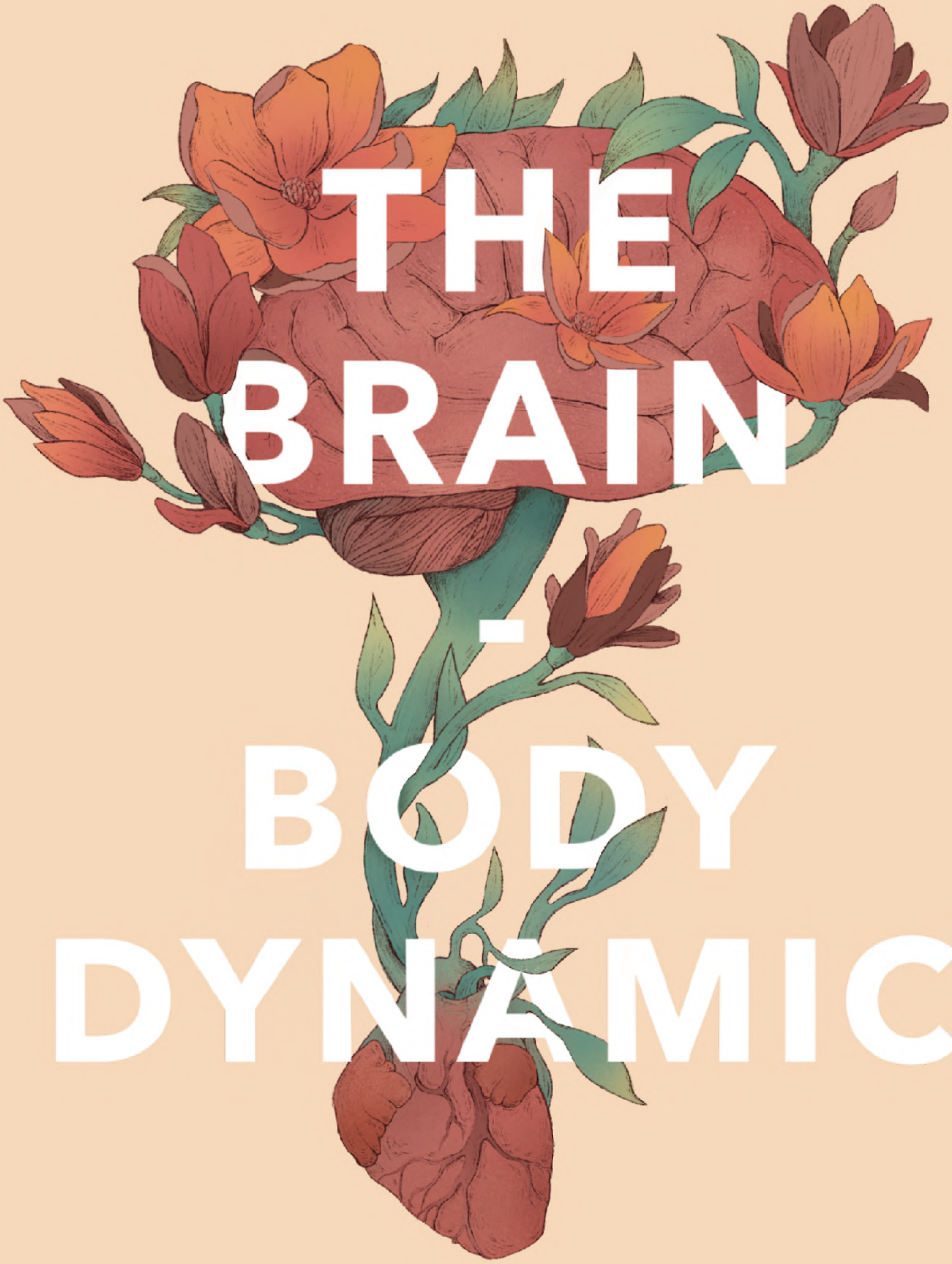
The relationship between attention and consciousness



THE BRAIN - BODY DYNAMIC

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The relationship between attention and consciousness: the brain-body dynamic

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A mi abuelo Emilio.
Quien me conectó con la naturaleza,
quien siempre me trató como su igual,
quien confió y animó en el camino que elegí.

The cover and illustrations for this doctoral thesis were
thoughtfully created by Klara Hemmerich,
a neuroscientist and a talented illustrator.

La portada y las ilustraciones de esta tesis doctoral fueron
cuidadosamente creadas por Klara Hemmerich,
neurocientífica y talentosa ilustradora.

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Resumen/Abstract in Spanish

El entorno de vida en el que vivimos está cargado de una gran cantidad de información de la cual tenemos la impresión de percibir escenas ricas en detalle. Sin embargo, si queremos describir o reportar una información concreta, nuestra capacidad de reporte es más más limitada. ¿Es entonces la consciencia perceptual un proceso cognitivo rico o limitado? La respuesta a esta pregunta genera un amplio debate hoy en día, como muchos otros temas de estudio relacionados con la consciencia. Block (2011) propuso que la consciencia perceptual se puede clasificar en consciencia de acceso y consciencia fenomenológica. Mientras que la consciencia de acceso tiene un carácter limitado (solo podemos reportar unos cuantos elementos a la vez), la consciencia fenomenológica hace referencia a una experiencia subjetivamente rica del entorno, pero que en ocasiones puede contener información errónea. Para que la información acceda a consciencia o para que nuestro sistema cree una experiencia perceptual es necesario prestar atención (Baars, 1997). Aunque son numerosos los trabajos que han mostrado el papel crucial de la atención en la consciencia, no todos los tipos de atención producen los mismos efectos.

Existen diferentes teorías que discuten el papel de la atención en el procesamiento consciente. Por ejemplo, la teoría del espacio de trabajo global de Dehaene & Changeux (2011) propone que la atención sería un pre-requisito para que se genere la consciencia perceptual, aunque la atención por sí sola no es suficiente para producir una experiencia consciente. Otras teorías

como la Teoría recurrente de Lamme & Roelfsema (2000) destacan la necesidad de comunicaciones feedforward y feedback entre regiones principalmente sensoriales para que se produzca la consciencia, aunque la atención podría tener un papel colaborativo en segundo plano. Estas teorías hipotetizan qué ocurre en el sistema nervioso central para que se produzca la experiencia consciente. Sin embargo, la aproximación del marco neural subjetivo de Park & Tallon-Baudry (2014) destaca la relevancia de la actualización entre el estado del organismo y el cerebro para que se produzca el procesamiento consciente, que por definición es un procesamiento que ocurre en primera persona ("yo veo"). Este debate abierto entre la necesidad o no de atención, así como el papel de la comunicación entre el cerebro y el organismo en la experiencia consciente, ha inspirado las preguntas y los estudios que componen esta tesis doctoral.

El objetivo general de esta tesis es explorar el papel de las interacciones entre la atención y la consciencia perceptual, así como explorar esta relación en modulaciones cerebro-organismo. La dinámica cerebral se mide mediante oscilaciones cerebrales, y la dinámica del organismo mediante medidas del sistema nervioso periférico como la tasa cardíaca. Para alcanzar estos objetivos se han realizado 4 estudios en los que se analiza cómo diferentes procesos atencionales interactúan o no con la consciencia de acceso y fenomenológica. En uno de estos estudios se analiza la dinámica cerebral en una tarea de integración de rasgos (que se usa como medida de la consciencia fenomenológica), y en 2 de estos estudios se analiza la actividad del sistema nervioso periférico (medidas de tasa cardiaca) en una tarea de consciencia de acceso y fenomenológica (integración de rasgos).

El primer estudio (capítulo 6) experimental de esta tesis explora la relación entre la alerta fásica y consciencia de acceso, así como sus modulaciones en tasa cardíaca. Los participantes debían detectar la presencia de un estímulo en el umbral de la consciencia, que podía ser precedido (en el 50% de los ensayos) por una señal de alerta.

En el segundo estudio (capítulo 7) se desarrolló una nueva línea experimental que exploraba la consciencia fenomenológica mediante un paradigma de integración de rasgos. A los participantes se les presentaba brevemente un conjunto de letras de diferente forma y color (ej: **8OL8**). Su objetivo era reportar el color de la letra L. Según el ejemplo dado, si los participantes contestaban "verde", el ensayo se consideraba un acierto (correcta integración de los rasgos de forma y color); si contestaban "azul", el ensayo se consideraba una ilusión perceptual (error de integración al utilizar la información del distractor); y si contestaban "rojo", un color que no se presentaba en pantalla, el ensayo se consideraba un error. Las ilusiones perceptuales son una herramienta útil que permite el estudio de la consciencia fenomenológica, ya que cuando se producen, la experiencia subjetiva es rica, pero se ha producido de manera errónea. Además, este estudio se compuso de 3 experimentos diferentes en los que se manipulaba la atención antes de la presentación del estímulo al que los participantes debían responder. Siguiendo la clasificación de Posner y Petersen (2012), se manipuló el sistema ejecutivo (atención dividida), el sistema de orientación endógena y el sistema de orientación exógena. En los experimentos 2 y 3 de este estudio se incluyó, al final del experimento, una manipulación de las expectativas, presentando de manera inesperada para los participantes el estímulo objetivo en un color inesperado (blanco).

En el tercer estudio (capítulo 8) se utilizó el paradigma de integración de características con el fin de explorar la dinámica cerebral en diferentes bandas de frecuencia relacionadas con una correcta o incorrecta integración de rasgos. Estudios previos se había focalizado en una única frecuencia, por lo que el objetivo de este estudio fue explorar de manera más amplia qué oscilaciones cerebrales caracterizaban una experiencia subjetiva correcta o incorrecta.

Finalmente, en el cuarto estudio (capítulo 9) se exploró la relación entre la alerta fásica y consciencia fenomenológica, así como sus modulaciones en tasa cardíaca. Usando el mismo paradigma que en los capítulos 7 y 8 presentamos un tono de alerta en la mitad de los ensayos, antes de que se presentase el estímulo objetivo, a la vez que medíamos la respuesta cardiaca de los participantes.

En general, los resultados de esta tesis han mostrado que la alerta fásica mejora la consciencia de acceso, pero no la consciencia fenomenológica (medida por la capacidad de integración de rasgos). En el caso de la consciencia de acceso, estudios previos han mostrado las mejoras en la detección consciente por la orientación atencional (especialmente exógena, (Chica et al., 2011), y una modulación menos consistente por la sobrecarga del sistema ejecutivo (Colás et al., 2017; Martín-Signes et al., 2018). En la consciencia fenomenológica hemos encontrado claras modulaciones por la orientación atencional, pero no por la atención ejecutiva. Además, la violación de expectativas ha mostrado una clara influencia sobre el proceso de integración de rasgos. Los resultados en la dinámica cerebral muestran que la información representada fenomenológicamente depende de procesos preparatorios (alfa temprano), de inhibición de distractores (alfa tardío), y de representación fiable de la información (alfa tardío y beta). Finalmente, los resultados de medidas periféricas, en concreto de tasa cardiaca, muestran claras modulaciones de este sistema periférico tanto cuando accedemos a consciencia como cuando integramos rasgos, aunque el patrón modulatorio es muy distinto en función del tipo de consciencia.

En conclusión, esta tesis doctoral destaca la necesidad de explorar la relación entre la atención y la consciencia mediante medidas del sistema nervioso central y periférico. Estudiar el comportamiento de ambos sistemas permite destacar la importancia de la comunicación entre el cerebro y el organismo durante la consciencia perceptual, así como incorporar este aspecto a futuros modelos que traten de explicar la consciencia

English abstract

Our environment contains large amounts of information, which gives us the impression of perceiving perceptual scenes that are rich in detail. However, when it comes to describing or reporting specific information, our ability to do so is more limited. This raises the question of whether perceptual consciousness is rich or limited. The answer to this question has prompted an important debate, along with many other unresolved issues related to the study of consciousness. Block (2011) proposed a classification of perceptual consciousness into access consciousness and phenomenological consciousness. Access consciousness has a limited capacity, allowing us to report only a few items at a time. In contrast, phenomenological consciousness involves a subjectively rich experience of the environment, which can sometimes contain erroneous information. Attention plays a crucial role facilitating access consciousness or creating perceptual experiences (Baars, 1997). Although numerous studies have demonstrated the fundamental role of attention in consciousness, not all types of attention produce comparable effects.

Different theories discuss the role of attention in conscious processing. For example, Dehaene and Changeux's (2011) Global Workspace Theory suggests that attention is a prerequisite for perceptual consciousness, although attention is insufficient to produce a conscious experience. Other theories, such as Lamme and Roelfsema's Recurrent Theory (2000), emphasize the need for feedforward and feedback communications between primarily sensory regions for gaining consciousness, with attention possibly

playing a collaborative role in the process. These theories theorize about how activity in the central nervous system enables conscious experience. However, the subjective neural framework approach proposed by Park and Tallon-Baudry (2014) emphasizes the importance of the interaction between the state of the organism and the brain for conscious processing, which, by definition, takes place from a first-person perspective (I see). This ongoing debates, concerning the necessity of attention and the role of brain-body communication, has inspired the questions and studies that constitute this dissertation.

The main goal of this thesis was to explore the interactions between attention and perceptual consciousness, as well as to investigate this relationship in terms of brain-body modulations. In our studies, brain dynamics were measured throughout brain oscillations, while body dynamics were examined using measures of the peripheral nervous system, such as heart rate. To achieve these goals, four studies were conducted to analyze how different attentional processes interact, or not, with phenomenological and access consciousness. One of these studies examines brain dynamics in a feature integration task (used as a measure of phenomenological consciousness), while two studies investigate peripheral nervous system activity, specifically heart rate measures, in tasks related to both access and phenomenological consciousness (feature integration).

The first experimental study (Chapter 6) of this thesis explores the relationship between phasic alerting and access consciousness, as well as their modulations in heart rate.

Participants were required to detect the presence of a stimulus at the threshold of consciousness, which could be preceded (in 50% of trials) by an alerting signal.

In the second study (Chapter 7), a new experimental line was developed to explore phenomenological consciousness using a feature integration paradigm. Participants were briefly presented with a string of characters of different shapes and colors (e.g., **8OL8**). Their goal was to report the color of the letter L. According to the example given, if participants answered "green", the trial was considered a hit (correct integration of shape and color features); if they answered "blue", the trial was considered a perceptual illusion (integration error produced by using the color of the distractor); and if they answered "red", a color that was not presented on screen, the trial was considered an error. Perceptual illusions are a useful tool that allows the study of phenomenological consciousness, because when they occur, the subjective experience is rich, but has been produced erroneously. In addition, this study was composed of 3 different experiments in which attention was manipulated prior to the presentation of the target stimulus. Following Posner and Petersen's (2012) classification, the executive system (divided attention), the endogenous orienting system, and the exogenous orienting system were manipulated. In Experiments 2 and 3 of this study, an expectancy manipulation was included at the end of the experiment by unexpectedly presenting the target stimulus in an unexpected color (white).

In the third study (Chapter 8) the feature integration paradigm was used in order to explore brain dynamics in different frequency bands related to correct or incorrect feature integration. Since previous studies had concentrated solely on a single frequency, the objective of this study was to broaden the exploration of the brain oscillations that distinguish between correct and incorrect subjective experiences.

Finally, the fourth study (Chapter 9) explored the relationship between phasic alerting and phenomenological consciousness, as well as their modulations in heart rate. Using the same paradigm as in Chapters 7 and 8, we presented an alerting tone in half of the trials before the target stimulus was presented while measuring the participants' cardiac response.

Overall, the results of this thesis have shown that phasic alerting enhances access consciousness, but not phenomenological consciousness (as measured by the ability to integrate features). In the case of access consciousness, previous studies have shown improvements in conscious detection by attentional orienting (especially exogenous, Chica & Bartolomeo, 2012), and less consistent modulation by executive attention (Colás et al., 2017; Martín-Signes et al., 2018). In phenomenological consciousness, we have found clear modulations by attentional orienting, but not by executive attention. Furthermore, expectancy violations clearly influenced the feature integration process. Results on brain dynamics showed that phenomenologically represented information depends on preparatory processes (early alpha), distractor inhibition (late alpha), and a reliable representation of information (late alpha and beta). Finally, the results of peripheral measures, in particular heart rate, show clear modulations of this peripheral system both when we access consciousness and when we integrate features, although the modulatory pattern is very different depending on the type of consciousness.

In conclusion, this doctoral thesis highlights the need to explore the relationship between attention and consciousness using measures of the central and peripheral nervous system. Studying the behavior of both systems allows us to emphasize the importance of the communication between the brain and the organism during perceptual consciousness, as well as to incorporate this aspect into future models that attempt to explain consciousness

Introduction

Chapter 1: A trip through the tangled world of consciousness

1.1 Defining consciousness

In the recent past and at this time, the study of perceptual consciousness and its neural correlates maintains a deep interest in the scientific field. While neural correlates try to identify brain activity related to conscious processing, some theories try to explain how conscious experience arises from such neural correlates (Seth & Bayne, 2022). Consciousness is a complex phenomenon (Delacour, 1995) whose experience can be phenomenologically rich (Block, 2011) but limited in report (Dehaene & Changeux, 2011). However, there is no consensus on a single definition. Some authors have provided different approaches to its definition, as well as its categorization.

A simple way to approach this categorization involves conceiving consciousness as either a "global state" or a "local state" (Seth & Bayne, 2022). The global state addresses what is commonly related to the arousal/activation state of the organism. This arousal can span from simply being awake, being in a sleep state, under the effects of anesthesia, minimally conscious state, comatose state, and vegetative state (currently known as unresponsive wakefulness syndrome) (Bayne et al., 2016; Boly et al., 2009; Laureys et al., 2004; Laureys & Schiff, 2012). Conversely, the "local state" refers to consciousness in terms of its content (access consciousness) and in terms of the individual's subjective experience of it (phenomenological consciousness).From this point of view, Block

(2011) proposed a distinction between access consciousness and phenomenological consciousness. While access consciousness has a limited capacity guided by the contents of working memory or by attentional resources, phenomenological consciousness is characterized by its perceptual richness, which "overflows" access consciousness, although accessible information may have errors (Block, 2007, 2011). Access and phenomenological consciousness are not completely independent of each other (Seth & Bayne, 2022). To illustrate this interrelationship, we can consider an everyday example such as choosing a fruit within a variety (bananas, oranges, and apples). The choice of a specific fruit may be influenced by past experiences and personal preferences. For example, a banana with many black spots might be perceived as delicious by someone who enjoys sweet, ripe flavors, while, to another, the same banana might seem too overripe. In this conscious experience, the content of the concept of 'banana' is mixed with the subjective and conscious experience associated with this food, showing how access consciousness and phenomenological consciousness come together. In summary, perceptual consciousness is a difficult construct to define, which seems to refer both to the arousal state of the organism and to the capacity to perceive from one's own perspective the content of a given stimulation. In the following sections, we try to explain the most current

1.2 Theories of consciousness

The following theories aim to clarify what is consciousness and which cognitive mechanisms are necessary and sufficient for conscious processing (the so called easy problem) and how conscious experience emerge of brain activity (the hard problem). Some of the following theories try to account for both problems, while others underpin only one of them. Some theories try to determine the relevance of other cognitive processes (such as attention and memory) for conscious processing.

1.2.1 The recurrent theory

Lamme and Roelfsema's theory (2000) proposes that conscious processing takes place in regions of the sensory cortex, through recurrent re-entry of information. Visual inputs (most authors focus on the visual system because it is the most studied) are registered in regions such as V1 and send feedforward signals to extrastriate and parietal visual regions. From these areas, the re-entry of information to visual regions is generated with the help of top-down signals (Boehler et al., 2008; Lamme, 2003; Lamme et al., 1998, 2000; Pascual-Leone & Walsh, 2001).

According to this theory, activity in sensory regions would be enough for consciousness to be produced. However, parietal and frontal regions would play a collaborative role in this process, contributing to the content of perceptual experience, reasoning and/or decision making (Lamme, 2006, 2010).

This theory attempts to explain the difference in brain processing in access and phenomenological consciousness. In the case of phenomenological consciousness, when different stimuli are presented, mechanisms of feedforward activity of neurons in visual sensory regions are activated (Figure 1.1, left, green dots). Then, as information travels to higher regions of the visual cortex, competition between different stimuli begins to emerge (Desimone

& Duncan, 1995). This competition may impair the perception of stimuli close to the target stimulus since not all information can be processed in detail to access consciousness. However, the identified features of the presented stimulation would activate the feedforward activity of neurons in visual sensory regions, allowing a minimal perceptual organization that alludes to phenomenological consciousness. This signal would have a weak and unconscious character but would allow a behavioral response (Figure 1.1 upper right, yellow and green dots When this feedforward activity is intensified, a top-down interaction is generated between these visual regions and parieto-frontal regions (higher-order regions). At this point, the attentional system would play a relevant role in the information to access consciousness, enhancing the top-down recurrence between visual and parieto-frontal regions (Lamme, 2003; Lamme & Roelfsema, 2000) (see Figure 1.1, bottom right, yellow and red dots).

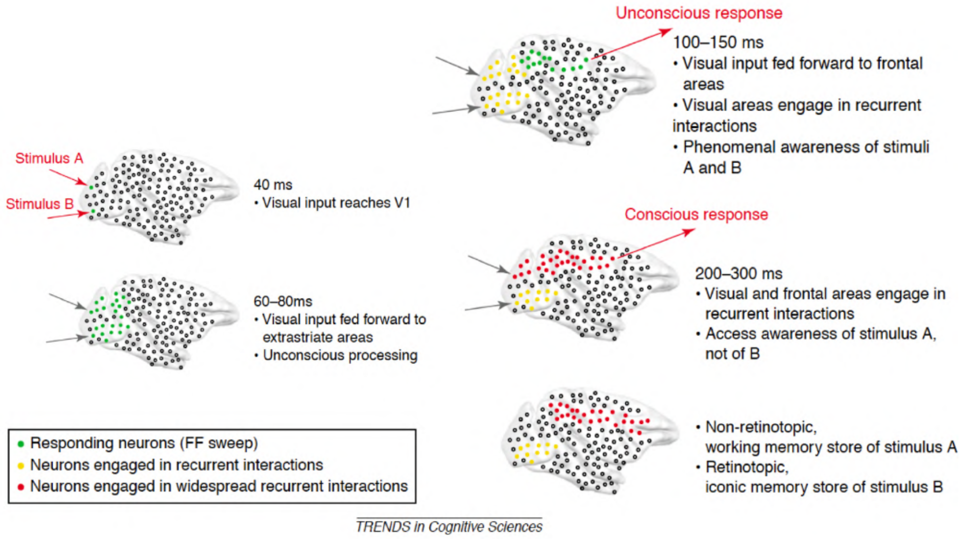


Figure 1.1: Schematic representation of Lamme's (2003) recurrent model including the differentiation between phenomenological and access consciousness. Green dots represent feedforward neural communication of multiple stimuli (A and B). Yellow and green dots represent competition between stimulus perception as well as signal recurrence that allows the creation of weak representations related to phenomenological consciousness. Yellow and red dots represent global top-down recurrence between parieto-frontal and visual regions. Figure with permission from (Lamme, 2003).

1.2.2 Higher order theories

There are different higher-order theoretical approaches: self-organizing metarepresentation theory (Cleeremans, 2007; Cleeremans et al., 2020), higher-order state space theory (Fleming, 2020), and perceptual reality supervision theory (Gershman, 2019; Lau, 2019). This section will not describe each of the theories, but rather will provide the common message of all of them.

These higher-order theories share the same premise about the importance of metarepresentations, in terms of their focus on differing why one is or is not conscious of different contents of the environment around us, and address the experienced nature of consciousness (Seth & Bayne, 2022). Metarepresentations are a set of higher-order representations that focus on other lower-order representations. For example, in the presence of a sunset there would be an initial representation of the image itself, the different colors of the sky, the presence of the sun or the clouds. This would correspond to a lower order representation, but when we think about how this image makes us feel or different thoughts emerge from this image, we are creating a meta-representation, since there is a representation of another previous representation. I.e., perceptual consciousness occurs as a result of a rewriting of lower-order processing (Cleeremans, 2007; Cleeremans et al., 2020), which may be due to subjective reporting results (Fleming, 2020) or it may result from a trusted "judgment" of the higher-order networks on the lower-order representation (Gershman, 2019; Lau, 2019), see Figure 1.2.

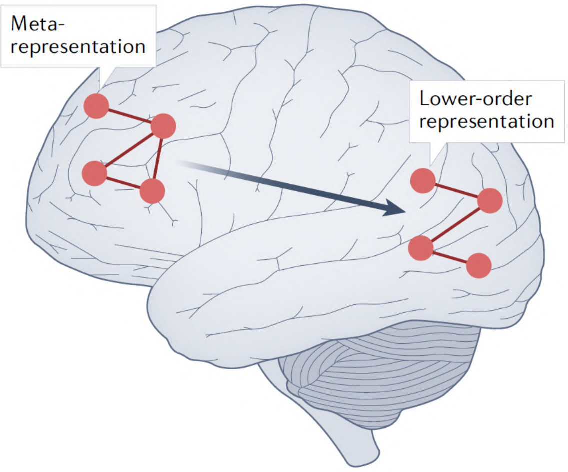


Figure 1.2: this figure illustrates the neural basis underlying the main idea of higher-order theories, in which a meta-representation over a lower-order representation would give rise to consciousness. Figure extracted with permission from Seth & Bayne, (2022).

Considering this premise, this theory suggests that information accesses consciousness because there is coherence between meta-representations and low-order representations. In contrast, information would be unconscious when coherence between the two representations (meta-representation and low-order representation) does not occur (Seth & Bayne, 2022). It should be noted that these higher-order theories do not explicitly differentiate between access consciousness and phenomenological consciousness. However, they seem to place more emphasis on the phenomenological aspects of consciousness, as meta-representations encompass the experiential subjectivity of the person perceiving his or her own world. It is necessary to remember that phenomenological consciousness seems to overflow access consciousness (Block, 2007, 2011), creating a subjective sense of perceptual richness but which is often partially incorrect (Kouider et al., 2010). Higher-order theories also attribute these errors to the overestimation of perceived information. In other words, despite the occurrence of weak coherence between meta-representations and low-order representations, the system considers this communication erroneously rich.

1.2.3 Integrated information theory (IIT)

Integrated information theory (IIT) follows a purely mathematical perspective, which describes a series of axioms that must be fulfilled for a complex system to have a conscious experience (Oizumi et al., 2014; Tononi, 2008, 2012; Tononi et al., 2016). This theory proposes that consciousness should be understood as the "power of cause-effect", further associated with an absolute maximum amount of integrated information. This maximum amount of integrated information is represented by the value of Φ (phi).

The power of cause-effect refers to the "local state" of consciousness (the content of consciousness; see point 1 of this chapter) (Tononi et al., 2016). This principle indicates that for a system to be physically meaningful and therefore conscious, it must be able to change its state based on its intrinsic perspective. Tononi et al. (2016) clarify this aspect by providing an example of the functioning of a neuron: "*A neuron complies with this principle because it has two or more internal states (active and inactive) that can be affected by inputs (cause) and outputs, making a difference to other neurons (effects)*".

On the other hand, the value of Φ is related to the "global state" of consciousness (state of consciousness; see point 1 of this chapter) (Tononi et al., 2016). The value of Φ refers to the maximum amount of irreducible integrated information given by a system. Therefore, the level of consciousness as a state will arise as a function of a given Φ value (Tononi, 2012; Tononi et al., 2016). Although this relationship fulfills mathematical principles, there is no way to measure the amount of Φ (Seth & Bayne, 2022). There are some indexes that seem to be approximated, for example, the perturbative complexity index (PCI), which is measured by the brain response given a determined transcranial magnetic stimulation (Casali et al., 2013).

In anatomical terms, IIT relates consciousness to posterior brain regions *("posterior hot zone")* that are constituted by occipital, temporal, and parietal areas (see Figure 1.3). These regions have enough capacity to generate high levels of integrated information (Tononi, 2004, 2008; Tononi et al., 2016). Communication between these areas is not related to information processing per se, but rather these structures intrinsically contain the previously mentioned cause-effect features. In other words, each of these structures has the capacity to influence others, which can have an impact on conscious experience.

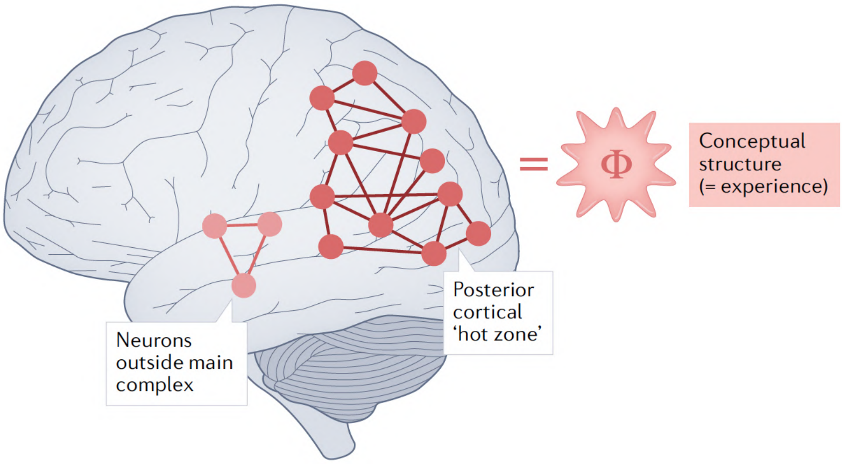


Figure 1.3: representation of regions involved in integrated information theory, as well as the influence of these regions on themselves. The role of Φ as a result of conscious experience is highlighted. Figure extracted with permission from (Seth & Bayne, 2022).

Regarding the difference between phenomenological and access consciousness, the IIT does not refer to this classification of consciousness. However, it does refer to the fact that consciousness can have phenomenological and accessible contents (Tononi et al., 2016).

1.2.4 Global workspace theory (GWT)

Baars (1997, 2002) was one of the first authors to propose a theory of consciousness in the framework of the global workspace. He proposed that consciousness, both globally and locally, is widely accessible to other complex cognitive processes such as attention, memory or verbal reporting (see Figure 1.4).

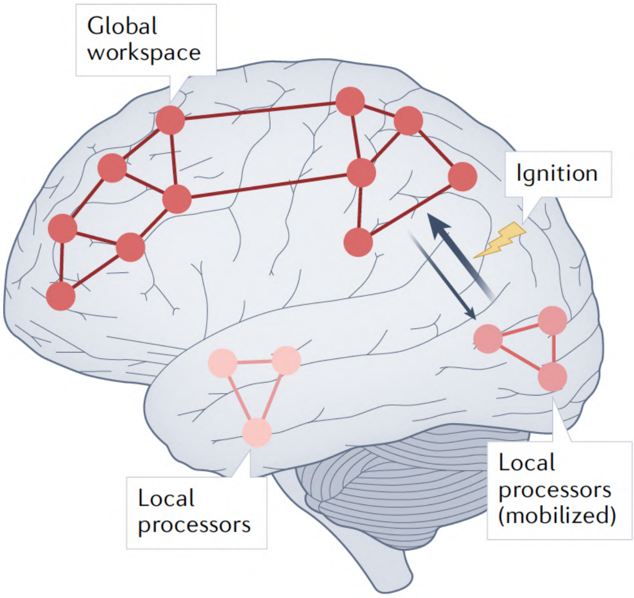


Figure 1.4: Graphical representation of the global workspace models of consciousness. Figure extracted with permission from (Seth & Bayne, 2022).

Based on this premise, Dehaene & Changeux (2011) developed the theory known as global neural workspace theory (GNWT). This theory emphasizes that a particular sensory stimulation gains access to consciousness when that information propagates within a broad neural workspace, through the phenomenon of ignition (Dehaene et al., 2003). This process is implemented through higher order association areas, mainly located in the prefrontal cortex (Dehaene & Changeux, 2011;

Mashour et al., 2020) (see Figure 1.4). Furthermore, another relevant aspect of this theory highlights the role of other cognitive processes such as attention and memory in conscious experience. On the one hand, attention allows the selection and amplification of the perceived sensory signal and, therefore, allows such stimulation to access consciousness (more details in chapter 2, section 2.3). On the other hand, working memory allows attending to and maintaining a certain number of items that use the global workspace for propagation to higher order areas (Mashour et al., 2020). As indicated by Mashour et al. (2020), "*attention and memory reflect what is on one's mind*".

This type of theory can explain access consciousness (Mashour et al., 2020), as well as the different levels of global consciousness. Any failure of access consciousness is related to a functional disruption of the global workspace (fronto-parietal regions) (Mashour, 2013). However, the subjective experience of phenomenological consciousness is not directly explained in this theory, being considered as unconscious processing.

1.3 Remarks and conclusions from theories of consciousness

As can be seen in the previous sections, the scenario of the study of perceptual consciousness is extensive and varied, but also incomplete. By way of synthesis, we will discuss the most relevant points in common with these theories and the points at odds with each other.

A first point to take into account refers to the brain regions involved for consciousness to be produced. On the one hand, IIT and information re-entry theories emphasize that posterior regions are enough for conscious experience to occur (Lamme, 2006, 2010; Lamme et al., 2000; Tononi, 2004, 2012; Tononi et al., 2016). Both theories indicate that the involvement of anterior regions (prefrontal cortex) is related to verbal reporting processes or the emission of a response, but not to consciousness per se (Boly et al., 2017; Raccah et al., 2021). On the other hand, higher-order theories and GNWT, do highlight the importance of fronto-parietal regions for conscious processing to take place (Dehaene & Changeux, 2011; Gershman, 2019; Lau, 2019; Mashour, 2013). Currently, there are different studies supporting the role of fronto-parietal regions in conscious perception, both in studies of healthy participants (Bor & Seth, 2012; Dehaene & Changeux, 2011; Dehaene & Naccache, 2001; Gaillard et al., 2009; Lau & Passingham, 2006; Lau & Rosenthal, 2011; Laureys & Schiff, 2012; Martín-Signes et al., 2018, 2019, 2021; Odegaard et al., 2017; Van Vugt et al., 2018), as well as in studies of patients with fronto-parietal lesions (Bartolomeo et al., 2007; Colás et al., 2019; Del Cul et al., 2007; Lau & Rosenthal, 2011). While higher-order theories and the GNWT emphasize the importance of these anterior regions in perceptual consciousness, higher-order theories propose that these regions would be important for the formation of meta-representations (Cleeremans, 2007; Cleeremans et al., 2020; Fleming, 2020; Gershman, 2019; H. Lau, 2019; Seth & Bayne, 2022). However, the GNWT associate the role of these areas in consciousness as part of the overall workspace (Baars, 2002; Dehaene & Changeux, 2011; Mashour et al., 2020). Finally, Dehaene and Changeaux's (2011) GNWT and re-entry theories (Lamme et al., 2000) emphasize the role of information amplification and maintenance in access consciousness, thanks to the cognitive processes of attention and working memory. However, GNWT links both attention and working memory to consciousness, whereas re-entry theories completely dissociate these cognitive processes from consciousness.

Another crucial aspect in this field is to understand how theories address the distinction between access consciousness and phenomenological consciousness (Block, 2011). Within the theories described in this chapter, the only one that attempts to explicitly explain Block's (2011) classification is Lamme and Roelfsema's (2000) recurrent theory. Meanwhile, in the framework of IIT, although no literal mention is made of both types of consciousness, there is an attempt to explain the contents of phenomenological and accessible character in a differentiated manner (Tononi et al., 2016). In the case of higher-order theories, no explicit differentiation is made between the two concepts either. However, they do emphasize the importance of meta-representations, which contain phenomenological features (Fleming, 2020; Seth & Bayne, 2022). In contrast, GNWT seems to emphasize only access to consciousness. This theory does not support the differentiation between phenomenological consciousness and conscious access, but rather argues that for conscious subjective experience (coffee aroma experience) to exist, the information must already be consciously accessible, otherwise it would be unconscious information (Mashour et al., 2020; Naccache, 2018).

A relatively novel aspect in the study of perceptual consciousness is the role that the state of the organism may play (Blanke, 2012; Critchley et al., 2004; Park & Tallon-Baudry, 2014). Different approaches suggest that the brain (or central nervous system) does not act in isolation to different cognitive processes, but rather there is constant communication between the brain and the organism (or peripheral nervous system) in order to keep both systems in balance (Beissner et al., 2013; Craig, 2009; Critchley et al., 2004; Critchley & Harrison, 2013; Damasio, 2010; Lang et al., 1990; Mayer, 2011; Park & Tallon-Baudry, 2014; Richter, Babo-Rebelo, et al., 2017; Saper, 2002; Thayer et al., 2012). The presence or not of homeostasis between the central and peripheral nervous system may define the cognitive, emotional, or behavioral response to a given environment (Critchley & Harrison, 2013; Damasio, 2010). None of the theories of consciousness described in this chapter address the importance of communication between the central and peripheral nervous systems. In Chapter 4 of this thesis, the functioning of communication between the central and peripheral nervous system is detailed, and various theoretical approaches that explain this communication are explored, one of them being focused on perceptual consciousness. In addition, some cognitive interpretations of peripheral measures such as heart rate are described.

1.4 How to measure consciousness

The measures of consciousness and unconscious processes have been complex and subject to considerable controversy (Peters et al., 2017). Thanks to the development of behavioral paradigms to measure the different states and contents of consciousness, in recent decades it has been possible to establish more rigorously how conscious and nonconscious processing occurs, as well as their neural bases. In this section, we will describe some paradigms that measure perceptual consciousness and detail those used in this thesis.

1.4.1 Experimental paradigms

The variety of experimental paradigms for measuring access consciousness is more extensive than the number of existing paradigms for measuring phenomenological consciousness. Possibly this is due to the complexity associated with analyzing the subjective aspects of consciousness, besides the difficulty of disaggregating phenomenological consciousness from access consciousness (Kouider et al., 2010).

Paradigms that measure perceptual consciousness encompass, among others, masking procedures, binocular rivalry, flash suppression, bistable figures, stimulus presentation at the conscious threshold, and feature integration. There are also paradigms that measure consciousness by interfering with the attentional system: inattentional blindness, change blindness, or attentional blink. Finally, we will refer to paradigms in which verbal report is not necessary to measure consciousness.

There are different types of masking paradigms. However, the main idea is to present a certain stimulus, which is masked with another image whose components may be similar to the target stimulus. Both elements are presented in close temporal and spatial proximity (Breitmeyer & Ogmen, 2006). The binocular rivalry paradigm consists of the presentation of two different images simultaneously. Each of the images is presented in a different eye, generating a conflict in which only one of the images gains access to consciousness, i.e., during the perceptual process an alternation between the two images occurs (Kovács et al., 1996; Tong et al., 1998). The flash suppression paradigms involve the presentation of flashing dynamic masks with high contrast in one of the eyes. This procedure can make the presentation of the target stimulus in the other eye invisible (Stein, 2019; Tsuchiya & Koch, 2005). The bistable figures approach is another way to measure consciousness, using visual patterns that can perceptually switch (Leopold et al., 1999, 2002). A classic example of these bistable figures is the presentation of a cube picture. Depending on the perceptual experience, the cube may show an upward or downward orientation. This change of orientation is known as perceptual switching. Another way to consciously measure accessibility is to modify certain characteristics of the target stimulus. For example, by manipulating the contrast of a Gabor stimulus (Pins & Ffytche, 2003; Tallon-Baudry, 2012). This is done in order for such a stimulus to be at each person's conscious threshold, being consciously perceivable at some times and not at others. Feature integration paradigms (see Chapter 2, Section 2.4.1 for details), provide information about the features of a stimulus that is always visually accessible. Although such information is always available, manipulating factors such as exposure time, the amount of information to be integrated, the place of presentation (fovea vs. periphery), or expectancies, allow for modulating its accessibility and generating perceptual illusions. These illusions make it possible to explore the functioning of phenomenological consciousness by allowing a rich and subjective experience that is partially incorrect (Kouider et al., 2010).

Other paradigms, such as inattentional blindness, change blindness, or attentional blink, measure perceptual consciousness by interfering with attentional resources. Inattentional blindness consists of the appearance of an unexpected object while the attentional focus is on another object, which sometimes results in the object going undetected (Mack, 2003; Mack & Rock, 1998). In change blindness, consecutive scene presentations that change in one element (usually with a mask between the two scenes) are used, and participants do not detect the change even though attention is not focused on another task (Simons & Ambinder, 2005; Simons & Levin, 1997). Attentional blink consists of the rapid serial presentation of visual stimuli (RSVP). Participants must detect two stimuli that are presented in that sequence. The second target is detected or not depending on whether or not the first one was detected and the time interval between the two (Dux & Marois, 2009; Shapiro et al., 1997).

As a result of the critique of paradigms involving verbal reports or motor response, non-report paradigms emerged. This critique alludes to the literature emphasizing the role of frontal regions during consciousness, among other regions (Baars, 2002; Boly et al., 2017; Cleeremans et al., 2020; Dehaene & Changeux, 2011; Lau, 2019; Mashour et al., 2020). However, in other studies the role of frontal regions is questioned, indicating that these frontal areas are not linked to conscious processing, but rather to post-perceptual functions such as the emission of the motor response or the verbal report of the perceived stimulus (Block, 2019; Raccah et al., 2021). Moreover, the necessity to emit an external response makes it difficult to study the consciousness of animals lacking verbal language (Tsuchiya et al., 2015). As a result of these problems, non-response paradigms emerge. These paradigms aim to relate the neural signal to perceptual consciousness using neuroimaging techniques (electroencephalography and/or functional MRI) or eye movement recording (Cohen et al., 2020; Haynes, 2009; Kapoor et al., 2020; Tsuchiya et al., 2015). For example, in the study by Kapoor et al. (2020), they used eye movement and intracranial electrode recording to find out whether the monkeys were conscious of the change in the grating motion of the presented stimulus.

Considering the wide variability of experimental paradigms to study perceptual consciousness, in this doctoral thesis we have chosen to manipulate the Gabor stimulus contrast to study access consciousness, and a feature integration paradigm to explore phenomenological consciousness. In the following section, we will elaborate on the details of both paradigms.

1.4.2 Experimental paradigms chosen to explore consciousness

Stimulation at the threshold of consciousness. The Gabor stimulus is frequently used in the field of visual perception since neurons in occipital areas have shown activity when a Gabor stimulus is presented (Huang et al., 2023). Furthermore, Gabor stimuli fit a convolution between a sinusoidal function and a Gaussian function that allows spanning the spatial and frequency domain. These features simplify the manipulation of different Gabor properties such as contrast, frequency, orientation, etc (Gabor, 1946). Thanks to this simple character, the Gabor stimulus can be used in detection tasks (Colás et al., 2019; Martín-Signes et al., 2021), discrimination tasks (Botta et al., 2017; Carrasco et al., 2008), and even for subjective reporting (Carrasco & Barbot, 2019). The Gabor stimulus has a circular shape whose perimeter is not delimited. In addition, they are made up of a series of undefined, black-and-white lines, whose quantity (frequency), orientation, and space between them can vary. In our case, the contrast of the stimulus is manipulated (see Figure 1.5).

