016, 2018; Cobos et al., 2019). It is plausible that the overlap between regions or neural mechanisms involved in executive control and conscious perception is less massive, resulting in a less consistent neural and behavioral interaction. In the present study, the neuromodulation of a frontal region, the right SMA, only affected perceptual sensitivity on incongruent trials when the integrity of the right SLF III or the left FAT were introduced in the analysis. Similarly, the stimulation of the right FEF only affected the response criterion on incongruent trials when the volume of the right SLF III was taken into account. Nevertheless, these findings do not rule out the implication of frontal regions in conscious perception and point to fronto-parietal and frontal networks as the possible shared neural substrates between both systems. Finally, the TMS-effects dependence on the micro- and macrostructure of some fronto-parietal and frontal tracts suggest that white matter properties might be taken into account as a source of individual variability and efficiency in TMS studies. While a direct implication of white matter tracts connecting the neuromodulated regions have been shown before (Barredo et al., 2019; Brodie et al., 2014; Quentin et al., 2013, 2015; Rodríguez-Herreros et al., 2015), these results (and others before, Martín-Signes, Pérez-Serrano, et al., 2019) suggest that an indirect modulation thought compensatory processes supported by different anatomical networks is also plausible.

6.6. Acknowledgments

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6.7. Open practices

The study in this article earned an Open Materials badge for transparent practices. Materials and data for the study are available at https://osf.io/g8ue5/?view_only=b54ba6ec57b54810b92a220f402da6e8. The conditions of our ethics approval do not permit public archiving or sharing of anonymized raw study data. We report sample size calculations, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures and analyses were pre-registered prior to the research being conducted.

GENERAL DISCUSSION

Chapter 7. General discussion and conclusions

7.1. General discussion

7.1.1. Attentional modulations of conscious perception

Attention is considered, by many models, as a mechanism for the selection of information accessing conscious experience. Given that we have a limited amount of processing resources, and that we live in a crowded environment, attention would serve as a filter (Dehaene et al., 2006). Others conceptualizations propose that attention is an independent mechanism, only combined with conscious perception in a later decisional stage, selecting information for the final report/response (Tallon-Baudry, 2012). However, any of the possible conceptions of the link between attention and conscious perception predicts that subject's reports would vary according to the allocation of attention. In the two studies of this thesis, we expected that the conflict generated by infrequent incongruent Stroop trials required the involvement of the executive control attentional network (as done before, Colás et al., 2017, 2018). We observed that conscious reports increased during congruent than incongruent Stroop trials. Additionally, when conflict generated by incongruent Stroop trials was presumably larger (for verbal instead of manual responses, and when the size of the stimulus set was increased), perceptual sensibility was also modulated.

Although these results do not allow to differentiate between the models exposed above, they bring the novelty of a further exploration of the executive control network. Given the heterogeneity of attention, we cannot presume that all attentional mechanisms have a similar impact over conscious perception (indeed, we already know that this is not the fact, Chica et al., 2011; Koch & Tsuchiya, 2007). Therefore, we can conclude that the deployment of executive control necessary in some situations (e.g. when conflict is present) modifies the subsequent conscious perception of near-threshold information, by modulating decision criteria (Colás et al., 2017, 2018), but also perceptual stages of processing (as in the present work). However, executive control is also a wide concept and this work was focused in one of its subfunctions (i.e. inhibitory control).