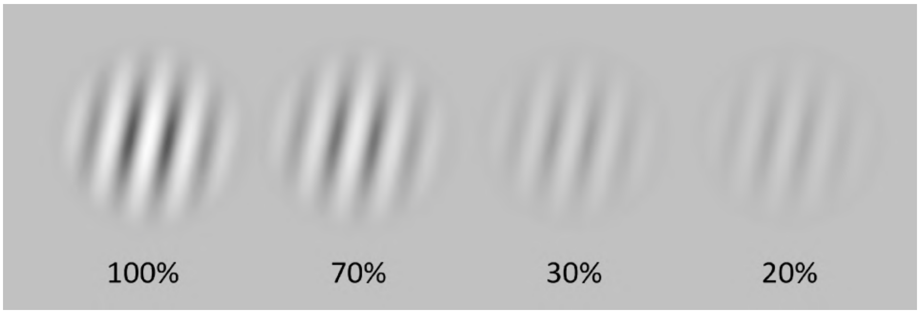


Figure 1.5: Representation of Gabor stimuli with a 3-degree frequency and a spatial frequency between lines of 4 cycles per degree. The inclination of the lines is 10 degrees. From left to right, the stimulus loses contrast to become less visible.

Experimental paradigms that use Gabor stimulus to measure consciousness include a titration procedure before the experimental phase. During this stage, each participant must detect the presence of the stimulus, being the responses categorized as hits (detecting a stimulus that was present), false alarms (detecting a stimulus that was actually absent), misses (not detecting a stimulus that was present), and correct rejections (not detecting a stimulus that was absent) (Chica, Botta, et al., 2012; Colás et al., 2018; Martín-Signes et al., 2018; Park et al., 2014). This range of possible response types aligns with the classification proposed by the Signal Detection Theory (SDT) (Abdi, 2007). The contrast used depends on whether it is above (almost always perceptible), below (very low perceptibility), or at the conscious threshold (approximately half the time perceptible). In our case, we use Gabor stimuli at the conscious threshold. Using contrast manipulation, the aim is to record the percentage of correct responses for each participant, who should get approximately 50% correct. Because the stimulus is always present, but sometimes enters consciousness and sometimes does not, it is said to be at the threshold of consciousness. These paradigms can also include confidence judgments, which are considered a measure of metacognition.

Feature Integration. In Chapter 2, section 2.4.1.1., the theory of feature integration (Treisman & Gelade, 1980) will be described. Briefly, this theory suggests that processing simple features of a stimulus can occur automatically (without attention) while integrating features requires the use of attentional resources. However, what is relevant in these paradigms is that despite the information being always available, its masking, brief presentation, or presentation in the periphery of the visual field allows for partial consciousness of the stimulus, which can sometimes be accurate and at other times erroneous (Kouider et al., 2010). These errors are known as perceptual illusions because the stimulus is experienced in its entirety, but its access does not correspond to the presented information (Block, 2007; Sergeant & Dehaene, 2004).

In this thesis, we have chosen a modified paradigm based on Esterman et al. (2004), which produces perceptual illusions. The stimulus consists of the presentation of 4 characters: two white flankers at the ends and two colored letters in between. The flanking characters can be either "8" or "S," while the inner letters are always an "L" and an "O." Among the inner letters, the target letter is the "L," and the "O" is the distractor, whose position can vary within the line of letters (see Figure 1.6). The participant's task is to correctly report the color of the letter "L" (a hit). Reporting the color of the distractor would result in a perceptual illusion. Reporting a color not presented on the screen would be an error, and if no color is perceived, the participant has the option to report that they did not see the stimulus.

To induce perceptual illusions, the set of letters is presented for a brief period and then masked. Additionally, each participant undergoes a titration procedure before the experimental phase. This procedure could manipulate exposure time, eccentricity, and/or stimulus size. For example, in the EEG study in Chapter 8, the string of characters is always presented briefly for 100 ms, and only the size is manipulated to achieve approximately 70% accuracy, assuming that around 30% of responses would be illusions. The chosen accuracy range depends on the number of trials in the titration block (see more details in Chapters 7, 8, and 9). This procedure means that if the percentage of accuracy in a block of trials is approximately 70%, the size of the set of letters decreases. If the percentage of accuracy is below 60% in the trials, the size of the string of character increases. The optimal size is determined when the percentage of accuracy is approximately between 70% and 60% in two consecutive calibration blocks.

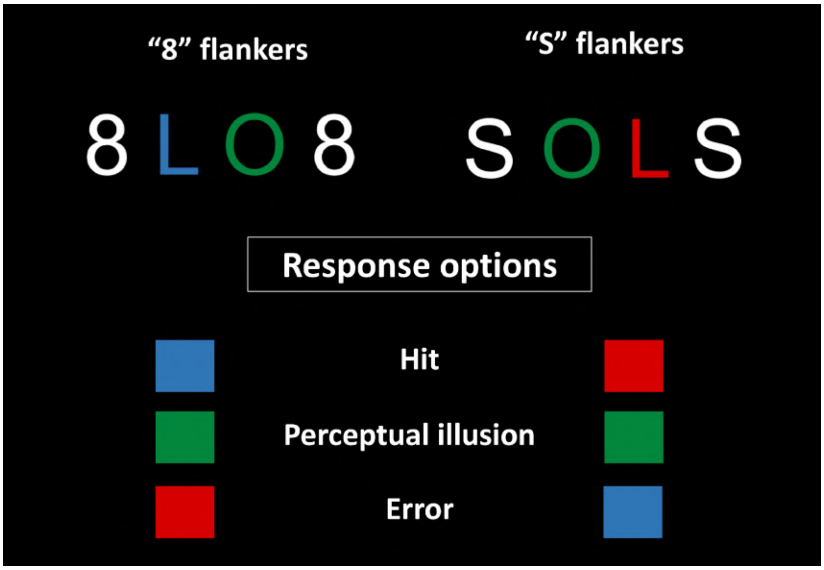


Figure 1.6: Examples of stimuli used in this doctoral thesis to measure phenomenological consciousness. These stimuli are an adaptation from Esterman et al. (2004). At the top, a set of characters is presented, consisting of two flanking characters ("8" or "S") and two colored letters within the set: the target letter "L" and the distractor "O." In the lower part, you can observe the possible types of responses associated with different colors: red, green, or blue.

Chapter 2: The theoretical framework of attention

2.1 What is attention?

In every moment, we find ourselves surrounded by a large amount of information. This information is selected and filtered according to its salience and our goals or objectives (Broadbent, 1958). Attention is one of the most important cognitive processes that allows the selection of information. The term attention is a difficult concept to approach given its heterogeneity. Colloquially, when something "catches your attention" it implies that the stimulus is novel for you or is interesting for your goals. Furthermore, asking for attention in a school classroom involves a sustained effort of concentration overtime on the part of the students. James' (1890) well-known quote indicated that "*everyone knows what attention is. It is the taking possession of the mind in clear and vivid form of one out of what seems several simultaneous objects or trains of thought* ". This approach to defining attention includes both its limited and heterogeneous nature. However, the concept of attention is complex, and disaggregating its properties simplifies its understanding. For example, Parasuraman & Davies (1984) proposed a division of attention into processes of selection, divided attention, sustained attention, or executive control of action; Van der Heijden (1992) differentiated between attention, expectation, and intention; LaBerge (1995) proposed that attention manifests itself in a selective, preparatory, or maintained form. Currently, one of the most widely used and cited models is Petersen and Posner's (Petersen & Posner, 2012; Posner & Petersen, 1990). This model proposed three different, but linked, functional networks that are part of the attentional system: the alerting, orienting, and executive control networks. The functionality and neural bases of these networks are described below.

2.1.1 The alerting system and how to measure it

The attentional alerting network plays a crucial role in the regulation of the optimal levels of arousal/activation, both in a sustained manner over time, as well as in a more transitory way (Funes & Lupiáñez, 2003; Posner & Petersen, 1990; Sturm & Willmes, 2001). According to this differentiation, the alerting system is divided into tonic and phasic alerting. Tonic alerting is responsible for the maintenance of the awake state over time (sustained attention). The way to measure tonic alerting involves temporally long and monotonous paradigms, such as the psychomotor vigilance task (PVT) (Drummond et al., 2005). These types of tasks are associated with faster responses to the task at the beginning of the experiment and slower responses when the vigilance state declines as time passes or more fatigue is experienced (Drummond et al., 2005; Loh et al., 2004).

On the other hand, phasic alerting acts in a more transient form, increasing the level of arousal/activation at a given time. A very common way of measuring phasic alerting involves including a warning signal (in any sensory modality) prior to the presentation of a target stimulus. This signal increases the level of arousal without providing information about where or when the stimuli will be presented. Phasic alerting is associated with faster responses to the stimulus (as compared to conditions without alerting), although these faster responses are sometimes accompanied by a greater number of errors. This trade-off between speed and accuracy of response is quite common with these type of manipulations (Posner et al., 1973; Townsend & Ashby, 1983; Vandierendonck, 2017) and indicates that the phasic alert signal is beneficial in terms of speed of response, but not in terms of improved processing quality (Posner, 1978) (more details in section 2.2.).

2.1.2 The orienting system and how to measure it

The spatial orienting system allows the selection of relevant information at a particular location in space (Posner, 1980; Posner & Petersen, 1990). Orienting can occur "overtly", through head or eye movements, or covertly, without motor activity (Liu et al., 2009; Posner, 1980; Rafal et al., 1989). In addition, spatial locations can be selected either exogenously or endogenously.

When orienting occurs exogenously it involves bottom-up processing, guided by the salient features of the stimulus. The saliency of a stimulus can be manipulated by changing its luminance, color, duration, and even its motion (Bartolomeo, 2008; Chica, Bartolomeo, et al., 2013; Chica, Martín-Arévalo, et al., 2014). Many examples of orienting occur in driving. E.g., while you are focused on your own driving, a driver behind you flashes a full beam at you. This signal has an unexpected and salient feature as it is produced by a change of lights. In addition, it orients you in space (towards the rear-view mirror) and often results in a further reorientation of your attention to locate and respond to the stimulation. One of the most commonly used paradigms to explore exogenous attention is the "cost-benefit" paradigm (Posner, 1980). In this paradigm, a peripheral cue signals a location, which can coincide or not with the location of the target. When the cue appears at the target location, these trials are considered valid. However, if the target stimulus appears at the opposite location, these trials are considered invalid (Chica, Martín-Arévalo, et al., 2014).

On the other hand, endogenous orienting is voluntarily initiated through top-down processing, driven by a goals or intentions (Bartolomeo, 2008; Chica, Bartolomeo, et al., 2013; Chica, Martín-Arévalo, et al., 2014; Jonides, 1981). Following the same example of driving, an endogenous signal could be a roadside billboard with an arrow indicating the entrance to a destination city. In this scenario, the arrow on the billboard guides the driver's attention endogenously because the driver's expectation or goal is to arrive to that city. To manipulate this type of attention, it is also common to use the cost-benefit paradigm (Posner, 1980). Unlike exogenous cues, endogenous cues indicate with high probability where the target is going to appear. A classic example involves associating the color of a centrally presented cue with a particular location. For instance, the color red might signify that the stimulus is likely to appear on the right, while the color green indicates a high probability of the stimulus appearing on the left. When the prediction of the cue is achieved (when the target stimulus appears where the cue indicated), these trials are considered valid.

However, if the prediction is not fulfilled, these trials are considered invalid (Chica, Martín-Arévalo, et al., 2014).

In both exogenous and endogenous spatial attention, a facilitation effect is usually observed: responses are faster and/or more accurate on valid vs. invalid trials (Chica, Martín-Arévalo, et al., 2014; Posner, 1980). However, this facilitation effect has been shown to depend on the time that elapses between the cue and the target stimulus (the stimulus onset asynchrony, SOA). Endogenous attention effects are optimal at SOAs longer than 300 ms, lasting a couple of seconds (Lupiáñez et al., 2006). However, in exogenous attention (directed by peripheral signals), if the SOA is longer than 300 ms, a phenomenon known as inhibition of return occurs. This phenomenon consists of faster responses for invalid vs. valid trials (Lupiáñez et al., 2006; Posner, 1980). Inhibition of return is considered a mechanism that favors the exploration of new locations, improving the efficiency of visual search (Klein, 2000).

2.1.3 The executive system and how to measure it

The executive system refers to a series of mental processes implemented in a voluntary/top-down manner when a given task or goal requires attention or concentration (Burgess & Simons, 2005; Diamond, 2013; Espy, 2004; Miller & Cohen, 2001). The executive system is activated when novel or difficult situations require voluntary control, planning, or decision-making to solve the problem (Norman & Shallice, 1986). There is some consensus that the executive system is composed of three essential cognitive cores: inhibitory control, working memory, and cognitive flexibility.

Inhibitory control involves controlling one's attention, behavior, thoughts, and emotions in order to provide adaptive responses (Diamond, 2013). An everyday situation of inhibitory control occurs when studying for an exam in a noisy context such as having a radio on. At that moment, the executive system is activated to focus attention on studying while inhibiting the meaning of the words that may be emitted by the radio.

Working memory is responsible for the maintenance and manipulation of the information (Baddeley & Hitch, 1994; Smith & Jonides, 1999). Imagine that you are solving a mathematical problem or constructing a sentence in a second language. Working memory is necessary to retrieve previously learned criteria on how to carry out an addition or where an adjective should be placed in English grammar, and to also establish connections between this prior knowledge and the future solution of the mathematical problem or the appropriate grammatical construction (Diamond, 2013). It should be noted that working memory is different to short-term memory. While working memory maintains and manipulates information, short-term memory only maintains information.

Cognitive flexibility entails a change of perspective towards a problem, a readjustment of the mental schema that requires a new situation, a change of rules, or a change of priorities (Diamond, 2013). For example, if every day of the week I have the habit of going for a run at 9:00 in the morning and, suddenly, it starts to rain until 11:00; having cognitive flexibility allows me to adapt my task (going for a run) to a new schedule in the day.

These three cores of the executive system are interconnected. That is, if I need to re-plan my running schedule, this involves inhibiting the previous schemas loaded in the working memory and re-activating the new information in working memory in order to carry out my new schema.

In the laboratory, the way to measure the executive system is to present tasks that manipulate these 3 nuclei. The best-known paradigms for the study of executive functions are Stroop-type, Simon-type, flanker, or dual-task tasks.

The Stroop task consists of the presentation of a stimulus that can present multiple features simultaneously. The best-known example is the presentation of words that name colors, written in a particular color. In some trials, the color of the word and the ink match, while sometimes they do not ("GREEN" or "GREEN"). Participants are required to indicate the color of the ink. When the word and the ink match, trials are congruent, and when they do not, trials are incongruent. Typical results involve faster and/or more accurate responses for congruent vs. incongruent trials. This result is known as the *Stroop effect* (Stroop, 1935).

The Simon task consists of the presentation of a stimulus at a certain location, which may or may not correspond to the location of the response key (Hommel, 2011). When both locations coincide, trials are compatible, whereas if the location of the stimulus and the response key are different, trials are incompatible. The Simon effect consists of faster and/or more accurate responses when trials are compatible vs. incompatible.

The flanker task consists of responding to a central stimulus surrounded by a series of irrelevant stimuli known as flankers (for example: "VVCVV", where "C" is the central stimulus and the "Vs" are the flankers). When the central stimulus and the flankers have the same shape, and are associated with the same response, trials are congruent; while, if they differ in shape or its associated response, trials are incongruent. As in the Stroop and Simon effect, in the flanker paradigm, it is common to emit faster and/or more accurate responses for congruent vs. incongruent trials (Eriksen & Eriksen, 1974).

Finally, dual-task paradigms involve the performance of two tasks simultaneously, whose sensory and cognitive content is usually different (Baddeley, 2020; Della Sala et al., 1995; Miyake & Shah, 1999). This type of paradigm allows attentional resources to be distributed in both tasks, resulting in a limitation or overload of the attentional system.

2.2 The role of previous knowledge: top-down expectancies

In the previous sections, we have defined attention as a selection mechanism. Until a few years ago, this concept of selection (and its experimental measurement) has not been properly dissociated from another form of information prioritization: expectancies (Rungratsameetaweemana & Serences, 2019).

Since it is not possible to process all the information in our environment, we use attention to filter and select relevant information. However, this selection may or may not be based on prior knowledge, i.e., prior expectancies of a given content (Jiang et al., 2013; Jiang & Chun, 2001). For instance, while driving in a city, we are more likely to encounter motorbikes (creating an expectancy), so we more often orient our attention to the rear-view mirrors in search of these motorbikes. This example underscore the interplay between attention and expectancies, highlighting how expectancies can modulate the way we direct our attention to certain stimuli in the environment. In the classical cost-benefit paradigm, the concepts of selection and expectancies have not always been properly dissociated, since a predictive cue selects a relevant location, but also includes a probability component that modifies our expectations. If a cue indicates that a stimulus will appear 80% of the trials on the right (and the remaining 20% of the trials on the left, it is leading to both an expectancy of appearance and a selection of the indicated region.

Both examples emphasize the challenging dissociation between expectancies and attention. Nowadays, different studies have revealed that the behavioral effects of both cognitive processes are similar, with improvements in the detection and recognition of stimuli when they are attended to and expected compared to unattended or unexpected stimuli (Summerfield & Egner, 2009; Summerfield et al., 2006). However, at the neural level, the effects of attention and expectation are dissociable. While attentional selection is associated with the fronto-parietal network activity (Corbetta & Shulman, 2002), the orbitofrontal cortex (OSF) plays an important role in the development of expectancies (Bar et al., 2006; Fenske et al., 2006).

The theoretical framework entailing expectancies and attention is framed in hierarchical perceptual inference. This model is based on the dynamics of predictive coding models (Friston, 2005; Lee & Mumford, 2003). This approach suggests that perception is formed through constant communication between different levels of processing in our brain. This bidirectional communication involves both bottom-up (external sensory stimulation) and top-down (what we expect based on previous experience) signals between higher and lower-level sensory regions. These signals are combined in a dynamic and iterative way, i.e. the brain constantly compares what we are seeing/perceiving (sensory information) with what we expect to see/perceive (expectations). If this dynamic, iterative process fails in either direction, perception occurs erroneously (Chennu et al., 2013; Feldman & Friston, 2010). When this system fails, expectancies entail a cost. An example reflecting such a failure may be the following: in a context in which one plans to go to the beach, prior expectancies involve the anticipation of perceiving stimuli such as the heat of the sun, ocean waves, beach umbrellas, or other objects, such as towels and sunscreen. However, prior knowledge in this context does not include the presence of an object such as a lamp. In this situation, the attentional system filters the stimuli of interest, such as the state of the water, to assess whether or not to swim. Together with the expectancies generated by the context (the mentioned objects that are expected), this unexpected object (the lamp) may go unnoticed, due to the incompatibility in both the selection system and the prior knowledge system.

In summary, the way in which a stimulus is perceived could be influenced by different attentional systems or as a function of prior expectancies. While expectancies often exhibit similar behavioral effects as attention (Summerfield & Egner, 2009; Summerfield et al., 2006), their neural bases are different (Fenske et al., 2006). In the perceptual domain, it is crucial to distinguish between these two processes. While attention allows us to evaluate the relevance of sensory information, expectancies are responsible for making predictions about specific features or specific locations (Summerfield & De Lange, 2014). The fulfillment of expectancies seems to enhance perceptual processing (Rohenkohl et al., 2014; Vangkilde et al., 2012), whereas the violation of expectancies often impairs perception (Aru & Bachmann, 2017; Mack et al., 2016).

2.3 The role of attention in access consciosness

Throughout this chapter, we have defined attention, characterize its different subsystems, and differentiated it from the concept of expectation. But how does attention influence cognitive processes such as consciousness?

Different theoretical approaches have considered that attention acts as a "gateway" to consciousness (Baars, 1997; Cohen & Dennett, 2011; Dehaene & Naccache, 2001; Dennett, 2001; Posner, 1994). The attentional system is proposed to enable the selection and amplification of information to gain access to consciousness, although attention is not sufficient for conscious experience (Dehaene et al., 2006; Dehaene & Changeux, 2011b). In contrast, neither the information integration theory nor higher-order theories propose a relevant role of attentional processes in consciousness. While the information integration theory indicates that the activity of sensory regions is already complex enough for consciousness to occur (Tononi, 2004, 2008; Tononi et al., 2016), higher-order theories emphasize the role of meta-representations in conscious experience (Cleeremans, 2007; Cleeremans et al., 2020; Fleming, 2020; Gershman, 2019; Lau, 2019, see Chapter 1 for further details). In the following paragraphs, we will briefly summarize some studies in which the effects of different attentional networks (alerting, orienting, and executive system) on access consciousness are explored.

Regarding phasic alerting, there are different studies that highlight the beneficial role of a warning signal presented before a near-threshold stimulus. In general, this benefit reflects faster response times and increased perceptual sensitivity when warning signals are present vs. absent (Botta et al., 2014; Chica et al., 2016; Kusnir et al., 2011; Martín-Signes et al., 2019; Petersen et al., 2017). In neglect patients, the presence of a warning signal also enhances their deficits in perceptual consciousness (Chica et al., 2012; Finke et al., 2012; Robertson et al., 1998).

The effect of the attentional orienting system on conscious perception depends on whether attention is oriented endogenously or exogenously. When near-threshold stimuli are used as targets, endogenous orienting can be dissociated from consciousness (Botta et al., 2014; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012; Kentridge et al., 2008; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008). However, this is a controversial issue as some studies have indeed shown improvements in perceptual consciousness with the use of endogenous cues (Liu et al., 2009; Vernet et al., 2019). In the case of exogenous orienting, there is more robust evidence demonstrating enhanced conscious detection at attended locations. Different studies have shown that the use of a peripheral cue enhances conscious detection in attended vs. unattended locations (Botta et al., 2014, 2017; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012; Hein et al., 2006).

The relationship between the executive system and consciousness is more complex than that observed in the alerting or orienting systems. Despite this, there is considerable evidence showing that executive system interference reduces the ability to perceive a stimulus. By overloading the WM in inattentional blindness (Akyürek et al., 2007) or attentional blink (Colzato et al., 2007) paradigms, an unexpected stimulus does not access consciousness. Also, in visual search paradigms, working memory overload increases the probability of erroneous responses (De Loof et al., 2013).

On the other hand, dual-task paradigms using stimuli at the conscious threshold have shown modulations in consciousness when the executive system is interfered. That is, conscious detection is impaired when concurrently presented with incongruent Stroop trials as compared to the presentation of congruent Stroop trials (Colás et al., 2017; Martín-Signes et al., 2018, 2021).

Results from the reported studies indicate that bottom-up processing (exogenous orienting and phasic alerting) modulates access consciousness (Botta et al., 2017; Chica et al., 2010, 2016, 2018; Chica, Paz-Alonso, et al., 2013; Chica & Bartolomeo, 2012; Kusnir et al., 2011). However, the role of top-down processing (endogenous orientation and executive system) in perceptual consciousness is less conclusive (Botta et al., 2014; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012; Colás et al., 2017; Liu et al., 2009; Martín-Signes et al., 2018; Vernet et al., 2019). Some studies have reported that endogenous attention does not modulate conscious perception (Botta et al., 2014; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012), although more recently, Vernet et al. (2019) reported improvements in visual consciousness produced by endogenous attention. The executive system interferes with conscious perception, modulating perceptual sensitivity (Martín-Signes et al., 2018), or response criterion (Colás et al., 2017).

The studies described in this section focus only on access consciousness. However, in this thesis, we follow the distinction proposed by Block (2011) which indicates that consciousness not only involves the limited nature of its content (access consciousness) but also implies a rich subjective experience (phenomenal consciousness). Furthermore, the study of how attention modulates our subjective experience is of particular interest today. This interest was previously highlighted by Helmholtz & Southall (2000) and James (1890), who suggested that attention could influence the subjective appearance of sensory stimuli. Recent studies have shown that different types of attention impact the subjective perception of visual stimuli (Carrasco et al., 2004, 2008; Carrasco & Barbot, 2019; Fuller et al., 2008, 2009; Liu et al., 2009). However, the approach chosen in this thesis to study the attentional modulation of conscious experience includes partial consciousness paradigms. In the following section, we will focus on the concept of partial consciousness as an important point of connection for the study of phenomenal consciousness. Additionally, we will explore the relationship between attention and classic partial consciousness paradigms, as well as the theoretical models that support this relationship.

2.4 Partial consciousness: An approach to bridging phenomenal consciousness and perceptual illusions

Despite the differentiation between access and phenomenal consciousness (Block, 2011), it is difficult to separate the level of accessibility of a given stimulus from its phenomenological character (Kouider et al., 2007).

According to Block, experimental paradigms for measuring phenomenological consciousness should contain "undetectable" stimuli or partially accessible stimuli (Block, 2007, 2011; Kouider et al., 2007). The first type of paradigms refers to those that contain accessible stimuli that due to experimental conditions such as inattention do not access consciousness (e.g., attentional blink or inattentional blindness) (Dux & Marois, 2009; Mack, 2003; Mack & Rock, 1998; Shapiro et al., 1997). In the second case, the paradigms should measure partial consciousness (de Gardelle et al., 2009; Kouider et al., 2007, 2010). In these paradigms, stimuli are presented above threshold, although the information does not always reach the appropriate levels of perceptual representation

(Kouider et al., 2007, 2010). For example, if a short text is presented for a limited time of five seconds, participants could detect a set of letters, sentences or even some words. However, the meaning of the whole text will not be accessible. Therefore, partial consciousness is achieved by a brief presentation, by masking, by presenting information in the visual periphery, by increasing the number of distractors, by overloading the attentional system, etc. (Kouider et al., 2007, 2010). This way of presenting stimuli to achieve their partial consciousness establishes a close similarity with the necessary conditions for creating some perceptual illusions (see section 2.4.2 of this chapter) (Block, 2007; Sergeant & Dehaene, 2004). Some illusions can occur because of a failure during the feature integration process. Therefore, the study of perceptual illusions can be considered as a useful tool for studying phenomenological consciousness.

The following section will detail some experimental paradigms in which perceptual illusions are produced in the field of feature integration. In addition, we will also review the role of attention on feature integration.

2.4.1 Experimental paradigms for partial consciousness and the role of attention

Sperling (1960) developed one of the main paradigms for measuring phenomenological consciousness. This paradigm consisted of the brief presentation of a 3x4 matrix of letters. Although participants reported to perceive the entire set of letters, they could only correctly report three or four of them (partial consciousness). After the display presentation, three auditory cues with different tone intensities were included. These different tonalities were related to the location of the different rows in the array. Thus, the tone indicated which row had to be reported (e.g., low tone instructed to recall the bottom row). The results showed that participants reported perceiving a matrix of letters, but were only able to fully integrate between 3-4 letters of which especially the tone-oriented letter row was reported. Moreover, de Gardelle et al. (2009) manipulated top-down expectancies by including different stimuli such as some pseudo-letters and symbols. While the symbols were perceived, the pseudo-letters were illusorily perceived as normal letters. These results reveal the relevance of attention in subjective report, and also emphasize the role of expectancies, as underscored by the Feature Confirmation Account (FCA; see section 2.4.3).

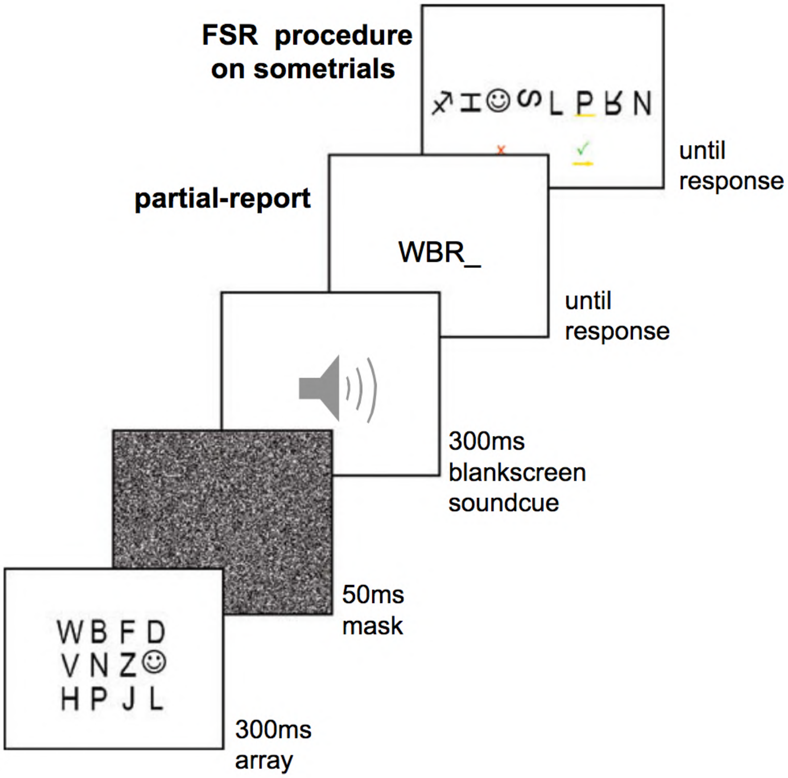


Figure 2.2: representation of the experimental paradigm of Gardelle et al. (2009). The letter matrix is presented for 300 ms. After the presentation of a mask (50 ms), a tone indicated the row of the matrix to be remembered. Without time pressure, participants typed the recalled letters. Sometimes, another response screen was presented asking to report the remaining unattended letters, pseudo-letters, or symbols (free subjective report: FSR) Figure extracted with permission of (de Gardelle et al., 2009).

Other paradigms consist of the presentation of stimuli whose color and shape features are manipulated. Figure 3 shows two types of paradigms: feature detection paradigms and visual search paradigms. In feature detection paradigms, stimuli are usually briefly presented and/or masked. In the example of Figure 3 (left), participants are required to report the shape and color of the letters. Feature integration occurs correctly in the case of reporting a red A and a blue X. However, if a blue A and a red X were reported, an illusory conjunction would occur. A shape error will be observed if reporting a red A and a blue T. Finally, a color error will be observed if reporting a red A and a green X.

In the visual search paradigm, participants are required to look for a target (e.g. a red "X"). When the distractors are very different from the target stimulus, targets are identified faster (independently of the number of distractors), since only the color neural map needs to be activated (Figure 3 right and above). However, if the distractors share features with the target stimulus, different feature maps must be activated and linked by spatial attention. Therefore, this search involves a greater amount of time for searching, which increases as the number of distractors also increases (Ivry & Prinzmetal, 1991; Robertson, 2003).

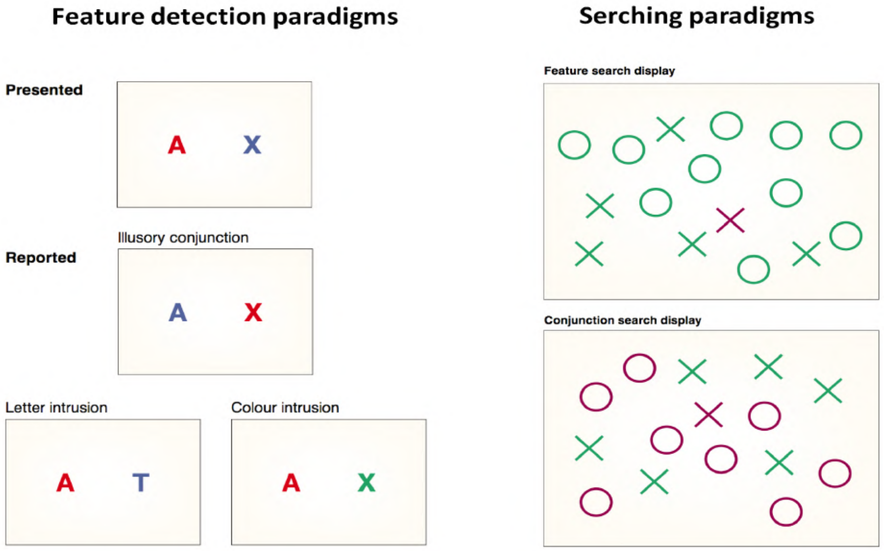


Figure 2.3: Representation of two types of feature integration paradigms for measuring phenomenological consciousness using perceptual illusions. On the left, a shape (type of letter) and/or color (red, green, or blue) feature detection paradigm is shown. On the right-above, a visual

search paradigm with simple distractors (color different from the target) is shown, and on the right-below the same task, but with more complex distractors (same color and shape). Figure extracted and modified from Robertson (2003).

It has been proposed that overloading the attentional system increases the proportion of perceptual illusions (Arend et al., 2013; Chen & Watanabe, 2021; Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982). However, in some studies, dividing attention did not increase the number of perceptual illusions (Li et al., 2002; Rodríguez-San Esteban et al., 2022).

Spatial orienting has been consistently proven to improve feature integration (Briand, 1998; Briand & Klein, 1987; Henderickx et al., 2010; Prinzmetal et al., 1986). Some of these studies provide more consistent results for the effects of exogenous orienting (Briand & Klein, 1987a), while others show lager effects of endogenous orienting (Henderickx et al., 2010).

The effect of alerting on feature integration has been largely underexplored. In Liu et al. (2013), the alerting system did not show modulations in feature integration (measured with the "feature overlap effect"). In study 9 of this thesis, we extend the evidence regarding how the alerting system modulates feature integration.

Perceptual expectancies also appear to affect perceptual processing and feature integration. That is, having prior experience with a given content facilitates the processing of that perceptual content (Sherman et al., 2015; Stefanics et al., 2010; Wyart et al., 2012). However, expectancies can also induce a greater amount of perceptual illusions when that content includes novel and/or unexpected information (Aru et al., 2018; Aru & Bachmann, 2017; de Gardelle et al., 2009; Harris et al., 2011; Humphreys, 2016; Moore et al., 1998; Wokke et al., 2013).

In summary, this section summarizes the undoubted importance of the attentional system in feature integration. In the following sections, we present two theories that try to explain who feature integration occurs and how does it relate to attentional selection: the Feature Integration Theory (FIT) of Anne Treisman (1996) and the FCA of Humphreys (2016).

2.4.1.1 Anne Treisman's approach

One of the most famous theories used over time in the field of perception (Kristjánsson & Egeth, 2020) is Anne Treisman's *FIT* (Treisman, 1996). This theory explains the process by which we perceive the stimuli around us in a unified way. According to this theory, the perception process occurs in a hierarchical manner and consists of an automatic stage, followed by another stage controlled by the attentional system (Kristjánsson & Egeth, 2020; Treisman, 1996; Treisman & Schmidt, 1982; Wolfe & Robertson, 2012). In the automatic stage, some simple features such as color, shape, or motion are analyzed without the need for attention. In parallel, maps are created for each feature, which are combined in a second stage by focusing attention. In this second stage, attention selects the stimulus to be perceived in a location map and correctly merges the information from the previous feature maps. According to this proposal, attention acts as a "glue" between the different features (Treisman & Gelade, 1980). If the stimulus or object is familiar, an association is made between the stimulus and the prior knowledge, resulting in the identification of the object (see Figure 2.4).

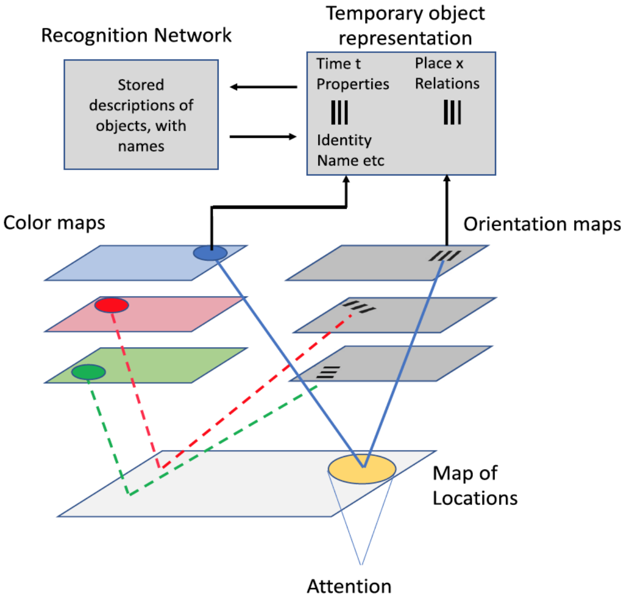


Figure 2.4: Schematic representation of the feature integration process according to Anne Treisman's theory (Treisman & Gelade, 1980). Figure extracted with permission from (Kristjánsson & Egeth, 2020).

According to the FIT, given the limited nature of attention, this integration process can erroneously occur. These errors are produced by an incorrect combination of different features and are called *illusory conjunctions or perceptual illusions* (Henderson & McClelland, 2020; Treisman & Gelade, 1980). These illusions occur when stimulation is presented briefly, masked, due to memory failures, attentional overload, or the creation of certain expectations (Aru et al., 2018; Aru & Bachmann, 2017; de Gardelle et al., 2009; Kuhn & Rensink, 2016; Mack et al., 2016).

At present, the debate on whether attentional failures produce perceptual illusions remains unresolved (Briand, 1998;

Han & Humphreys, 2007; Humphreys, 2016; Pelli et al., 2007; Prinzmetal et al., 1986; Shafritz et al., 2002; Whitney & Levi, 2011). In the next section, we present a further approach, suggesting a different role of attention during the process of feature integration.

2.4.1.2 The Feature Confirmation approach

Alternatively to FIT, the *FCA* by Humphreys (2016) proposes a role of attention in feature integration, but not as a prerequisite for successful integration to occur. Specifically, the FCA indicates that feature integration is a bottom-up process (Humphreys, 2016; Li et al., 2002; Treisman, 1998). However, this processing can sometimes fail, producing unstable representations. In that case, attention would be required to send top-down feedback signals. This "attentional confirmation process" would be responsible for stabilizing the noisy or unstable signal (Humphreys, 2016). This slow confirmation process is carried out by the parietal cortex (Braet & Humphreys, 2009; Gillebert & Humphreys, 2010; Humphreys, 2016). The involvement of this area in the integration process is a matter of debate since its activity could be related to attention processes (Kastner & Ungerleider, 2000; Shafritz et al., 2002a) or else to feature confirmation mechanisms (Humphreys, 2016). The role of parietal regions in attention has been largely discussed (Braet & Humphreys, 2009; Hochstein & Ahissar, 2002; Humphreys, 2016; Matthews et al., 2018; Mordkoff & Halterman, 2008; Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982; Wolfe & Robertson, 2012). However, it is undebated that patients with brain damage in the parietal lobe show difficulties in feature integration (Cohen & Ivry, 1989; Cohen &

Rafal, 1991; Friedman-Hill et al., 1995; Humphreys et al., 2000). Transcranial magnetic stimulation studies have also demonstrated an attenuation on illusory binding when stimulating the parietal cortex (Esterman et al., 2007). Other studies have found alterations in perception only when multiple features need to be integrated, but not when a single feature is presented (Robertson, 2003). On the other hand, Braet & Humphreys (2009) used transcranial magnetic stimulation in parietal regions, and found that the integration process was impaired in late, but not in early phases of integration.

Throughout this chapter, we have reviewed Posner's attentional model, which has inspired some of the studies in this thesis. We have also presented some studies that demonstrate the role of attention in access consciousness and phenomenal consciousness. It is worth noting that the experimental approach chosen for the study of phenomenal consciousness is based on partial consciousness paradigms involving the correct or incorrect integration of stimulus features. This integration process is explained by well-established theories such as the FIT, and more recent theories like the FCA. Both theories debate the role of attention during the integration process. However, they do not explicitly discuss the involvement of other cognitive processes such as memory in the process of feature integration. This issue will be explored in Study 8 of this thesis, in which we explore the brain oscillations that occur during correct and incorrect integration. In the following chapter, we delve into how the meaning of brain oscillations and their relationship with various cognitive processes such as feature integration, memory, attention, and perceptual consciousness.

Chapter 3: Brain oscillations in different cognitive processes

3.1 Introduction to brain oscillations

The use of neuroimaging techniques has contributed extensively to the field of Cognitive Neuroscience. Techniques such as functional magnetic resonance imaging (fMRI) provide rich spatial information, but its temporal resolution is more limited. In contrast, electroencephalography (EEG) provides brain activity information with a temporal resolution of milliseconds, adjusting to the dynamic nature of brain activity. In other words, while fMRI provides information on where a given cognitive process occurs, EEG provides a better answer to the question of *when* the process occurs (Cohen, 2017).

There are different measures to be obtained from the EEG signal such as evoked potentials, brain oscillations, source localization, or functional connectivity. Since this thesis analyzes brain oscillations using time-frequency analysis (see chapter 8), we will focus on their relationship with different cognitive processes such as attention or perceptual consciousness among others (see section 3.2).

Brain oscillations refer to a set of fluctuations that follow a certain rhythm and change according to the postsynaptic activity of a group of neurons (subsystem) in the brain (system) (Buzsáki & Watson, 2012; Cohen, 2015). These fluctuations can vary in time and reveal themselves in the form of waves characterized by their frequency, amplitude, and phase (see figure 3.1). Frequency refers to the speed of an oscillation and is measured in Hertz (Hz). Hzs are equivalent to the number of fluctuations that a wave has over one second. In Figure 3.1 (top part) a 1Hz oscillation is observed, since in one second a single cycle containing its corresponding rise and fall is observed. However, in the bottom part of Figure 3.1, the wave is 4Hz, since, in one second, four cycles are shown for each second. The frequency range of interest in the study of cognitive processes spans from 2Hz to 90 Hz. Depending on this range, oscillations are often categorized as delta (0.5-3 Hz), theta (3-8 Hz), alpha (8-13 Hz), beta (13-30 (Hz), or gamma (30-90 Hz) (Başar et al., 2001; Ergenoglu et al., 2004). Given the literature reviewed in Chapter 8 of this thesis, we will focus on frequencies from the theta to gamma.

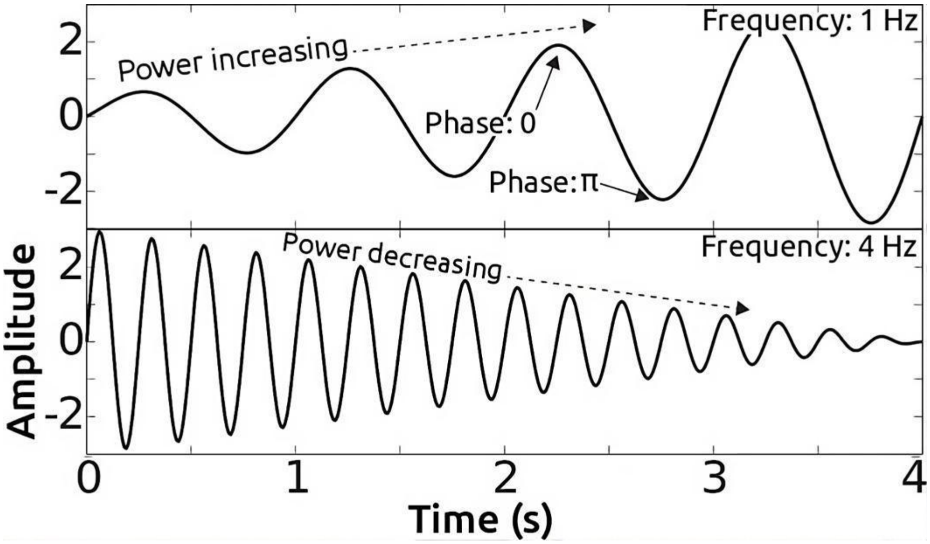


Figure 3.1: graphical representation of two sine waves showing their frequency, power, and phase properties. Figure taken from Cohen (2015).

The amplitude of a wave is related to the magnitude of the change in brain oscillation, with the understanding that these changes represent brain activity. One way to measure these changes in magnitude is power. Power, as indicated by Cohen (2015), can be understood as a line that envelops changes in brain oscillations over time (see figure 3.2). Importantly, power can fluctuate, increasing or decreasing (see figure 3.1).

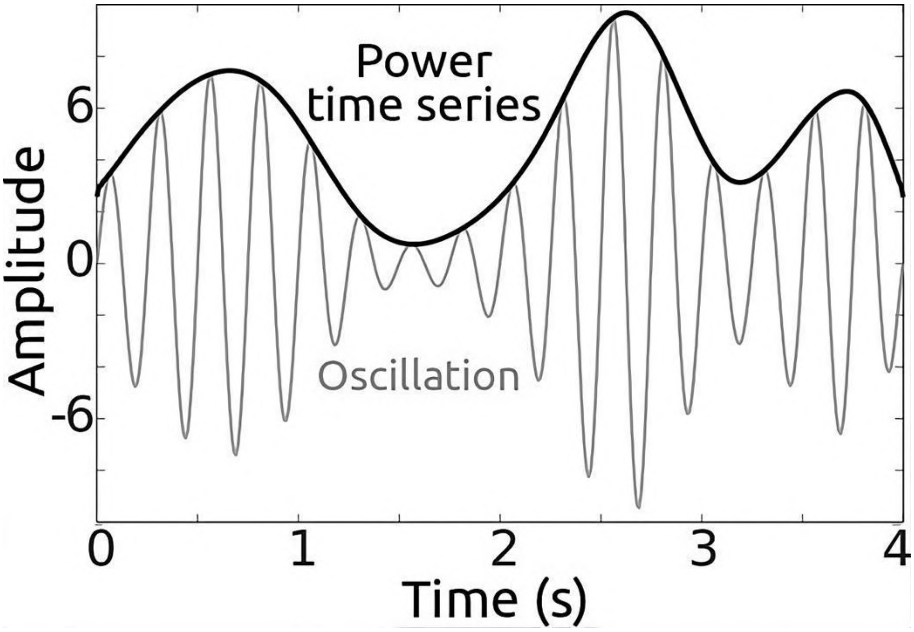


Figure 3.2: graphical representation of the changes in magnitude of the amplitude of the brain oscillations of a sine wave. The power is represented by a line enveloping these changes over time. Figure taken from Cohen (2015).

The third property of brain oscillations refers to phase. The phase is related to the transient state of an oscillation that varies between the lowest and the highest point within a cycle. Figure 3.1 shows the beginning of a high point ("phase 0") of the oscillatory cycle and a low point named "phase Π".

Now that the main properties of brain oscillations have been briefly described, it is important to understand the contribution of the study of brain oscillations to our comprehension of the cognitive system. The cyclic and dynamic aspects of oscillations are found naturally in different contexts: in the rotational motion of the Earth, in the changes of the tide, or within the changes of day and night. Without this periodicity, there would be no possibility of building up temporal dimensions of past, present, and future. Not only in the external context we find this oscillatory activity, but different parts of our organism also function with this oscillatory character: the heartbeat, breathing, or even the different hormonal states (Buzsáki, 2006). Therefore, oscillations are found naturally throughout our environment, and the same occurs in the brain. Neural activity constantly oscillates in a natural way. But this oscillatory activity is not always noisy or random, but it has been associated with different cognitive functions. One of the first oscillations that were identified and studied in history of cognitive neuroscience was alpha. Particularly, Berger (1929) found that during the resting state, alpha activity was predominant (~ 10Hz) in posterior regions. Furthermore, the alpha frequency is usually designated as the "idling" rhythm (for a review Pfurtscheller et al., 1996). From then until the present, the interest in the study of brain oscillations has been increasing. This is due to the valuable information that oscillations provide on the neural mechanisms underlying human cognition. The study of brain oscillations has also allowed to create a link between human and non-human neurophysiology, as well as exploring biomarkers of different psychopathologies (Cohen, 2017; Crone et al., 2006; Niedermeyer, 2003; Oswal et al., 2013). However, the evidence supporting the relationship between brain oscillations and cognitive processes, the specific location of these oscillations in the brain, and their underlying mechanisms is still incomplete (Cohen, 2015).

In summary, during the first part of this chapter, we have presented the basic notions to understand the basic properties of brain oscillations, as well as their importance in the relationship with brain activity. In the following section, we describe more specifically which brain oscillations have been linked to different cognitive processes such as attention, memory, error detection, or perceptual consciousness, among others.

3.2 Brain oscillations and their relationship to cognitive processes

In this thesis, we focus on cognitive processes that broadly include attention and perceptual consciousness, reviewing some processes of interest in our empirical work such as feature integration, memory, object representation, or error detection. Given the results obtained in study 8 of this thesis, the role of frequencies, theta, alpha, beta, and gamma will be described.

3.2.1 The theta-band

The theta frequency band has been associated to focused attention (Başar-Eroglu et al., 1992) and error detection (Cavanagh et al., 2009; Cohen, 2011; Fusco et al., 2018; Kalfaoğlu et al., 2018; Luu et al., 2004; Trujillo & Allen, 2007). Given the clear relationship between perceptual errors and the theta-band, one could consider a perceptual illusion (involving a failure to integrate features) as a perceptual error. Indeed, Mathes et al. (2014) found that theta power increased during the occurrence of the perceptual illusion of motion in bistable figures. However, the literature in this type of paradigm importantly supports the relationship between theta-band with conflict resolution or the coherence of object perception instead of perceptual illusions.

A further fundamental role of theta involves the cognitive process of memory. This frequency band plays a crucial role in both long-term memory and working memory (Klimesch et al., 2010; Sauseng et al., 2010). In addition, the theta band is closely linked to memory encoding (Roux & Uhlhaas, 2014; Sammer et al., 2007; Sauseng et al., 2010) and the generation of false memories/recalls (Mapelli & Özkurt, 2019; Sweeney-Reed et al., 2012).

The theta-band also plays an important role in the coordination and communication of information between different and distant brain regions (von Stein & Sarnthein, 2000), as well as in the maintenance of integrated information (Kayser et al., 2012).

In summary, because of a perceptual illusion is a type of error, the most relevant information for the context of this thesis would be the association of theta frequency with error detection or the generation of false memories (Mapelli & Özkurt, 2019). This frequency band has also been associated with attention (Başar-Eroglu et al., 1992; Fiebelkorn & Kastner, 2019), memory encoding (Roux & Uhlhaas, 2014; Sammer et al., 2007; Sauseng et al., 2010) or the communication of different cortical networks (Kayser et al., 2012). The role of brain oscillations in brain connectivity is not exclusive of the theta-band; as it will be reviewed below, the alpha, beta, and gamma bands also play a similar role in this context (Fiebelkorn et al., 2018; Fiebelkorn & Kastner, 2019; Fries, 2005; Rohenkohl et al., 2018). In section 3.2.5 of this chapter, this communicative function will be explored in detail, analyzing different approaches and emphasizing the unique contributions of each frequency band.

3.2.2 The alpha-band

As indicated above, the alpha band was one of the first oscillations to be discovered and studied (Berger, 1929; Pfurtscheller et al., 1996). Currently, this frequency band has been associated with the optimal attentional state (Lange et al., 2014; Romei et al., 2008), consciousness (Palva & Palva, 2007), visual perception (VanRullen, 2016), as well as cortical excitability (Romei et al., 2008). Decreased alpha band power has been related to attentional optimal states (Lange et al., 2014; Romei et al., 2008) or increased cortical excitability (Romei et al., 2008), while changes in its phase are linked to consciousness (Palva & Palva, 2007). On the other hand, several studies have shown that the alpha-band exhibits modulations even before stimulus presentation, which are related to preparatory states that enhance detection (Ergenoglu et al., 2004; Wutz et al., 2018) and discrimination processes (Hanslmayr et al., 2007; van den Berg et al., 2016; van Dijk et al., 2008).

More recently, the alpha-band has been related to the inhibition of irrelevant (distracting) information (Capilla et al., 2014; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007a; Klimesch, 2012; Lange et al., 2014; Min et al., 2008;

Min & Herrmann, 2007; Schroeder et al., 2018). Alpha power is usually enhanced at ipsilateral posterior electrodes (e.g., if the target stimulus appears on the left, alpha is enhanced in left hemisphere electrodes). In parallel, decreased alpha power at contralateral parieto-occipital electrodes (opposite hemispheric location to the target location) has been related to spatial attention (Busch & VanRullen, 2010; Capilla et al., 2014; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006a).

Consistent evidence has suggested that spatial attention is important during the feature integration (Cohen & Rafal, 1991; Grubb et al., 2013; Montaser-Kouhsari & Rajimehr, 2005; Prinzmetal et al., 1986; Yeshurun & Rashal, 2010), therefore, it is expected to observe modulations in the alpha-band related to the correct or incorrect integration of features. Some studies have observed a causal relationships between the alpha-band and feature integration using transcranial magnetic stimulation (Müller et al., 2015; Zhang et al., 2016, 2019, 2020).

In short, the alpha-band has been extensively studied in Cognitive Neuroscience and has been closely related to attentional processes. It has also been related to the process of feature integration, although, as we will review below, other frequency bands have also been related to feature integration (see section 3.2.4).

3.2.3 The beta-band

The beta-band is widely recognized for its close association with the generation of motor responses (Engel & Fries, 2010). However, its role in the feature integration, attention, or consciousness is considerably limited. The role of the beta-band in feature integration is related to the number of stimuli to integrate rather than to the correct or incorrect integration of features. Beta-band power decreases in parietal regions as the number of features to integrate increases (Zaretskaya & Bartels, 2015). In contrast, in illusory motion paradigms, the beta-band increases during perceptual switching (Shafritz et al., 2002a).

On the other hand, increased beta-band power has been associated with spatial attention (Buschman & Miller, 2007; Fiebelkorn et al., 2018; Fiebelkorn & Kastner, 2021). Recently, it has been proposed that the relationship between beta-band and spatial attention is related to inhibitory mechanisms. It has been proposed that the beta band might allow for a flexible relationship between exogenous and endogenous selection. I.e., the presence of beta activity allows the inhibition of exogenous (bottom-up) processes, enhancing endogenous (top-down) processes to resolve a conflict (Dubey et al., 2023).

In relation to feature integration, this flexible role between exogenous and endogenous mechanisms may be relevant. As indicated in section 3.2.1, the beta-band, along with other oscillatory frequencies, allows the efficient communication between different brain regions. There is plenty of evidence supporting that beta-band sends top-down feedback signals and, at the same time, could facilitate bottom-up feedforward brain communication (Bastos et al., 2014; Lee et al., 2013; Michalareas et al., 2016; Richter, Thompson, et al., 2017; Richter et al., 2018;

Veniero et al., 2021). This communicative role is further explained in Section 3.2.5.

The beta-band has been strongly related with motor processes (Engel & Fries, 2010; Tzagarakis et al., 2010) and also with spatial attention (Buschman & Miller, 2007; Fiebelkorn et al., 2018; Fiebelkorn & Kastner, 2021). Regarding perceptual consciousness, the beta band has been associated with perceptual switching, but not with the content of consciousness per se (Engel & Fries, 2010; Smith et al., 2006). To our knowledge, the beta band has not been associated with feature integration, but the optimal communication between different brain regions could be indirectly involved in the correct or

3.2.4 The gamma-band

The gamma band is widely recognized for its close relation to complex cognitive processes, such as consciousness (Burgess & Ali, 2002; Crick & Koch, 1990; Panagiotaropoulos et al., 2012; Rieder et al., 2011; Schurger et al., 2006) or attentional selection mechanisms (Gruber et al., 1999; Keil & Müller, 2010; Strüber et al., 2000). Furthermore, it has been related to the processing of novel stimuli (Bauer et al., 2014; Engel et al., 2001; Engel & Fries, 2010; Rohenkohl et al., 2018), and it is modulated by task difficulty (Senkowski & Herrmann, 2002; Tamura et al., 2017).

The gamma-band has also been associated with working memory (Herrmann, Lenz, et al., 2004; Herrmann, Munk, et al., 2004; Miller et al., 2018). Gamma band power increases when the working memory load is higher (Bastos et al., 2018; Honkanen et al., 2015; Howard, 2003; Lundqvist et al., 2011; Miller et al., 2018; Roux & Uhlhaas, 2014).

Additionally, the gamma-band has been considered a crucial marker of feature integration (Singer, 2013; Singer & Gray, 1995; Tallon-Baudry, 2009; Tallon-Baudry & Bertrand, 1999). Gamma activity increases when the number of features to integrate increase (Honkanen et al., 2015; Keil & Müller, 2010; Morgan et al., 2011; Vidal et al., 2006). Moreover, gamma activity increases when the integration process occurs correctly (as compared to incorrect integration) (Bertrand & Tallon-baudry, 2000; Buschman & Miller, 2007a; Phillips et al., 2012; Phillips & Takeda, 2009; Vidal et al., 2006).

In short, the gamma-band is associated with various high-level cognitive functions like attention, consciousness, memory, and information integration (Herrmann, Munk, et al., 2004; Miller et al., 2018; Rieder et al., 2011; Singer, 2013). The gamma-band also serves as a crucial bottom-up communication mechanism between different brain regions during visual perception (Richter, Thompson, et al., 2017), indicating its importance in visual processing and feature integration. For further details, refer to Section 3.2.5.

3.2.5 Cross-frequency communication

Electrophysiological activity is generated in large sets of long-range neurons, whose activity is dynamic (Breakspear et al., 2010; Klausberger et al., 2003; Traub et al., 1996). These sets of neurons are in constant communication establishing functional brain network (Stankovski et al., 2017). There are different approaches to analyzing this communication. The cross-phase-phase coupling (Varela et al., 2001), the cross-phase-power coupling (Canolty et al., 2006), and the cross-frequency-power-power correlation (Bengson et al., 2012; Mazaheri & Jensen, 2010; Popov et al., 2018).

In different cognitive processes such as visual perception (Carrasco, 2011), attentional processing (Siegel et al., 2008) or feature integration (Hochstein & Ahissar, 2002) the existence of a hierarchy between feedforward (bottom-up) and feedback (top-down) processes has been demonstrated. The optimal working of feedforward and feedback processes allows perception to occur successfully. Theta and gamma activity are generally related to bottom-up processes, whereas alpha and beta activity are more related to top-down processes (Bastos et al., 2014; Buschman & Miller, 2007; Michalareas et al., 2016; Richter, Thompson, et al., 2017; Richter et al., 2018; von Stein & Sarnthein, 2000).

In the literature, the coupling between theta and gamma has been related to feature binding (Köster et al., 2018), attentional mechanisms (Papaioannou et al., 2022), or encoding working memory (Friese et al., 2013; Heusser et al., 2016; Staudigl & Hanslmayr, 2013). Coupling between theta and beta is related to enhanced executive control and increased vigilance state (Angelidis et al., 2016, 2018; Putman et al., 2010, 2014; van Son et al., 2019).

The coupling between theta and beta has also been reported using a theta-to-beta ratio (TBR) index. In patients with attention deficit and/or hyperactivity disorder (Lubar, 1991), low TBR values were associated with better functioning of cognitive processes, whereas high values were related to lower connectivity in executive networks and increased connectivity of the default neural network (Son et al., 2019; van Son et al., 2019). On the other hand, coupling between theta and alpha has been associated with the fluctuating nature of attention. This fluctuation is related to worse behavioral performance when “poor” theta phase occurs along with an increase in alpha activity. When a good performance of an attentional task occurs, “good” theta phase and an increase of beta and gamma activity happen (Fiebelkorn et al., 2013, 2018; Fiebelkorn & Kastner, 2020, 2021).

In summary, understanding how brain oscillations and their interaction provides rich information. It helps uncover the underlying neural mechanisms of various cognitive processes and their involvement in achieving a specific goal (e.g., perception). The study of brain oscillations is gaining significant interest in the field of Neuroscience since an individual brain region does not operate in isolation. However, cognitive processes not only involve brain communication. For decades, it has been known that the brain interacts with the rest of the body, particularly in the field of emotions and attention (Lang et al., 1990). Currently, the communication between the brain and the body, both at the cerebral and peripheral levels, is gaining special importance in the research of cognitive processes such as perceptual consciousness (Park et al., 2014), as modulations at these levels have been observed to have a significant impact in the field of perception. In the following chapter, we will delve into the brain and body communication.

Chapter 4: Brain-body interactions

4.1 Introduction to the pathways of brain-body communication

In the field of Cognitive Neuroscience, it is common to explore the neural basis of different cognitive processes by focusing on techniques that only take into account the activity of the central nervous system (CNS) (e.g. EEG, MEG, fMRI). However, this perspective is currently undergoing a major shift, as more attention is drawn to the fact that cognitive processes do not occur in an isolated brain (Craig, 2009; Critchley et al., 2004; Critchley & Harrison, 2013; Lang et al., 1990; Park et al., 2014). It is well recognized in the literature that in different cognitive processes and emotions, the central and peripheral nervous systems (PNS) constantly communicate with each other (Craig, 2009; Lang et al., 1990; Park et al., 2014; Reisenzein et al., 1995). The PNS is further divided into the Somatic Nervous System (SNS) and the Autonomic Nervous System (ANS). While the SNS is responsible for sending sensory and motor information to the CNS, the ANS regulates involuntary functions of the organism such as heartbeat, digestion, or respiration. Both systems are composed of afferences, which carry information from the PNS to the CNS, and efferences, which carry information from the CNS to the PNS (Ripoll, 2010; Vila & Guerra, 2010). The ANS comprises two systems: sympathetic and parasympathetic. The sympathetic branch is in charge of distributing the organism's resources (e.g. blood and glucose) to more external areas of the body to emit a visible behavior (e.g.

escape behavior), while the parasympathetic system distributes these same resources to the internal part of the body (organs). Both branches, sympathetic and parasympathetic, constantly send signals to each other to maintain homeostasis in the organism. Homeostasis does not only dependent on the activity of the sympathetic and parasympathetic systems, it is also needs constant communication between the brain and the rest of the organism (Canales-Johnson et al., 2015; Craig, 2002; Critchley & Harrison, 2013; Lang et al., 1990; Park & Tallon-Baudry, 2014; Reisenzein et al., 1995). This communication maintains the balance between the CNS and PNS through feedback from visceral afferent pathways. Thanks to this balance, the brain builds a representation that facilitates the understanding of emotions, behavior, and different cognitive processes (Critchley & Harrison, 2013; Damasio, 2010). At the brain level, a number of important regions have been found to register this visceral activity. Different authors agree on the relevance of the insula as a "hub" of communication between the brain and the rest of organism (Craig, 2009; Critchley et al., 2004; Critchley & Harrison, 2013; Park et al., 2018; Park & Tallon-Baudry, 2014). As seen in Figure 4.1, Critchley & Harrison (2013) described two PNS-CNS communication pathways: an indirect visceral pathway (pink color) and a direct pathway coming from the spinal cord (green color). Both pathways communicate with the nucleus of the solitary tract (NTS), sending information to the thalamus, which, in turn, projects the information to regions of the cortex such as the Posterior Insula (PI), the Anterior Insula (AI), and the Anterior Cingulate Cortex (ACC) (Critchley et al., 2004; Critchley &

Harrison, 2013; Menon & Uddin, 2010; Park & Tallon-Baudry, 2014). The ACC is closely related to cognitive functions such as executive attention (Colás et al., 2017, 2018; Egner & Hirsch, 2005; Fan et al., 2005; Miller et al., 2018; Pardo et al., 1990) and perceptual consciousness (Martín-Signes et al., 2018).

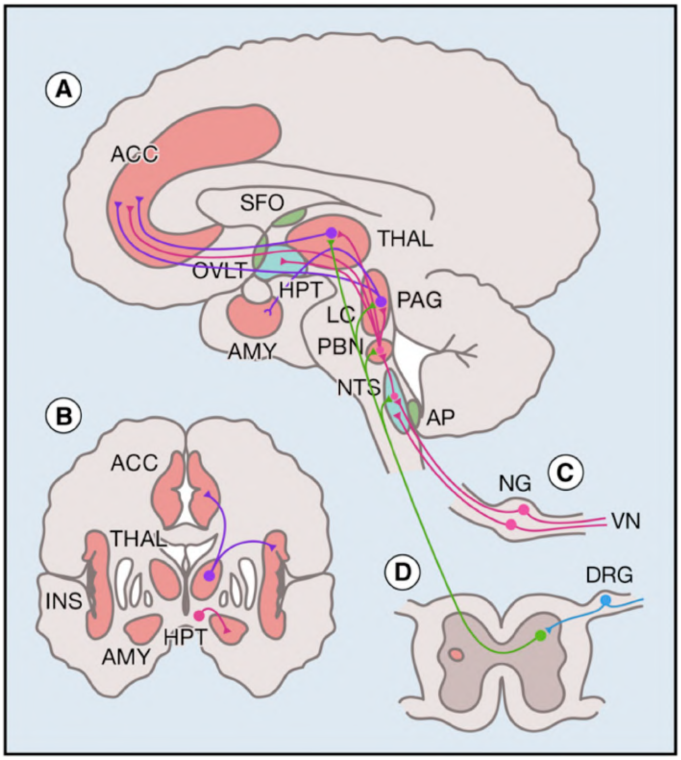


Figure 4.1: Direct (green) and indirect (pink) communication pathways between PNS and CNS. Figure extracted with permission from Critchley & Harrison (2013).

Besides the plethora of central indexes at our disposal that can shed light into the workings of different cognitive processes, a more accurate picture could rise by combining those with physiological measures belonging the PNS. In that sense, one of the most promising approaches comes from the recording of cardiovascular activity which, in turn, yields different measures that can be related to cognition, such as heart rate variability (HRV), heart rate (HR), or heart-evoked potentials (HEP) (Pollatos & Schandry, 2004; Skora et al., 2022).

These indexes are derived from the recording of the electrocardiogram, which is a representation of the electrical events associated to each heartbeat. The heartbeat is usually represented as a waveform known as the PQRST (see Figure 4.2). The different parts of the waveform can be divided into three steps with different associated functions that are produced by electrical potentials. The P wave involves the depolarization of the atrium (auricular contraction); the QRS set represents ventricular depolarization (ventricular contraction), and the T wave indicates the moment of repolarization, i.e., when the ventricles return to the previous state.

In this thesis, we will focus on the heart rate measurement (R-wave distance between consecutive beats). To understand in depth the relationship between heart rate dynamics and brain function, as well as cardiac patterns that could be interpreted as cognitive functions, it is necessary to grasp some fundamental approaches. In particular, the baroreceptor reflex hypothesis (Lacey & Lacey, 1958; Lacey, 1970) and the neurovisceral model of integration (Thayer & Lane, 2009). Since this thesis focuses on advancing knowledge about consciousness at central and peripheral levels, this chapter will conclude by introducing a novel proposal with a specific focused on perceptual consciousness, known as the Subjective Neural Frame (Park et al., 2014).

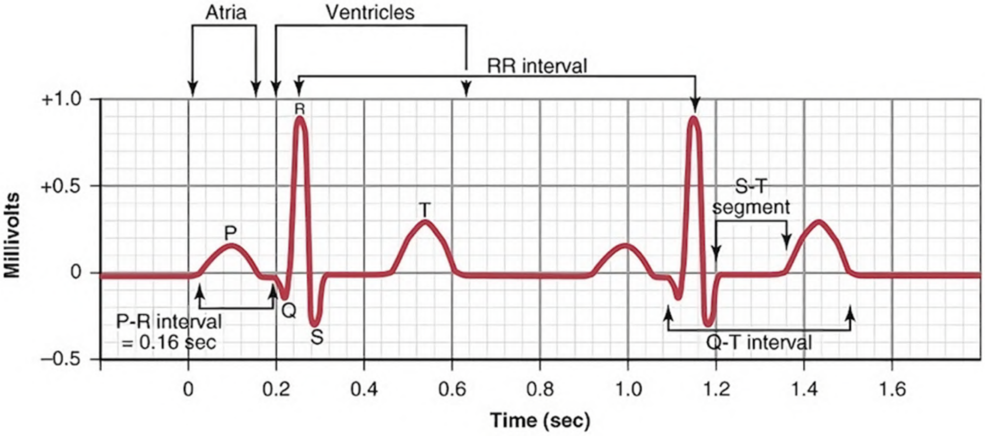


Figure 4.2: Schematic illustration of two heartbeats showing the waveforms PQRST. Figure extracted with permission from Hall (2021).

4.1.1 the baroreceptor hyphotesis

The baroreceptor hypothesis (Lacey & Lacey, 1958; Lacey, 1970) is one of the oldest approaches to explain brain-body communication through cardiac measurements. Besides regulation by the sympathetic and parasympathetic systems, the nervous system also includes the baroreceptor reflex. This reflex is an involuntary mechanism that helps to adjust changes in blood pressure. Its primary purpose is to ensure a continuous and adequate blood flow between the brain and the heart. The control center for this reflex is located in the medulla oblongata. This reflex sends afferent signals that occur during systole (cardiac contraction) resulting in an attenuation of cortical excitability (Duschek et al., 2015; Elbert & Rau, 1995; Lacey & Lacey, 1958; Makovac et al., 2015; Rau et al., 1993; Rau & Elbert, 2001), which would translate into a general inhibitory effect of such neuronal excitability and interfere with external stimulus processing

(Duschek et al., 2013; Elbert & Rau, 1995). This cortical inhibition results in a cardiac acceleration that would impair exteroceptive processing, but enhance the process of performing an action. In contrast, in diastole (cardiac distension), baroreceptor activity would decrease, leading to cardiac deceleration, which would imply greater cortical excitability and, therefore, improved perceptual processing (Skora et al., 2022).

Cortical excitability is closely associated with the concept of neural gain (Kolasinski et al., 2017). Neural gain refers to the constant mapping between input and output signals (from external stimuli and sensory organs, respectively), where the probability of a given output is linked to the strength of a given input. The gain concept can be understood as an amplification of the brain communication that would modulate the success of information processing. Whether the value of this gain increases, it enhances the processing of the stimulus being focused on while diminishing attention to distractor or irrelevant stimuli, which should not be processed (Eldar et al., 2013). This modulation occurs at the brain level, affecting cognitive processes such as attention, learning, sensory processing, and multimodal integration (Ferguson & Cardin, 2020). The relationship between the baroreceptor reflex and cortical excitability may reflect a global gain modulation that influences the organism's internal signal accuracy and, in turn, impacts the balance between exteroceptive and interoceptive signal accuracy (Skora et al., 2022).

4.1.2 Thayer & Lane Model

The neurovisceral integration model supports the idea that the brain and the heart communicate through direct and indirect pathways (see Figure 4.1 from Critchley & Harrison, 2013). This model suggests that, besides its implications for regulatory processes, this communication is also related to different cognitive processes (R. Smith et al., 2017; Thayer & Lane, 2009).

Unlike the previous model, Thayer & Lane's model (2009) emphasizes the role of the prefrontal cortex (PFC) in these processes. Together with the amygdala, the PFC is part of an inhibitory circuit that interacts with through an indirect pathway: the vagus nerve (R. Smith et al., 2017; Thayer & Lane, 2009). This model assumes the inhibitory role of prefrontal activity on the amygdala via a GABAergic neuronal pathway. This inhibition leads to either a decrease in HR or an increase in HRV given the excitatory effect of the amygdala on cardiac activity. Conversely, if the amygdala is not inhibited by frontal structures, HR would increase and HRV would decrease.

In emotional processing, the frontal cortex is inhibited in situations of fear/threat, increasing the amygdala sympathetic branch activity, and affecting cardiovascular activity. In cognitive processing, the opposite pattern is observed: performance enhancement in various tasks is accompanied by a lower heart rate, larger inhibition of frontal areas and their inhibitory connections with the amygdala.

This model highlights that the communication between the brain and the body implies greater flexibility in the system, allowing for better adaptation to the external environment (Lechinger et al., 2015; Smith et al., 2017; Thayer & Lane, 2009).

4.1.3 The neural subjective frame

As seen in previous chapters of this thesis, there are different models of perceptual consciousness, which attempt to explain the subjective experience of perceiving a stimulus (Baars, 2002; Dehaene & Changeux, 2011b; Lamme & Roelfsema, 2000; Melloni et al., 2023; Tononi, 2004). Imagine two people sunbathing in the same moment and place. The exposition to the warm weather is exactly the same, but the experience of feeling the temperature, for example in their faces, is different. This feeling is difficult to understand since it depends on the physiological state of each person. One of the most recent approaches that takes into account these subjective aspect of conscious experience is the neural subjective framework (Park & Tallon-Baudry, 2014).

This approach holds special relevance because it emphasizes the importance of constant communication between the brain and the body for cognitive processes like consciousness, although the proper brain-body communication is not enough for conscious experience (Park & Tallon-Baudry, 2014). This concept implies a constant updating between proprioception ("I perceive") (Blanke, 2012) and specific neural maps derived from visceral information about the internal state of the organism (Critchley & Harrison, 2013; Damasio, 2010). Both systems, under constant monitoring, would give rise to the conscious experience (Park & Tallon-Baudry, 2014). Similar to the previously described models, the subjective neural frame approach emphasizes the role of afferent and efferent connections in brain-organism communication (Beissner et al., 2013; Critchley & Harrison, 2013; Mayer, 2011; Park & Tallon-Baudry, 2014; Richter et al., 2017; Saper, 2002; Thayer et al., 2012). The afferents are responsible for communicating the state of the organism to the brain. This model specifically focuses on the HEP to explore the neural subjective frame, as this measure of cardiac and brain activity has shown modulation by task relevance, cardiac self-perception, or access consciousness (Montoya et al., 1993; Park et al., 2014; Schandry & Weitkunat, 1990). Recently, various studies have shown that HEP indeed serves as a neural marker of brain-organism interactions, involving the insula (both anterior and posterior) and central and posterior frontal regions (Babo-Rebelo, Richter, et al., 2016; Babo-Rebelo, Wolpert, et al., 2016; Canales-Johnson et al., 2015; Park et al., 2014, 2018; Sel et al., 2016). Different cognitive processes have been linked to various brain regions, but they all converge on one common area: the insula. Specifically, the role of the anterior insula is highlighted as a hub of interoceptive processes and an error detector in brain-organism communication at the subjective level (Craig, 2003, 2009; Damasio & Carvalho, 2013; Oppenheimer et al., 1992; Park & Tallon-Baudry, 2014; Seth, 2013). Currently, the relevance of the neural subjective frame is difficult to demonstrate at the experimental level, although it gains support from a series of premises that lend it credibility. The first premise concerns the repeated communication through afferent and efferent pathways between the brain and organism (Critchley & Harrison, 2013; Hansen et al., 2003; Lacey & Lacey, 1978; Lacey, 1970; Park et al., 2018; Park & Tallon-Baudry, 2014; Thayer & Lane, 2009). The second premise is that cardiac activity has consistently been associated with emotions, as well as other perceptual processes without emotional content (Crone et al., 2005; De Pascalis et al., 1995a; Jennings et al., 2009; Lacey, 1972; Motyka et al., 2019; Park et al., 2014; Ribeiro & Castelo-Branco, 2019; Skora et al., 2022; Sokolov, 1963; van der Veen et al., 2004; Vila et al., 2007). The third premise is that alterations in this cardiac activity can affect behavioral performance (Park et al., 2018; Pollatos et al., 2016; Ronchi et al., 2015).

4.1.4 Cognitive processes modulations associated with cardiac changes

The sympathetic and parasympathetic systems operate continuously to adapt the physiological response and/or behavioral response commensurate with the demands of the external environment (Lechinger et al., 2015; Smith et al., 2017; Thayer & Lane, 2009). The joint action translates into transient changes in heart rate (Skora et al., 2022) that, in general, involve a cardiac deceleration-acceleration pattern.

Cardiac deceleration (increased time lag between consecutive R-waves of consecutive beats) has been related to orienting to salient stimuli (Lacey & Lacey, 1977; Lacey, 1972; Sokolov, 1963; Vila et al., 2007), high attentional demands (De Pascalis et al., 1995; Dehais et al., 2011; Ribeiro & Castelo-Branco, 2019; Salvia et al., 2012; Zimmer et al., 1990), preparatory/anticipatory processes related to alertness, orienting and inhibitory functions (Jennings et al., 2009; Jennings & van der

Molen, 2005; van der Veen et al., 2004), response speed (Jennings & Wood, 1977; Reyes del Paso et al., 2015), detection processes (Barry & Tremayne, 1987; Motyka et al., 2019; Park et al., 2014), efficient sensory and motor processing (Ribeiro & Castelo-Branco, 2019), and error perception (Crone et al., 2003, 2005; Danev & de Winter, 1971; Fiehler et al., 2004; Skora et al., 2022; van der Veen et al., 2004; Wessel et al., 2011).

Regarding the subsequent cardiac acceleration (shorter time lag between consecutive R-waves), this has been related to the motor execution of a response (Börger & van der Meere, 2000; Graham & Clifton, 1966; Jennings & Wood, 1977; Obrist, 2012), reduced attention to external events, enhanced action tendencies and behavioural readjustment (Skora et al., 2022; Vila et al., 2007; Vila & Guerra, 2010), increased executive demands of the task (Backs & Seljos, 1994; Chang & Huang, 2012; Duschek et al., 2009; Luque-Casado et al., 2016; Mathewson et al., 2010), or conscious detection (Park et al., 2014).

To put in briefly, cardiac deceleration, in general, has been associated with stimulus detection (Barry & Tremayne, 1987; Motyka et al., 2019; Park et al., 2014), whereas cardiac acceleration has generally been linked to the response and/or action associated to stimulus detection (Börger & van der Meere, 2000; Obrist, 2012; Park et al., 2014; Vila et al., 2007).

To sum up, this introductory chapter provides a general theoretical background to understand how the communicates with the rest of the organism and how this communication affects cognition and emotion. We present certain cognitive interpretations related to HR, which are relevant within the main framework of this thesis: attention and consciousness.

Motivation and aims

Chapter 5: Motivation, research aims, and significance

5.1 Motivation

Through the years, perceptual consciousness has been one of the most debated cognitive processes in the field of Cognitive Neuroscience. At present, no consensus has been reached on its definition, the way to measure it, how to dissociate it from other cognitive processes, as well as its neural basis. Block, (2011) proposed the distinction between access consciousness (the ability to report a perceived stimulus) and phenomenological consciousness (the subjective experience of perception, which generally overflows access consciousness). Furthermore, there is much debate about whether the attentional system serves as a "gateway" to perceptual consciousness or whether, on the contrary, consciousness and attention can be dissociated.

In our research group, we have studied the importance of attention in perceptual consciousness both at the behavioral level (Botta et al., 2014, 2017; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012; Colás et al., 2017; Kusnir et al., 2011), and at the neural level, using measures of the central nervous system (CNS) such as EEG (Chica, Botta, et al., 2012; Chica et al., 2010), fMRI (Chica et al., 2018; Chica, Paz-Alonso, et al., 2013; Martín-Signes et al., 2018) and transcranial magnetic stimulation (TMS) (Chica, Valero-Cabre, et al., 2014; Martín-Signes et al., 2019, 2021). The scientific evidence on the interaction between attention and consciousness at the CNS level is more extensive than at the PNS level. The interest in the study of the PNS and its relationship with cognitive processes is long-standing. However, most research has focused on emotions (Seth, 2013; Van Diest et al., 2009; Vila & Guerra, 2010) rather than cognitive processes such as working memory, attention, or perceptual consciousness (Thayer & Lane, 2009). Recently, interest in how consciousness modulates the PNS activity is growing (Park et al., 2014; Park & Tallon-Baudry, 2014; Tallon-Baudry et al., 2018).

In the context of access consciousness, phasic alerting and exogenous orienting have been shown to behaviorally enhance the conscious perception of a near-threshold stimulus (Botta et al., 2017; Chica et al., 2010; Chica, Paz-Alonso, et al., 2013; Chica et al., 2016a, 2018; Chica & Bartolomeo, 2012). As indicated above, these interactions between access consciousness and attention have been extensively explored at the CNS level, demonstrating the relevance of the fronto-striatal network for alerting –Chica et al., (2016), and fronto-parietal network for orienting –Chica et al., (2013). However, at the PNS level, the evidence is sparse. Recently, the research group led by Catherine Tallon-Baudry has shown the importance of studying the PNS in relation to access consciousness (Park et al., 2014; Tallon-Baudry et al., 2018). When consciously perceiving a stimulus at the threshold of consciousness, cardiac deceleration was enhanced when that stimulus was perceived, as compared to non-perceived stimuli. However, no modulations related to attentional manipulations were explored (Park et al., 2014). This study served as the inspiration to begin this doctoral thesis. In the first experimental study, we explored the interplay between phasic alerting and consciousness while recording heat rate to 1) replicate the results of Park et al., (2014) and 2) further explore the influence of the alerting system in conscious perception and its relation to heart rate modulations.

The study of phenomenal consciousness is more complex. A relevant property of this type of consciousness is that it involves a subjective experience of great perceptual richness, which often contains inaccurate information. Therefore, one way to approach the study of phenomenal consciousness is by analyzing these perceptual errors, commonly known as perceptual illusions. To achieve this, in this thesis we employ a feature integration paradigm in which the stimulus is always accessible, but its features (color and shape) can be correctly or incorrectly combined. According to Anne Treisman's (1996) theory, feature integration can fail because of the overload of the attentional system. Some studies have shown that divided attention (Aru et al., 2018; Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982), the "absence" of spatial attention (Briand, 1998; Cohen & Rafal, 1991; Grubb et al., 2013; Montaser-Kouhsari & Rajimehr, 2005; Pelli et al., 2007; Prinzmetal et al., 1986; Yeshurun & Rashal, 2010) or incorrect expectancies (Aru et al., 2018; Aru & Bachmann, 2017; de Gardelle et al., 2009; Harris et al., 2011; Moore et al., 1998; Wokke et al., 2013) impair integration processes, increasing errors. A further way to explore how and when this integration process fails at the CNS level is to study brain dynamics through brain oscillations. The brain naturally contains these oscillations, which change depending on cognitive processing or when it is necessary to communicate with different brain regions to perform a given task (Cohen, 2015). Recent studies have associated alpha (Ghiani et al., 2021; Müller et al., 2015; Zhang et al., 2019) and gamma oscillations (Honkanen et al., 2015; Keil & Müller, 2010; Morgan et al., 2011; Tallon-Baudry, 2009; Tallon-Baudry et al., 1996; Vidal et al., 2006) with the process of feature integration. However, no studies have explored so far the involvement of different brain oscillations during the integration process.

Additionally, studies exploring the role of the PNS in perceptual illusions or in the cognitive processes that modulate them are almost absent in the literature. There is scientific evidence supporting the relationship between PNS and error perception when receiving feedback (O'Connell et al., 2007; Wessel et al., 2011). Specifically, it has been observed that heart rate tends to decelerate when an error is perceived (Crone et al., 2003; Danev & de Winter, 1971; Fiehler et al., 2004; van der Veen et al., 2004; Wessel et al., 2011). Yet, this deceleration also occurs when correctly detecting stimuli (Barry & Tremayne, 1987; Motyka et al., 2019; Park et al., 2014) or when the response to that stimulus is efficient (Graham & Clifton, 1966; Jennings et al., 2009; Jennings & van der Molen, 2005; Lacey & Lacey, 1977; Skora et al., 2022). Therefore, the relationship between the PNS activity and feature integration is still unexplored.

5.2 Research aims

The main goal of this thesis was to explore the interactions between attention and perceptual consciousness, as well as to investigate this relationship in terms of brain-body modulations. To achieve this aim, we used behavioral measures, measures that record CNS activity such as EEG, and measures that record peripheral activity such as EKG. In the first study of this thesis, we explored how HR and skin conductance (SC) are modulated by phasic alertness and access consciousness (Chapter 6). Subsequently, we opened a new line of research that explores phenomenological consciousness through a feature integration paradigm. In Chapter 7 and 9, we developed the paradigm to assess how different attentional systems (executive system, spatial orientation, and phasic alertness), as well as top-down expectancies, modulate perceptual illusions. Finally, we include two studies of central (Chapter 8) and peripheral (Chapter 9) measures showing brain and cardiac dynamics during the integration process.

Chapter 6: Heart-rate modulations reveal attention and consciousness interactions

In this first study, we manipulated phasic alerting in a conscious detection task, and aimed to replicate the results observed in previous behavioral studies; that is, we expect an increase in the number of perceived targets following a warning signal (compared to no-signal trials). Second, we explored cardiac modulations (HR measures) and SC produced by phasic alerting and access consciousness.

Chapter 7: Attention does not always help: the role of the expectancy, divided, and spatial attention on illusory conjunctions

This study had several goals:

1) To develop an experimental paradigm in which an adequate percentage of perceptual illusions occurred (over 30% of total trials).

2) To explore how manipulations of divided attention (executive system), and endogenous and exogenous attentional orienting affect the feature integration process (3 different behavioral studies).

3) To explore the contribution of top-down expectancies in feature integration. This manipulation was conducted by adding, at the end of the experiment and unexpectedly, a different feature in the target stimulus. After the experimental phase, participants were categorized as aware or not aware of this manipulation thanks to a structured interview.

Chapter 8: The role of brain oscillations in feature integration

In order to characterize the brain dynamics of feature integration, an EEG study was conducted. The experimental paradigm included a dual task in which divided attention was manipulated while participants discriminated a target which required the combination of shape and color features. The aim of this study was to explore which frequency bands (theta, alpha, beta, and gamma) were involved in the feature integration process. Top-down expectancies were also manipulated to explore the oscillatory modulations observed in those participants who were aware of the expectancy manipulation and for those who were not.

Chapter 9: Heart rate modulations during phasic alertness and feature integration

This experiment studied how phasic alertness may (or may not) modulate phenomenal consciousness by using the feature integration paradigm. Likewise, its most important goal was to explore brain-body modulations by means of electrocardiogram (EKG) recording. As in previous chapters, different cardiac modulations were explored between those participants who were aware of the manipulation of top-down expectancies and those who were not aware.

5.3 Statements of significance

There are different models that, over the years, have attempted to provide a unified explanation for the phenomenon of perceptual consciousness (Dehaene & Changeux, 2011b; Melloni et al., 2023; Tononi, 2004). Some of these models have considered attention a prerequisite of consciousness (Chica et al., 2018; Chica, Paz-Alonso, et al., 2013; Dehaene & Changeux, 2011; Petersen & Posner, 2012). Both cognitive processes are highly heterogeneous in nature, which complicates their study, and have make it difficult to extract firm conclusions about their relationship. For example, demonstrating that one type of attention, e.g. endogenous attention, is not necessary for consciousness does not imply that other types of attention, e.g., exogenous attention, are not (Chica, Botta, et al., 2012). Within the field of perceptual consciousness, there is a wide debate about whether conscious experience is rich or limited. Given a certain visual scene, one may have the impression of perceiving most aspects of the environment (i.e. we have the subjective impression of perceiving with great perceptual richness). However, when observers are asked to report what they perceive, their accuracy is very low, limited to a few elements (i.e. the perceptual experience seems to be limited). This could be accounted for the fact that access to specific elements involves the use of mechanisms such as attention or working memory, which would limit the amount of information that humans are able to report. On the other hand, there is no consensus about which models better explains perceptual consciousness. The IIT of Tononi et al., (2016) proposes that consciousness depends on the amount of integrated information, represented as Φ (phi), in a specific network, mainly located in the posterior cerebral cortex. According to this theory, it is proposed that a specific value of Φ determines the coherence of information, giving rise to the conscious experience. On the other hand, the GNWT of Dehaene & Changeux, (2011) postulates that consciousness emerges after the ignition phenomenon, produced by the interconnection between higher-order sensory, parietal, and frontal areas. While IIT does not consider the attentional system to be of great relevance in perceptual consciousness, GNWT does consider attention as a necessary mechanism for consciousness.