7.1.2. Common neural substrates for attention and conscious perception in the frontal lobe

In the understanding of the relationship between attention and conscious perception, it is fundamental to distinguish the NCC from those of attention. Models proposing that they are intrinsically linked predict shared or partially shared neural mechanisms for attention and conscious perception (De Brigard & Prinz, 2010; Dehaene et al., 2006; Posner, 1994). In the search for those common neural mechanisms, the frontal lobe has been pointed out. According to some models, frontal regions are fundamental for the emergence of conscious perception (e.g. Del Cul et al., 2009; Lau & Rosenthal, 2011; Odegaard et al., 2017). On the other hand, they are also involved in many attentional processes (Fan et al., 2005). Indeed, prefrontal and frontal regions has been pointed out as key regions in executive control processes (e.g. Macdonald et al., 2000; Miller & Cohen, 2001; Posner & Petersen, 1990). In accordance, in the two studies of this thesis, we explored the neural basis of the interaction between executive control and conscious perception. Such interaction was observed in the functional connectivity of some fronto-parietal regions, whose strength coupling was greater for seen compared to unseen trials, only for congruent Stroop trials. Besides, two frontal regions (the SMA and the FEF) demonstrated a causal involvement but solely when white matter properties of the SLF or the FAT were taken into account.

These results suggest partially shared neural correlates for attention and conscious perception in frontal regions. Importantly, this result is supported by correlational, but also causal evidence. However, we reckon that while evidence is clear for the interaction between phasic alerting and conscious perception (Chica et al., 2016; Martín-Signes, Pérez-Serrano, et al., 2019), and between exogenous orienting and conscious perception (Chica et al., 2013; Chica, Valero-Cabré, et al., 2014), it is somewhat weaker for executive control. This late interaction was only found in functional connectivity analysis in the fMRI study, or when white matter measures were taken into account in the TMS study. Therefore, it is plausible that executive control and conscious perception share less extensive common neural mechanisms. However, it is also possible that the Stroop task employed is not generating a strong enough conflict (maybe due to participants' training with this or similar tasks). Indeed, only when conflict generated by incongruent Stroop trials was presumably larger (as in the second experiment), perceptual sensibility was modulated. We believe that other tasks (e.g. learning of new rules) could cause a greater conflict, helping in the understanding of the modulation of executive control over conscious perception and its neural mechanisms.

Regarding the debate about the involvement of frontal regions in the NCC, the fMRI study of this thesis pointed to a set of fronto-parietal regions that were more activated for consciously perceived than non-consciously perceived targets. However, this study was not specifically designed for the search of the NCC, and thus, the activations reported comprise both the conscious perception of the

Gabor and the Stroop task. In the second study of this work, some frontal cortical regions (i.e. right SMA and right FEF) were neuromodulated by using TMS. None of the stimulated regions generally increased the detection of near-threshold Gabor stimuli. Although some theories propose that frontal regions are crucial for conscious perception, they state that consciousness is a very distributed process, relying in a wide network of fronto-parietal regions. Therefore, the stimulation of a single cortical area is not hypothesized to modulate conscious perception processes (but see Kanai et al., 2008; Quentin et al., 2015, 2016).

7.1.3. The role of fronto-parietal white matter

The last objective of this doctoral thesis was to explore the involvement of long-range fronto-parietal white matter tracts in the interaction between executive control and conscious perception. This interest is supported by theories proposing that both, conscious perception and some attentional processes, rely on a distributed fronto-parietal network. We expected that structural properties of the SLF could correlate with measures demonstrating attentional or conscious perceptual effects. In accordance with this hypothesis, we observed an association between the micro- and macrostructural properties of the different branches of the SLF, and behavioral, TMS, and fMRI effects of the interaction between executive attention and conscious perception.

7.1.3.1. The role of the SLF I, II, and III in attention and conscious perception

As reviewed before, the SLF is organized in three parallel branches – SLF I, II and III – from dorsal to ventral positions (Makris et al., 2005). Anatomically, the SLF I overlaps with the dorsal fronto-parietal network, the SLF III overlaps with the ventral network, and the SLF II probably communicates both (Thiebaut de Schotten et al., 2011). However, a large majority of studies consider the SLF as a single pathway, limiting possible investigations of their separated functions. We believe that the spherical deconvolution deterministic DWI tractography employed in this work offers an advantageous approach to explore SLF I, II, and III functions in healthy participants.