In different studies, it has been shown that perceptual consciousness is enhanced by the attentional system (Botta et al., 2017; Chica, Botta, et al., 2012; Dehaene & Changeux, 2011b; Kusnir et al., 2011). This interaction between attention and consciousness could depend on the type of consciousness (access vs. phenomenological) and the type of attention (executive system, orienting, alerting, or perceptual expectancies). At the brain level, the scientific evidence about attention-consciousness interactions is abundant (Chica, Valero-Cabre, et al., 2014; Chica et al., 2016; Dehaene & Changeux, 2011; Martín-Signes et al., 2018, 2019; Melloni et al., 2023; Rodríguez-San Esteban et al., 2022). However, scientific evidence on how the PNS participates in this interplay of attention and consciousness is scarce. In this context, the current doctoral thesis continues the experimental line of the research group, related to access consciousness, but with special emphasis on the modulations produced at the peripheral level. On the other hand, it develops a new experimental line related to phenomenological consciousness by using a feature integration paradigm. The studies of this thesis found that feature integration is modulated by spatial orienting and top-down expectancies, and not so much by phasic alerting or the executive system (divided attention). Furthermore, through the study of brain oscillations, we observed the contribution of several cognitive processes that could fail and give rise to perceptual illusions during feature integration. Finally, and in harmony with the first experimental study (chapter 6), we add results of peripheral measurements showing differences in the feature integration process, which, again, highlight the relevance of the study of the PNS in different cognitive processes.

In summary, this doctoral thesis aims at expanding the evidence about the relationship between perceptual consciousness and attention. It highlights the role of different recording techniques (e.g. EEG and EKG) to better understand the contribution of both the central and peripheral nervous systems to cognition. The evidence collected throughout this doctoral thesis suggests that access and phenomenal consciousness are distinctly affected by different attentional manipulations. While phasic alertness interacts with access consciousness, it does not interact with phenomenological consciousness. In the case of the spatial orienting system, both endogenous and exogenous orienting modulate phenomenological consciousness, while only exogenous orienting modulates access consciousness (Chica, Lasaponara, et al., 2011; Cobos & Chica, 2022). In the present studies, the executive system does not modulate phenomenological consciousness (Cobos & Chica, 2022), while its manipulation interferes with some aspects of access consciousness (Colás et al., 2018; Martín-Signes et al., 2018). Moreover, we observe a clear effect of top-down expectancies on phenomenological consciousness (Cobos & Chica, 2022). Brain dynamics show that errors associated with phenomenological consciousness may be due to the intervention of different cognitive processes such as preparatory attentional processes, perceptual representations, or expectancies. Furthermore, this thesis demonstrates the role of the PNS in both access consciousness and phenomenological consciousness. The research presented in this doctoral thesis represents a modest advance in the field of consciousness and attention, but it also opens many future perspectives focused on improving the understanding of this complex process such as perceptual consciousness, both in the basic experimental and applied fields.

Experimental studies

Chapter 6: Heart-rate modulations reveal attention and consciousness

The content of this chapter has been published in Cobos, M. I., Guerra, P. M., Vila, J., & Chica, A. B. (2019). Heart-rate modulations reveal attention and consciousness interactions. *Psychophysiology, 56*(3), e13295.

6.1 Abstract

Our environment is constantly overloaded with information, although we cannot consciously process all the stimulation reaching our senses. Current theoretical models are focused on the cognitive and neural processes underlying conscious perception.

However, cognitive processes do not occur in an isolated brain but in a complex interaction between the environment, the brain, and the organism. The brain-body interaction has largely been neglected in the study of conscious perception. The aim of the present study was to explore if HR and SC are modulated by the interaction between phasic alertness and conscious perception. We presented near-threshold visual stimuli that could be preceded by an alerting tone on 50% of the trials. Behaviorally, phasic alerting improved perceptual sensitivity for detecting a near- threshold stimulus (along with changes in response criterion). Following the alerting tone, a cardiac deceleration-acceleration pattern was observed, which was more pronounced when the near-threshold stimulus was consciously perceived in comparison with unconsciously perceived stimuli. SC results further showed some degree of subliminal processing of unseen stimuli. These results reveal that cardiac activity could be a marker of attention and consciousness interactions, emphasizing the need for taking into account brain-body interactions for

current theoretical models of consciousness.

6.2 Introduction

Conscious perception has been a topic of great interest since even before psychology was born as a discipline. Its scientific study has been especially challenging because of the difficulty of disentangling conscious experience from verbal reports. Block's (2011) characterization of “phenomenal” and “access” consciousness captures this distinction between the experience of seeing (phenomenal consciousness) and the ability to report this perception (access consciousness).

Another challenge in the study of conscious perception is the characterization of the mechanisms that allow the selection of information. From all the information reaching our senses, only a small fraction can be consciously reported. Attention has been postulated as one of the mechanisms allowing this selection. According to Petersen & Posner, 2012, the attentional system can be divided into three anatomically and functionally distinct subsystems: alerting, orienting, and executive control. In this study, we will focus on the alerting system, which maintains an optimal vigilance state (tonic alerting) or increases the activation of the organism for a brief period of time following a salient event (phasic alerting; Petersen & Posner, 2012). Phasic alerting has been demonstrated to improve perceptual sensitivity for detecting targets presented near the threshold of consciousness (Botta et al., 2017; Kusnir et al., 2011; Petersen et al., 2017), producing its effects through a frontostriatal network (Chica et al., 2016).

Until now, current theoretical models of conscious perception have mainly focused on cognitive and neural processing (Dehaene & Changeux, 2011; Lamme et al., 2000; Tononi, 2012; Zeman, 2001). However, cognitive processes do not happen in an isolated brain, and thus it is important to understand the interaction between the brain and the environment, and between the brain and the organism (Craig, 2009; Critchley et al., 2004; Critchley & Harrison, 2013; Park & Tallon-Baudry, 2014). Even though brain-body interactions have received some attention in the study of self-awareness (Tsuchiya & Adolphs, 2007) and emotions (Seth, 2013), only recently have Tallon-Baudry and colleagues started to explore the relationship between body signals and consciousness (Park et al., 2014; Park & Tallon-Baudry, 2014). The central nervous system monitors the state of the internal organs (e.g., the heart) to regulate the homeostatic state of multiple biological parameters. The heart has a group of mechanosensory neurons that send information reflecting fast events (Armour & Ardell, 2004; Park et al., 2014) through ascending afferent pathways to the central nervous system. According to Park & Tallon-Baudry, (2014), the continuous updating of these neural maps about the internal state of the body gives rise to the so-called neural subjective frame, a first-person experience of conscious perception.

Physiological studies have associated cardiac changes with several cognitive processes. For example, following an alerting tone, there is a cardiac deceleration followed by an acceleration (Lacey & Lacey, 1978). While the cardiac deceleration has been associated with preparatory processes, cardiac acceleration has instead been associated with stimulus identification and response preparation

(Vila et al., 2007).

Moreover, the amplitude of the decelerating cardiac pattern has been demonstrated to depend on stimulus relevance (Somsen et al., 2004). In the field of consciousness, Park et al., (2014) demonstrated a cardiac deceleration before a to-be-detected target was presented and acceleration after response delivery. Moreover, conscious perception increased the observed cardiac deceleration as compared to nonconsciously perceived stimuli, especially after participants delivered the motor response to signal their decision.

The objective of the present study is to explore cardiac modulations associated with the interaction between attention and consciousness. We manipulated phasic alertness and measured its impact on the conscious perception of a near-threshold Gabor stimulus (titrated to be consciously perceived on ~50% of the trials). Behaviorally, the alerting tone should increase perceptual sensitivity to detect the near-threshold stimulus (Botta et al., 2017; Kusnir et al., 2011). We expected to observe an increase in the deceleration-acceleration cardiac pattern following the alerting tone. If an interaction between phasic alerting and consciousness were observed, the deceleration-acceleration pattern should be greater for consciously perceived as compared to nonconsciously perceived stimuli, especially following the alerting tone. These data may be important for understanding brain-body interactions in the study of attention and conscious perception.

6.3 Method

6.3.1 Participants

Twenty-six healthy volunteers (16 female, mean age of 23 years, *SD* = 3.5, all right-handed) participated in the experiment in exchange for course credit. All participants were undergraduate students from the Faculty of Psychology (University of Granada), who had not previously participated in similar experiments. One participant was excluded from the sample because his behavioral data were not properly recorded, and a further participant was excluded because she never responded to the objective task (see Procedure). All participants reported having normal or corrected-to-normal vision and audition and had no clinical history of neurological or psychiatric disorders. Signed informed consent was collected before the study, and participants were informed about their right to withdraw from the experiment at any time. The local research ethics committee from the University of Granada approved the experiment, which was carried out in accordance

6.3.2 Apparatus and stimuli

E-prime software was used to control stimuli presentation, timing operations, and behavioral data collection (Schneider et al., 2002). Participants were seated at an approximate distance of 57 cm from the computer screen. At this distance, 1 cm corresponds to 1º of visual angle. All stimuli were presented on a gamma-corrected LCD monitor (17", Benq FP731, 1,024 × 768 pixels) with a refresh rate of 60 Hz. The experimental display consisted of three markers (6º width × 5.5º height) presented on a gray background (luminance = 64.6 cd/m^2). A fixation point (a black plus sign, 0.5º ×

0.5º) was presented within the central marker. The other two markers were presented 11.5º to the right and to the left of the fixation point (distance measured from the center of fixation point to the center of the marker). The target could appear inside one of two lateral boxes, and consisted of a Gabor with a spatial frequency of 4 cycles/degree spatial frequency, a diameter of 3º, and with its inner lines tilted 10º to either the left or the right.

A MATLAB script was used to create 100 Gabor stimuli, with a maximum and minimum Michelson contrast of 0.92 and 0.02, respectively.

Two arrowlike stimuli (<<< or >>>) were presented above and below the fixation point to collect the subjective response (see Procedure).

The alerting tone consisted of a beep burst presented at 97.5 dB. It was presented through headphones (Philips adjustable SHP2000; frequency range of 15–22000 Hz; maximum sensitivity 100 dB; impedance 32 ohm; maximum input power of 500 mW).

6.3.3Psychophysiological variables and apparatus

Psychophysiological recording was accomplished by means of a Biopac System, model MP150, and a PC running AcqKnowledge acquisition software (v. 3.9.1.6). The EKG was obtained by placing three disposable electrodes, filled with hypertonic gel, at Lead II. Frequencies below 0.5 and above 35 Hz were filtered out by means of a Biopac amplifier, model MEC110C. Although our main hypotheses referred to heat rate measures, we also recorded SC, using a Biopac EDA100C amplifier. All signals were acquired at a sampling rate of 2000 Hz.

6.3.4 Procedure

Figure 6.1 shows the sequence and timing of the stimuli in a given trial. Each trial started with a fixation display (493–986 ms). This fixation display was followed by an alerting tone (17 ms) in 50% of the trials. After an interstimulus interval (ISI) varying randomly between 204–306 ms, the Gabor could be presented. On 50% of the trials, no Gabor was presented (catch trials). On the remaining 50% of the trials, the Gabor was equally likely to appear at either the left or the right marker for 34 ms. Therefore, the Gabor could be presented between 714–1,309 ms after onset of the fixation point. Participants were asked to discriminate the orientation of the lines composing the Gabor as fast and as accurately as possible (objective response). Participants used the mouse to respond with their right hand, clicking the left button with their index finger if the lines were oriented to the left, or clicking the right button with their middle finger if the lines were oriented to the right. No response was required when no Gabor was perceived. In previous work (Botta et al., 2017), we asked participants to respond to the objective task even if no Gabor was perceived in order to equate motor preparation requirements for seen and unseen stimuli. However, it was very difficult to ask for an objective response when no tone was presented and no Gabor was perceived given the long jitter interval between trials (the intertrial interval, ITI, varied randomly between 4,012–8,024 ms to allow heart rate, HR, to reach the baseline). The random duration of the ITI and the fixation period made it difficult to estimate the moment in which a response was required.

After the objective response, we presented participants with two arrowlike stimuli, one below and the other one above the fixation point (>>> or <<<). We provided participants with three keys (to be pressed with the left hand): an upper key (*d*, pressed with the middle finger), a lower key (*c*, pressed with the index finger), and the space bar (pressed with the thumb). The upper key always corresponded to the arrow presented in the upper part of the fixation point, while the lower key was associated with the arrow presented in the lower part of the fixation point. Participants were asked to report, as accurately as possible, whether they had seen the target or not. If they had not, they were required to press the space bar. If they had seen the target, they were asked to indicate its location on the screen, left or right, when the arrows were presented. This procedure prevented lateralized response preparation until the arrow display appeared. This response is considered subjective because there is no correct response. Instead, participants indicated their conscious perception of the Gabor (seen or unseen). Participants were required to respond as accurately as possible, with no time pressure.

The experiment consisted of five blocks of 48 trials each, separated by a 2-min pause after each block.

Before the experimental trials, Gabor contrast was manipulated in a separate titration block until participants perceived ~50% of the Gabors presented. During titration, trials were similar to the experimental task except that no tone was presented (fixation point = 493–986 ms; ISI = 204–306 ms; Gabor = 34 ms; objective response = 2,975 ms; subjective response = until response). Titration began with a suprathreshold stimulus (Michelson contrast = 0.184), of which the contrast was manipulated in successive blocks depending on the mean percentage of seen Gabors every 16 trials. After each block, if participants reported seeing 63% or more targets, Gabors of the subsequent lower contrast level (Michelson contrast minus 0.009) were presented during the next block of trials; on the contrary, if the percentage of seen targets was equal to or lower than 38%, the next block of trials used Gabors at the subsequent higher contrast level (Michelson contrast plus 0.009). The titration procedure stopped when Gabor contrast yielded a percentage of seen targets ranging between ≥ 38% and ≤ 63% for two consecutive blocks of trials. This contrast value was used in the experimental task. During titration, participants were required to keep the percentage of false alarms below 20%.

After titration, participants were informed about the procedure used to record the psychophysiological data, including the place of electrode location, the need to clean the skin, and to use electrolytic gel. For HR recording, three disposable electrodes were placed following the Lead II configuration: the negative pole on the right wrist, the positive pole on the left ankle, and ground sensor on the right ankle. This configuration was chosen to optimize the R wave of the ECG. Lead III configuration was used with one male participant (negative pole: left wrist; positive pole: left ankle; ground: right ankle) because he had a bandage on his right arm. For SC, two electrodes were placed in the hypothenar eminence of the left hand.

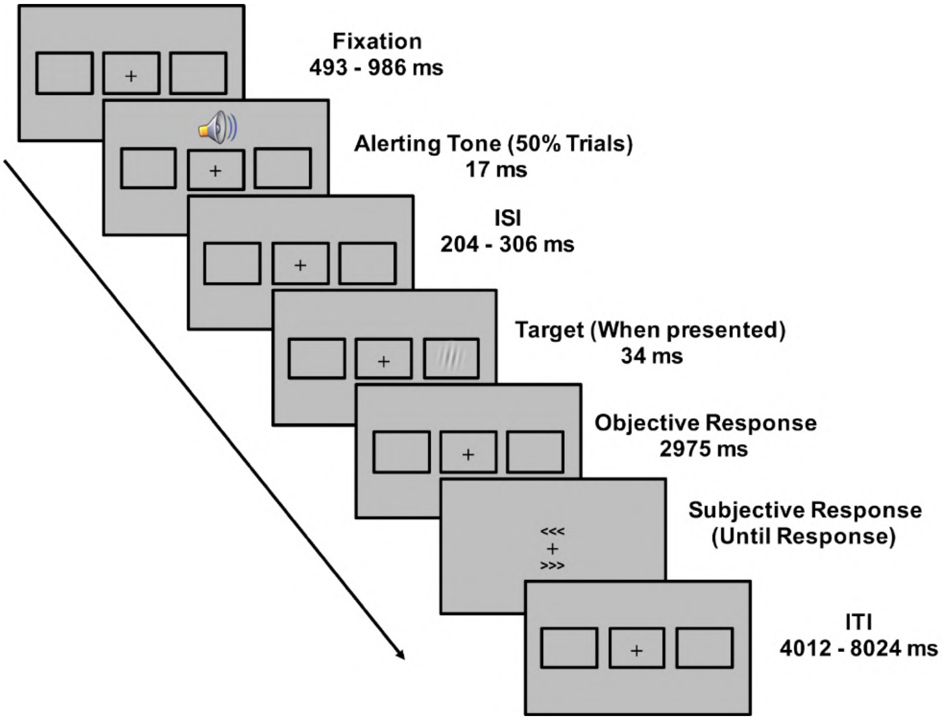


Figure 6.1: Sequence of events in a given trial. In the trial presented as an example, the alerting tone and the Gabor were presented (although in the experiment, there were 50% of the trials without alerting tone, and 50% of the trials without Gabor).

6.3.5 Data reduction and statistical analyses

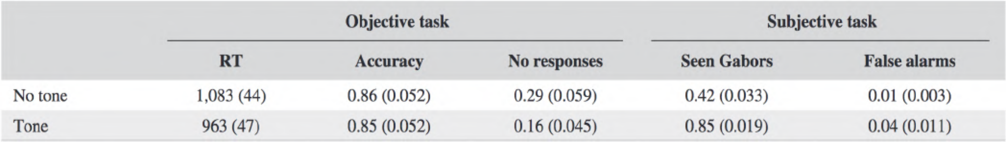
ECGLAB RR software (Vicente et al., 2013) was used to calculate the HR from the EKG. We measured each cardiac period (i.e., the R-R interval) in milliseconds and transformed it into HR in beats per minute. Then, the Kardia software (Perakakis et al., 2010) was used to obtain, for each trial, the weighted average of the HR every 100 ms, for an interval of 5 s (starting with the onset of the fixation point). These HR values were finally transformed into differential scores by subtracting the weighted average of the HR during the 400 ms prior to the presentation of the fixation point. Due to artifacts in the ECG, five participants were excluded from the HR analysis.

SC in microSiemens was first averaged every 500 ms, for an interval of 5 s (starting with the onset of the fixation point) and then transformed into differential scores by subtracting the average SC during 1 s prior to presentation of the fixation point. Due to artifacts, three participants were excluded from the SC analyses.

6.4 Results

6.4.1 Behavioral data analysis and results

Data from the objective and the subjective tasks were analyzed using *t* tests to compare trials in which the alerting tone was absent or present. In the objective task, we analyzed response accuracy, the percentage of no responses, and reaction time (RT) for seen Gabors (only of trials with correct responses in the objective task; see Table 6.1).



	Objective task			Subjective task	
	RT	Accuracy	No responses	Seen Gabors	False alarms
No tone	1,083 (44)	0.86 (0.052)	0.29 (0.059)	0.42 (0.033)	0.01 (0.003)
Tone	963 (47)	0.85 (0.052)	0.16 (0.045)	0.85 (0.019)	0.04 (0.011)

Table 6.1: Results of the objective and subjective tasks as a function of the alerting tone presence. Note: Mean (SE) are presented. TRs are expressed in milliseconds; all other measures are rates (0-1). RT = reaction time; SE = standard error.

No anticipations or responses shorter than 150 ms were observed. For the subjective task, we analyzed the percentage of seen targets and the percentage of false alarms (FA), as well as perceptual sensitivity and response criterion according to signal detection theory (Macmillan, 2002). We computed a nonparametric index of perceptual sensitivity (A’), and response criterion (β’’) to detect the Gabor.

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

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).

6.4.2 Objective task analysis

When the Gabor was consciously perceived, response accuracy for the objective task was 0.70. This value was significantly greater than chance (0.50; t (25) = −3.58, p < 0.001, Cohen’s d = 0.70). No responses were given in most trials when the Gabor was not consciously perceived (only 0.01 responses were recorded). No alerting effect was observed in the accuracy analysis for correct responses, t (23) = 0.875, p = 0.391, Cohen’s d = 0.179. However, the percentage of no responses to the target decreased when the alerting tone was presented as compared to conditions with no alerting tone, t (25) = 3.366, p = 0.002, Cohen’s d = 0.660 (see Table 6.1). RT results demonstrated a main effect of alerting, with shorter responses when the alerting tone was presented as compared to conditions with no alerting tone, t (22) = 6.406, p = 0.001, Cohen’s d = 1.336.

6.4.3 Subjective task analysis

Participants consciously perceived more targets, t (25) =

−14.55, p = 0.001, Cohen's d = −2.854, but also produced more false alarms, t (25) = −2.533, p = 0.018, Cohen's d = 0.497, when the alerting tone was presented as compared to conditions with no alerting tone (see Table 1). Signal detection theory analyses demonstrated that perceptual sensitivity increased, t (25) = −7.625, p = 0.001, Cohen's d = −1.495, and response criterion was less conservative, t (25) = 2.423, p = 0.023, Cohen's d = 0.475, when the alerting tone was presented as compared to conditions with no alerting tone (see Figure 6.2).

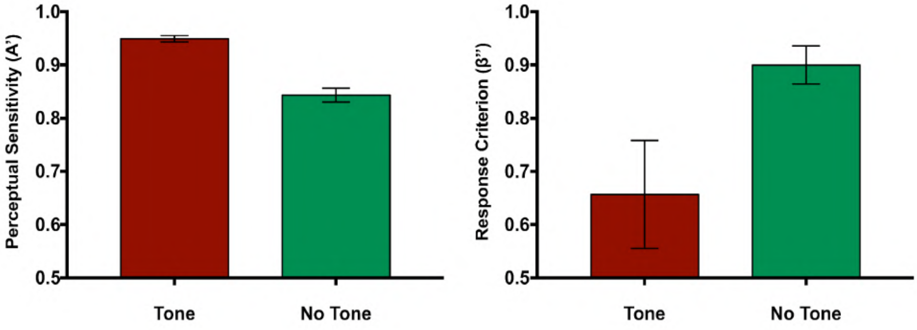


Figure 6.2: Perceptual sensitivity (a') and response criterion (β'') for detecting the Gabor when the alerting tone was present versus absent. Bars represent the standard error of the mean.

6.4.4 HR analysis

HR data were analyzed using repeated measures analysis of variance (ANOVA) with three independent variables manipulated within participant: alerting tone (absent or present), consciousness of Gabor (seen or unseen), and time (50 time points from the presentation of the fixation point—each 100 ms long). The analysis demonstrated a main effect of time, $F(49, 980) = 27.48$, $MSE = 4.19$, $p < 0.001$, $\eta_p^2 = .58$, showing the traditional cardiac deceleration-acceleration pattern along the trial. Four significant interactions were found: an interaction between alerting tone and consciousness of Gabor, $F(1, 20) = 5.74$, $MSE = 127$, $p = .027$, $\eta_p^2 = .22$; between alerting tone and time, $F(49, 980) = 9.13$, $MSE = 1.79$, $p < 0.001$, $\eta_p^2 = .31$; between consciousness of Gabor and time, $F(49, 980) = 5.25$, $MSE = 13.01$, $p < 0.001$, $\eta_p^2 = .21$; and between alerting tone, consciousness of Gabor, and time, $F(49, 980) = 4.83$, $MSE = 1.43$, $p < 0.001$, $\eta_p^2 = .19$ (see Figure 6.3). We used Fisher post hoc comparisons to explore the latter interaction, comparing the HR when the Gabor was seen and unseen at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, HR significantly differed for seen and unseen trials between 3,200 and 5,000 ms after fixation onset (all ps < 0.05). However, when the alerting tone was present, HR significantly differed for seen and unseen trials between 1,100 and 3,600 ms after fixation onset (all ps < 0.05; see Figure 6.3).

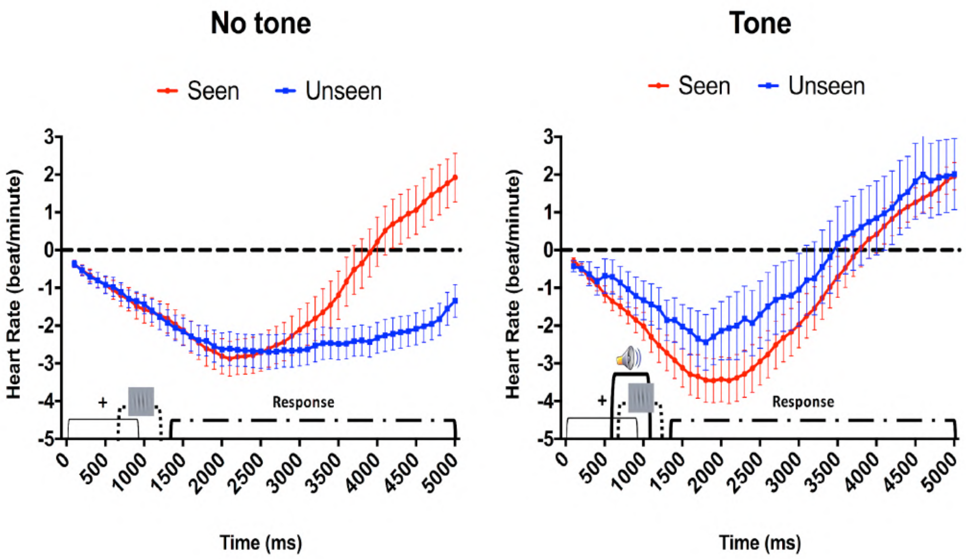


Figure 6.3: Changes in HR (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the *x* axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. In both tone and no tone conditions, the deceleration-acceleration pattern is observed. A significant interaction between phasic alerting, consciousness, and the time is also observed (see Results). Bars represent the standard error of the mean.

The above-described analysis, locked to the appearance of the fixation point, demonstrated that HR on seen and unseen conditions differed at earlier time points when the alerting tone was presented as compared to conditions with no alerting tone. Target onset time was variable (714 to 1,309 ms from the onset of the fixation point), and the subjective response occurred on average 2,975 ms after the fixation display was presented. Therefore, data indicate that in the no tone condition, HR differentiated between seen and unseen conditions only after the subjective response was given, while in the tone condition differences in HR between seen and unseen trials occurred approximately at the time of Gabor onset. To better understand the timing of the interaction between phasic alertness and conscious perception, the above-described ANOVA was repeated but locked to the appearance of the target (instead of the fixation display). This analysis demonstrated an interaction between alerting tone, consciousness of Gabor, and time, $F(39, 780) = 4.56$, $MSE = 1.13$, $p < 0.001$, $\eta_p^2 = .18$. Fisher post hoc comparisons demonstrated that, when the alerting tone was absent, HR significantly differed in the tone and no tone conditions from 2,200 ms after target onset until the end of the interval (all *p*s < 0.05), coinciding on average with the moment of the subjective response time window. However, when the alerting tone was present, HR significantly differed from the onset of the target until 2,600 ms later (all *p*s < 0.05).

We also wondered whether HR would differentiate between unseen trials when the target was actually present but it was reported as unseen, and when the target was absent and it was reported as unseen. Data from the HR were analyzed using a repeated measures ANOVA with three independent variables manipulated within participant: alerting tone (absent or present), condition (unseen absent vs. unseen present), and time (50 time points from the presentation of the fixation point—each 100 ms long). This analysis demonstrated a main effect of alerting tone, $F(1, 20) = 8.50$, $MSE = 136$, $p = 0.008$, $\eta_p^2 = .30$, and a main effect of time, $F(49, 980) = 15.74$, $MSE = 3.23$, $p < 0.001$, $\eta_p^2 = .44$. The interaction between alerting tone and time was also significant, $F(49, 980) = 18.62$, $MSE = 1.78$, $p < 0.001$, $\eta_p^2 = .48$; however, neither the main effect of condition nor any of its interactions with the other variables were significant (all *p*s > 0.221).

6.4.5 SC analysis

SC data were analyzed using a repeated measures ANOVA with three independent variables manipulated within participant: alerting tone (absent or present), consciousness of Gabor (seen or unseen), and time (10 time points from presentation of the fixation point—each 500 ms long).

A main effect of tone was observed, $F(1, 22) = 14.28$, $MSE = 0.24$, $p < 0.001$, $\eta_p^2 = .39$, showing increased SC when the alerting tone was presented as compared to conditions with no alerting tone. A main effect of time was found, $F(9, 198) = 6.53$, $MSE = 0.04$, $p < 0.001$, $\eta_p^2 = .23$, with increased SC as time passed within the trial. Three significant interactions were found: between alerting tone and time, $F(9, 198) = 12.47$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = .36$; between consciousness of Gabor and time, $F(9,198) = 2.08$, $MSE = 0.01$, $p = 0.032$, $\eta_p^2 = .09$; and between alerting tone, consciousness of Gabor, and time, $F(9, 198) = 4.38$, $MSE = 0.01$, $p < 0.001$, $\eta_p^2 = .16$ (see Figure 6.4). We used Fisher post hoc comparisons to explore the latter interaction, comparing the SC when the Gabor was seen and unseen at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, SC for seen and unseen Gabors significantly differed from 4,000 ms from fixation onset until the end of the trial (all *p*s < 0.001). However, when the alerting tone was present, SC differed significantly for seen and unseen Gabors between 3,000 and 4,000 ms (all *p*s < 0.05) (see Figure 6.4).

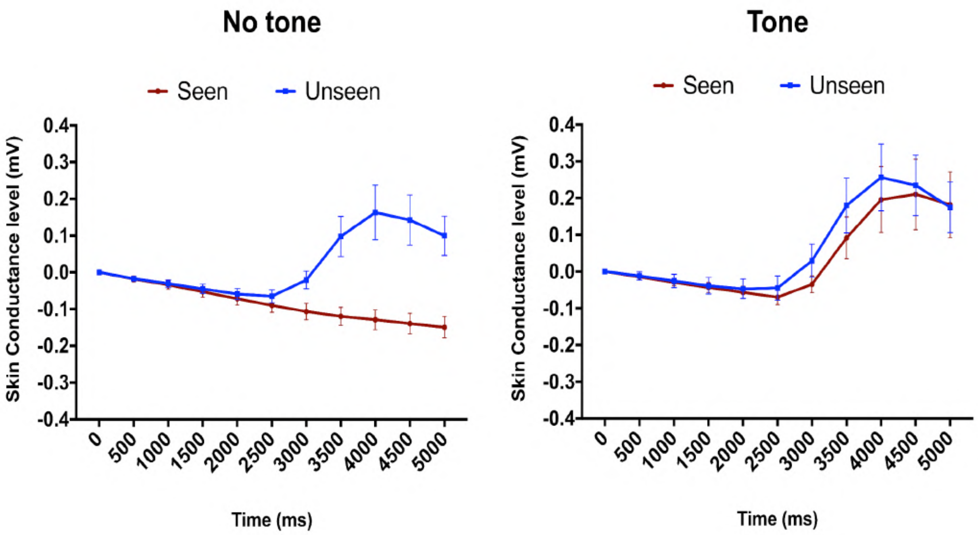


Figure 6.4: Changes in SC (relative to baseline) for seen and unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the *x* axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. A significant interaction between phasic alerting, consciousness, and time is observed (see Results). Bars represent the standard error of the mean.

We also wondered whether SC would differentiate between unseen trials when the target was actually present and when the target was absent. Data were analyzed using a further repeated measures ANOVA with three independent variables manipulated within participant: alerting tone (absent or present), condition (unseen absent vs. unseen present), and time (10 time points from presentation of the fixation point—each 500 ms long). This analysis demonstrated a main effect of alerting tone, $F(1, 22) = 16.32$, $MSE = 0.25$, $p < 0.001$, $\eta_p^2 = .42$, and a main effect of time, $F(9, 198) = 4.95$, $MSE = .03$, $p < 0.001$, $\eta_p^2 = .18$. Three significant interactions were found: between alerting tone and time, $F(9, 198) = 14.39$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = .39$; between condition and time, $F(9, 198) = 2.20$, $MSE = 0.003$, $p = 0.023$, $\eta_p^2 = .09$;

and between alerting tone, condition, and time, $F(9, 198) = 2.94$, $MSE = 0.003$, $p = 0.003$, $\eta_p^2 = .12$ (see Figure 6.5). We used Fisher post hoc comparisons to explore the latter interaction, comparing SC when the Gabor was present but unseen, and when it was absent and unseen, at each time point and for each alerting tone condition (present or absent). When the alerting tone was absent, there were no significant results (all *ps* > 0.05). However, when the alerting tone was present, SC significantly increased for present but unseen Gabors as compared to absent Gabors. This effect was observed from 3,000 ms after fixation onset until the end of the trial (all *ps* < 0.002).

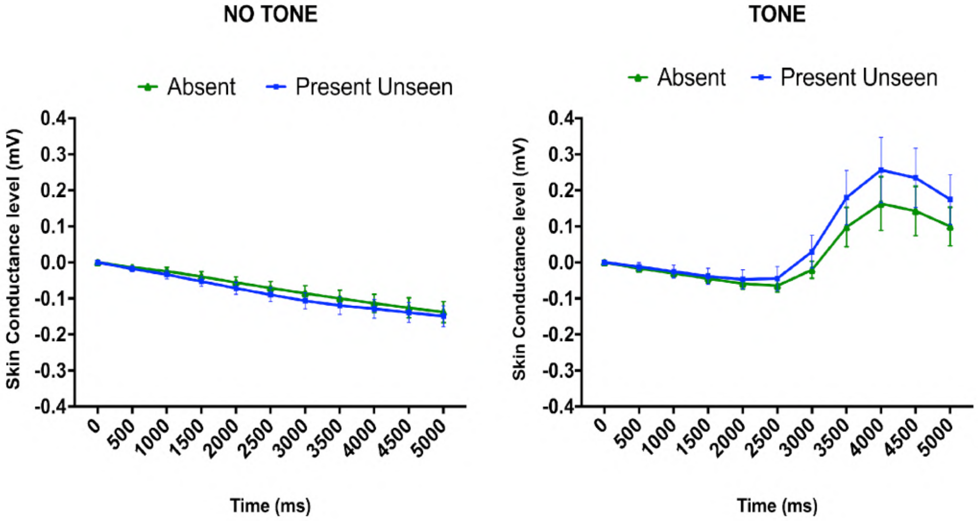


Figure 6.5: Changes in SC (relative to baseline) for absent versus present but unseen Gabors when the alerting tone was absent (left) and present (right). The 0 value on the x axis represents the moment of fixation onset. The moment of presentation of the alerting tone and the Gabor was variable. A significant interaction between alerting, consciousness, and time is observed (see Results). Bars represent the standard error of the mean.

6.5 Discussion

The present study was designed to examine brain-body interactions in the relation between attention and consciousness. Brain-body interactions have been demonstrated to be important in many cognitive processes such as self-consciousness (Canales-Johnson et al., 2015; Critchley & Harrison, 2013) and emotions (Craig, 2009; Critchley & Harrison, 2013; Lang et al., 1990; Reisenzein et al., 1995). Consistent with previous observations, HR results demonstrated the traditional deceleration-acceleration pattern (main effect of time; Lacey & Lacey, 1978). As expected, cardiac deceleration was more pronounced when the alerting tone was presented than when it was absent (Vila et al., 2007), confirming previous observations of heart rate modulations by phasic alerting.

Importantly, the heart rate deceleration-acceleration pattern demonstrated an interaction between phasic alerting and consciousness. When the alerting tone was absent, HR only differed between seen and unseen Gabors after the subjective response was given, probably reflecting postdecisional, evaluative processes (Andreassi, 1980; Lacey & Lacey, 1978; Lacey, 1967; Vila & Guerra, 2010). However, when the alerting tone was presented, HR deceleration was more pronounced for seen as compared to unseen Gabors before the presentation of the Gabor stimulus and until 2,600 ms later. The alerting modulation was also associated with shorter RTs, as well as changes in both perceptual sensitivity and response criterion (see also Botta et al., 2017; Kusnir et al., 2011).

SC results revealed some kind of subliminal processing of stimuli reported as unseen. Despite participants' inability to perform the objective task when the Gabor was reported as unseen in this and in previous studies (Chica, Lasaponara, et al., 2011; Kusnir et al., 2011), SC increased for unseen, but present, Gabors as compared to unseen, and absent, Gabors when the alerting tone was presented. Subliminal processing has been demonstrated in multiple experiments (Duschek et al., 2009; Gaillard et al., 2006; R. Kentridge, 2004; Kentridge et al., 1999; Sklar et al., 2012; Van Gaal et al., 2010, 2014). Although near-threshold Gabors in our experiments do not usually demonstrate subliminal effects, a recent investigation using machine learning decoding techniques have demonstrated that present but unseen Gabors can affect MEG responses for a sustained period of time (King et al., 2016). To our knowledge, SC has never been explored in the context of attention-consciousness interactions. Our results suggest that phasic alerting increases subliminal processing, although more research is needed to understand the level of processing of these subliminal Gabors that did not affect behavior (the objective response).

The results reported here highlight that attentional processing (phasic alerting) boosts conscious perception of near-threshold stimuli (Botta et al., 2017), as proposed by the Global Neuronal Workspace model (Dehaene & Changeux, 2011b). The neural interaction between phasic alerting and consciousness has been associated with the activity of a frontostriatal network, including structures such as the caudate nucleus, the thalamus, the ACC, the supplementary motor area (SMA), and the frontal eye fields (Chica et al., 2016). According to Sturm & Willmes, (2001), the ACC, midbrain, and thalamus constitute the anterior alerting system, while the pre-SMA is involved in response selection and preparation. An important theoretical question is how the CNS influences the PNS. Many authors agree with a main role of the insula in this interaction (Craig, 2002; Critchley et al., 2004; Critchley & Harrison, 2013; Park et al., 2014).

Critchley & Harrison, (2013) described two communication pathways between the CNS and PNS: direct and indirect. Both pathways send information to the thalamus, which projects to the posterior insula (PI; Danev & de Winter, 1971; Park et al., 2014), which is involved in homeostasis and regulation of the body and physiological state (Critchley et al., 2004; Critchley & Harrison, 2013; Menon & Uddin, 2010; Park et al., 2014). PI sends information to the AI, which transmits the information to ACC (Menon & Uddin, 2010; Uddin, 2015), an important region of the frontostriatal network involved in phasic alerting. The communication between the AI and the ACC has also been related to the salience network (Menon & Uddin, 2010; Uddin, 2015). As proposed by Critchley & Harrison, (2013), the CNS-PNS systems coordinate and integrate their functioning through dynamic feedback. Although theoretically unlikely, we have no data to disprove that PNS effects might be secondary to the main CNS effects (observed in the frontostriatal network;(Chica et al., 2016).

Brain-body interactions have been largely neglected in the consciousness literature. Our study was inspired by Park et al., (2014), who measured the conscious detection of a near-threshold Gabor and observed a similar cardiac deceleration- acceleration pattern to that observed in our study for seen as compared to unseen Gabors. The present study has demonstrated that this brain-body interaction mediates the phasic attentional modulation of conscious perception. In particular, cardiac deceleration was more pronounced at the time of Gabor onset for seen as compared to unseen trials, but only when the alerting tone was presented. Park et al., (2014) complemented EKG data with MEG data, locked to the heartbeat-evoked response.

Brain sources were located in the ACC, the right posterior medial insula, inferior parietal regions of the right hemisphere, and somatosensory cortex (Park et al., 2014). These brain structures resemble the visceral projection described in the Introduction, and some of them have also been associated with conscious perception (Kranczioch et al., 2005). The insula, in particular, seems to be implicated in conscious perception (Craig, 2009; Tsuchiya & Adolphs, 2007) and has also been proposed as a network hub of the salience network (Menon & Uddin, 2010; Uddin, 2015). It is one of the first regions to receive information from the PNS (Craig, 2009; Critchley & Harrison, 2013; Menon & Uddin, 2010; Uddin, 2015), and it belongs to a circuit—including the ACC and other limbic and subcortical structures—which is associated with the integration of the external sensory information with the internal state of the body (Seeley et al., 2007; Uddin, 2015). We therefore hypothesize that the phasic alerting and consciousness interaction observed in the HR response might be associated with this neural circuit, which is considered important in the integration of signals from the body and the brain. Alerting signals modulate the HR and the saliency network (Corbetta et al., 2008; Uddin, 2015), and these peripheral and central signals might be integrated in structures such as the insula. As we have previously demonstrated both with phasic alerting (Botta et al., 2017; Chica et al., 2016; Kusnir et al., 2011) and exogenous attention manipulations (Botta et al., 2017; Chica et al., 2010; Chica, Lasaponara, et al., 2011; Chica, Botta, et al., 2012), the interactions between attention and consciousness occur in frontoparietal and frontostriatal regions, distant from the primary sensory regions in which perceptual information is initially processed. This observation argues against the so-called low order theories of consciousness (Zeki & Bartels, 1999), postulating that consciousness depends mostly on the activation of primary sensory regions.

In summary, the present study replicates previous behavioral results demonstrating attentional boosting of near-threshold stimuli (Botta et al., 2017; Chica, Lasaponara, et al., 2011; Kusnir et al., 2011). In addition, these effects are reflected in the organism (HR and SC), generating the need to take into account brain-body interactions for current theoretical models of consciousness (Park & Tallon-Baudry, 2014).

6.6 Acknowledges

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Chapter 7: Attention does not always help: the role of expectancy, divided, and spatial attention on illusory conjunctions

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7.1 Abstract

Humans have the subjective impression of a rich perceptual experience, but this perception is riddled with errors that might be produced by top-down expectancies or failures in feature integration. The role of attention in feature integration is still unclear. Some studies support the importance of attention in feature integration (Paul & Schyns, 2003), whereas others suggest that feature integration does not require attention (Humphreys, 2016). Understanding attention as a heterogeneous system, in this study we explored the role of divided (as opposed to focused – Experiment 1) attention, and endogenous-exogenous spatial orienting (Experiments 2 and 3) in feature integration. We also explored the role of feature expectancy, by presenting stimulus features that were completely unexpected to the participants. Results demonstrated that both endogenous and exogenous orienting improved feature integration while divided attention did not. Moreover, a strong and consistent feature expectancy effect was observed, demonstrating perceptual completion when an unexpected perceptual feature was presented in the scene. These results support the *feature*

confirmation account (Humphreys, 2016), which proposes that attention is important for top-down matching of stable representations

7.2 Introduction

Attention is a mechanism that prioritizes the processing of relevant information. When the perceptual load exceeds our capacity (Lavie, 2006, 2010; Murphy et al., 2016), attentional mechanisms are necessary to select the information that will eventually access consciousness (Petersen & Posner, 2012). Many studies have demonstrated that attention is important for conscious access (Dux & Marois, 2009; Martens & Wyble, 2010; Rensink et al., 1997; Simons & Ambinder, 2005), thus favoring models that highlight the role of attention in conscious perception (Chica & Bartolomeo, 2012; Dehaene & Changeux, 2011; Posner, 1994). However, more recent studies have demonstrated that at least some types of attention are not necessary for consciousness (Chica & Bartolomeo, 2012; Chica et al., 2011; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008). Endogenous or top-down attention can indeed be dissociated from conscious perception (Chica et al., 2011; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008), while exogenous forms of attention (Chica et al., 2013), alerting (Chica et al., 2016; Petersen et al., 2017) and executive control (Colás et al., 2017; Martín-Signes et al., 2018) mechanisms modulate conscious access.

Nevertheless, perceptual consciousness might be richer than the information we can access and report. Block (2011) proposed that larger amounts of information can be represented in the so called "phenomenal consciousness", although we can only consciously access and report a small fraction of it. Interestingly, many studies have demonstrated that our phenomenal experience, although rich, is riddled with errors that might be produced by failures in feature integration, memory, or top-down expectancies (Aru et al., 2018; Aru & Bachmann, 2017; de Gardelle et al., 2009; Kuhn & Rensink, 2016; Mack et al., 2016). We can better understand how phenomenal consciousness might not be entirely trustable if we think of color perception in peripheral vision. Because we do not have many cones in the peripheral parts of the retina (Goldstein, 2013), color perception is not accurate for stimuli presented in the periphery (Hansen et al., 2009). However, we do not have the subjective impression of unclear color perception outside the fovea. Yet, if we were asked to report colors, our responses would often be erroneous, either by reporting the color of an object nearby (incorrectly integrating features of different objects), reporting a color from memory (reporting a green tree), or reporting an expected color (reporting a yellow tree if we are in autumn).