When the interaction between executive control and conscious perception was explored with fMRI, we found a positive correlation between functional connectivity measures of the interaction between executive control and perceptual consciousness and the microstructure of the left SLF II. As mentioned above, the SLF II is hypothesized to serve as a link between dorsal and ventral networks, and may be important for the resolution of a dual task in which conflict has to be monitored, while detecting targets appearing at unpredictable locations (Corbetta & Shulman, 2002). Indeed, abnormalities in this SLF medial branch has been reported in attention-deficit/hyperactivity disorder (Makris et al., 2008; Wu et al., 2020).

Findings of the second study of this work confirmed an involvement of the right SLF III in the interaction between executive control and conscious perception, explored while stimulating the SMA with TMS. Previous results (Martín-Signes, Paz-Alonso, et al., 2019) related the microstructure of this same tract on the rTMS-SMA effects over the interaction between phasic alerting and conscious perception. On the left hemisphere, the SLF III was predictive of the neural interactions observed (in BOLD measures) between exogenous orienting and phasic alerting, and conscious perception (Chica et al., 2018). Furthermore, the microstructure of the right SLF III has been recently associated with the necessary contrast to perceive near-threshold Gabors in patients with frontal damage (Colás et al., 2019). Attending to the macrostructural properties of this branch, we also showed that the volume of the right SLF III was involved in the interaction between executive control and conscious perception, explored while stimulating the FEF with TMS.

Few studies have specifically explored or reviewed the functional role of the SLF I, II, and III in cognitive processes. Parlatini and collaborators (2017) combined tractography in a large sample of participants with a meta-analysis of fMRI studies. They concluded that the SLF I was associated with a dorsal cluster involved in spatial functions, such as saccades, voluntary oriented attention, or motor sequences, while the SLF III was related with a ventral cluster of non-spatial functions, such as working memory, response inhibition, automatically captured attention, or decision making. The SLF II was associated to all areas shared between the two clusters. In a recent review, Nakajima and collaborators (2019) collected existing knowledge regarding SLF functions. Their work supports a role of the dorsal segment of the SLF mainly in visuospatial attention and motor control. The ventral segment, primarily from the left hemisphere, would be involved in the language network, while the right homologous would be involved in attentional functions, specially bottom-up attention.

Even though we are not in the position of undoubtedly disentangle the separated contributions of the different branches of the SLF, we can conclude that they play a role in healthy and dysfunctional attentional and conscious perceptual processes. Our data (and other before, Chica et al., 2018; Martín-Signes, Pérez-Serrano, et al., 2019) point to the right SLF III as an important fasciculus reflecting the interactions between attention and conscious perception. This is reinforced by data showing a role of this tract in the conscious perception of near-threshold stimuli after prefrontal brain damage (Colás et al., 2019), and in attention and conscious perception deficits accompanying neglect (Bartolomeo et al., 2012; Lunven et al., 2015). However, future investigation should disentangle – if possible – their hemispheric functional differences, and the coherence between micro- and macrostructural measures. The role of the left SLF II in the interaction between executive control and conscious perception, suggested by the fMRI-DWI data of our second study, is not entirely clear in the literature and should be deeper explored in future studies.

7.1.3.2. White matter structure as a source of individual variability and neuromodulation efficiency

When white matter micro and macro-structural properties are studied in healthy participants, it is not expected that tracts integrity is compromised as it is in the study of participants suffering from brain damage or diseases, such as attention-deficit/hyperactivity disorder or autism. However, we know that variability in micro- and macrostructural measures does exist between healthy individuals, and that inter-subject variations correlate with individual differences in performance in a wide range of cognitive domains (Niogi, 2010). Results of the present work, reviewed in the previous section, confirm this idea specifically for attentional and conscious perception processes.

In line with this conception, some studies have demonstrated that TMS-induced neuromodulation is related with structural properties of white matter tracts. As one might expect, properties of pathways connecting the TMS-targeted region and other key regions are fundamental (Barredo et al., 2019; Brodie et al., 2014; Quentin et al., 2013, 2015; Rodríguez-Herreros et al., 2015). Data from the second study of this work demonstrated that the microstructure of a tract segment connecting the targeted SMA and the SPL, was a significant predictor for the TMS effects.