Studying these types of perceptual errors can shed some light on phenomenal consciousness because observers often have a rich phenomenal/subjective experience that is only partially correct (Kouider et al., 2010). Illusory conjunctions refer to errors in which two features belonging to different objects are combined to produce a single percept of one object. The best known theory about feature conjunction is the *Feature Integration Theory* proposed by Treisman and colleagues (Treisman, 1996; Treisman & Schmidt, 1982; Wolfe & Robertson, 2012). This theory proposes that basic features such as form, motion, color, etc. can be extracted pre-attentively, but the process of integrating different features to perceive an object requires attention. When attention fails, observers are more likely to erroneously integrate features from different objects as part of a single object. Many studies have supported the assumptions of this theory, demonstrating an increased number of illusory conjunctions when attention is diverted (Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982). Other studies have however demonstrated that perceptual processing does not always depend on attentional manipulations (Humphreys, 2016; Matthews et al., 2018; Mordkoff & Halterman, 2008). E.g. Li et al. (2002) demonstrated that with diverted attention in a dual task paradigm, participants are able to correctly discriminate natural scenes, but they cannot identify a simpler object in which form-color integration is necessary. It has been proposed that for certain complex stimuli, attention may not be necessary for conscious perception, a result that has been taken as empirical evidence for a dissociation between top-down attention (in manipulations of divided attention) and (conscious) perception (Matthews et al., 2018).

Contrary to the predictions of the FIT, some studies have demonstrated bottom up binding without attention (Braet & Humphreys, 2009; Gillebert & Humphreys, 2010; Hochstein & Ahissar, 2002). According to the *feature confirmation account*, proposed by Humphreys (2016), rather than being critical for feature integration, attention plays a role in feature confirmation—the establishment of stable representations by top-down matching of rich but unstable input data. Feature conjunctions are coded early on in visual processing but they are noisy and relatively transient unless supported by top-down activation from the posterior parietal cortex. The *feature confirmation account* does not explicitly state if different attentional systems modulate this initial feature binding process differentially, although top-down influences from the parietal cortex might be related to endogenous or top-down attention (implemented in brain regions containing spatial maps, such as the superior/inferior parietal cortex and frontal eye field according to Corbetta et al.'s model, 2008), rather than to exogenous or stimulus-driven attention (implemented in regions such as the temporo-parietal junction and inferior frontal gyrus according to Corbetta et al.'s model, 2008). Based on the evidence demonstrating fewer illusory conjunctions for known than new feature combinations (e.g. a red tomato vs. a blue tomato), the *feature confirmation account* also proposes that stored knowledge (perceptual expectations) about objects modulate perceptual integration (Humphreys, 2016).

Feature integration, and its relation to attention, has been investigated with different paradigms. Using visual search tasks in which feature integration is needed in some conditions (conjunction or serial search) but not in others (feature or parallel search), Briand and Klein (1987) and Briand (1998) demonstrated that exogenous orienting effects (faster and/or more accurate responses when targets are presented at the valid location as compared to an invalid location) were larger for conjunction than for feature tasks, while endogenous orienting lead to equivalent orienting effects for feature and conjunction tasks. More recently, Henderson & McClelland (2020) distinguished between proximal and distal illusory conjunctions. Proximal illusory conjunctions occur between closely neighboring target and distractor stimuli, while distal illusory conjunctions occur between two stimuli that are spaced far enough apart that neither is crowding the other. Henderson (2014) argued that proximal illusory conjunctions errors can be explained by the crowding effect, a limitation of visual perception such that stimuli placed within a certain critical spacing of each other will interfere with each other's perception (Pelli et al., 2004; Pelli & Tillman, 2008; Whitney & Levi, 2011).

Another important consideration about this literature is that attention refers to a complex set of mechanisms that allow for the selection of relevant information. According to Petersen and Posner's taxonomy (2012), attentional processing can be subdivided into spatial orienting, alerting, and executive control mechanisms. These three attentional systems are implemented in different brain networks (Fan et al., 2005; Petersen & Posner, 2012) and can likely modulate feature integration differently.

The aim of the present study was to test the role of different sub-mechanisms of attention in feature integration. We adapted a paradigm, previously developed by Esterman and colleagues (2004, 2007), to produce proximal illusory conjunctions of features. A string of characters was presented to either the left or right of the fixation point. It consisted of two central characters ("L" and "O"), printed in blue, green, or red color, surrounded by two white distractors. Participants were required to report the color of the letter "L", and a calibration procedure ensured around 70% of hits in each participant. In the first experiment, we tested the paradigm and introduced a manipulation of divided attention with a number task composed of two conditions, which varied in difficulty.

According to the FIT, more illusory conjunctions should be observed when attention is diverted. In our paradigm, we expected to observe more illusory conjunctions when the number task was more demanding (eliciting longer RT and/or more errors) as compared with a less demanding condition (eliciting shorter RT and/or fewer errors). In Experiments 2 and 3, endogenous and exogenous spatial attention were respectively manipulated. We have no reason to believe that the FIT would make different predictions for endogenous vs. exogenous attention; in both cases, fewer illusory conjunctions are expected at the attended location than at the unattended location. The feature confirmation account, on the contrary, highlights the role of top- down information (from the parietal cortex), which might be more related to endogenous attention. Therefore, this theory would predict fewer illusory conjunctions at the attended location than at the unattended location for endogenous attention, while exogenous attention might not modulate feature integration. If illusory conjunctions were produced by crowding, they should be similarly modulated by both endogenous and exogenous attention. Based on the reported effects of both endogenous and exogenous attention on crowding (Carrasco & Barbot, 2014), we have no reasons to hypothesize a larger effect of one type of attention over another.

Finally, feature expectancy was manipulated by presenting the target letter in a different and unexpected color during the last blocks of trials. This kind of manipulation has previously been used to explore the role of top-down expectations in visual perception (Aru et al., 2018; Aru & Bachmann, 2017; Kok et al., 2017). Because this manipulation does not involve spatial attention, the FIT will not predict a modulation of feature integration. However, the *Feature Confirmation Accoun*t proposes that stored knowledge (perceptual expectations) about objects modulate perceptual integration, and would therefore predict that the presence of an unexpected feature might increase erroneous feature integration.

7.3 Method of experiment 1: divided attention

The aim of this experiment was to adapt Esterman and colleagues' (2004, 2007) procedure to produce illusory conjunctions in healthy participants, while introducing a secondary task. Participants were asked to discriminate the color of a target letter which was peripherally presented and surrounded by distractors. The secondary task consisted of responding to numbers presented above and below the fixation point. In the demanding condition, the numbers were either the same or different, and participants made a same-different judgment. In the less demanding condition, the numbers were always the same, and participants identified the number presented (Arend et al., 2013). We expected longer RTs and/or lower accuracy for the same-different judgment as compared to the identification response. If focused attention was important for feature integration, according to the FIT, we should observe more illusory conjunctions when a more demanding (same-different) task was concurrently presented as compared to the less demanding (identification) task.

7.3.1 Participants

G*power (Faul et al., 2009) was used to calculate sample size based on the effect size of the illusory conjunctions reported in Esterman et al. (2004) (dz = 1.27, large effect). Our main result relates to the comparison of the proportion of illusory conjunctions in the two number task conditions (same-different vs. identification task). We therefore calculated sample size for a non-parametric Wilcoxon paired t-test (matched samples, dz=1.2 - large effect, α = 0.05; Power = 0.80). A sample of 8 participants was required. However, Esterman et al.'s manipulation had a different experimental design than ours, and our effects might be smaller. For medium effect dz=.7; (Cohen, 1992; Fritz et al., 2012), 19 participants are required. Anticipating that data from some participants would have to be excluded due to possible technical errors, excessive eye movements, etc., we decided to collect a larger sample of 30 participants.

Thirty healthy volunteers (27 females, mean age of 21 years, SD = 2.59, all right-handed) participated in the experiment in exchange for course credit. One participant was excluded because he was unable to maintain fixation. Another participant was excluded from the number task analysis because there were no RT/accuracy data for illusory conjunctions in one of the two Number Task conditions. All participants in this and the following experiments were undergraduate students from the Faculty of Psychology of the University of Granada, who had not previously participated in similar experiments. All participants reported having normal or corrected-to-normal vision, normal color perception, and had no clinical history of neurological or psychiatric disorders. Signed informed consent was collected before the study, and participants were informed about their right to withdraw from the experiment at any time. The Granada's Biomedicine Ethic Research Committee (CEIM/CEI Granada) approved the experiment, which was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

7.3.2 Apparatus and stimuli

E-prime software was used to control stimuli presentation, timing operations, and behavioral data collection (Schneider et al., 2002). Participants were seated at an approximate distance of 47 cm from the computer screen. All stimuli were presented on a LCD monitor (17", LG L1718S, 1,280 x 1,024 pixels) with a refresh rate of 60 Hz. A video-based, eye tracking system (Eyelink 1000 Plus, 5.09 software version) was used to monitor the direction of gaze every 2ms, with a spatial resolution <0.01°. The experimental display, adapted from Esterman and colleagues' (2004, 2007), consisted of a central fixation point (a white plus sign, 0.6° x 0.6°) presented against a black background. Two numbers (6 or 9) were presented, one of them 1.2° above, and the other one 1.2° below, the fixation point. A string of characters could randomly appear either at the left or right peripheral location. The distance between the string of characters and the fixation point varied from 9.5 to 17.5° (measured from the center of fixation point to the center of the string of characters), according to a previous titration procedure (see below). The duration of the string of characters also varied between 83 and 210 ms according to the titration procedure. The string of characters was presented in Arial font (see figure 7.1), subtending 4.6° x 1.2°. The two external characters consisted of the distractors “S” or “8”, printed in white ink. The two inner characters were the letters “L” and “O”, which were colored in red (RGB: 215,0,0), blue (RGB: 46,118,182), or green (RGB: 0,135,61). In each trial, the “L” and “O” letters had different colors. Both letters were presented randomly at either the inner leftmost or rightmost location (see Procedure section).

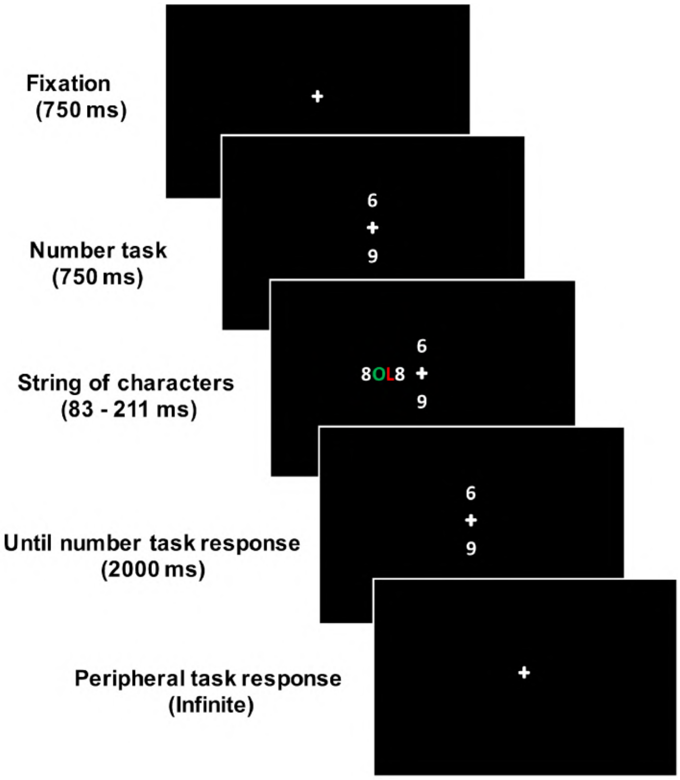

Figure 7.1: Sequence and timing of events in a given trial in Experiment 1. Participants first responded to the number task, making (in different blocks of trials) either an identification or a same-different response. After this speed response was made, participants indicated the colour of the “L” letter with no time pressure.

7.3.3 Procedure

The experiment consisted of ten blocks of 48 trials each, each one of them separated by a brief pause. Before the beginning of each block, an eye tracking calibration and a drift correction were performed.

Figure 7.1 shows the sequence and timing of the stimuli in the given trial. Participants responded to the number task and to the peripheral task (string of characters) as indicated below.

In half of the trial blocks (same-different task), the numbers above and below the fixation point could be either the same (6-6 or 9-9) or different (6-9 or 9-6). Participants' task was to indicate if the two numbers were the same or if they were different. In the remaining blocks (number identification task), the numbers above and below the fixation point were always the same (6-6 or 9-9) and participants were asked to report if the number 6 or 9 was presented. In the same-different task, participants responded to the number with their right hand, using the mouse, and pressing the left button for one of the responses and the right button for the other one (the response mapping was counterbalanced between participants). In the number identification task, participants always pressed the left button when the number 6 was presented, and the right button when the number 9 was presented. The response had to be given before the number display disappeared (see figure 7.1), and they were instructed to provide fast and accurate responses.

After the response to the number was given, participants were required to verbally report the color of the letter "L". To ensure accurate responses, with no time pressure, and to minimize the probability of interchangeable responses, participants were instructed to respond accurately, with no time pressure, and the experimenter manually recorded their responses using the keyboard (z=blue, x=green, c=red, space=unseen). Responses to this peripheral task were categorized as hits (when the correct color of the letter "L" was reported), illusions (when participants reported the color of the letter "O"), errors (when participants reported a color that was not presented in the display), and unseen (when participants could not report the color of the letter).

Before the experimental blocks, a titration block was presented to achieve ~70% of hits in each participant. We expected a low proportion of errors and unseen responses, achieving around ~30% illusions in each participant. During titration, trials were identical to the experimental task. Two attributes of the string of characters were manipulated during the titration block: presentation time (ranging from 83-211 ms) and eccentricity (5 positions). Titration began with the more eccentric condition (17.5° to the left or right of the fixation point, measured from the fixation point to the center of the string of characters) and a presentation time of 147 ms. After every 12 trials (a titration block), the mean proportion of hits was calculated. If participants correctly reported 75% or more targets, presentation time was reduced by 32 ms for the next titration block (if the shortest stimuli duration were achieved (83 ms) and participants still performed over 75% correct, titration would have stopped —although this condition was not met for any participant). If participants correctly reported 66% or fewer targets, presentation time was increased by 32 ms for the next titration block. If the longest stimuli duration was achieved (211 ms) and participants correctly reported 66% or fewer targets, eccentricity of the target was reduced by 2°, making the string of characters closer to the center during the next titration block. If the closer condition was achieved (9.5°), presentation time increased up to 211ms for the next titration block. In alternated titration blocks, participants performed either the same-different or the identification central tasks. Titration stopped when the proportion of hits ranged between ≥66% and ≤75% for two consecutive titration blocks. The presentation time and eccentricity of the string of characters obtained for each participant during the titration phase was used during the experimental blocks. The experiment lasted for about 1h 30 min., including the initial titration procedure.

7.3.4 Results

We eliminated trials in which participants fixated (longer than 50 ms) 2° away from the fixation point before the offset of the string of characters, which accounted for 2.17% of the trials (SD=3.46).

Data from the peripheral task were analyzed by using non-parametric paired samples t-tests (Wilcoxon signed-rank) to compare the mean proportion of hits, illusions, errors, and unseen responses for the two Number Task conditions (same-different and identification tasks). The effect size is reported by the rank-biserial correlation (r_B). A score <.1 is considered a trivial effect, 0.1 a small effect, 0.3 a medium effect, and 0.5 or more a large effect (Goss-Sampson, 2019). The proportion of hits (W = 243, p = .594, r_B = .117), illusions (W = 266, p = .304, r_B = .223), and errors (W = 174, p = .980, r_B = -.009) were not significantly modulated by the Number Task condition; i.e. the proportion of hits, illusions, and errors was similar when participants performed the same-different or the identification task. However, more unseen responses were observed when the same-different task was concurrently performed as compared to the identification task (T = 71, p = .005, r_B = - .624) (see figure 7.2).

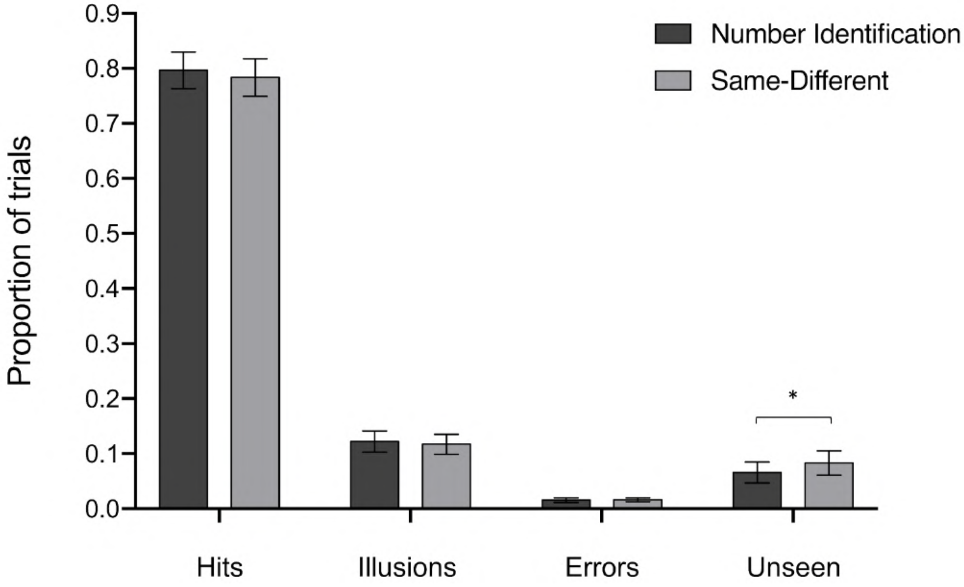

Figure 7.2: Proportion of hits, illusions, errors, and unseen responses for each Number Task condition (identification and same-different) in Experiment 1. The figure shows a comparable number of hits, illusions, and errors in both tasks, but a larger proportion of unseen responses in the more demanding same-different task as compared with the identification task.

For the Number Task, both accuracy and RT were emphasized. It is well known that under these conditions, speed-accuracy trade-off-based strategies can be adopted. For example, participants can respond faster but less accurately in a given condition. We thus used the Linear Integrated Speed-Accuracy Score (LISAS), a measure that combines RT of correct responses (cr) and the proportion of errors (PE) (Vandierendonck, 2017). S_{RT} refers to the participant's overall RT standard deviation, and S_{PE} refers to the participant's overall PE standard deviation.

$$LISAS = RTcr + \frac{S_{RT}}{S_{PE}} * PEcr$$

LISAS provides an index of behavioral effects which is free of speed-accuracy trade-offs, with a similar weight of the RT and PE components. In LISAS, smaller values indicate faster and/or more accurate responses. Data were analyzed with a repeated measure analysis of variance (ANOVA) with the variables of Number Task condition (same-different and identification tasks), and Trial Type for the peripheral task (hits and illusions). Responses were more efficient for the identification task than for the same-different task (F (1,27) = 24.898, MSE = 13221.671, p < .001, η_p^2=.48). Even though participants had not responded to the peripheral task yet, responses to the Number Task were more efficient if participants correctly reported the color of the target letter later on the trial (hits) than if an illusion was observed (F (1,27) = 5.932, MSE = 8708.714, p = .022, η_p^2=.18) (see figure 7.3). Number Task condition and Trial Type did not significantly interact (F<1)[1].

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[1] RT analyses showed a main effect of the Number Task condition (F (1,27) = 27.312, MSE = 9110.482, p < .001, η_p^2=.503), and a main effect of Trial Type (F (1,27) = 11.321, MSE = 3991.113, p = .002, η_p^2=.295). The interaction was not significant (F<1). In the accuracy analysis, the main effects (Number Task: F (1,27) = 1.628, MSE = .016, p = .213, η_p^2=.057; Trial Type: F (1,27) = 2.957, MSE = .003, p = .097, η_p^2=.099) and the interaction (F<1) were not significant.

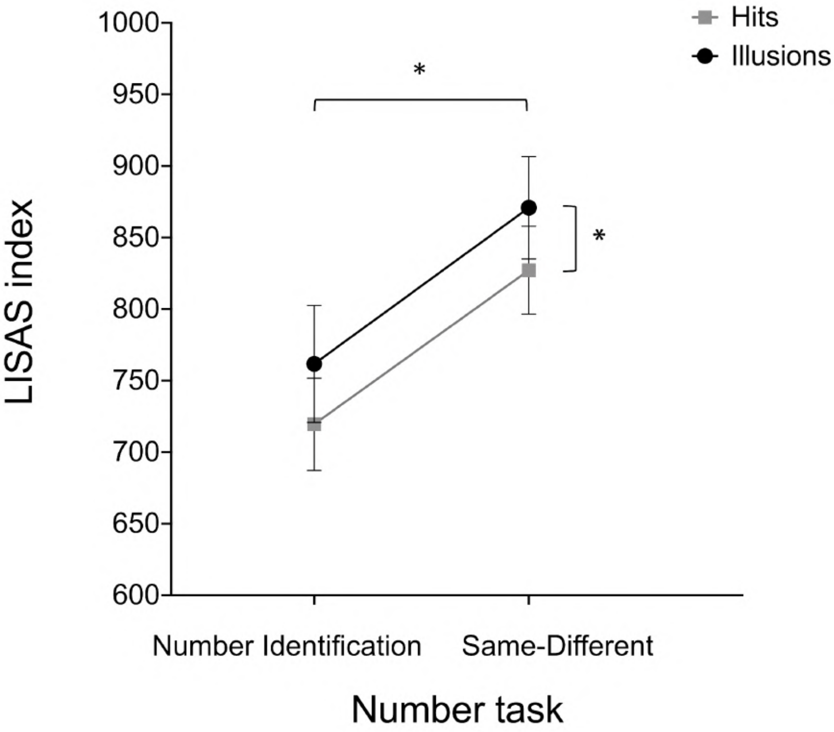

Figure 7.3: LISAS index for the Number Task response for each experimental condition in Experiment 1. This figure shows the main effect of Number Task and Trial Type. Bars represent standard errors; asterisks represent statistically significant effects (p<.05).

In summary, Experiment 1 demonstrated that our manipulation was effective to produce illusory conjunctions (~30% in each participant). According to the predictions of the FIT, participants are more likely to erroneously report the color of the distractor than a color not presented on the screen; i.e. under conditions of rapid presentation, participants erroneously bound together features of different objects. Moreover, contrary to the predictions of the FIT, the number of illusory conjunctions did not increase when a more demanding secondary task was being performed as compared with a less demanding secondary task. This result supports Prinzmetal, Henderson, & Ivry's (1995) findings, who demonstrated that proximal illusory conjunctions are not affected by a secondary task. In contrasts, other studies have demonstrated that secondary tasks impair performance of peripheral tasks (Li et al., 2002; Matthews et al., 2018; Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982). However, some of these previous studies compared conditions in which participants responded to the secondary task with conditions of no response (Aru et al., 2018; Aru & Bachmann, 2017; Li et al., 2002; Matthews et al., 2018; see also Henderson & McClelland, 2020). Attentional demands are extremely different when responding vs. not responding, two conditions that differ in attentional demands, task load, response preparation, and execution. In our experiment, the two conditions compared were very similar except for the task at hand (same-different vs. number identification), and elicited different RTs and accuracy. Moreover, even if task demands did not modulate the number of illusory conjunctions in our experiment, participants responded slower to the number when an illusion was reported later on in the trial as compared to hits, especially when the Number Task was more demanding. This result indicates that a common preparatory attentional process might be mediating performance in both tasks. These findings imply that attention might be important for feature integration, but rather than focused (as opposed to divided) attention, a more general preparatory process might be modulating both feature integration and the execution of the number task response in this experiment.

7.4 Method experiment 2: Endogenous Attention

In Experiments 2 and 3, we tried and replicated the results of Experiment 1 with a different secondary task. We used a number comparison task with a standard in memory (Krajcsi & Kojouharova, 2017; Viarouge et al., 2014). Participants had to report whether a given number was larger or smaller than 5. It is well known that it takes longer to respond the closer the numbers are to the standard (5). We therefore divided our stimuli into those closer to 5 (3, 4, 6, 7) and those far from 5 (1, 2, 8, 9). In Experiment 2, the string of characters was presented more often in one location of the screen than the other, allowing the manipulation of endogenous spatial attention (Chica et al., 2013, 2014). We expected to observe fewer illusions in the attended than the unattended spatial location. Finally, feature expectancy was manipulated in the last blocks of trials (Aru & Bachmann, 2017). During the experiment (576 trials), the color of the to-be-discriminated target was red, green, or blue. Unknown to the participants, in the last two blocks of trials, the target was printed in white on half of the trials. If feature expectancy was important for feature integration, then illusory conjunctions should significantly increase in this block of trials, even if some participants may be unaware of the presence of this unexpected color.

Moreover, in Experiment 1, it could be argued that the fact that the digits of the number task were presented for 750 ms prior to the onset of the display containing the critical peripheral stimuli makes it possible that the participant might have completed the perceptual encoding of the central task digits prior to the onset of the critical peripheral stimuli. In order to address this concern, in Experiments 2 and 3, the interval between the onset of the central and the peripheral task was reduced to 300 ms.

7.4.1 Participants

G*power was used to calculate sample size based on the effect size of Experiment 1 for unseen responses (d = 1.6). A sample of 6 participants was required. However, in this experiment, we also planned to compare the number of illusions in the last two blocks of trials (when the "L" letter was printed in white) with the number of illusions during the rest of the experiment (when the "L" letter was printed in red, blue, or green). Because we could not anticipate how many participants would be aware of the presence of the white "L" (and those participants will be removed from the feature expectancy analysis), we decided to check with Bayesian paired samples t-tests statistics after recruiting 30 participants. If the Bayesian factor (BF) provided conclusive evidence in favor of the alternative (BF>3) or the null hypothesis (BF<.33), and, in case of inconclusive evidence, we would increase sample size until evidence is conclusive. We used the default priors of JASPs for these analyses.

Thirty healthy volunteers (25 females, mean age of 21 years, SD=2.65, all right-handed) participated in the experiment in exchange for course credit. Four participants were eliminated from the sample because they broke fixation in more that 30% of the trials. The total sample was therefore 26 participants. Two further participants did not respond in one condition of the experiment to the analysis of the Number Task. For this reason, number task analysis had 24 participants, while peripheral task analysis had 26 participants.

7.4.2 Apparatus and stimuli

Everything was the same as in Experiment 1, with some exceptions. In this experiment, a single number was presented 1° above the fixation point. The number task consisted of a number comparison task with a standard in memory (Krajcsi & Kojouharova, 2017). Numbers from 1 to 9 were presented (excluding 5). Participant's task was to indicate whether the number was larger or smaller than 5. According to the numerical distance effect, numbers 3, 4, 6, and 7 correspond to the "near" condition (in which longer RTs were expected), while numbers 1, 2, 8, and 9 correspond to the "far" condition (in which shorter RTs were expected). The string of characters could randomly appear 6.4° to the left or right of the fixation point (distance measured from the center of fixation point to the center of the string of characters). It consisted of four characters presented in Arial font (see figure 7.4), subtending 4.4°x1.2°. After the string of characters a mask was presented (characters "&&&&"), printed in white ink, and subtending 4.4°x1.2°.

In the last two blocks of trials, the letter "L" was displayed in white on 50% of the trials.

7.4.3 Procedure

Figure 7.4 shows the sequence and timing of the stimuli in the given trial. As in Experiment 1, participants were required to perform two responses. First, they reported if the number was larger or smaller than 5. They had 2500 ms to respond from the appearance of the number, by clicking the right button of the mouse if the number was greater than 5, or the left button of the mouse if the number was smaller than 5. They were required to respond as fast and as accurately as possible. Then, they had to verbally report the color of the letter "L". They were required to respond accurately, with no time pressure, and the experimenter manually recorded their responses using the keyboard.

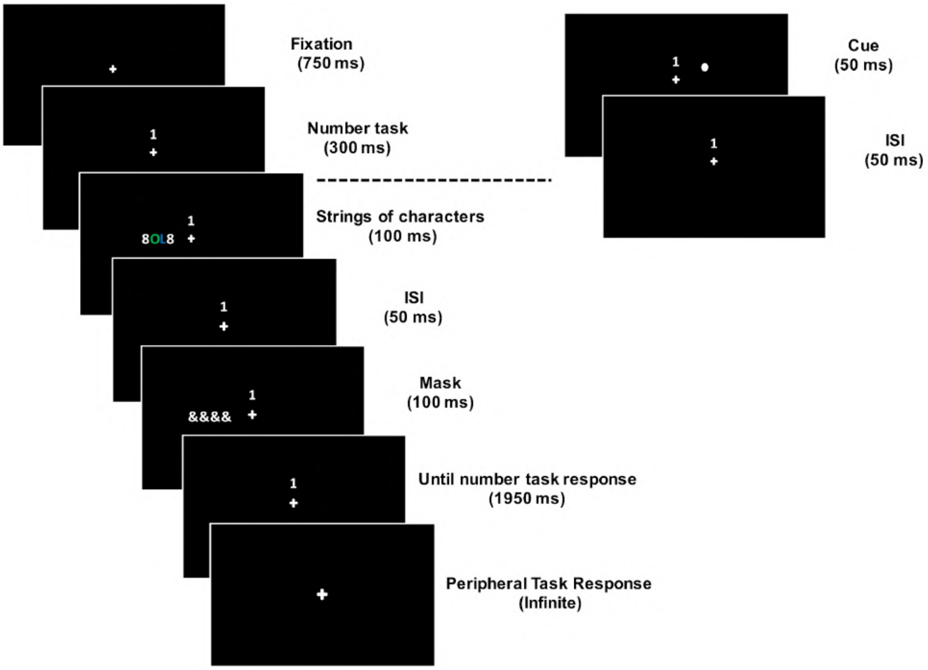

Figure 7.4: Sequence and timing of events in a given trial in Experiment 2 (left) and an example of invalid trial in Experiment 3 (right).

To study the effect of endogenous attention on illusory conjunction, the location of the string of characters was manipulated. In half of the blocks, it appeared on the left location on

75% of the trials, and on the right location on the remaining 25% of the trials. On the other half of the blocks, the string of characters appeared on the right location on 75% of the trials, and on the left location on the remaining 25% of the trials. Participants were informed at the beginning of each block that the string of characters was more likely presented in one location or the other, although they were not informed about the exact probability of the string of characters' location. Half of the participants started with the block containing 75% left location – 25% right location trials, and the other half of the participants started with the block containing 75% right location – 25% left location trials.

The experiment consisted of 8 blocks of 72 trials each, separated by a brief pause. Unknown to the participants, in the last two blocks (72 trials each), the letter "L" was printed in white on 50% of the trials. At the end of the experimental session, a brief structured interview was completed to explore whether participants were aware of the appearance of the white letter. Three questions were asked: "Do you have any comments about the experiment?"; "Did you find any color combination more difficult than the others?"; "Have you noticed anything different at the end of the experiment?".

Before the experimental blocks, a separate titration block was presented in order to achieve ~70% of hits in each participant. During titration, trials were similar to the experimental task. Two features of the string of characters (and the mask) were manipulated during the titration block: size and eccentricity. Titration began with the easier condition (size = 4.4° x 1.2°;

eccentricity from fixation = 6.4°, measured from the fixation point to the center of the string of characters). After every 14 trials (a titration block), the mean proportion of hits was calculated. If participants correctly reported 78% or more targets, size was decreased by 0.5° x 0.2° for the next titration block. If participants correctly reported 62% or fewer targets, size was increased by 0.5° x 0.2° for the next titration block. If the smaller size was achieved (2.4° x 0.4°), titration continued by manipulating eccentricity. If participants reported 78% or more targets, the string of characters was presented 4° further from the fixation point; and if participants reported 62% or fewer targets, the string of characters was presented 4° closer to the fixation point. The titration procedure stopped when the proportion of hits ranged between ≥62% and ≤78% for two consecutive titration blocks. The size and eccentricity obtained for each participant was used during the experimental trials. The experiment lasted for about 1h and 30 min., including the initial titration procedure.

7.4.4 Results

Trials in which participants fixated (longer than 50 ms) 2° away from the fixation point before the offset of the string of characters were eliminated, which accounted for 6.04% of the trials (SD=6.27). For the peripheral task, we used non-parametric paired sample t-tests (Wilcoxon signed-rank) to analyze the proportion of hits, illusions, errors, and unseen trials depending on the Number Task condition (“far” vs. “near”), and the Endogenous Attention condition (attended vs. unattended location trials). To analyze the possible interaction between the Number Task and Endogenous

Attention in the proportion of hits, illusions, errors, and unseen trials, we computed for each participant the proportion of hits in the far-attended condition minus the near-attended condition and compared this index with the far-unattended condition minus the near-unattended condition (the same was done for illusions, errors, and unseen trials). We used non-parametric paired sample t-tests (Wilcoxon signed-rank) to compare these conditions. No significant interactions were observed, and therefore, no further planned comparisons were conducted.

The proportion of hits increased (W = 237, p = .012, r_B = .580), and the proportion of illusions decreased (W = 53, p = .004, r_B = - .647), on attended location trials as compared to unattended location trials (see figure 7.5). For hits and illusions, there were no other main effects or interaction (all ps>.34). The t-test on errors and unseen responses provided no evidence for main effects or interaction (all ps>.069).

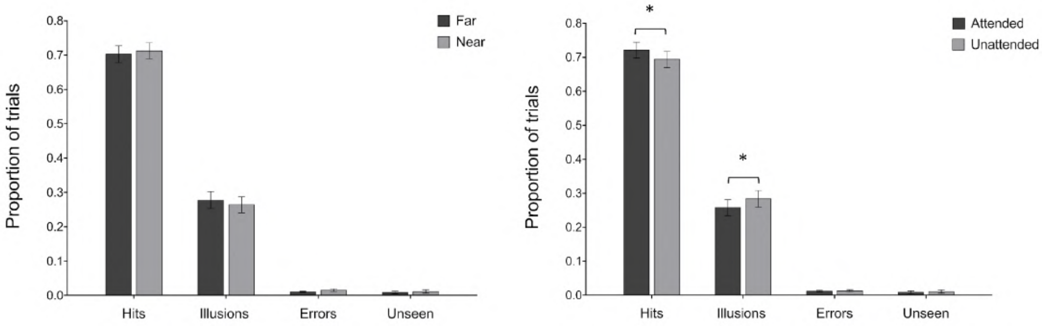

Figure 7.5: Proportion of trials for each experimental condition of the Number Task ("far" and "near") and Endogenous Attention (attended and unattended) in **Experiment 2**. The graph shows a significant increase of hits and decrease of illusions in the attended as compared to the unattended condition. Bars

represent standard errors; asterisks represent statistically significant effects ($p<.05$).

The analysis of the LISAS to respond to the Number Task demonstrated a main effect of the Number Task condition (F (1,23) = 51.460, MSE = 3681.559, $p < .001$, $\eta_p^2=.691$) (see figure 7.6). Responses were more efficient in the "far" as compared to the "near" condition. The main effect of Trial Type was not significant (F (1,23) = 3.008, MSE = 2896.519, $p = .096$, $\eta_p^2=.116$). There was no significant interaction between both factors (F (1,23) = 1.073, MSE = 1473.116, $p = .311$, $\eta_p^2=.045$)[2].

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[2] RT and accuracy analyses demonstrated a main effect of the Number Task condition, (RT: F (1,23) = 38.177, MSE = 2053.058, $p < .001$, $\eta_p^2=.624$, accuracy: F (1,23) = 21.584, MSE = .001, $p < .001$, $\eta_p^2=.484$). There was no evidence for other main effect or interaction (all ps>.067).

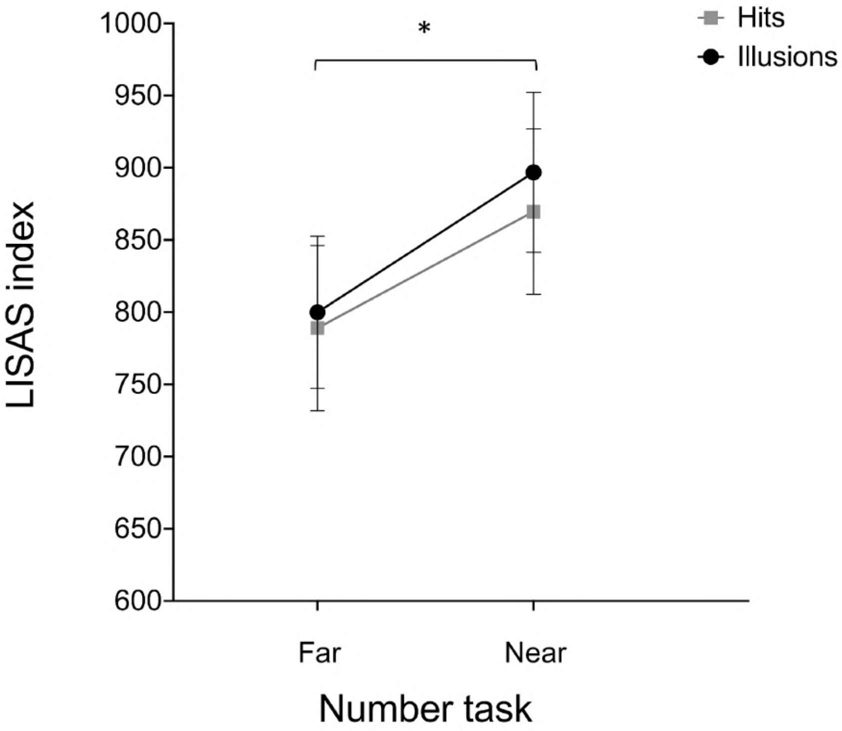

Figure 7.6: LISAS index for the Number Task response for each experimental condition in **Experiment 2**. The figure shows the main effect of Number Task. Bars represent standard errors; asterisks represent statistically significant effects (p<.05).

In order to explore the effect of feature expectancy on illusory conjunctions, we compared the proportion of illusions, errors, and unseen trials in the last two blocks of trials (when, unexpected to participants, the "L" target was printed in white on 50% of the trials) with the trials of the experimental blocks (in which the "L" target was always printed in red, green, or blue). For this analysis, we eliminated fifteen participants who noticed that the "L" was printed in white in some trials. The remaining participants (i.e. those that did not report having seen the white "L" in the last blocks of trials) made significantly more illusions ($W = 3$, $p = .001$, $r_B = - .934$, $BF_{10} = 476.717$), and errors ($W = 0$, $p < .001$, $r_B = - 1.0$, $BF_{10} = 210.272$), when the “L” was printed in white as compared to the expected block (“L” in chromatic color). The effect of expectancy on unseen trials did not reach significance ($W = 15$, $p = .221$, $r_B = - .455$, $BF_{10} = 1.182$) (see figure 7.7).

To directly compare the increase in illusions and errors in the unexpected block as compared to the expected block, we computed for each participant the increase in illusions for the unexpected as compared to the expected block, and compared this index with the increase in errors for the unexpected as compared to the expected block. We used non-parametric paired sample t-tests (Wilcoxon signed-rank) to compare these conditions. The comparison did not reach significance (W = 66, p = .168, r_B = .451). Although a comparable increase of illusions and errors was observed in the unexpected block as compared to the expected block, the proportion of illusions was larger than the proportion of errors both in the expected block (W = 91, p <.001, r_B = 1.000) and the unexpected block (W = 79, p =.017, r_B = .736).

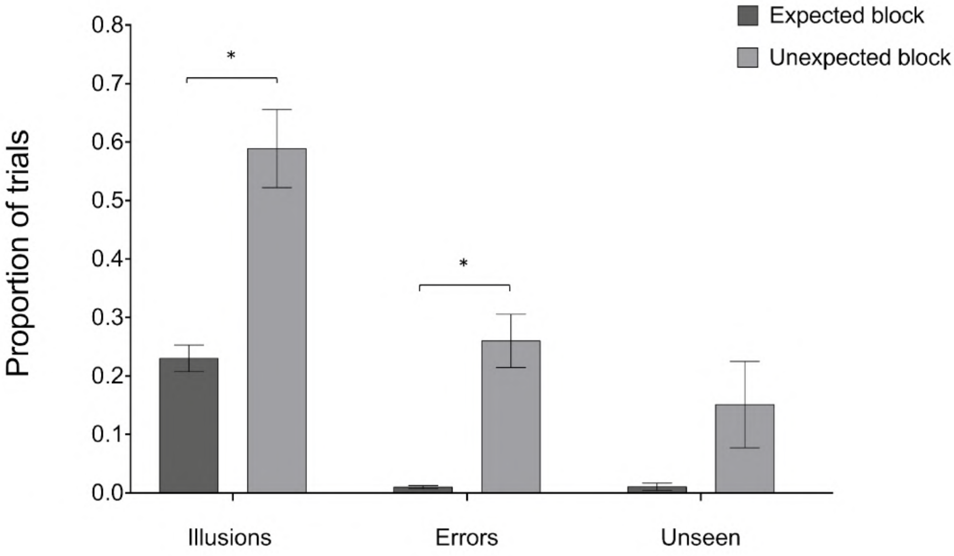

Figure 7.7: Proportion of illusions, errors, and unseen trials for the expected block and unexpected block for participants that did not notice that the "L" was printed in white on 50% of the trials in **Experiment 2** (N = 13). In the unexpected block, only trials in which the "L" was printed in white are presented. The graph shows the significant increase of illusions and errors in the unexpected

block in comparison with the expected block. Bars represent standard errors; asterisks represent statistically significant effects (p<.05).

In summary, Experiment 2 replicated the results of Experiment 1: the number of illusions was comparable when the Number Task was more or less demanding. Moreover, this experiment demonstrated that expecting the target at a certain spatial location decreased illusory conjunctions. Therefore, endogenous spatial attention was more effective for correct feature integration than focused (as opposed to divided) attention. Finally, feature expectancy demonstrated to powerfully modulate phenomenal consciousness. When, unknown to participants, the letter target was printed in white ink after being presented in red, blue, or green ink during 576 trials, ~50% of the participants did not notice at all this manipulation. In these unexpected trials, participants reported either a color not presented on display (errors) or the color of the letter aside the target (illusory conjunctions), demonstrating perceptual completion for unexpected events. Although both illusory conjunctions and errors increased in the unexpected block as compared to the expected block, illusory conjunctions were more likely than errors, demonstrating that perceptual completion is often solved by integrating features of the target and the distractor.

7.5 Method experiment 3: Exogenous Attention

Experiment 3 was identical to Experiment 2 but we manipulated exogenous spatial attention using a spatially non-informative peripheral cue (Chica et al., 2013, 2014).

7.5.1 Participants

Because the design and analyses were identical to experiment 2, the same sample size was used. Thirty healthy volunteers (22 females, mean age of 24 years, SD= 2.85, all right-handed) participated in the experiment. Five participants were excluded because they broke fixation in more than 30% of the trials. The total sample size was therefore 25 participants.

7.5.2 Apparatus and stimuli

Everything was identical to Experiment 2 except for the following: a spatially non-predictive peripheral cue (presented for 50 ms) and a cue-target inter-stimulus interval of 50 ms preceded the string of characters. The peripheral cue consisted of a white circle subtending 0.6°x0.6°, presented 2° above the location of the string of characters (see figure 7.4, right panel).