However, we consider that one of the most relevant results of this doctoral thesis is the role of indirectly involved tracts as significant predictors for TMS effects. For example, in the second study, the right SLF III and the left FAT were related to the effects caused by TMS over the right SMA, even though none of them innervate the targeted region. We hypothesized that those participants with high connectivity between relevant anatomical networks are probably sheltered from the TMS modulation. We reckon that this relationship between white matter tract structure and cognitive abilities is more significant when behavioral effects are weak or variable. Chechlacz and collaborators' work (2015) support this idea. They employed a search task to explore shifts in the spatial allocation of visual attention produced by TMS over the right and left posterior parietal cortex (PPC). When the right PPC was stimulated, most of the participants showed a rightward shift. However, TMS effects over the left PPC were more variable (13 participants presented rightward attentional shifts and 9 presented leftward attentional shifts), and correlated with the microstructure of the corpus callosum. In the TMS study of this thesis, modulations of behavioral interactions between executive control and conscious perception were only demonstrated when inter-subject white matter variations were introduced in the analysis. Similarly to the study reviewed above, SMA-TMS effect over perceptual sensitivity in Stroop incongruent trials was numerically more variable (SD = 0.058) than in congruent trials (SD = 0.050). Also, participants showing a low HMOA mean of the right SLF III had a numerical more variable TMS effect (SD = 0.063) than participants with high HMOA mean (SD = 0.047). However, this hypothesis could be better confirmed by a meta-analysis exploration of DWI-TMS studies with complex behavioral tasks (where variability among participants is expected due to low ceiling or floor effects).

Also supporting this view, there is evidence in patients with brain damage that white matter integrity in the intact hemisphere is a reliable predictor of outcome and recovery (Forkel, Thiebaut de Schotten, Dell'Acqua, et al., 2014; Lunven et al., 2015; Pani et al., 2016). White matter integrity is also a key factor in patients' response to behavioral (Lunven et al., 2019) and TMS (Nyffeler et al., 2019) treatment after brain damage. For example, inhibitory TMS over the contralesional hemisphere has generally been shown to ameliorate neglect signs. However, variability in responses to TMS seems to be determined by the integrity of parieto-parietal interhemispheric connections (Nyffeler et al., 2019).

7.2. Limitations and future perspectives

The results of this doctoral thesis need to be understood in the context of some limitations. Some of them are intrinsically related to the methods employed. The low temporal resolution of the fMRI does not allow to stablish a precise timeline of the processes involved in the resolution of the task. In consequence, it does not permit to select the specific moment of time in which TMS stimulation would be optimal. In the TMS study, targeted regions were selected from normalized coordinates from previous fMRI studies. Although this method has advantages over others (e.g. utilizing 10–20 EEG position), it also causes inter-individual variances in the actual target stimulation (Sack et al., 2009). This and other well-known factors (Bijsterbosch et al., 2012; Casula et al., 2018; Rocchi et al., 2018) are sometimes responsible of variable or weak TMS effects in cognitive studies. However, we have tried to overcome some of these limitations by including two control conditions: vertex stimulation and the stimulation of another cortical region with a different predicted outcome. This constitutes a good proof that TMS effects found are region specific of the targeted area. However, we consider that our investigations would benefit from more sophisticated methods such as individual fMRI-guided TMS neuronavigation or combined TMS-EEG, that allow to explore the neural correlates of TMS modulations (Tremblay et al., 2019).

This work has also limitations related to DWI methods. Contrary to some approaches that explore white matter properties at a voxel level (which does not permit to isolate specific pathways; e.g. Smith et al., 2006), DWI tractography provides a tool that allows to extract individual dissections (subject by subject), using prior anatomical knowledge. ROIs can be delineated over normalized templates (De Groot et al., 2015; Lawes et al., 2008), or be generated in each brain native space (Catani & Thiebaut de Schotten, 2008; Rojkova et al., 2016). This last approach makes it possible to more precisely differentiate between different portions of the tracts, but has the disadvantage of being dependent of researcher’s anatomical knowledge and subjectivity (Makris et al., 2005). Also, the spherical deconvolution algorithm employed in this work (Dell’Acqua et al., 2010; Dell’Acqua & Tournier, 2019) provides an important advancement to reconstruct white matter tracts in regions with multiple fiber crossings (as the SLF). However, promising DWI developments (e.g. multi-shell data or multi-slice acquisition) open further possibilities of exploration that could complement and expand the findings of this work.