7.5.3 Procedure

Everything was the identical to Experiment 2 except for the following: 1) The string of characters was presented on the left hemi field on 50% of the trials, and on the right hemi field on 50% of the trials. 2) A peripheral cue was presented, which could appear at the same location that the string of characters (valid trials, 50%) or at the opposite position (invalid trials, 50%).

The experiment consisted of 8 blocks of 96 trials each, separated by a brief pause. Unknown to the participants, in the last two blocks (96 trials each), the letter “L” was printed in white on 50% of the trials. As in the previous experiment, before the experimental block, a separate titration block was conducted to achieve ~30% of illusions in each participant. The experiment lasted for about 1h and 30 min., including the initial titration procedure.

7.5.4 Results

We eliminated trials in which participants fixated (longer than 50 ms) 2° away from the fixation point before the offset of the string of characters. Only 7.57% of the trials were eliminated (SD=8.89).

We used non-parametric paired sample t-tests (Wilcoxon signed-rank) to analyze the proportion of hits, illusions, errors, and unseen trials in the peripheral task, depending on the Number Task condition ("far" vs. "near"), and the Exogenous Attention condition (invalid vs. valid location trials). As in Experiment 2, to analyze the possible interaction between the Number Task and Exogenous Attention in the proportion of hits, illusions, errors, and unseen trials, we computed for each participant the proportion of hits in the far-valid condition minus the near-valid condition and compared this index with the far-invalid condition minus the near-invalid condition (the same was done for illusions, errors, and unseen trials). We used non-parametric paired samples t-tests (Wilcoxon signed-rank) to compare these conditions. When a significant interaction was observed, planned comparisons were conducted using non-parametric paired samples t-tests (Wilcoxon signed-rank).

For both hits and illusions, the main effects of Number Task (for hits: $W = 191$, $p = .458$, $r_B = .175$; for illusions: $W = 119$, $p = .252$, $r_B = - .268$) and validity (for hits: $W = 100$, $p = .096$, $r_B = - .385$; for illusions: $W = 223$, $p = .107$, $r_B = .372$) did not reach significance.

However, there was an interaction between Number Task and Exogenous Attention for hits (W = 75, p = .017, r_B = - .538), and illusions (W = 263, p = .006, r_B = .618). The proportion of hits increased for valid as compared to invalid trials in the “far” (W = 81, p = .027, r_B = - .502) but not in the “near” condition (W = 151, p = .771, r_B = - .071). Similarly, the proportion of illusions decreased for valid as compared to invalid trials in the “far” (W = 263, p = .006, r_B = .618) but not in the “near” condition (W = 160, p = .958, r_B = - .015). No main effects or interactions were significant for errors and unseen responses (all ps>.166) (see figure 7.8).

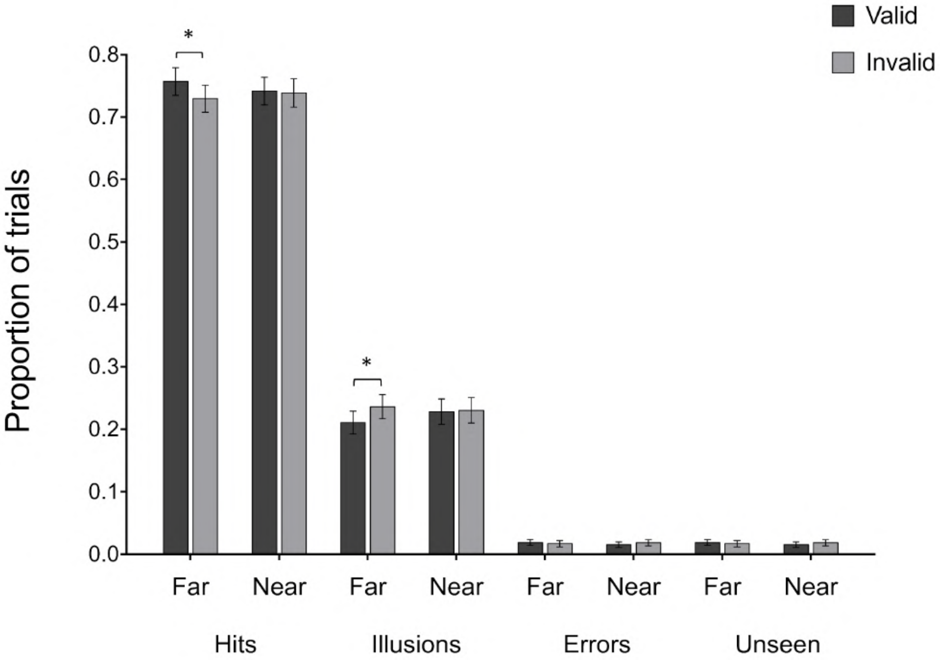

Figure 7.8: Proportion of trials for each experimental condition of Number Task condition (“far” and “near”) and Exogenous Attention (valid and invalid) in **Experiment 3**. The graph shows the interaction between Number Task and Exogenous Attention. Hits increase and illusions decrease in the valid as compared to the invalid condition, but only in the “far” condition. Bars represent standard errors; asterisks represent statistically significant comparisons (p<.05).

For the Number Task analysis, responses were faster and more accurate in the “far” as compared to the “near” number condition (F (1,24) = 33.864, MSE = 5567.299, $p < .001$, η_p^2=.585), and for hits as compared to illusions (F (1,24) = 9.994, MSE = 1744.643, p = .004, η_p^2=.294). Both factors interacted (F (1,24) = 4.508, MSE = 1135.643, p = .044, η_p^2=.158) (see figure 7.9), demonstrating more efficient responses for hits as compared to illusions in the “near” (F (1,24) = 12.186, MSE = 20726.006, p = .002), but not in the “far” condition (F (1,24) = 1.551, MSE = 1829.447, p = .225)[3].

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[3] RT analyses showed a main effect of the Number Task condition (F (1,24) = 34.068, MSE = 1407.667, $p < .001$, η_p^2=.587). The accuracy analysis demonstrated a main effect the Number Task condition (F (1,24) = 25.733, MSE = .002, $p < .001$, η_p^2=.517), and a main effect of Trial Type (F (1,24) = 16.741, MSE = 4.089e^-4, $p < .001$, η_p^2=.411). In the accuracy analysis, the interaction between both factors was significant (F (1,24) = 11.165, MSE = 3.671e^-4, p = .003, η_p^2=.317).

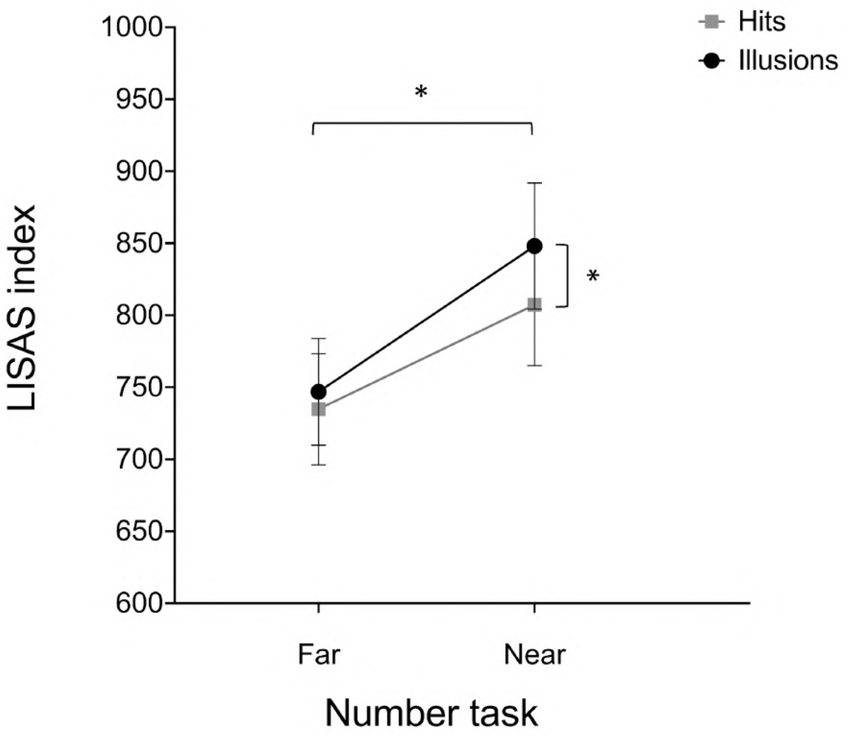

Figure 7.9: LISAS to respond to the Number Task as a function of the Number Task condition (“far” and “near”) and Exogenous Attention (valid and invalid) in **Experiment 3**. The figure shows main effects of Number Task, Trial Type, and the interaction between both variables. Bars represent standard errors; asterisks represent statistically significant comparisons (p<.05).

To explore the effect of feature expectancy on illusory conjunctions, we compared the proportion of illusions, errors, and unseen trials in the last two blocks (when, unexpected to participants, the “L” target was printed in white on 50% of the trials) with the rest of the blocks. For this analysis, we eliminated sixteen participants who noticed that the “L” was printed in white in some trials. The remaining participants (N=9) made more illusions (W = 0, p = .004, r_B = - 1.0, BF_{10} = 148.728) and errors (W = 0, p = .004, r_B = - 1.0, BF_{10} = 4.842) in the unexpected block than in the expected block. Unseen responses were comparable between both blocks (W = 2, p = .093, r_B = - .810, BF_{10} = 1.043) (see figure 7.10). As in Experiment 2, we compared the increment between illusions and errors in the unexpected block compared to the expected block, which was not significant (W = 37, p = .098, r_B = .644). Although a comparable increased of illusions and errors was observed in the unexpected block compared to the expected block, the proportion of illusions was larger than the proportion of errors both in the expected block (W = 45, p =.004, r_B = 1.000) and the unexpected block (W = 44, p =.008, r_B = .956).

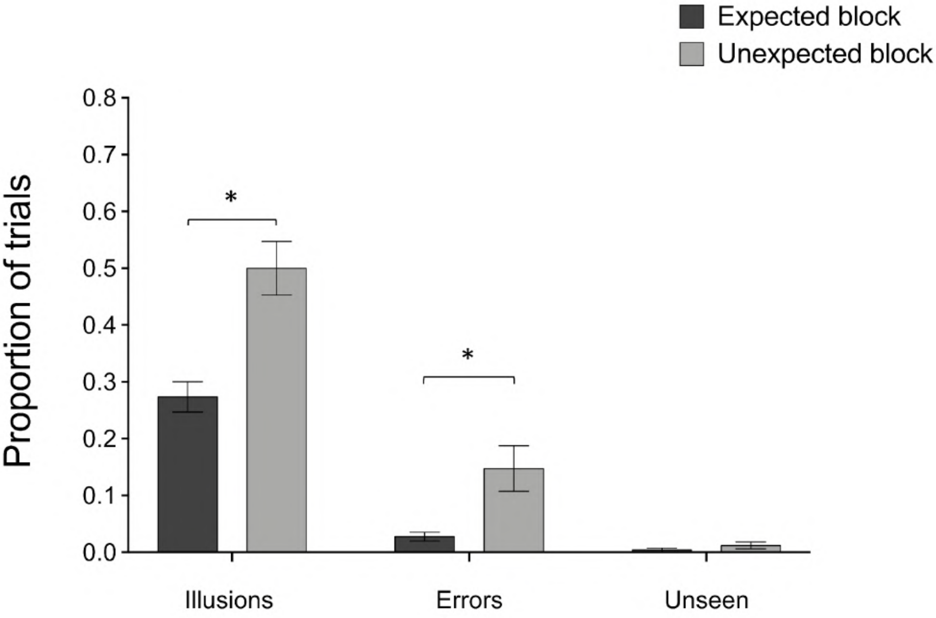

Figure 7.10: Proportion of illusions, errors, and unseen trials for the expected block and unexpected block for participants that did not notice that the “L” was printed in white on 50% of the trials in **Experiment 3** (N = 9). In the unexpected block, only trials in which the “L” was printed in white are presented. The graph shows the significant increase of illusions and errors in the unexpected blocks in comparison with the expected blocks. Bars represent standard errors; asterisks represent statistically significant effects (p<.05).

The results of Experiment 3 confirmed that, overall, divided attention did not modulate feature integration. As in Experiment 2 (endogenous attention), exogenous attention decreased the number of illusory conjunctions, but only in the less demanding ("far") condition, demonstrating an interaction between exogenous attention and divided attention in this perceptual task. Moreover, feature expectancy produced a reliable effect on the proportion of illusions and errors when an unexpected feature was presented.

7.6 Control analyses

One of the main results of these experiments is that divided attention does not modulate the proportion of hits and illusions. To conclude in favor of the null hypothesis, we collapsed the data of the 3 experiments and tested with Bayesian statistics if we had evidence in favor of the null hypothesis (comparable number of hits and illusions in the two number task conditions: more or less demanding task). For hits, illusions, and errors, Bayesian statistics demonstrated evidence in favor of the null hypothesis (hits: BF_{10}=.144; illusions: BF_{10}=.190; errors: BF_{10}=.191). We did have evidence in favor of the alternative hypothesis for unseen responses (BF_{10}=.7.538), i.e. more unseen responses were observed when the number task was more demanding as compared to the less demanding task.

The Number Task in Experiments 2 & 3 consisted of a number comparison task with a standard in memory. Participants indicated if numbers were smaller or larger than 5. According to the literature, numbers are represented along a "mental line" horizontally aligned, with smaller numbers being represented on the left and larger numbers being represented on the right (Dehaene et al., 1993; Fischer et al., 2003; Fischer & Shaki, 2014). It has been demonstrated that numbers can orient spatial attention to left-right locations according to their position in this mental line (Fischer et al., 2003). To test if the Number Task in Experiments 2 & 3 oriented attention to spatial locations, we codified the trials as "correspondent" if the number was 1-4 and the string of characters was presented on the left, or if the number was 6-9 and the string of characters was presented on the right. Trials in which the number was 1-4 and the string of characters was presented on the right, and trials in which the number was 6-9 and the string of characters was presented on the left, were codified as "non-correspondent". We analyzed the LISAS index as a function of Experiment (2 & 3), Correspondence, and Trial Type. Responses were more efficient for correspondent trials as compared to non-correspondent trials (F (1,47) = 9.938, MSE = 12381.523, p = .003, η_p^2=.175). This factor did not interact with other factors (all ps>.112). We also analyzed the proportion of hits, illusions, errors, and unseen responses using non-parametric T-tests (Wilcoxon signed-rank). Correspondence did not modulate the proportion of hits (all ps>.101, for the main effect of correspondence and its interaction[4] with other variables),

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[4] To analyze the possible interaction between the Correspondence and Attention in the proportion of hits, illusions, errors, and unseen trials, we computed for each participant the proportion of hits in the correspondent-attended condition minus the non-correspondent-attended condition and compared this index with the correspondent-unattended condition minus the non-correspondent -unattended

illusions (all ps>.110, for the main effect of correspondence and its interaction with other variables), errors (all ps>.557, for the main effect of correspondence and its interaction with other variables), or unseen responses (all ps>.094, for the main effect of correspondence and its interaction with other variables).

Another variable to consider for control analyses is the inner location of the target within the string of characters. More illusions are expected when the target was presented more peripherally than when it was presented closer to the fixation point. We reanalyzed the data of Experiments 2 & 3, and observed that the proportion of hits increased ($W = 1006$, $p < .001$, $r_B = .642$), and the proportion of illusions decreased ($W = 228$, $p < .001$, $r_B = - .628$), for inner as compared outer locations. "Inner target location" did not modulate the proportion of errors ($W = 419$, $p = .269$, $r_B = - .190$) or unseen responses ($W = 257$, $p = .236$, $r_B = - .228$). Although the attentional manipulation was different in both experiments (endogenous vs. exogenous attention), a combined analysis of both experiments demonstrated that the attention condition did not interact[5] with

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condition (the same was done for illusions, errors, and unseen trials). We used non-parametric paired samples t-tests (Wilcoxon signed-rank) to compare these conditions.

[5] To analyze the possible interaction between the Inner Target Location and Attention in the proportion of hits, illusions, errors, and unseen trials, we computed for each participant the proportion of hits in the inner-attended condition minus the outer-attended condition and compared this index with the outer-attended condition minus the outer-unattended condition (the same was done for illusions, errors, and unseen trials). We used non-parametric paired samples t-tests (Wilcoxon signed-rank) to compare these conditions.

"inner target location" (all ps>.290). However, in Experiment 1, the effect of inner target location was not significant for either hits (W = 257, p = .405, r_B = 0.182) or illusions (W = 178, p = .405, r_B = -0.182).

7.7 Discussion

The aim of the present study was to explore the effect of attention on feature integration, while considering attention as a heterogeneous construct, which involves several independent mechanisms (Petersen & Posner, 2012). In the present experiments, we used a paradigm that produced proximal illusory conjunctions of color-form features, and explored the role of divided (as opposed to focused) attention, as well as endogenous and exogenous spatial attention in feature integration. We also investigated the role of feature expectancy, by introducing an unexpected feature on the target in the last blocks of trials (the "L" target was printed in white on 50% of the trials, while it had been red, green, or blue on hundreds of trials experienced before). Approximately half of the participants did not notice this new feature. As we usually do in real life, perceptual information from the rest of the scene was used to complete this missing information, increasing the number of illusory conjunctions and errors. This result was consistently observed in Experiments 2 & 3, demonstrating the large influence of top-down expectations on visual perception (Aru & Bachmann, 2017; Harris et al., 2011; Moore et al., 1998; Wokke et al., 2013). The effect of stored knowledge on feature integration is a central process of the *Feature Confirmation Account*, which proposes that the stronger the stored representation of the stimulus, the fewer the demands on attention. I.e. in our paradigm, participants' knowledge about the possible color of the target (red, blue, or green) was so strong, that the attentional modulation from regions such as the parietal cortex (top-down feedback) might have been reduced, increasing the number of illusory conjunctions and errors when an unexpected feature was encountered.

It has been argued that proximal illusory conjunctions can be explained by the crowding effect, a limitation of visual perception such that stimuli placed within a certain critical spacing of each other will interfere with each other's perception (Henderson, 2014). Both endogenous (Montaser-Kouhsari & Rajimehr, 2005) and exogenous (Grubb et al., 2013; Pelli et al., 2007; Yeshurun & Rashal, 2010) attention decrease crowding (see Carrasco & Barbot, 2014 for a review of endogenous and exogenous attentional effects on spatial resolution), and our results have also demonstrated that both endogenous and exogenous attention decrease the number of illusory conjunctions (although the effect of exogenous attention was not observed when the secondary task was more demanding). This result demonstrates that spatial attention is important for correct feature integration, as it has been previously demonstrated (Briand et al., 1987; Briand, 1998; Cohen & Rafal, 1991; Prinzmetal et al., 1986). Although it is not explicit in the theory, we reckon that the *Feature Confirmation Account* accommodates these findings better than the FIT. The *Feature Confirmation Account* proposes an initial bottom-up stage of feature integration based on the activation of neurons sensitive to conjunctions of visual features. This initial process is subsequently confirmed through top-down feedback from the parietal cortex, and this is an attention-demanding process. Although the parietal cortex is important for both endogenous and exogenous attention (Chica, Bartolomeo, et al., 2011), according to Corbeta et al.'s model (2008), endogenous or top-down attention is implemented in regions such as the superior/inferior parietal cortex and the frontal eye field, which contain spatial representations. Exogenous or stimulus-driven attention (on the other hand) is related to the temporo-parietal junction and the inferior frontal gyrus, which do not contain spatial representations. The *feature confirmation account* can accommodate the results presented in this paper, i.e. demonstrating a more consistent effect of endogenous attention independently of the demands of the secondary task, while the effect of exogenous attention depends on the secondary task demands.

As expected, the RT and accuracy results of the number task (analyzed through the LISAS index) demonstrated faster and/or more accurate responses in the number comparison task when numbers were farther from the criterion (Verguts & Van Opstal, 2005). This indicates that our manipulation of secondary task demands was effective. Some previous studies using dual tasks have reported trade-offs while participants currently performed the two tasks. Accuracy of the number task could be sacrificed in order to respond to the peripheral task (see e.g. Matthews et al., 2018). We did not observe such a trade-off but RT to the secondary task increased (and/or accuracy decreased) when an illusion was later reported as compared to hits. This result suggests that a general preparatory process modulates the processing of both tasks. In some trials, participants could be more alerted (vigilant) than others, enhancing performance on the number task and preventing illusory conjunctions in the peripheral task. In a different paradigm in which near-threshold to-be-detected Gabor stimuli were used as targets (Chica et al., 2010), we also hypothesized that cue-induced capture of attention is not an all or none process. In each trial, the cue can capture attention to a greater or to a smaller degree, perhaps depending on the state of preparation of the brain. This was indexed by a different P1 component. Valid cues led to the conscious perception of the subsequent targets when they captured attention to their location, as indexed by the P1 component distributed over occipito-parietal areas. On the other hand, invalid cues led to the conscious perception of the subsequent targets only when they failed to capture attention at their location (opposite to the target location) (see also Chica et al., 2013, for similar fMRI results). It could be argued that the time to generate an answer is not a strong manipulation of attentional resources, especially in Experiments 2 and 3, in which the number task condition was manipulated in a trial by trial basis. Shore et al., (2001) failed to find an effect of T1 difficulty upon the magnitude of the Attentional Blink which was observed if T1 difficulty was manipulated between blocks of trials. However, in our experiments, the number task did not modulate the proportion of illusory conjunctions in Experiment 1, in which task demands were manipulated between blocks of trials. Our results are in line with previous literature demonstrating that divided attention manipulations affect illusory conjunctions in distal but not proximal set ups (Henderson & McClelland, 2020).

Contrary to previous studies (Paul & Schyns, 2003; Treisman & Gelade, 1980; Treisman & Schmidt, 1982), our manipulation of divided attention did not require participants to perform a secondary task as compared to not performing such a task. We compared participants' performance in two different conditions in which the secondary task was always performed, by varying attentional demands. In all the three experiments our manipulation was effective in producing longer RTs and/or lower accuracy for the more demanding condition as compared to the less demanding condition. The manipulation was also effective because more unseen responses were reported in the more demanding condition (as compared to the less demanding condition). However, the number of hits, illusions, errors, and unseen responses was comparable in both conditions. This result indicates that task demands did not modulate perceptual processes and feature binding. Moreover, RT to respond to the number task was delayed in those trials in which participants later on reported an illusion as compared to a hit (significantly in Experiments 1 and 3, and with a similar trend in Experiment 2). This result has been replicated in two other studies from our lab (currently in preparation), and indicates that attentional demands from the secondary task affect response preparation and/or execution but not perceptual processes associated to feature binding.

We also analyzed the orienting of attention to space related to the magnitude of the centrally presented numbers (Arend et al., 2013; Fischer & Shaki, 2014). Although the numbers did orient attention to the location they are mentally represented, this attentional orienting did not modulate feature integration. Additionally, more illusions were observed when the inner target location was presented more peripherally than when it was presented closer to the fixation point (a result that was significant in Experiments 2 & 3). The fact that more illusory conjunctions were observed for more external targets argues against the idea that crowding itself can produce the observed illusory conjunctions without any contribution of spatial selection. The further the target, the larger the influence of inner distractors in incorrect feature binding.

In summary, previous studies have demonstrated that different forms of attention modulate access consciousness differently. While exogenous spatial orienting (Chica, Bartolomeo, et al., 2011) and alerting (Chica et al., 2016; Kusnir et al., 2011) modulate perceptual sensitivity to detect near-threshold stimuli, endogenous attention (Chica, Bartolomeo, et al., 2011; Koch & Tsuchiya, 2007; Wyart & Tallon-Baudry, 2008) and executive control (Colás et al., 2017; Martín-Signes et al., 2018) produce weaker modulations of conscious access. These observations indicate that conscious access interacts with bottom-up forms of attention, but not with top-down forms of attention. On the other hand, phenomenal consciousness (as measured in the present design) is modulated by both endogenous and exogenous attention, but not by divided attention. This observation indicates that feature binding is related to spatial forms of attention, probably given the well-known role of the parietal cortex both in orienting spatial attention (Chica, Bartolomeo, et al., 2011; Corbetta et al., 2008) and feature binding (Cohen & Rafal, 1991; Esterman et al., 2007; Shafritz et al., 2002). The different interaction of access consciousness and phenomenal consciousness with different forms of attention might also be related with recent proposals that associate phenomenal consciousness with processing in the "back of the brain" (parietal and sensory regions) and access consciousness with processing in the "front of the brain" (prefrontal cortex). Because the three attentional systems are implemented in different brain networks (Petersen & Posner, 2012), they are expected to interact differently with different forms of consciousness.

In conclusion, our experiments showed that endogenous and exogenous spatial attention, as well as feature expectancy, modulated feature integration while divided attention did not, demonstrating the important role of top-down expectancies in visual perception. Although the *Feature Confirmation Account* made no explicit predictions about the different role of endogenous and exogenous attention on feature integration, we reckon this theory can easily accommodate the present findings.

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7.9 Author contributions

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Chapter 8: The role of brain oscillation in feature integration

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8.1 Abstract

Our sensory system is able to build a unified perception of the world, which although rich, is limited and inaccurate. Sometimes, features from different objects are erroneously combined. At the neural level, the role of the parietal cortex in feature integration is well-known (Braet & Humphreys, 2009; Shafritz et al., 2002). However, the brain dynamics underlying correct and incorrect feature integration are less clear. To explore the temporal dynamics of feature integration, we studied the modulation of different frequency bands in trials in which feature integration was correct or incorrect. Participants responded to the color of a shape target, surrounded by distractors. A calibration procedure ensured that accuracy was around 70% in each participant. To explore the role of expectancy in feature integration, we introduced an unexpected feature to the target in the last blocks of trials. Results demonstrated the contribution of several frequency bands to feature integration. Alpha and beta power was reduced for hits compared to illusions. Moreover, gamma power was overall larger during the experiment for participants who were aware of the unexpected target presented during the last blocks of trials (as compared to unaware participants). These results demonstrate that feature integration is a complex process that can go wrong at

different stages of information processing and is influenced by top-down expectancies.

8.2 Introduction

At any given moment, our sensory system is overloaded with stimuli that cannot be perceived in isolation. Our perceptual experience is rich and stimuli need to be integrated into coherent percepts and scenes. Even if our goal is relatively simple (e.g., hit a ball in a tennis match), we cannot only perceive single features such as movement, because other features such as color and shape are important to hit the ball and not another object (a bird passing by). Moreover, humans have the subjective impression of perceiving the whole scene in a very detailed way (in our example, the court, the trees around, the tennis net, etc.). However, this unified perception of large amounts of information has been found to be largely unreliable and full of errors (Block, 2011). Some of these errors consist of incorrect integration of features, e.g., erroneously integrating shape and color features from two objects located close to each other (Humphreys, 2016; Kouider et al., 2010; Pelli et al., 2004; Pelli & Tillman, 2008; Treisman & Gelade, 1980; Treisman & Schmidt, 1982; Whitney & Levi, 2011).

From a modular conception of the brain, it has been proposed that feature integration is a necessary process because features are processed in different brain regions of the visual hierarchy. Although this problem was partially solved by the discovery of neurons that respond to more than one feature in sensory regions such as V1 (Groen et al., 2017; Shu et al., 2015;

Tootell et al., 1998), the computational issue remains unsolved, since additional features may characterize the perceived object.

Behaviorally, errors in feature integration (known as illusory conjunctions) increase when the attentional system is overloaded, in conditions of divided attention (Treisman, 1996; A. M. Treisman & Gelade, 1980), when stimuli are briefly presented (Chen & Watanabe, 2021; Henderson & McClelland, 2020; Prinzmetal et al., 1995), when they are presented in the periphery of the visual field (Cohen & Ivry, 1989; Henderson & McClelland, 2020b; Prinzmetal et al., 1995; Robertson, 2003; Treisman & Schmidt, 1982), when top-down expectancies are manipulated (Aru et al., 2018; Aru & Bachmann, 2017; Cobos & Chica, 2022; de Gardelle et al., 2009; Kuhn & Rensink, 2016; Mack et al., 2016), and when spatial attention is diverted (Briand, 1998; Cobos & Chica, 2022; Cohen & Rafal, 1991; Grubb et al., 2013; Montaser-Kouhsari & Rajimehr, 2005; Prinzmetal et al., 1986; Yeshurun & Rashal, 2010). Top-down expectancies about perceptual information are well known to bias perception and decision making. Research has demonstrated larger amounts of errors (Engel et al., 2001; Engel & Fries, 2010; A. Mayer et al., 2016; Min & Herrmann, 2007), including illusory conjunctions, when an unexpected feature appears. Thus, our system tends to complete missing information with the expected perceptual features that we normally encounter in this context.

At the neural level, neuropsychological studies have stressed the role of the parietal cortex in feature integration (Baumgartner et al., 2013; Donner et al., 2000; Esterman et al., 2007; Leonards et al., 2000; Rodríguez-San Esteban et al., 2022; Shafritz et al., 2002); illusory conjunctions increase after damage to this brain area in syndromes such as hemispatial neglect (Bernstein & Robertson, 1998; A. Cohen & Rafal, 1991; Cohen-Dallal et al., 2021; Robertson, 2003) or the Balint's syndrome (Chechlacz, 2018; Cohen & Rafal, 1991; Soto & Humphreys, 2009). Brain lesions and fMRI data have been important to determine the brain regions supporting correct and incorrect feature integration. Nevertheless, cognitive processing is simultaneously distributed across several spatiotemporal scales, raising the question of how these distinct spectral signatures dynamically interact to enable effective cortical processing and communication (Buzsáki & Draguhn, 2004; Engel et al., 1992, 2001; Fries, 2009; Jensen et al., 2007; Senkowski et al., 2008).

To explore the temporal dynamics of feature integration, we studied the modulation of different frequency bands in trials in which feature integration was correct or incorrect (illusory conjunctions). Previous studies have reported gamma band modulations related to feature integration. For example, gamma activity is higher as the number of features to integrate increases (Honkanen et al., 2015; Keil & Müller, 2010; Morgan et al., 2011; Vidal et al., 2006). This frequency band has been considered a landmark of feature integration (Morgan et al., 2011; Tallon-Baudry, 2009; Tallon-Baudry et al., 1996; Tallon-Baudry & Bertrand, 1999; Vidal et al., 2006), although it has also been related with other cognitive processes such as working memory (Herrmann, Lenz, et al., 2004; Herrmann, Munk, et al., 2004; Miller et al., 2018), selective attention (Gruber et al., 1999; Keil & Müller, 2010; Strüber et al., 2000), and top-down expectancies (Bauer et al., 2014; Rohenkohl et al., 2018). The relation between the beta-band and feature integration is more limited. Beta band modulations are usually associated with motor responses (Engel & Fries, 2010) and top-down signals generated within attentional regions (such as the frontal eye field), which can change the excitability of lower-level visual areas (Veniero et al., 2021). Alpha modulations at parieto-occipital electrodes are related to spatial attention (Busch & VanRullen, 2010; Capilla et al., 2014; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006b) and, as outlined above, spatial attention is one of the most important cognitive processes modulating feature integration (Briand, 1998; Cobos & Chica, 2022; Cohen & Rafal, 1991; Grubb et al., 2013; Montaser-Kouhsari & Rajimehr, 2005; Prinzmetal et al., 1986; Yeshurun & Rashal, 2010). In particular, alpha lateralization has been related to spatial selection and inhibition of distractors (Capilla et al., 2014; Klimesch, 2012; Klimesch et al., 2007b; Lange et al., 2014; Min & Herrmann, 2007; Schroeder et al., 2018). Conjunction search paradigms have also supported the causal role of alpha oscillations in correct feature integration (Müller et al., 2015). More recently, it has been proposed that alpha/beta power decreases track the fidelity of stimulus-specific information represented within the cortex (Griffiths et al., 2019). Moreover, early modulations in alpha power (before the stimulation is presented) has been associated to preparatory processes that improve target detection (Ergenoglu et al., 2004; Wutz et al., 2018) and discrimination (Hanslmayr et al., 2007; van den Berg et al., 2016; van Dijk et al., 2008). Finally, there is abundant correlational evidence (Cavanagh et al., 2009; Cohen, 2011; Luu et al., 2004; Trujillo & Allen, 2007) about the role of theta power in error detection, as well as in memory encoding (Roux & Uhlhaas, 2014; Sammer et al., 2007; Sauseng et al., 2010) and false memories (Mapelli & Özkurt, 2019; Sweeney-Reed et al., 2012).

The paradigms used to explore feature integration and illusory conjunctions are diverse, and only one or two frequency bands have been explored in most of the studies addressing the brain dynamics of oscillatory processes associated to correct and incorrect perception (see e.g., Tallon-Baudry & Bertrand, 1999; Zhang et al., 2019). Nevertheless, we posit that different cognitive failures can lead to incorrect feature integration (failures in preparation, spatial attention, or working memory). In order to study the cascade of events that can produce an incorrect feature integration, we used a dual task paradigm (designed to increase the probability of finding erroneous feature integration), titrated to produce ~30% of illusory conjunctions while measuring high-density EEG. Our aim was to compare the spectral signatures of different frequency bands (theta, alpha, beta, and gamma), previously associated to error detection (Cavanagh et al., 2009; Cohen, 2011; Fusco et al., 2018; Luu et al., 2004; Romei et al., 2011; Trujillo & Allen, 2007), preparation (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Mathewson et al., 2009; van den Berg et al., 2016; van Dijk et al., 2008; Wutz et al., 2018), spatial attention (Busch & VanRullen, 2010; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006b), perceptual information representation (Griffiths et al., 2019), top-down influences over visual perception (Veniero et al., 2021), working memory (Herrmann, Munk, et al., 2004; Miller et al., 2018), and feature integration itself (Morgan et al., 2011; Tallon-Baudry, 2009; Tallon-Baudry et al., 1996; Tallon-Baudry & Bertrand, 1999; Vidal et al., 2006). To explore the role of expectancy in feature integration, as done in previous studies (Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022), we introduced an unexpected feature to the target in the last blocks of trials, and compared brain oscillatory modulations of participants that were aware of this unexpected feature and those that were not aware.

According to the above-reviewed studies, we predicted that incorrect feature integration leading to illusions (as compared to hits) would be characterized by: 1) an increase in theta power (Cavanagh et al., 2009; Cohen, 2011; Luu et al., 2004; Mapelli & Özkurt, 2019; Roux & Uhlhaas, 2014; Sammer et al., 2007; Sauseng et al., 2010; Sweeney-Reed et al., 2012; Trujillo & Allen, 2007), 2) increased alpha power at early (Ergenoglu et al., 2004; Hanslmayr et al., 2007; van den Berg et al., 2016; van Dijk et al., 2008; Wutz et al., 2018) and late stages, especially at contralateral locations (Busch & VanRullen, 2010; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006), 3) increased beta power (Griffiths et al., 2019; Veniero et al., 2021), and 4) reduced gamma power (Honkanen et al., 2015; Keil & Müller, 2010; Morgan et al., 2011; Vidal et al., 2006). We had no a-priori hypothesis about the modulations that would be associated to the expectancy manipulation.

8.3 Method

8.3.1 Participants

G*power (Faul et al., 2007) was used to calculate the sample size based on the effect size of the proportion of illusions reported in Cobos & Chica (2022; Experiment 3). The effect size in this experiment, reported by rank-biserial correlation (r_B), revealed a large effect (r_B= -.502; d = 1.2, Cohen, 1992; Fritz et al., 2012). We calculated sample size for T-test Wilcoxon signed-rank test (matched pairs, $\alpha = 0.05$; Power = 0.95). A minimum sample of 12 participants was required. Because we planned to contrast data from aware and unaware participants in the expectancy manipulation (see Method), and because some participants were expected to be excluded from data analyses due to artefacts and noise in the EEG signal, we decided to collect a larger sample of 30 participants.

Thirty healthy volunteers (21 females; mean age of 24 years, SD = 2.87 years) participated in the study in exchange for a monetary compensation of 10€/h. They all reported normal or corrected-to-normal vision, normal color perception, and had no prior experience with the task. Signed informed consent was collected before the study, and participants were informed about their right to withdraw from the experiment at any time. The CEIM/CEI Granada's Biomedicine Ethic Research Committee approved the experiment, which was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

8.3.2 Apparatus and stimuli

E-Prime software version 2.0 (Schneider et al., 2002) was used to control stimuli presentation, timing operations, and behavioral data collection. Participants were seated at an approximate distance of 60 cm from the computer screen (an LCD monitor, 24'', Benq BL2405HT, 1920x1080 pixels, with a refresh rate of 60 Hz). The experimental procedure was adapted from Esterman and colleagues (Esterman et al., 2004, 2007; see also Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022).

The display consisted of a central fixation point (a white plus sign, 0.47° × 0.47°) presented against a black background. A number was presented above (0.95°) the fixation point, printed in white. It could take values between 1 and 9, excluding 5. According to the numerical distance effect (Verguts & Van Opstal, 2005), the numbers conformed two possible conditions: a more demanding "near" condition (numbers closer to 5: 3, 4, 6, 7) and a less demanding "far" condition (numbers further away from 5: 1, 2, 8, 9). The peripheral stimulus consisted of a horizontal string of four characters (3.8° x 1.05°) presented in Arial font. The peripheral stimulus could randomly appear 5.7° to either the right or left side of the fixation point (measured from the center of the fixation point to the inner corner of the string of characters), and 0.24° above the horizontal axis. The two external characters consisted of the flankers "S" or "8", printed in white. The two inner characters were the letters "L" and "O", which were colored in red (RGB: 215,0,0), blue (RGB: 46,118,182), or green (RGB: 0,135,61). In each trial, the "L" and "O" letters always had different colors. Both letters were presented randomly at either the inner leftmost or rightmost location (see Procedure section). A mask (&&&&) was also presented after the string of characters (see Figure 8.1).

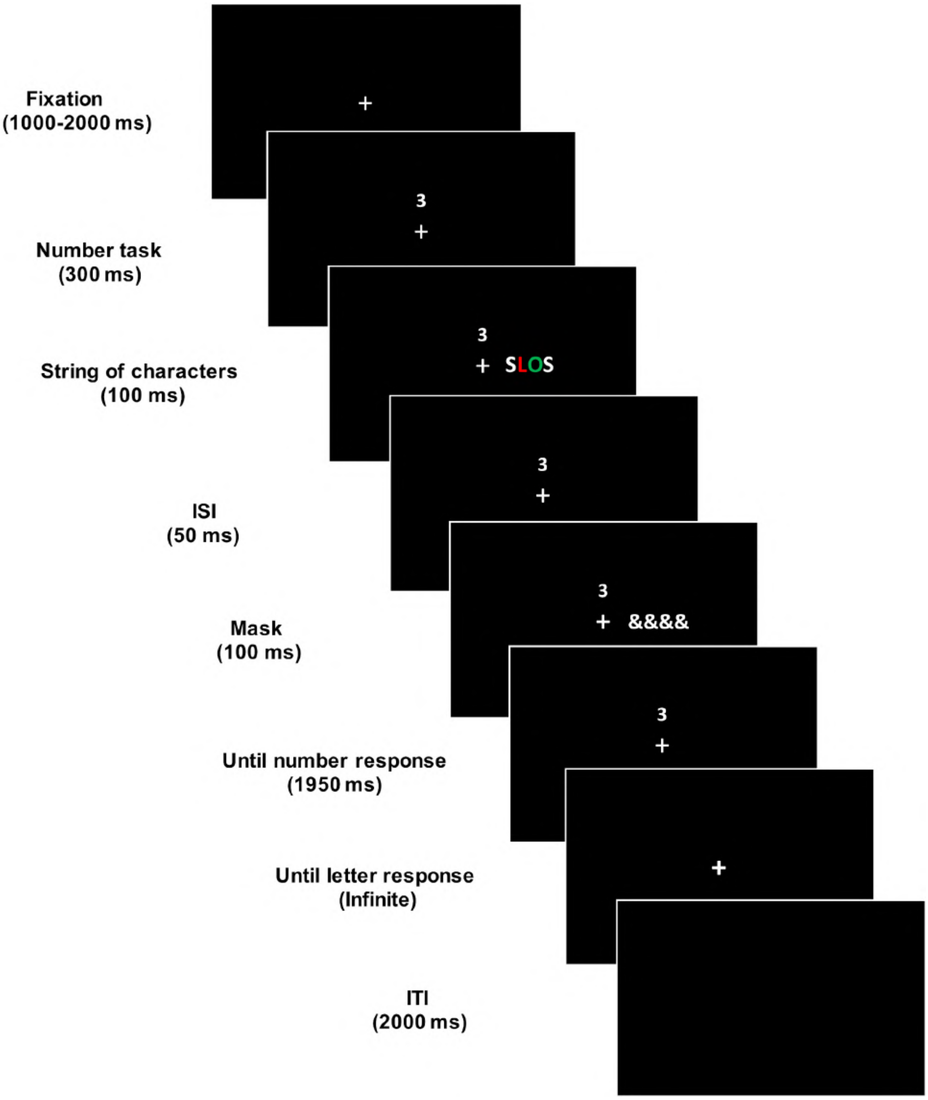

Figure 8.1: Sequence and timing of events in a given trial. Participants first responded to the central task reporting if the number was larger or smaller than 5. After this speeded response was given, participants responded to the peripheral task, indicating the color of the "L" letter with no time pressure.

8.3.3 Procedure

The experiment consisted of fourteen blocks of 48 trials, each of them separated by a brief pause. Figure 8.1 shows the sequence and timing of stimuli in a given trial. Trials began with a fixation screen (with a random duration between 1000-2000 ms), followed by the presentation of the number (displayed for a total of 2500 ms). Numbers from the far and the near condition were randomly presented. After 300 ms from the number onset, the peripheral target was shown for 100 ms. Its location was determined randomly, appearing 50% of the trials at each side of the fixation point. After an inter-stimulus interval (ISI) of 50 ms, the mask was displayed for 100 ms.

Participants were first required to respond to the number (central task). As soon as the number was presented, they reported whether it was smaller or larger than 5 (using the left or right mouse button, respectively). They used their right hand for this response, performing as fast and accurate as possible.

Once the answer to the central task was given, participants were required to carry out the peripheral task. They were instructed to respond accurately, but without time pressure, using the left hand to press the “z”, “x”, and “c” keys to report the color of the letter “L” (either red, blue, or green). The correspondence between color and response key was counterbalanced between participants. They could also press the space bar if they were not able to report the color of the target letter. Responses to the peripheral task were categorized as hits (when the correct color of the letter “L” was reported), illusions (when participants reported the color of the letter “O”), errors (when participants reported a color that was not presented in the display), and unseen (when participants could not report the color of the target letter).

Unknown to the participants, in the last four blocks of trials, the target letter was printed in white on 50% of the trials. In these trials, there was no correct response. If participants realized of the presence of the white target, they could report “unseen”. They could also respond by saying the color of the distractor (illusion) or a color not presented in the display (error). We will refer to the first 10 blocks as the “expected blocks” and to the last 4 blocks as the “unexpected blocks”. At the end of the experimental session, a brief structured interview was completed to explore whether participants were aware of the appearance of the white letter. Three questions were asked: “Do you have any comments about the experiment?”; “Did you find any color combination more difficult than the others?”; “Have you noticed anything different at the end of the experiment?”. After the interview, the objectives of the experiment were explained to the participants, and they were informed about the presence of the white target in the last blocks of trials. At this time, the experimenter confirmed again if participants had perceived the white target or not.

Before the experimental blocks, a separate titration block was presented in order to achieve ~70% hits in each participant. We assumed that the remaining 30% of the trials would be mostly illusions. During titration, trials were similar to the experimental task, except for the size of the string of characters (and the mask). Titration began with the easier condition (size = 3.8° x 1.05°; eccentricity from fixation = 5.7°). After every 14 trials (a titration block), the mean proportion of hits was calculated. If participants correctly reported the color of the peripheral target in 78% or a larger proportion of trials, the size of the string of characters (and the mask) was decreased by 0.3° x 0.1° for the next titration block. If participants correctly reported the color of the peripheral target in 62% or a fewer proportion of trials, the size of the string of characters (and the mask) was increased by 0.3° x 0.1° for the next titration block. The titration procedure stopped when the proportion of hits ranged between ≥62% and ≤78% for two consecutive titration blocks. The stimulus size obtained for each participant was used during the experimental trials. The experiment duration (including titration and experimental blocks) was around two and a half hours.

8.3.4 Behavioral statistical analysis

Behavioral data from the central and the peripheral tasks were analyzed by using non-parametric paired sample t-tests (Wilcoxon signed-rank) to compare the mean of proportion of hits, illusions, errors, and unseen responses for the two Central Task conditions (far and near). The effect size is shown by the rank-biserial correlation (r_B). If the score is <.1, it is considered a trivial effect; values around 0.1 are interpreted as small effects, around 0.3 as a medium effect, and >0.5 as a large effect (Cohen, 1992; Fritz et al., 2012). The Cousineau-Morey's method (Cousineau, 2005; Morey, 2008) was used to calculate the standard errors of the means represented as error bars.

For the analysis of the central task, accuracy and RT were emphasized. Under these conditions, speed-accuracy trade-off-based strategies can be adopted. That is why we employed the linear integrated speed-accuracy score (LISAS), a measure that combines RT of correct responses (cr) and the proportion of errors (PE) (Vandierendonck, 2017) providing an index of behavioral effects free of these speed-accuracy trade-offs. S_{RT} refers to the participant's overall RT standard deviation, and S_{PE} refers to the participant's overall PE standard deviation. Using this index, small values represent faster and/or more accurate responses.

$$LISAS = RTcr + \frac{S_{RT}}{S_{PE}} * PEcr$$

To analyze this index, we run a repeated measures ANOVA with the independent variables of Central Task condition (far and near) and Trial Type (hits and illusions).

To explore the effect of expectancy on feature integration, we performed two analyses. We divided participants into those that were aware of the expectancy manipulation (N=14; according to the post-experiment questionnaire) and those that were not aware (N=16).Firstly, we compared the proportion of illusions, errors, and unseen trials in the Unexpected blocks (where the peripheral target was printed in white on 50% of the trials; last 4 blocks of trials) with the trials of the Expected blocks (where the peripheral target was always printed in red, green, or blue; first 10 blocks of trials), introducing Awareness as a between participants' factor in the ANOVA. Secondly, we compared their responses to the Central Task condition (far vs. near) in each Trial Type (hits, illusions, errors, and unseen) during the first 10 blocks of trials. For each group, we subtracted the proportion of responses in each trial type in the far minus the near condition, and compared this index between groups (using a non-parametric independent sample Mann-Whitney test).

Since we did not anticipate the number of participants who would be aware of the white target, Bayesian Factor (BF) analysis was applied after recruiting all participants. BF analyses provide conclusive evidence in favor of the alternative (BF>3) or the null hypothesis (BF<.33).

8.3.5 EEG recording

EEG signal was acquired using a 64-channels system mounted on a cap (actiCAP snap, Brain Products) and a computer running the BrainVision Recorder software (version 1.20.0601). Impedances were kept below 5 kΩ, following the recommendations of the amplifiers' manufacturer, and the signal was digitized at a sampling rate of 1000 Hz. EEG activity was referenced to the FCz electrode online. Electrical activity elicited by horizontal eye movements was monitored by electro-oculogram (EOG), recorded from two electrodes (TP_9-TP_{10}) on the outer canthi of both eyes.

8.3.6 EEG analysis

While Fieldtrip software (Oostenveld et al., 2011) and in-house built Matlab scripts were used to analyze EEG data, the statistical analysis of these results was performed with JASP (Goss-Sampson, 2019). The general aim of the EEG analyses was to explore how different brain oscillations were related to correct (hits) or incorrect responses (illusions) to the peripheral task, and to the different demands of the central task (near vs. far).

8.3.6.1 Preprocessing

Data were segmented into 4000 ms long epochs, starting 2000 ms before the number onset. These long epochs were used to avoid undesirable edge effects in the time-frequency (TF) analysis.

Only trials in which the participants correctly responded to the central task and provided a response to the peripheral task were used in further analysis.

Five different steps were followed for preprocessing and artifact rejection. 1) The power line artefact at 50 Hz and harmonics (100 Hz and 150 Hz) was reduced via spectrum interpolation (Leske & Dalal, 2019). 2) The baseline was corrected from -2000 to 0 ms to facilitate subsequent visualization of EEG traces. 3) All EEG data were visually inspected trial-by-trial and subject-by-subject. Trials which included artifacts such as swallowing, cable movement, or muscular activity were manually rejected. Trials containing blinks or eye-movements 600 ms before or 800 ms after the number onset were also manually rejected. This procedure excluded 11% of the trials (SD=6.5). 4) Independent Component Analysis ("runica" algorithm in Fieldtrip) was used to eliminate any remaining blinks. 5) An average of 2.37 (SD = 2.12) channels were interpolated using the signal recorded by neighboring electrodes. Two participants were eliminated because the number of rejected trials exceeded two deviations above the mean. Another participant was discarded because he/she had 9 bad channels. Finally, EOG electrodes were removed and EEG data were re-referenced to the common average.

Data were split into different experimental conditions based on the combination of Trial Type (hit or illusion) x Peripheral Target Location (left or right).

8.3.6.2 Time frequency analysis

Power was calculated for each trial using a (multi-) taper approach (Percival & Walden, 1993). The frequencies analyzed ranged from 2 to 100 Hz in 1 Hz steps. For low frequencies (<30 Hz) a 400 ms sliding window was applied, while for the gamma frequency (>30Hz) we used a 200 ms sliding window. In both cases, the signal was analyzed in 25 ms steps. The resulting TF maps were normalized at the participant level by calculating the relative change from baseline (-500 to -200 ms locked to number onset).

The selection of electrodes and frequency bands is detailed in the supplementary material, section 8.6.1. To avoid the problems of “double dipping” (i.e., the use of the same data for selection and selective analysis Kriegeskorte et al., 2009), we employed the TF representations of all conditions pooled together. Thus, we selected the electrodes with the maximum power peak for each frequency band: PO7 and PO8 for theta band (3-6 Hz), PO3 and PO4 for alpha band (9-12 Hz), C3 and C4 for beta band (17-23 Hz) and F7, F8, and CPz for gamma band (30-40 Hz) (Figure 8.2). FC1 (for the theta band) and CP1 (for the beta band) were also analyzed for showing an additional peak, although the analysis revealed non-significant results in these electrodes (see supplementary material, section 8.6.1.2).

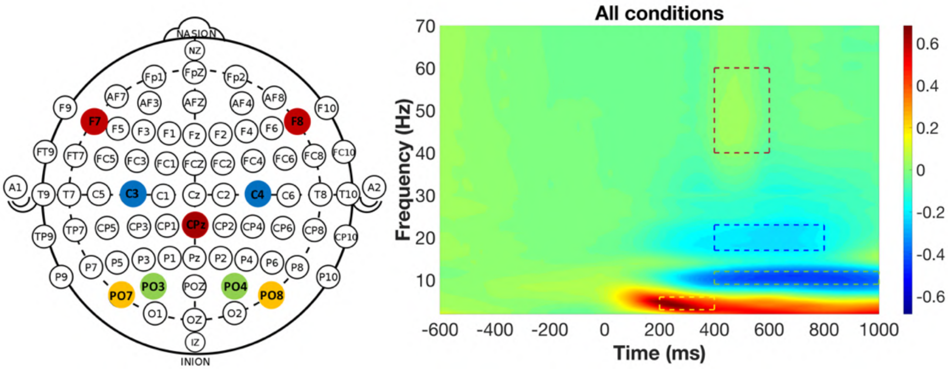

Figure 8.2: Sketch of the electrodes' distribution around the scalp as viewed from above (the top of the figure represents the frontal area). Additional sites according to the 10-20 International System are shown for further reference. Electrodes selected for analyses of each frequency band are highlighted: PO7-PO8 (yellow circles) for the theta frequency (3-6 Hz); PO3-PO4 (green circles) for the alpha frequency (9-12 Hz); C3-C4 (blue circles) for the beta frequency (17-23 Hz); CPz, F7, and F8 (yellow circles) for the gamma frequency (40-60 Hz). On the right, averaged normalized TF representation (2-70 Hz and -600 to 1000 ms; time 0 ms represents the number onset) for all conditions, participants, and electrodes after bootstrapping. The colorbar indicates relative change to baseline (-500 to -200 ms). Dashed lines represents the range of each frequency and the period of time analyzed. The color of the dashed lines corresponds to the color of electrodes.

The variables of interest in our paradigm were Central Task condition (far and near) and Trial Type (we focused on hits and illusions for the TF analysis). However, trials were sorted as hits or illusions according to participants' responses, and hits were more likely than illusions (mean of 53.68% hits and 24.74% illusions). The mean number of trials per condition after preprocessing was as follows: Hit-right target: average of 134 (+/- 33) trials; Hit-left target: average of 124 (+/- 34) trials; Illusion-right target: average of 56 (+/- 25) trials, Illusion-left target: average of 63 (+/- 31) trials. In order to deal with the effect of this difference in trial number, we used a parametric bootstrapping approach. Firstly, for each participant, we selected the condition with the minimum number of observations (e.g., 30 trials). Then, we randomly selected the same number of trials (30 trials in the example) for each of the other conditions. Secondly, selected trials were averaged leading to a single time series for each condition (Trial Type and Peripheral Target Location) and electrode of interest. This procedure was repeated 1000 times for each participant resulting in a time x 1000 matrix per condition and electrode, that was finally averaged across the bootstrapping dimension.

Finally, we selected the time windows of interest for each frequency band based on the grand-average of the temporal spectral evolution of all conditions pooled together. Time windows of interest were selected ±100ms from the maximum/minimum peak in each frequency

8.3.6.3 Statistical analysis of time-frequency maps

Statistical analyses were performed by paired sample t-test for peaks observed before the peripheral target was presented (before 300 ms). In these t-tests, hits and illusions were compared. Nonetheless, repeated measures analyses of variance (ANOVAs) were applied for peaks observed after the peripheral target was presented (after 300 ms). In these ANOVAs, the variable Laterality was also included in the ANOVA. Electrodes were considered ipsilateral or contralateral to the target location: for example, left targets were ipsilateral to the F7 electrode and contralateral to the F8 electrode. When a significant interaction was observed, planned comparisons were conducted using simple main effects in the

ANOVA. The variable Central Task was not introduced in this analysis because it did not behaviorally modulate the proportion of hits and illusions produced by the participants. When only one electrode (i.e., CPz) was statistically tested, paired samples t-tests were also applied instead of ANOVAs.

To explore the effect of expectancy on feature integration, we divided participants into those that were aware of the expectancy manipulation (N=14; according to the post-experiment questionnaire) and those that were not aware (N=16). We compared the overall power in the different frequency bands (theta, alpha, beta and gamma) during the first 10 blocks of trials for participants that were aware and not aware. We did not analyze the results of the last 4 blocks of trials, because we had not enough trials for this TF analysis.

8.3.6.4 Post-hoc cross-frequency power-power correlation analysis

Given that some of the observed modulations in the TF analysis were contrary to our hypothesis, we decided to run a post-hoc cross-frequency correlation on a trial-by-trial basis. The range of frequencies (theta: 3-6; alpha: 9-12; beta: 17-23; gamma: 40-60 Hz), electrodes (theta:PO7-PO8; alpha: PO3-PO4; beta: C3-C4; gamma: F7-F8), and time windows selected for the analysis was the same as described above. Trial-by-trial power-power cross-frequency correlations were calculated for each participant and each condition. For each frequency range, random trial selection was performed based on the minimum number of trials among the conditions for each participant. The data was segregated for each channel, allowing for the consolidation of information based on ipsilateral and contralateral data. Note that the CPz electrode in the gamma band was not introduced in this analysis as it was not lateralized. The time period was defined according to the predetermined time window associated with the maximum/minimum peak of each frequency, and the data within that window was averaged. Pearson's correlation scores were calculated between all frequency ranges of interest (early alpha, theta, late alpha, beta, and gamma band) at ipsilateral and contralateral sites. The described procedure was repeated 1000 times, resulting in different sets of randomly selected trials along with corresponding Pearson's correlation scores. The bootstrapped Pearson's correlation scores and the participant’s dimensions were averaged. By utilizing the atanh function in Matlab, Z-scores were obtained (as done in Bengson et al., 2012; Mazaheri et al., 2009; Mazaheri & Jensen, 2010), leading to the generation of four different matrices (ipsilateral hits, contralateral hits, ipsilateral illusions, and contralateral illusions). We first compared if the correlations observed for each condition (hit and illusion) were statistically significant from 0 using a paired sample t-test. If one of the correlations (for hits or illusions) in each pair was statistically significant from 0, paired samples t-tests were applied to find statistical differences between the z-score in each condition (hits vs. illusions for ipsilateral electrodes and hits vs. illusions for contralateral electrodes; see Figure 8.11).

8.3.7 Data availability

All behavioral data analysis and Matlab home-made scripts can be obtained from the open access web: Open Science Framework (OSF). Use the following link to access the information: https://osf.io/tbwf6/?view_only=5efed32f7fb747799cb51952c0917208. The following software is required to run the data: JASP (Goss-Sampson, 2019), Matlab, and Fieldtrip (Oostenveld et al., 2011).

8.4 Results

8.4.1 Behavioral results

We first analyzed the influence of the Central Task condition in the responses provided to the peripheral task. Neither the proportion of hits (W=298, p=.184, r_B=.282), illusions (W=189, p=.382, r_B=-.187), errors (W=219, p=.792, r_B=-.058), or unseen responses (W=36500, p=.552, r_B=-.198) were significantly modulated by the Central Task condition (see Figure 8.3).

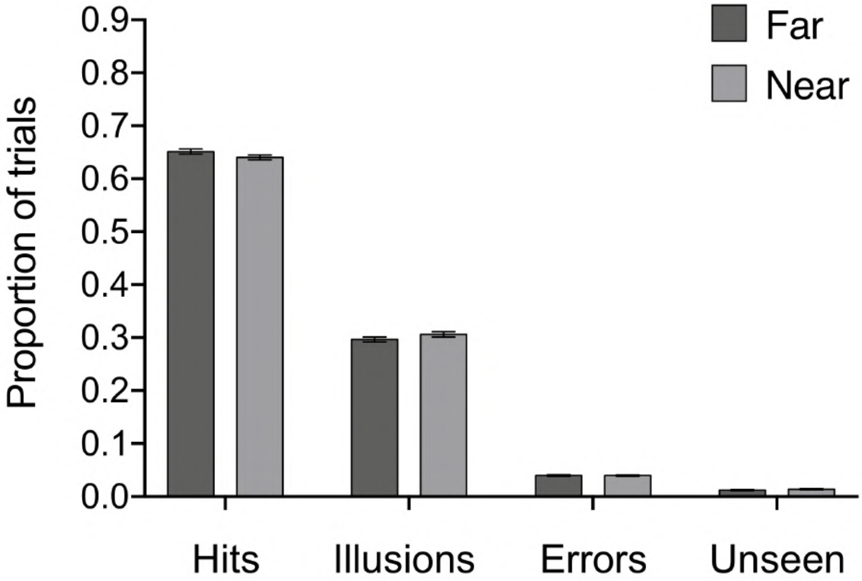

Figure 8.3: Proportion of hits, illusions, errors, and unseen responses for each Central Task condition ("far" and "near"). This figure shows a comparable number of hits, illusions, errors, and unseen responses in both conditions.

We then analyzed RT and accuracy to the central task, as a function of Central task condition (far, near), and categorized the trials as hits or illusions depending on participants' responses to the peripheral task. The analysis of the LISAS index (which combines RT and accuracy, see Methods) demonstrated that responses were more efficient for the "far" as compared to the "near" condition (F (1, 28) = 65.207, MSE = 414,409, $p < .001$, $\eta_p^2 = .70$)[1]. Even though participants had not responded to the peripheral task yet, responses to the central task were more efficient if participants correctly reported the color of the target letter later on the trial (hits) than if an illusion was observed (F (1, 28) = 22.447, MSE = 92,579, $p < .001$, $\eta_p^2 = .445$) (see Figure 8.4). The interaction between Central Task and Trial Type was not significant (F (1, 28) = 2.890, MSE = 4772, p = .100, η_p^2 = .094)[6].

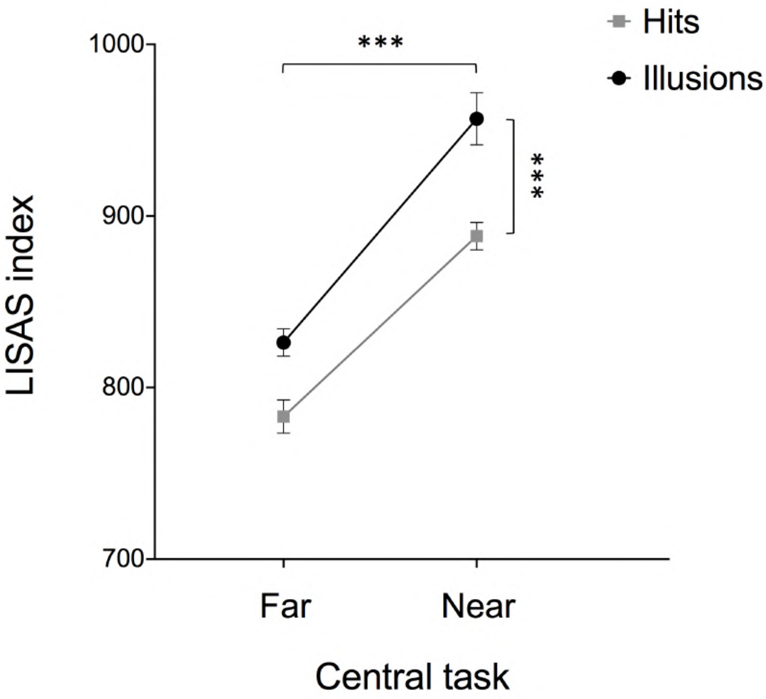

Figure 8.4: LISAS index to respond to the central task as a function of Central Task condition and Trial Type. This figure shows the main effects of Central Task and Trial Type. Asterisks represent significant effects (***p<.001).

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[6] RT and accuracy were also analyzed separately (see section 8.6.2 figures: S6 and S7, in the supplementary material). For RT (in which only trials with correct responses to the central task were analyzed), the ANOVA demonstrated both a main effect of Central Task condition (F (1, 28) = 88.231, MSE = 159,975, p < .001, η_p^2 = .759), and a main effect of Trial Type (F (1, 28) = 38.206, MSE = 43,193, p < .001, η_p^2 = .577). The interaction between both variables did not reach significance (F (1, 28) = .954, MSE = 525, p = .337, η_p^2 = .033). For the accuracy analysis, a main effect of Central Task (F (1, 28) = 24.114, MSE = .047, p < .001, η_p^2 = .463), and a main effect of Trial Type (F (1, 28) = 5.884, MSE = .005, p = .022, η_p^2 = .174) were found. The interaction between these factors was not statistically significant (F (1, 28) = 3.375, MSE = .001, p = .077, η_p^2 = .108).

In order to explore whether aware and unaware participants of the presence of the white target during the last blocks of trials did already differ in their performance during the expected bocks, Awareness was introduced in the analysis as a between-participants factor. No main effect of Awareness or interactions with this factor were observed (all ps>.430).

To explore the role of expectancy on illusory conjunctions, we analyzed the proportion of illusions, errors and unseen responses when the target letter was printed in white in the Unexpected blocks (last 4 blocks of trials) compared to the Expected blocks (first 10 blocks of trials). Participants who were aware (N=14) and not aware (N=16) of the expectancy manipulation (presence of the white target in the last block of trials) responded similarly to the task. Both groups made more illusions (not aware: W=8, p<.001, r_B=-.882, BF_{10} =102.807; aware: W=3, p<.001, r_B=-.943, BF_{10}=264.07), errors (not aware: W=1, p<.001, r_B=-.985, BF_{10} =54.97; aware: W=8, p=.003, r_B=-.848, BF_{10}=6.842), and unseen responses (not aware: W=1, p=.005, r_B=-.970, BF_{10}=6.02; aware: W=0, p=.022, r_B=-.848, BF_{10}=4.582), in the Unexpected block compared to Expected block (Figure 8.5). A direct comparison between both groups (subtracting the proportion of responses in each trial type in the expected block minus the unexpected block and comparing this index between groups using a non-parametric independent sample Mann-Whitney t-tests), indicated that the expectancy effect was comparable for illusions, errors, and unseen responses between groups (all ps>.166; BF_{10}=0.678).

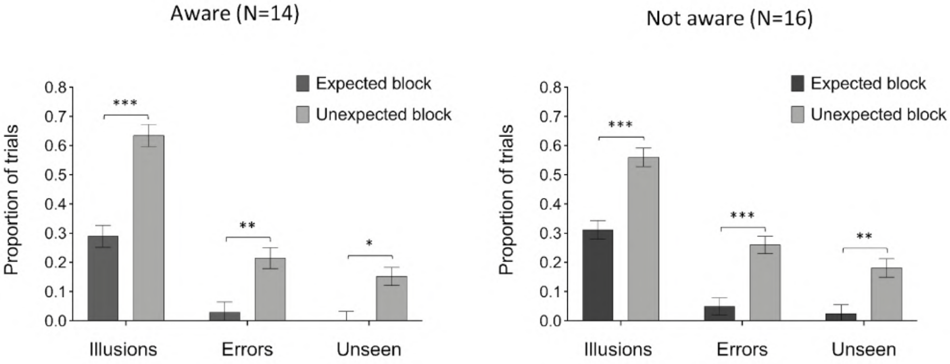

Figure 8.5: Proportion of illusions, errors, and unseen trials for the Expected blocks and Unexpected blocks. Left panel: aware participants (N = 14), who noticed that the peripheral target was printed in white in some trials. Right panel: unaware participants (N=16), who did not notice that the peripheral target was printed in white in some trials. In the Unexpected block, only trials in which the white target was presented were included in the analysis. Both graphs show the significant increase of illusions, errors, and unseen trials in the Unexpected blocks in comparison with Expected blocks. Asterisks represent statistically significant effects (***p<.001; **p<.005; *p<.05).

Finally, we wondered whether aware and unaware participants responded similarly to the peripheral task during the first 10 blocks of trials (expected blocks; data represented in Figure 8.3). A direct comparison between both groups (by subtracting the proportion of responses in far minus near condition), and conducting non-parametric independent sample Mann-Whitney t-tests, revealed that there were no significant differences in the central task effect for illusions, errors, and unseen responses between groups (all ps>.093; BF_{10} = 1.190).

To sum up, behavioral results show that this paradigm was successful to yield illusory conjunctions (~30% for each participant). A comparable number of illusions were observed for the different Central Task conditions, suggesting that divided attention did not effectively modulate feature integration (Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022).

Although Central Task demands did not modulate the proportion of illusory conjunctions, we found that participants were slower and less accurate in responding to the central task when, later in the trial, an illusion was reported as compared to hits. Regarding the effect of feature expectancy, the proportion of illusions, errors, and unseen responses significantly increased when the target was unexpectedly presented in white on 50% of the trials (as compared to the expected block), and this effect was comparable for participants who were aware of the expectancy manipulation and for participants who were not aware.

8.4.2 Time-frequency results

8.4.3 Power analysis in the peripheral task

The aim of these analyses was to understand the brain oscillatory mechanisms underlying correct vs. incorrect feature integration (i.e., hits vs. illusions).

Theta power peaked at 200 ms after number onset (100 ms before the peripheral target; see supplementary material: S2). Theta power from PO7-PO8 electrodes did not differ between hits and illusions (t (26) =-0.008, p=.994, Cohen’s d=-0.002). Alpha power decreased along the trial, peaking at 675 ms (see supplementary material: S3). Alpha power decrease was enhanced for contralateral as compared to ipsilateral PO3/PO4 electrodes (F (1, 26) = 36.356, MSE = 0.005, p < .001, η_p^2 = .583) (see Figure 8.6).

Interestingly, this Laterality effect interacted with Trial Type (F (1, 26) = 9.819, MSE = .002, p = .004, η_p^2 = .274). The planned comparisons showed a greater decrement for hits compared to illusions for ipsilateral electrodes (F=4.686, MSE=.062, p=.040), while the contralateral electrodes showed no differences (F=0.337, MSE=.004, p=.566) (see Figure 8.6).

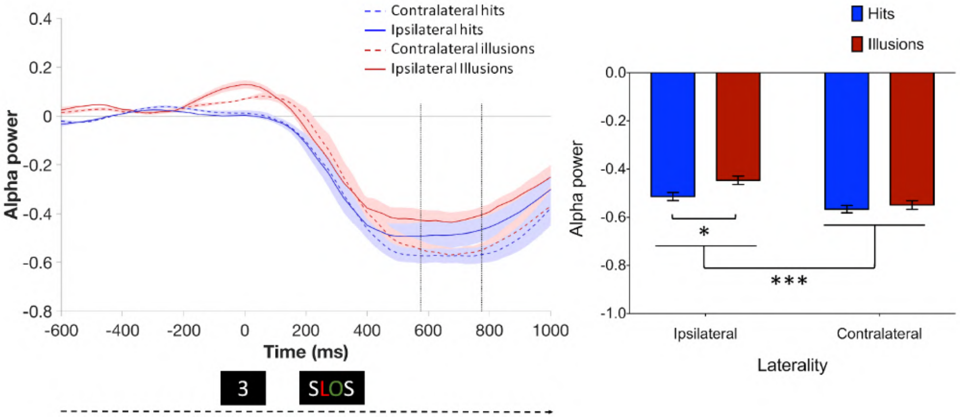

Figure 8.6: Left panel: Alpha power over time for PO3-PO4 channels averaged. Time 0 represents the onset of the central number. The peripheral target was presented at 300 ms. The vertical dotted lines mark the time interval analyzed (575-775 ms). The shaded area represents the SE of the mean. The right panel represents the main effect of laterality (enhanced alpha suppression for contralateral compared to ipsilateral targets). At ipsilateral electrodes, alpha power showed a greater decrement for hits compared to illusions. Asterisks represent statistically significant effects (***p<.001; *p<.05).

As it can be observed in figure 8.6, hits and illusions clearly differed in an early time window around time 0. This window (-100 to 100 ms) was analyzed post-hoc, showing a decreased alpha power for hits than illusions before the peripheral target was presented (t (26) =-2.175, p=.039, Cohen's d=-0.419, see Figure 8.7).

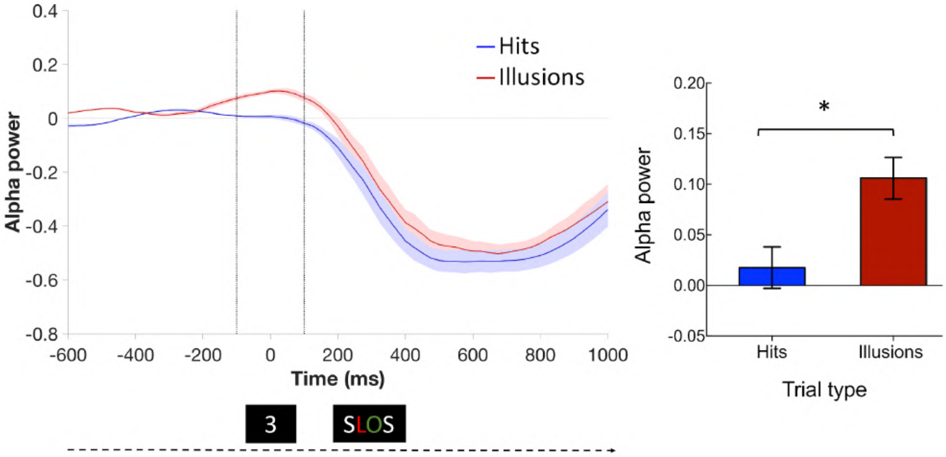

Figure 8.7: Left panel: Alpha power over time for PO3-PO4 channels averaged. Time 0 represents the onset of the central number. The peripheral target was presented at 300 ms. The vertical dotted lines mark the time interval analyzed (from-100 to 100 ms). The shaded area represents the SE of the mean. The right panel represents the main effect of Trial Type. Alpha power was lower for hits compared to illusions. Asterisks represent statistically significant effects (*p<.05).

Beta power also decreased after stimuli were presented (peak at 600 ms for C3-C4 electrodes; see supplementary material: S4), and this decrement was enhanced for hits compared to illusions (F (1, 26) = 10.416, MSE=.006, p=.003, η_p^2=.286) (see Figure 8.8).

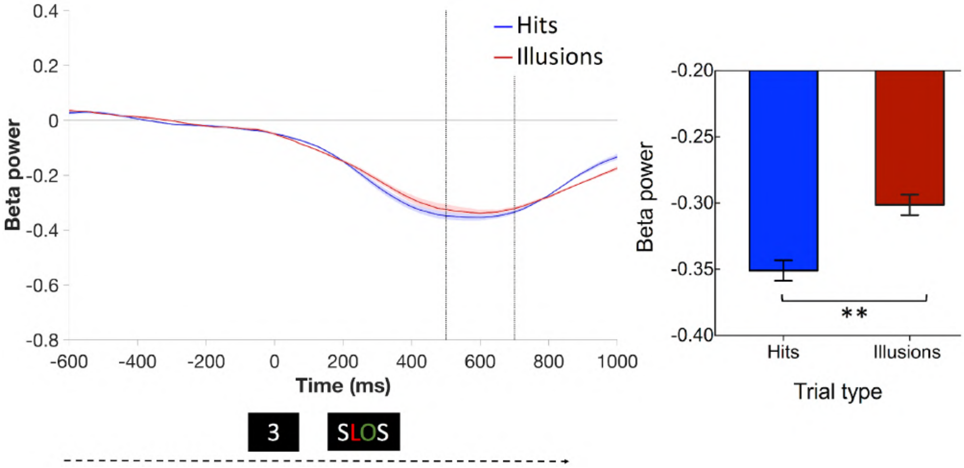

Figure 8.8 Left panel: Beta power over time for C3-C4 channels averaged. Time 0 represents the onset of the central number. The peripheral target was presented at 300 ms. The vertical dotted lines mark the time interval analyzed (500-700 ms). The shaded area represents the SE of the mean. The right panel represents the main effect of Trial Type. Beta power was more negative for hits compared to illusions. Asterisks represent statistically significant effects (**p<.005).

Finally, gamma-band activity (peak at 450 ms; see supplementary material, S5) was larger at frontal locations, and its power was increased for ipsilateral as compared to contralateral electrodes (F (1, 26) = 21.008, MSE = .084, p < .001, η^2_p = .447) (see figure 8.9). There were no other significant main effects or interactions (all Fs<3.606; all ps>. 069).

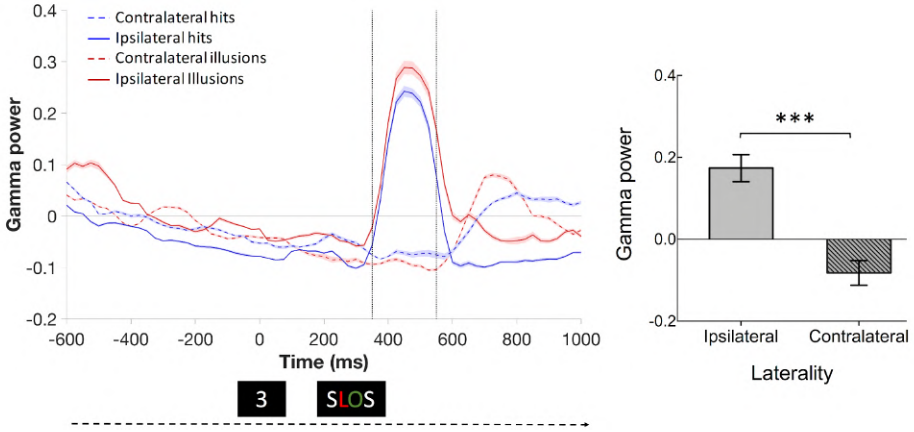

Figure 8.9: Left panel: Gamma power over time for F7-F8 channels averaged. Time 0 represents the onset of the central number. The peripheral target was presented at 300 ms. The vertical dotted lines mark the time interval analyzed (350-550 ms). The shaded area represents the SE of the mean. The right panel represents the main effect of Laterality: gamma power increased for ipsilateral compared to contralateral target. Asterisks represent statistically significant effects (***p<.001).

The behavioral results demonstrated that 16 (out of 30) participants were not aware of the presence of the white target during unexpected blocks of trials (for EEG analyses only 14 of these participants could be analyzed). We wondered whether aware and unaware participants might have followed a different strategy during the task, that could be captured in the TF analyses. To explore this, we repeated the above reported analyses, including the factor Awareness as a between-participants factor. These analyses demonstrated that gamma-band at frontal electrodes was increased for those participants who were aware of the white target as compared to participants who were not aware (main effect of awareness, F (1, 25)=12.817, MSE=.101, p=.001, η_p^2=.339; see Figure 8.10), especially at ipsilateral electrodes (interaction Laterality x Awareness: F (1, 25)=10.983, MSE=.061, p=.003,

η_p^2=.305.; awareness comparison at ipsilateral electrodes: F(1,25)=13.166; MSE=1.907; p=.001; awareness comparison at contralateral electrodes F(1,25)=3.052; MSE=0.051; p=.093).Gamma power was also increased for those participants who were aware of the white target as compared to participants who were not aware in electrode CPz (F (1,25) =7.625, MSE=.059, p=.011, η_p^2=.234). There were no other significant main effects or interactions with the factor Awareness (all Fs<12.817 all ps>.113).

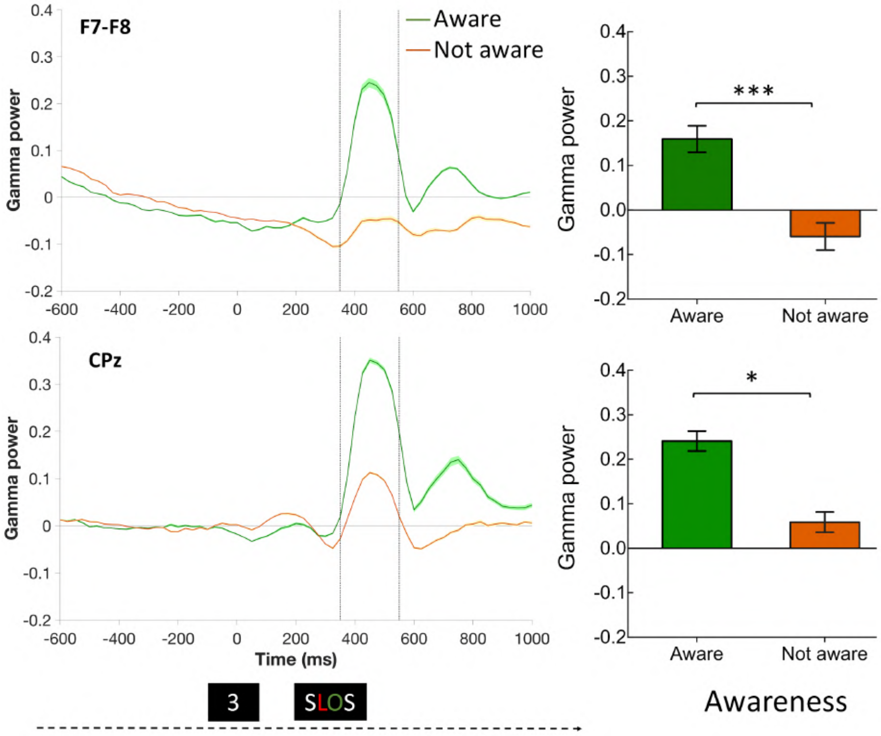

Figure 8.10: Left panel: Gamma power over time for F7-F8 (averaged) and CPz electrodes. Time 0 represents the onset of the central number. The peripheral target was presented at 300 ms. The vertical dotted lines mark the time interval analyzed (350-550 ms). The shaded area represents the SE of the mean. The right panel represents the main effect Expectancy: gamma power was increased for aware participants compared to not aware participants during the expected block. Asterisks represent statistically significant effects (***p<.001; *p<.05).

To sum up, these results suggest that errors during feature integration occur at different time intervals and different frequency bands. Illusory conjunctions are associated with oscillations in the alpha and beta bands. Moreover, gamma band activity was also related to the participants' capacity to perceive unexpected features. The implications of these data for feature binding and its relation to attentional processes will be discussed below.

8.4.4 Post-hoc cross-frequency power-power correlation analyses

Given that some of the observed results in the TF analysis were not expected, we decided to perform trial-by-trial cross-frequency power-power correlations. This analysis demonstrated that the correlation between ipsilateral theta and early alpha was larger for illusions than hits (Z = 0.143 vs. 0.080, t (27) =-2.535, p=.018). Contralateral early and later alpha showed a larger correlation for illusions than hits (Z = 0.092 vs. 0.047, t (27) =-2.239, p=.034). The correlation between contralateral theta and beta power was also larger for illusions than hits (Z = 0.043 vs. 0.001, t (27) =-2.284, p = .031).

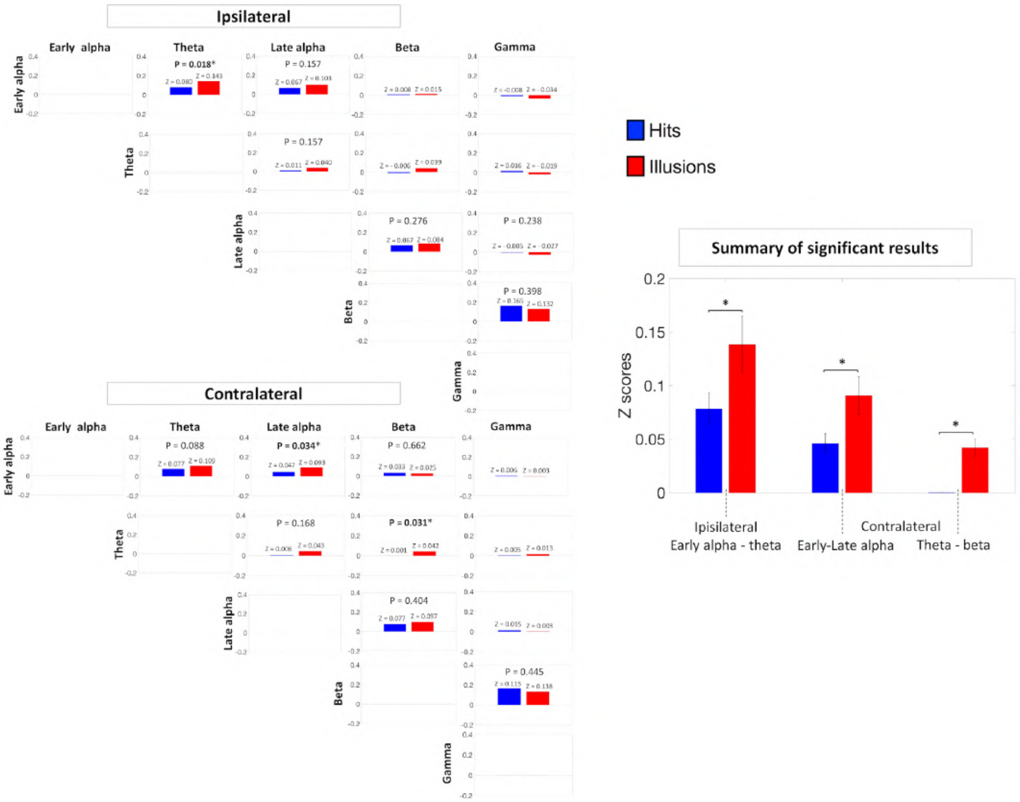

Figure 8.11: Trial-by-trial Z values correlation for hits vs. illusions at ipsilateral and contralateral electrodes. Above the bars, Z and p values are provided. No p values are reported in the comparisons for those pairs in which none of the conditions (hits or illusions) was statistically different from 0. Right panel: summary graph with only the significant correlations (p<.05).

8.5 Discussion

This study aimed at exploring the role of different brain oscillations in feature integration. The experiment involved a dual-task combining a central number task (which manipulated attentional demands) and a peripheral task in which color and shape features needed to be integrated (Cobos & Chica, 2022; Esterman et al., 2004, 2007; Rodríguez-San Esteban et al., 2022). Responses were classified as correct (hits, around 70% of the trials) or incorrect (illusions, around 30% of the trials). Behavioral results replicated the observations of previous studies (Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022): The attentional demands of the number task did not modulate the proportion of trials in which the integration was correct or incorrect. However, responses to the central task were more efficient when feature integration occurred correctly (hits) rather than incorrectly (illusions). This result has been associated with a preparatory process that can occur even before stimuli are presented, and that can affect performance in both tasks (Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022) (see also the early alpha modulations discussed below). At the end of the experiment, an unexpected target (a white target) appeared in a proportion of trials. This top-down expectancy manipulation increased illusions, errors, and unseen responses similarly for participants who were aware of the manipulation and for those participants who were not aware of it. It could be argued that the increase in illusions, errors, and unseen trials could be attributed to a decline in sustained attention, indicating fatigue. We analyzed performance as across blocks (see supplementary material section 8.6.2.1 and figure S6) and observed that the proportion of illusions, errors, and unseen trials remained relatively constant during the expected blocks. Only when non-expected blocks started, we observed a sudden impact on the proportion of illusions, errors, and unseen trials. Therefore, we can confidently conclude that the reported behavioral effects of top-down expectations are not influenced by fatigue.

The literature on feature integration is heterogeneous, and generally, only one frequency band is explored. We hypothesized that an incorrect feature integration may be due to failures at different moments and cognitive processes. Thus, in this study, we investigated the contribution of several frequency bands to feature integration and report both early and late modulations. During the early interval (before the peripheral target was presented), alpha power increased for illusions compared to hits. After the peripheral target, alpha and beta power reduction was higher for hits compared to illusions. Finally, a post-hoc trial-by-trial power-power correlation analysis was performed, showing different correlation patterns for correct and incorrect feature integrations.

Previous studies have focused on the gamma band when exploring the brain mechanisms associated with feature integration (Herrmann, Lenz, et al., 2004; Phillips & Takeda, 2009; Singer, 2013; Tallon-Baudry, 2009). Although there are a large number of experimental paradigms to study errors in feature integration (ambiguous figures, visual search, movement and color, etc.), the gamma band usually increases its power at occipito-parietal electrodes; moreover, gamma power enhancements are more pronounced as task demands for feature integration also increase, and when feature integration is correct rather than incorrect (Bertrand & Tallon-baudry, 2000; Buschman & Miller, 2007a; Phillips et al., 2012; Phillips & Takeda, 2009; Vidal et al., 2006). We therefore expected to observe increased gamma power at occipito-parietal electrodes for hits compared to illusions. Instead, gamma power was overall enhanced at frontal electrodes in our results. This apparently contradictory finding might be best accounted for by the literature on working memory, where gamma power increases with increasing memory load (Bastos et al., 2018; Honkanen et al., 2015; Howard, 2003; Lundqvist et al., 2011; Miller et al., 2018; Roux & Uhlhaas, 2014). Note that our paradigm required maintaining information in working memory, given the brief presentation of stimuli and the use of a dual task. The synaptic attractor model (SAM) states that working memory sample capacity is limited (Awh et al., 2007; Buschman et al., 2011; Cowan, 2010) and the accumulation of elements to be recalled simultaneously causes an amassing of synaptic interference associated with increased gamma activity (Lundqvist et al., 2011; Mi et al., 2017). This suggests that apart from perceptual demands, this task required maintaining information in short-term memory, which might be associated to increases in frontal gamma.