Another general limitation is the restricted number of participants employed in the studies, especially important for correlational analysis. Consequently, associations between white matter structure and TMS or fMRI effects found in this work need to be interpreted with caution. In addition to sample size, some of the analysis were performed over white matter tracts that were delineated *post hoc*. For example, the FAT was delineated as a suggestion of a reviewer. This lead to interesting results that motivate for further exploration of frontal lobe association tracts and their potential role in the interaction between executive control and conscious perception. In sum, new studies with determined *a priori* hypothesis and larger sample size, over the SLF or new suggested tracts, will be very illuminating. Recently, our group has started a new project using TMS that aims at collecting a large sample of participants (N=60) and exploring white matter structure correlations. This and future projects will help disentangle more precisely white matter contributions in cognitive processes and TMS effects, with clinical and research applications. Indeed, fascinating tools that are coming will enable to track white matter pathways in real time for performing navigated TMS (Aydogan et al., 2020).

7.3. Highlights

The main results of this doctoral thesis can be summarized in some key contributions:

- Attentional modulations of conscious perception depend on the specific attentional function deployed. Executive control required for conflict resolution has a detrimental effect over conscious perception of near-threshold stimuli.
- Functional coupling between some fronto-parietal regions is related to the interaction between executive control and conscious perception. Two of such frontal regions, the right SMA and the right FEF, are causally involved in the interaction between executive control and

conscious perception, but only when white matter properties are taken into account. This suggest, at least, partially shared neural substrates between executive attention and conscious perception.

- Fronto-parietal long-range white matter pathways (i.e. the SLF) are related to attention and conscious perception, supporting models that emphasize the role of distributed networks.
- White matter structure is an important predictor of behavioral outcomes and TMS effects and variability.

SCIENTIFIC DISCLOSURE

Summary for the general public

In our everyday life, we are surrounded by a huge amount of information that reaches our senses. However, we are not aware (conscious) of all of them, simply because this would not be adaptive for our survival. Our attentional state (for example, being concentrated or distracted) can influence which information is consciously perceived. We all have the experience of some tasks being performed without paying too much attention (for example, driving along a well-known route). On the contrary, when we have to deal with a difficult, dangerous or new task (driving when it is raining and there is a lot of traffic) we need to use all or many of our attentional resources. Following the example, if you are driving under a demanding situation, it is more probable that you have to suddenly stop the car because you may have not seen a pedestrian that is going to cross the street. In this work, we wonder how conscious experience is affected when we need to deploy our attentional resources to a difficult task. To investigate this effect, we asked participants to solve a task at varying levels of difficulty, while they had to detect the appearance of visual stimuli that were hard to perceive. As in the pedestrian example, our results showed that our perception is worst when the attentional demands are high. Furthermore, we were interested in exploring how the brain solves this kind of situation. When participants performed the same task inside of a magnetic resonance imaging (MRI) scanner, some frontal regions of the brain were activated in a different way when they perceived or did not perceive the stimuli, and based on the difficulty of the task. Also, employing a neurostimulation non-invasive methodology (named transcranial magnetic stimulation or TMS), we demonstrated that the stimulation of frontal regions can modulate the perceptual capacities. This stimulation technique did not affect all participants in the same way, but those participants with a greater integrity of some anatomical pathways connecting frontal areas with other regions of the brain, were less affected by the stimulation. Frontal regions are the newest regions in the evolution of the brain, and also those that mature later in life. The results of this thesis highlight the importance of frontal regions for attention and conscious perception, and they suggest that all healthy brains are not equally affected by neuromodulation. This thesis offers a piece of new knowledge in the functioning of our cognitive abilities and our brains. In the future, it may help to develop new approaches for the treatment of patients with brain damage that present impairments in attention or conscious perception.

Resumen divulgativo / Summary for the general public in Spanish

Constantemente, una gran cantidad de información llega a nuestros sentidos. Sin embargo, no somos conscientes de toda esta información, simplemente porque esto no sería lo más adecuado para nuestra supervivencia. Nuestro estado atencional (por ejemplo, estar concentrado/a o distraído/a) puede influir en qué información es percibida conscientemente. Existen algunas tareas que podemos realizar sin prestar demasiada atención (por ejemplo, conducir por un camino que conocemos muy bien). Por el contrario, cuando tenemos que enfrentarnos a una situación difícil, peligrosa o nueva (por ejemplo, conducir cuando está lloviendo y hay mucho tráfico) necesitamos utilizar todos o muchos de nuestros recursos atencionales. Siguiendo el ejemplo anterior, si estás conduciendo durante una situación demandante, es más probable que no seas consciente de un peatón que se dispone a cruzar la calle y tengas que dar un frenazo repentino. En esta tesis doctoral nos preguntamos cómo la experiencia consciente se ve afectada cuando tenemos que utilizar nuestros recursos atencionales en una tarea o situación difícil. Para investigar esta cuestión, pedimos a participantes que resolvieran una tarea con diferentes niveles de dificultad, mientras que al mismo tiempo debían detectar la aparición de estímulos visuales que eran difíciles de percibir. Como ocurría con el peatón, los resultados mostraron que la percepción es peor cuando las demandas atencionales son altas (durante tareas difíciles). Además, en esta tesis doctoral estábamos interesadas en explorar cómo nuestro cerebro resuelve este tipo de situaciones. Cuando los/as participantes realizaban la misma tarea dentro del escáner de resonancia magnética (o MRI por sus siglas en inglés), algunas regiones frontales del cerebro se activaron de manera diferente dependiendo de si habían percibido el estímulo o no y de la dificultad de la tarea. Además, cuando se utilizó una técnica no invasiva de estimulación cerebral (llamada estimulación magnética transcraneal o TMS, por sus siglas en inglés), demostramos que la estimulación de regiones frontales puede modificar la capacidad de detectar estímulos difíciles de percibir. Esta técnica de estimulación no afectó a todas las personas que participaron en el experimento de la misma forma. Aquellas personas con una “mejor” conexión entre las regiones frontales y otras regiones del cerebro, se vieron menos afectadas por la estimulación. Las regiones frontales son las regiones más nuevas en la evolución del cerebro y también las que maduran más tarde durante el desarrollo. Los resultados de esta tesis destacan la importancia de las regiones frontales en los procesos atencionales y de consciencia y sugieren que no todos los cerebros sanos responden de la misma forma a la estimulación cerebral. Esta tesis ofrece una porción de conocimiento nuevo sobre cómo funcionan nuestras habilidades cognitivas y nuestro cerebro. En el futuro, esperamos que nuestros resultados puedan servir para desarrollar nuevas estrategias de tratamiento para pacientes con daño cerebral que presentan alteraciones en la atención o la percepción consciente.

ABBREVIATIONS

ACC, anterior cingulate cortex

BOLD, blood-oxygen-level dependent

DWI, diffusion-weighted imaging

EEG, electroencephalography

FA, false alarm

FAT, frontal aslant tract

FDR, false discovery rate

FEF, frontal eye field

fMRI, functional MRI

HMOA, hindrance modulated orientational anisotropy

IFL, inferior longitudinal fasciculus

IFOF, inferior fronto-occipital fasciculus

MRI, magnetic resonance imaging

NCC, neural correlates of consciousness

ROI, region of interest

RT, reaction time

rTMS, repetitive transcranial magnetic stimulation

SDT, signal detection theory

SLF, superior longitudinal fasciculus

  SLF I, dorsal branch of the SLF

  SLF II, middle branch of the SLF

  SLF III, ventral branch of the SLF

SMA, supplementary motor area

TMS, transcranial magnetic stimulation

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