Alpha-band results exhibited early and late modulations. Early modulations (increased alpha for illusions than hits) are in line with the literature showing that alpha power increase is associated with impaired perception (Ergenoglu et al., 2004; Limbach & Corballis, 2016; van Dijk et al., 2008). This result indicates that one of the cognitive processes influencing correct feature integration is the general preparatory state of the organism, which can be related to arousal and activation. In regard to the late alpha modulations observed, it is well-known that alpha power decreases at contralateral as compared to ipsilateral stimulus locations, and this is related to the spatial selection of this location (contralateral modulations) (Busch & VanRullen, 2010; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006b), and the inhibition of distractors (ipsilateral modulations) (Capilla et al., 2014; Klimesch, 2012; Klimesch et al., 2007b; Lange et al., 2014; Min et al., 2008; Min & Herrmann, 2007; Schroeder et al., 2018). We expected a larger decrease in contralateral alpha power for hits than illusions. In contrast, we observed an ipsilateral modulation, which might be related to the inhibition of distractors. In general, our data show a larger reduction of alpha and beta power for hits than illusions. Many studies have observed this alpha/beta power reduction in a wide range of cognitive tasks, from visual perception (Pfurtscheller et al., 1996) to memory retrieval (Michelmann et al., 2016). Alpha/beta desynchronization has been associated to information processing in specialized cortical modules during the perception of an event (Jensen & Mazaheri, 2010; Klimesch, 2012). Using representational similarity analysis during the perception and retrieval of videos, (Griffiths et al., 2019) have recently demonstrated that alpha/beta power decreases track the fidelity of stimulus-specific information represented within the cortex. This proposal fits well with our data, as alpha and beta power decreases were enhanced for hits compared to illusions, which could be indexing a more reliable representation of perceptual information within the cortex.

Although theta oscillations are strongly associated with perceptual errors (Cavanagh et al., 2009; Cohen, 2011; Fusco et al., 2018; Kalfaoğlu et al., 2018; Mathes et al., 2014), our data showed no modulation in this frequency band. It should be noted that 1) in our data, theta power had its maximal peak before the onset of the peripheral target, and, 2) contrary to previous reports in which frontal theta activity is related to error detection (Cavanagh et al., 2009; Cohen, 2011; Fusco et al., 2018; Luu et al., 2004; Romei et al., 2011; Trujillo & Allen, 2007), theta activity was overall larger at parieto-occipital electrodes in the present study. One possibility is that given the masking and the titration procedure to produce 30% illusions, participants could not distinguish between hits and illusory responses, and therefore, error detection mechanisms were not activated. This possibility will be tested in future studies by introducing a confidence scale after the response.

Given the extensive literature arguing that complex cognitive processes involve communication between different brain oscillations (Fries, 2005, 2009; Rohenkohl et al., 2018), we decided to perform a trial-by-trial power-power correlation between the different frequency bands here explored. We observed an increased correlation for illusions than hits within the alpha band for early and late periods, which indicates that the decrease in alpha power is less pronounced for illusions than for hits throughout the trial. More interestingly, early alpha and theta power correlated positively, and this correlation was increased for illusions as compared to hits. It has been proposed that attention fluctuates in a periodic fashion (Fiebelkorn et al., 2013, 2018; Fiebelkorn & Kastner, 2019; Helfrich et al., 2018), and these fluctuations are associated to performance fluctuations (Busch et al., 2009). For example, Busch and colleagues (Busch et al., 2009; Busch & VanRullen, 2010; van Es et al., 2022) observed that before stimulus onset, alpha and theta phase can account for 16% of variability in detection performance and allow the prediction of performance on the single-trial level (Busch et al., 2009). Our results are in line with these observations, demonstrating that theta and early alpha power are not only associated with stimulus detection but also with the quality of perception; in the current study, increased theta and early alpha power in a given trial is associated with incorrect feature integration.

The theta-beta cross-frequency power-power analysis demonstrated a positive correlation for illusions compared to hits. It means that the correlation implies a higher theta power and a higher decrement in beta power, but other studies indicate the relation between theta and beta using the theta/beta ratio (TBR). The TBR has been applied in different populations (such as Attention-Deficit / Hyperactivity Disorder, ADHD) (Arns et al., 2013; Snyder & Hall, 2006) and in conditions in which attention fluctuated during mind wandering (Son et al., 2019). These studies have demonstrated an increased theta/beta ratio for ADHD as compared to controls (Arns et al., 2013; Snyder & Hall, 2006), and increased theta/beta ratio during mind wandering (which was related to a decreased connectivity in the executive attention network and increased connectivity in the default mode network (Son et al., 2019; van Son et al., 2019). In the non-clinical population, reduced TBR has also been linked to better cognitive control, executive control, and increased vigilance (Angelidis et al., 2016, 2018; Putman et al., 2010, 2014; van Son et al., 2018). Moreover, TBR may reflect inhibitory cortical and subcortical communications (Knyazev, 2007; Putman et al., 2014; Schutter & Van Honk, 2005), leading by bottom-up and top-down reciprocal systems. In this regard, the TBR may represent the activation of cortical top-down system vs. subcortical bottom-up processes (Angelidis et al., 2018; Knyazev, 2007; Putman et al., 2010; Schutter & Van Honk, 2005; van Son et al., 2018). Although the analyses reported in this paper are different from the TBR analysis, the increased correlation of theta-beta observed in illusions as compared to hits could indicate reduced attentional focusing when feature integration failed or bad communication between bottom-up and top-down systems.

In relation to the influence of top-down expectancies in feature integration (Aru et al., 2018; Aru & Bachmann, 2017; Cobos & Chica, 2022; Han & Humphreys, 2007; Humphreys, 2016; Kok et al., 2017), some studies have explored the brain dynamics of different forms of expectancy. Early modulations in alpha power has been related to temporal and multisensorial expectancies (Mayer et al., 2016; Min & Herrmann, 2007). The strength of attentional alpha/beta modulations increases with the predictability of the anticipated sensory target (Bauer et al., 2014; Roehe et al., 2021). Additionally, the presentation of novel stimuli has also been related to increased gamma power (Engel et al., 2001; Engel & Fries, 2010). Our results demonstrate that gamma power was overall larger during the Expected blocks (before the unexpected target presentation) for participants who were aware of the unexpected target presented during the last blocks of trials (as compared to unaware participants). Gamma power increases have been related to attentional selection (Gruber et al., 1999; Herrmann, Lenz, et al., 2004) and to the individual capacity to attend and perceive multiple visual objects concurrently (Rouhinen et al., 2013). Therefore, the difference in gamma power between aware and unaware participants might be due to better attentional selection or capacity to attend to multiple items of the former.

To conclude, our results support that feature integration is a complex process that can go wrong at different stages including attentional processes (early alpha) and perceptual representations (late alpha and beta). They also highlight the influence of expectations in visual perception, linking gamma-band modulations with the participants' awareness of unexpected events.

8.6 Supplementary materials

8.6.1 Time frequency analysis

8.6.1.1 Plots of selected frequencies and electrodes

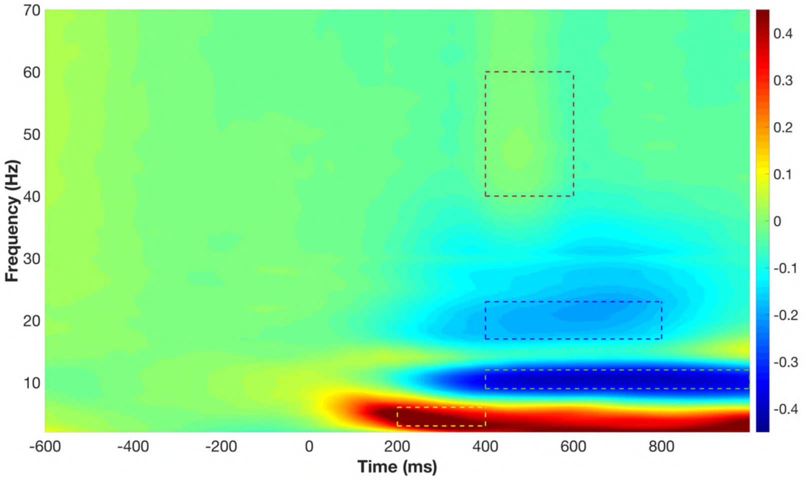

Figure S1: Averaged normalized TF representation (2-70 Hz and -600 to 1000 ms; time 0 ms represents the number onset). The colorbar indicates relative change to baseline (-500 to -200 ms). Data were averaged for all conditions, participants, and electrodes before bootstrapping.

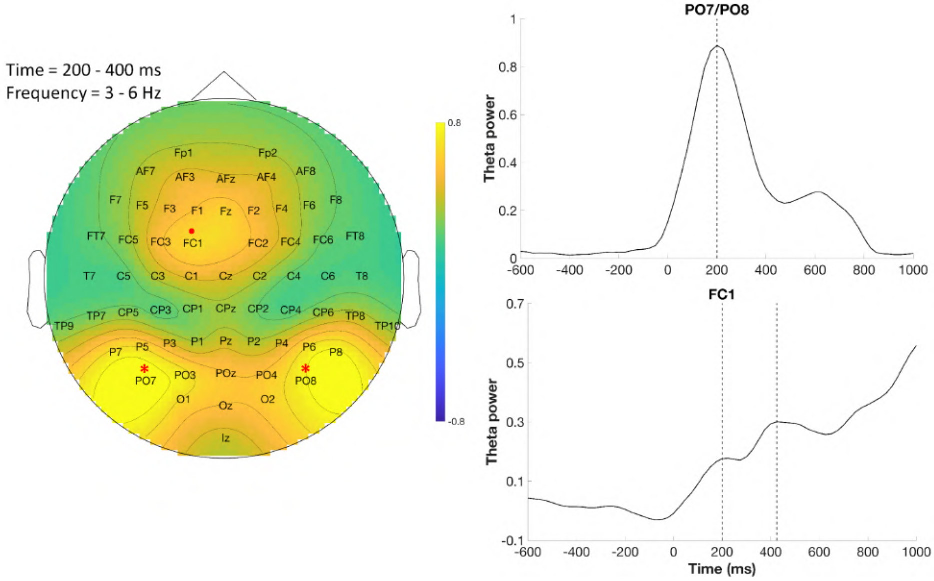

Figure S2: On the left, topoplot showing the distribution of theta power (3-6 Hz) from 200 to 400 ms. The red asterisks represent the analyzed electrodes. The red circle represents a supplementary electrode analyzed for showing the additional peak (although with slightly lower values than parieto-occipital sites). On the right, the averaged theta power for all conditions in PO7/PO8 electrodes (up) and FC1 (bottom). The dashed line represents the maximum peaks of theta power. In PO7/PO8, the peak occurred at 200 ms, while FC1 showed two different peaks that occurred at 200 and 425 ms.

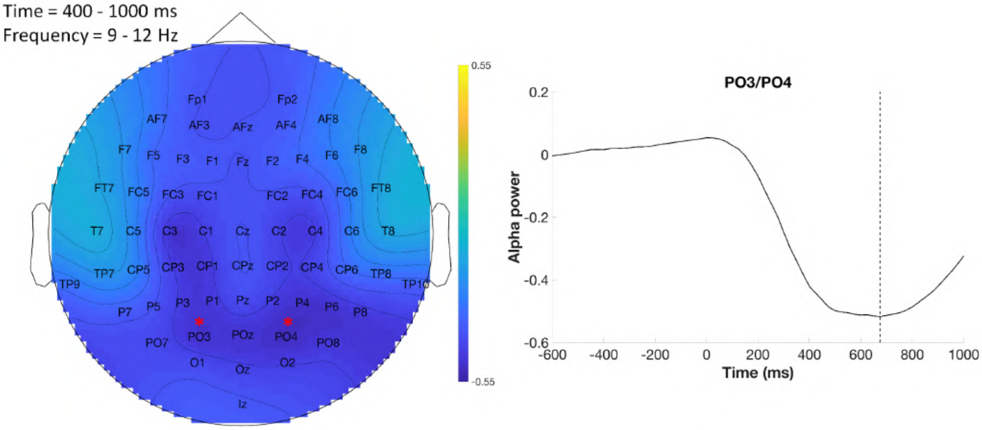

Figure S3: On the left, topoplot showing the distribution of alpha power (9-12 Hz) from 400 to 1000 ms. The red asterisks represent the analyzed electrodes. On the right, the averaged alpha power for all conditions in PO3/PO4 electrodes. The dashed line represents the peak of alpha power suppression at 675 ms.

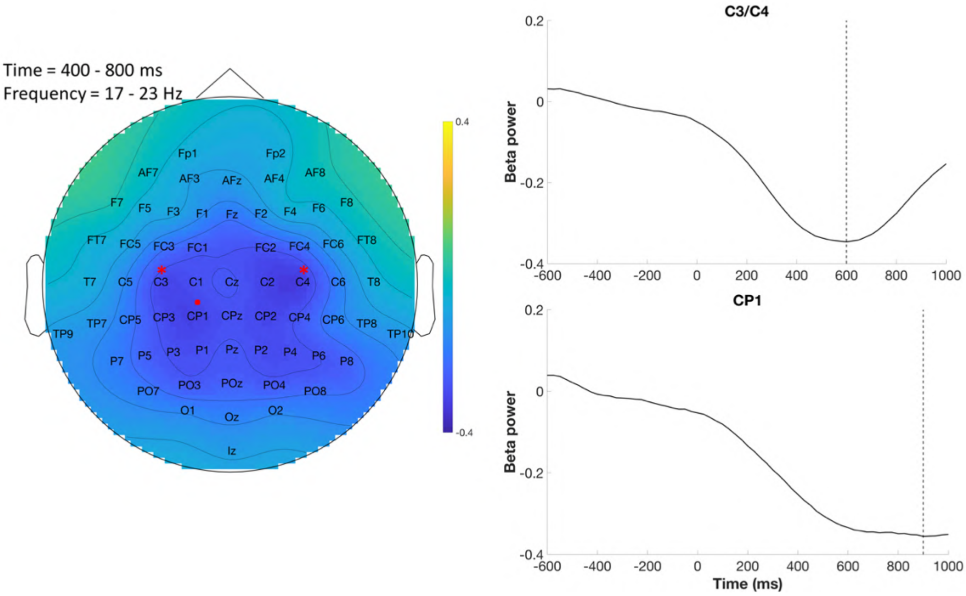

Figure S4: On the left, topoplot showing the distribution of beta power (17-23 Hz) from 400 to 800 ms. The red asterisks represent the analyzed electrodes. The red circle represents a supplementary electrode analyzed for showing the additional peak (although with slightly higher values than C3/C4 electrodes). On the right, the averaged beta power for all conditions in C3/C4 electrodes (up) and CP1 (bottom). The dashed line represents the peak of beta power suppression. In C3/C4, power reduction peaked at 575 ms, while in CP1 it peaked at 900 ms.

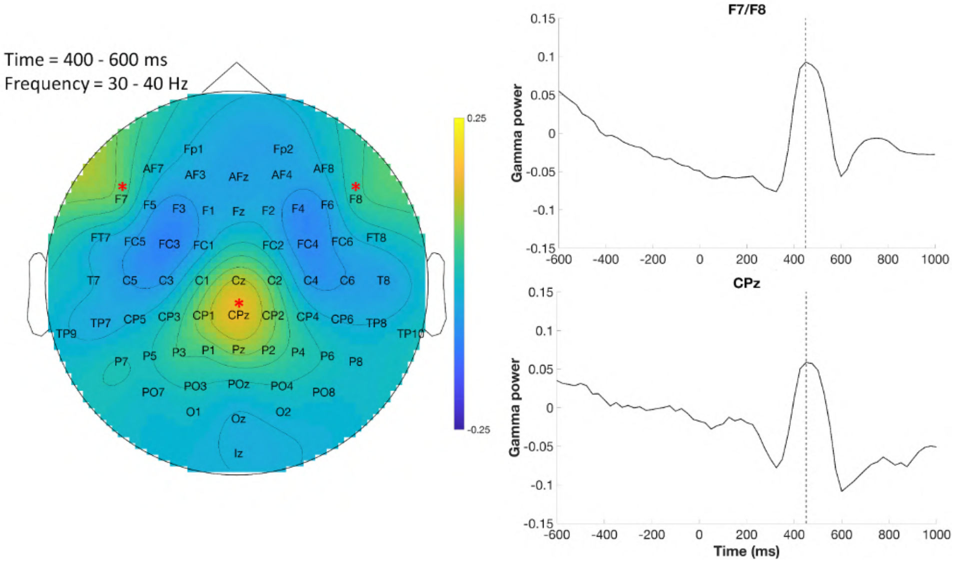

Figure S5: On the left, topoplot showing the distribution of gamma power (40-60 Hz) from 400 to 600 ms. The red asterisks represent the analyzed electrodes. On the right, the averaged gamma power for all conditions in F7/F8 (up) and CPz (bottom) electrodes. The dashed line represents the maximum peak of gamma power for frontal and central electrodes at 450 ms.

8.6.1.2 Statistical analysis of supplementary electrodes

Paired sample t-tests were conducted to compare hits vs. illusions. The statistical of the supplementary electrodes did not yield significant results: theta power for FC1 at 200 ms peak: t (26) =- 1.519, p=.141, Cohen's d=- 0.292; and at 425 ms peak: t (26) =- 1.230 p=.230, Cohen's d=- 0.237. Beta power for CP1: t (26) =- 0.603 p=.552, Cohen's d=- 0.116.

8.6.2 Supplementary behavioral control analysis

8.6.2.1 Analysis of the proportion of trial types across blocks

In the last 4 blocks of trials, unexpectedly to participants, the target letter was printed in white. This manipulation increased the number of illusions, errors, and unseen responses (as compared to the expected block). Because these unexpected blocks were always presented at the end of the experiment, it could be argued that the increase in illusions and errors could be due to fatigue. To test for this hypothesis, we analyzed the proportion of each Trial type across blocks. We used a non-parametric paired-sample t-test (Wilcoxon signed-rank) to compare (for each Trial type) two consecutive blocks. As shown in figure S6, the proportion of hits, illusions, errors, and unseen responses remained fairly constant during the expected blocks (1-10). Drastically, when the unexpected block started (transition from block 10 to 11), the proportion of hits decreased (W=464, p<.001, r_B=.996), and the proportion of illusions (W=26.5, p<.001, r_B=-.886), errors (W=55, p<.001, r_B=-.763), and unseen trials (W=0, p<.001, r_B=-1.0) increased (as compared to the previous block).

It seems therefore clear that fatigue was not the underlying cause for the increase of illusions, errors, and unseen responses in the unexpected block.

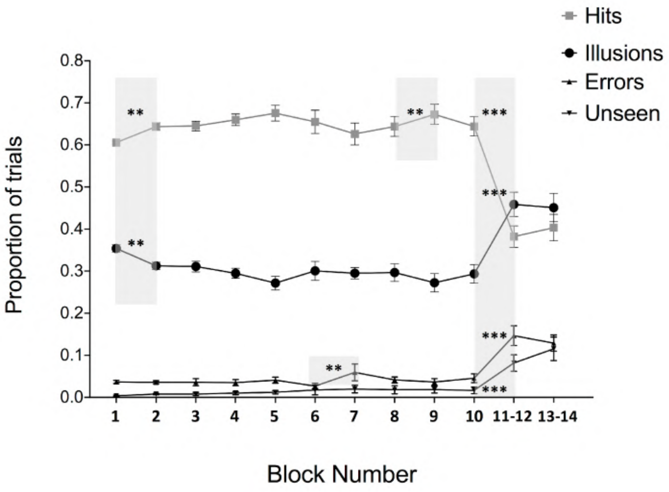

Figure S6: The proportion of hits, illusions, errors, and unseen responses across blocks. In blocks 1-10, the target letter was always colored in green, blue, or yellow (expected blocks). In blocks 11-12, the target letter was colored in white in 50% of the trials (unexpected blocks). The asterisks represent significant differences in the proportion of each trial type between consecutive blocks (indicated by gray shading) (***p<.001; **p<.005; *p<.05).

8.6.2.2 RT and ACC analyses of central task

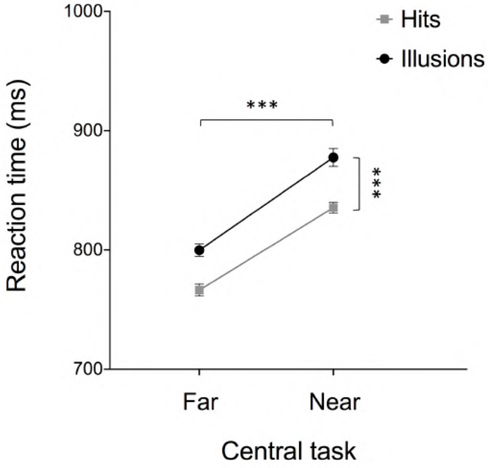

Figure S7: Mean RT to respond to the central task as a function of Central Task condition and Trial Type. This figure shows the main effects of Central Task and Trial Type. Asterisks represent significant effects (***p<.001).

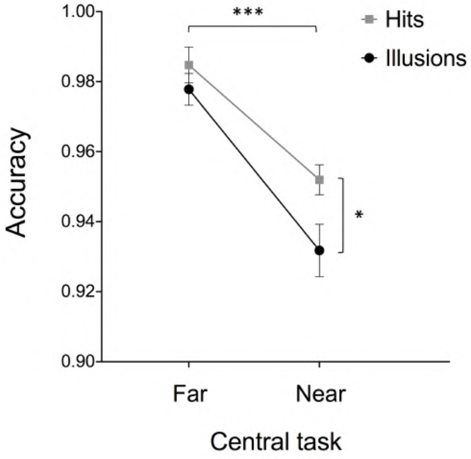

Figure S8: Mean ACC in the central task as a function of Central Task condition and Trial Type. This figure shows the main effects of Central Task and Trial Type. Asterisks represent significant effects (***p<.001; *p<.05).

8.7 Acknowledges

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8.8 Author contributions

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Data analysis: MIC, MM, AC
Writing original draft: MIC, ABC
Review & Editing: MIC, MM, PRSE, AC, ABC
Supervision and funding: ABC

Chapter 9: Heart-rate modulation during phasic alertness and feature integration

The content of this chapter is in preparation as: Cobos, M. I., Guerra, P. M., & Chica, A. B. Heart-rate modulations during phasic alertness and feature integration.

9.1 Abstract

Subjective experience is rich, although it can be inaccurate. When tasks require the integration of features (for example peaking a red apple), they can be erroneously integrated, creating illusory perceptions. Some studies have explored the brain responses associated to subjective perception and correct/incorrect feature integration, although brain-body interactions have largely been neglected in this field. The main goal of the present study was to explore if heart rate is modulated by the perceptual process of feature integration. A color-shape discrimination task, titrated to produce 70% correct (hits) and 30% incorrect (illusions) responses, was used. Targets were preceded by an alerting signal on 50% of the trials to manipulate phasic alerting. Moreover, the role of top-down expectancies over feature integration was explored by presenting an unexpected feature at the end of the experiment. Behavioral results indicated that phasic alertness did not modulate the feature integration process, but faster responses were observed when the alerting signal was presented (as compared to no alerting signal trials), and when feature integration occurred correctly (hits) vs. incorrectly (illusions). Heart rate patterns revealed a significantly larger deceleration for correct vs. incorrect feature integration in the absence of alerting signals. Top down expectations largely affected feature integration, and revealed a distinguishable pattern of heart rate responses for participants who were

aware of the expectancy manipulation and for those participants who were not aware. The heart rate decreased more when the aware participants correctly integrated, while the not aware ones did so more for illusions, but only with an alerting signal. These findings highlight the importance of considering the interaction between the brain and the body in the study of perception.

9.2 Introduction

Research in Cognitive Neuroscience has mostly focused on studying the relationship between cognitive processes and the activity of the CNS. However, the nervous system is not only composed of the brain and the spinal cord. This system is in constant communication with the PNS (Craig, 2009; Critchley et al., 2005; Critchley & Harrison, 2013; Park et al., 2014), which comprises a series of afferent and efferent nerves that maintain constant communication between the PNS and CNS (Armour & Ardell, 2004; Park et al., 2014; Park & Tallon-Baudry, 2014). Thus, in order to understand cognitive processes such as attention or perception, it is important to not only study what happens in the brain when we attend or perceive, but also how these processes modulate the activity of the PNS. Currently, there are a number of studies that highlight the importance of the PNS in the emotional domain (Seth, 2013; Van Diest et al., 2009; Vila & Guerra, 2010), as well as in some cognitive processes such as learning, memory, and attention (Thayer & Lane, 2009).

One way to study the PNS consists of anchoring the occurrence of external events (stimuli) to peripheral measures such as HR. In the field of attention, consistent associations have been found between patterns of cardiac deceleration-acceleration and different attentional states (Lacey & Lacey, 1978). For instance, cardiac deceleration has been associated with the orienting reflex (Barry & Tremayne, 1987; Sokolov, 1963; Vila et al., 2007), increased attentional demands (De Pascalis et al., 1995b; Dehais et al., 2011; Ribeiro & Castelo-Branco, 2019; Salvia et al., 2012;

Zimmer et al., 1990), stimulus detection (Barry & Tremayne, 1987; Cobos et al., 2019; Motyka et al., 2019; Park et al., 2014), or even preparatory processes (Graham & Clifton, 1966; Jennings et al., 2009, 2009; Jennings & van der Molen, 2005; Lacey & Lacey, 1977; Lacey, 1970; Skora et al., 2022). On the other hand, cardiac acceleration has been linked to processing load, stimulus identification, and response preparation (Börger & van der Meere, 2000; Obrist, 2012; Park et al., 2014; Vila et al., 2007). In the field of perceptual consciousness, the literature on how PNS activity is modulated by conscious processing is more sparse and recent. The pioneering study by Park & Tallon-Baudry (2014) demonstrated how access consciousness (which refers to perceptual information that can be reported) could be reflected in cardiac deceleration-acceleration patterns. In particular, cardiac acceleration was less pronounced for consciously detected than for non-consciously detected stimuli. Expanding upon this prior research, we devised a comparable study to investigate the influence of phasic alertness on access consciousness and how this relationship can be measured through fluctuations in heart rate (Cobos et al., 2019). We presented participants with near-threshold stimuli, which were titrated to be perceived 50% of the time, and which could be preceded by an alerting tone on 50% of the trials. In addition to showing the typical deceleration-acceleration pattern, results demonstrated that cardiac deceleration was enhanced when the alerting tone was presented and stimuli were consciously perceived, as compared to non-perceived stimuli. These data indicated that, similarly to the results observed with different measures of the CNS such as functional Magnetic Resonance Imaging (fMRI) (Chica et al., 2016c), the cardiac pattern is also modulated by access consciousness.

In the field of consciousness, a distinction has been made between access consciousness (the ability to report on a perceived stimulus) and phenomenological consciousness (the subjective experience of perception, which can occur without conscious report, and is often inaccurate) (Block, 2011). In previous studies, we used a feature integration task (in which feature integration failed in about 30% of the trials) to study phenomenological consciousness. In these studies, we observed that spatial attention improved feature integration (Cobos & Chica, 2022), while divided attention did not (Cobos et al., 2023; Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022). Furthermore, and in order to manipulate top-down expectancies (Aru et al., 2018; Aru & Bachmann, 2017; Cobos & Chica, 2022; Harris et al., 2011; Kok et al., 2017; Moore et al., 1998; Wokke et al., 2013), we included an unexpected feature at the end of the experiment: during the last blocks of, in 50% of the trials, the target was presented in a color that was unexpected to the participants. A robust and reliable effect of feature expectancy was observed, indicating perceptual completion when an unforeseen perceptual feature was introduced in the scene (Cobos et al., 2023; Cobos & Chica, 2022).

The current study aimed to explore brain-body interactions in conscious perception in order to determine if, as previously shown in the context of access consciousness (Cobos et al., 2019; Park & Tallon-Baudry, 2014), HR is modulated by phenomenological consciousness (using a feature integration paradigm). We hypothesize that phasic alerting would improve RT; if phasic alerting modulated phenomenal consciousness, illusions will be reduced when the alerting tone was present as compared to tone absent trials. As found in previous studies (Cobos et al., 2023; Cobos & Chica, 2022), we expected that the proportion of illusions would increase in the last blocks when the unexpected stimulus was presented. As regards the HR, we would expect to find a deceleration-acceleration pattern (main effect of time), as well as an increased deceleration in the presence of the alerting tone compared to the no-tone condition. Finally, based on the results observed in Cobos et al. (2019), we would expect a more pronounced deceleration pattern on trials with the alerting tone when correct feature integration (hits) occurs compared to incorrect feature integration (illusions). We did not have any a-priori hypothesis regarding

9.3 Method

9.3.1 Participants

G*Power (Faul et al., 2007) was used to calculate sample size according to the effect of endogenous attention on illusory conjunctions reported in Cobos & Chica (2022; Experiment 2, dz=0.56, large effect). Based on a priori sample size for a non-parametric Wilcoxon paired t-test (matched samples, dz=0.56, α=.05; power=0.80), a sample of 29 participants was required.

Consequently, thirty healthy volunteers (20 females, mean age of 23.45, SD = 4.45) participated in this experiment in exchange for a financial reward (10€ per hour). All participants were undergraduate students from the University of Granada who had not previously participated in similar experiments. All of them reported having normal or corrected-to-normal vision, normal color perception, no heart conditions, and no clinical history of neurological or psychiatric disorders. Before the experiment, they read the information sheet, and signed the COVID-19 informed consent and self-responsibility statement. They were also informed about their right to withdraw from the study at any time. The Granada's Biomedicine Ethic Research Committee (CEIM/CEI Granada) approved this experiment, which was carried out in accordance with the ethical standards of the Declaration of Helsinki.

9.3.2 Apparatus and stimuli

E-prime software 2.0 (Schneider et al., 2002) was used for stimuli presentation, timing and behavioral data collection. Participants were seated at an approximate distance of 64 cm. from the computer screen. All stimuli were presented on an LCD monitor (17", LG L1718S, 1280 x 1024 pixels) with a refresh rate of 75 Hz. A video-based, eye tracking system (Eyelink 1000 Plus, 5.09 software version), was used to monitor the direction of gaze every 1 ms, with a spatial resolution <0.001º.

The experimental display was an adaptation from Esterman and colleagues (2004, 2007). Each trial contained a white central fixation point (0.4º x 0.4º), presented against a black background. The peripheral target consisted of a string of four characters: the outermost characters (flanks) consisted of two white "S" or two "8", and the innermost characters consisted of an "L" (target letter) and an "O" (distractor). The target letter and the distractor could be presented in red (RGB: 215, 0, 0), blue (RGB: 46, 118, 182), or green (RGB: 0, 135, 61). In every trial, the target letter and distractor were presented in different colors and could randomly appear either at the left or right of the fixation point. The distance between the string of characters and the fixation point varied from 4.2º to 10.5 º (measured from the center of the fixation point to the center of the string of characters). Both letters were randomly presented at the inner leftmost or rightmost location (see Procedure section).

To manipulate phasic alertness, participants wore headphones (Philips SHP2000 adjustable; frequency range de 15-22000 Hz; maximum sensitivity 100 dB; impedance 32 ohms; maximum input power de 500 mW) that reproduced a tone of a frequency of 500 Hz at an intensity of 97.5 dB.

9.3.3 Procedure

The experiment consisted of 10 blocks of 48 trials each, with a break of approximately 2 minutes after every 2 blocks. Before the beginning of the experiment, and after every pause, the eye tracker was calibrated.

Figure 9.1 shows the sequence and timing of stimuli in a given trial. Each trial started with a fixation point (randomly lasting between 1008 and 2016ms). A tone (14ms) was randomly presented on 50% of the trials. After an Inter-Stimulus Interval (ISI), which could randomly last between 210 and 322ms, the peripheral target (for a duration of 112ms), either to the right or to the left of the fixation point. After another ISI (56ms), a mask was presented (112ms), followed by an interval of motor response preparation of 2002ms in which only the fixation point was displayed. After that, the fixation point increased 0.2º in size for another 2002ms, indicating that participants should then report the color of the target letter, using the left hand to press the “z”, “x” or “c” keys (the color-key assignment was counterbalanced between participants). If participants did not perceive the color of the target letter, they could respond by pressing the spacebar. Finally, an Inter-Trial Interval (ITI) of 2002ms was presented.

Responses were categorized as hits (when the correct color of the target letter was reported), illusions (when the color of the distractor letter was reported), errors (when a color not displayed on the screen was reported), and unseen (when participants could not report the color of the target letter).

To measure the effect of top-down expectancies on perception, during the last 4 blocks, unexpectedly to participants, the target letter was presented in white ink in 50% of the trials (192 in total). We will refer to these blocks as the “unexpected blocks”. At the end of the experiment, a short structured interview was conducted to check whether participants were aware of the white target during these “unexpected blocks”. The following questions were asked: “Do you have any comments on the experiment?” “Was any color combination harder to perceive/report?” “Did you notice anything different at the end of the experiment?”

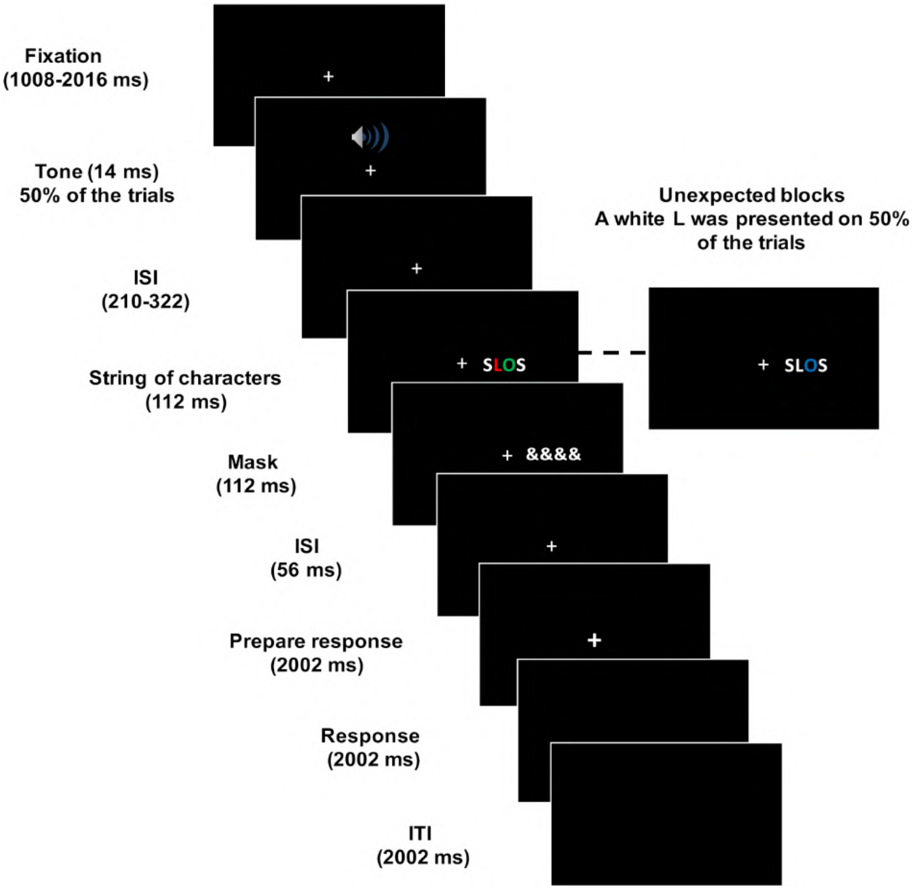

Figure 9.1*:* Sequence and timing of events in a given trial.

Before the experimental blocks, participants underwent a calibration procedure to achieve a hit rate of ~70%. Titration blocks (each composed of 12 trials) were identical to experiment blocks. Two features of the peripheral target (and the mask) were manipulated during titration: size (5 sizes) and eccentricity (2 positions). Titration began with the easiest condition (size: 4.6ºx1.2ºhigh; eccentricity from fixation: 4.2º —measured from the center of the fixation point to the center of the string of characters). After each titration block, the percentage of hits was calculated. If participants correctly reported the color of 75% or more targets, the size of the string of characters (and the mask) was reduced by 0.5 º x 0.2 º. If participants correctly reported 58% or fewer targets, size was increased by 0.5º x 0.2º. If the smallest size was achieved (3.2 x 0.4º), titration continued with an eccentricity manipulation. If participants correctly reported 75% or more targets, the peripheral target was presented 6.3º further from the fixation point; if participants reported correctly 58% or fewer targets, the peripheral target was presented 6.3º closer to the fixation point. Titration ended when the proportion of hits ranged between >58% and <72% during two consecutive blocks. The size and eccentricity achieved by each participant during titration, were used during experimental blocks. The experiment lasted for approximately 1 hour and 40 minutes (including the initial titration procedure).

9.3.4 Data reduction and statistical analyses

A digital finite impulse response high-pass filter was applied in Acqknowledge software to cancel out frequencies below 2.5 Hz (Blackman window, 61 dB roll-off). ECGlabRR software (Vicente et al., 2013) was run to derive the HR from the EKG. On a first stage, each cardiac period was measured as the distance -in milliseconds- between successive R waves, and subsequently transformed into beats per minute. Then, Kardia software (Perakakis et al., 2010) was used to obtain, for each trial, the weighted average of the HR every 100 ms for an interval of 4000 ms that was time-locked to the fixation point. Finally, HR differential scores were obtained by subtracting the average of HR activity occurring during the 1000 ms immediately prior to the fixation point onset.

9.3.4.1 Behavioral statistical analyses

Participants who broke fixation (with saccades larger than 2 degrees of visual angle from fixation and longer than 50 milliseconds during the target presentation and before the response was required) were eliminated. These eliminated trials accounted for 4.88% (SD=6.68%) of the trials. A total of 5 participants were excluded from the analysis due to either excessive (23% of the trials) eye movements (1 participant), problems with the recording of ocular activity (3 participants), or because the recording of the EKG failed (1 participant). The final sample size was 26 for behavioral data, and 25 for the HR analysis.

The proportion of hits, illusions, errors, and unseen responses for each alerting condition (tone - no tone) was analyzed using mixed-effects logistic regression models (GLMM) with the *glmer* function of the lme4 R package (Bates et al., 2014). For each trial type, data were binomially coded (0 or 1). We first analyzed the blocks in which the target was always colored in green, blue, or red (expected blocks: 6 blocks of 48 trials each). The full fixed structure of the model included the Alerting condition (no tone - tone), whereas the random structure contained the participant factor (Trial type ~ Alerting + (1|participant)). The second stage of the analyses involved exploring the expectancy manipulation in which, unknown to participants, a white target could be presented on 50% of the trials (unexpected blocks: 4 blocks of 48 trials each). The full fixed structure of the models contained the main factor of Alerting (no tone - tone), Block type (expected vs. unexpected), and the interaction between both factors. In the unexpected blocks, only trials in which the white target appeared were analyzed. As described above, the participant factor was used as a random factor (Alerting + Block type + Alerting:Block type + (1|participant)).

Participants were divided in two groups according to the post-experiment interview: a) those who were aware of the white target (N =11) and b) those who were not (N = 15). In order to explore if aware and not aware participants differed in their performance, we repeated the analysis including the Awareness factor. For the expected blocks the fixed structure was (Alerting + Awareness + Alerting:Awareness). For the comparison between expected and unexpected blocks, the fixed structure was (Alerting + Block type + Awareness + Alerting:Block type + Alerting:Awareness + Blocktype:Awareness + Alerting:Block type:Awareness). In both cases, Awareness factor was also applied as random factor. The optimal random structure was found using data-driven model comparison by running the *anova* function of the *stats* package of R (Chambers & Hastie, 1992). The slower AIC and BIC parameters indicated the fittest model to choose the random factor.

Mean RTs in the expected blocks were analyzed by linear-mixed effects models (LME) with the *lmer* function of the lme4 R package (Bates et al., 2014). The full fixed structure of the model contained the main effect of Trial type (only hits and illusions), the main effect of Alerting (no tone and tone condition), and the interaction of both factors. The random structure only included the participant factor (Trial type + Alerting + Trial type:Alerting + (1|participant)). The effect size for LME was informed by the eta square (η^2), extracted by the *eta_square* function of the sjstats R package (Lüdecke, 2015). This statistic measures the effect size of ANOVA being the analog of R^2. Values of η^2 range from 0 to 1, with ~.01 being a small effect, ~.06 a medium effect, and <.14 a large effect (Fritz et al., 2012). To qualify any two-way or three-way interactions, we used the *testInteractions* function of the phia R package (De Rosario-Martinez et al., 2015). RT analyses were repeated including Awareness as a fixed and random factor.

For all analyses, the X^2 and p values were provided by the *Anova* function of the car package (Fox et al., 2022). The effect size for MELR was reported using the odds ratio and the 95% confidence interval, by the *tab_model* function of the SjPlot R package (Lüdecke, 2015). The odds ratio indicates the constant effect of a specific predictor on the likelihood that one outcome will occur, while the confidence interval estimates the precision of the odds ratio (i.e., a smaller confidence interval signals a higher precision).

9.3.4.2 HR statistical analyses

The HR was only analyzed in the expected blocks, as there were not enough trials in the unexpected block to perform this analysis. Lineal-mixed models (LME) with the lmer function of the lme4 R package (Bates et al., 2014) were used. The full fixed structure of the model contained the main effect of Trial type (hits and illusions), the main effect of Alerting (no tone and tone condition), the main effect of Time (40 points of time of 100 ms), the 2-way interactions, and the triple interaction between factors. The random structure only included the participant factor (Trial type + Alerting + Time + Trial type:Alerting + Trial type:Time + Alerting:Time + Trial type:Alerting:Time + (1|participant)). The Anova function was used to obtain X^2 and p values. The effect size for LME was informed by the eta square (η^2), extracted by the eta_square function of the sjstats R package (Lüdecke, 2015). To qualify the two-way or three-way interactions, we used the testInteractions function of the phia R package (De Rosario-Martinez et al., 2015). As in the behavioral results, Awareness was introduced as a fixed and random factor.

9.4 Results

9.4.1 Behavioral data analysis and results

9.4.1.1 Expected blocks results

As it can be observed in figure 9.2, the proportion of hits (X^2 (1) = 2.399, p=.121, odds ratio =1.08, confidence interval = 0.98-1.20), illusions (X^2 (1) = 0.119, p=.730, odds ratio =0.98, confidence interval = 0.88-1.10), and errors (X^2 (1) = 1.440, p=.230, odds ratio =0.90, confidence interval = 0.75-1.07) was similar for the tone and no tone conditions. However, the proportion of unseen trials decreased when the tone was presented, compared to no tone trials (X^2 (1) = 4.049, p=.044, odds ratio =0.67, confidence interval = 0.45-0.99).

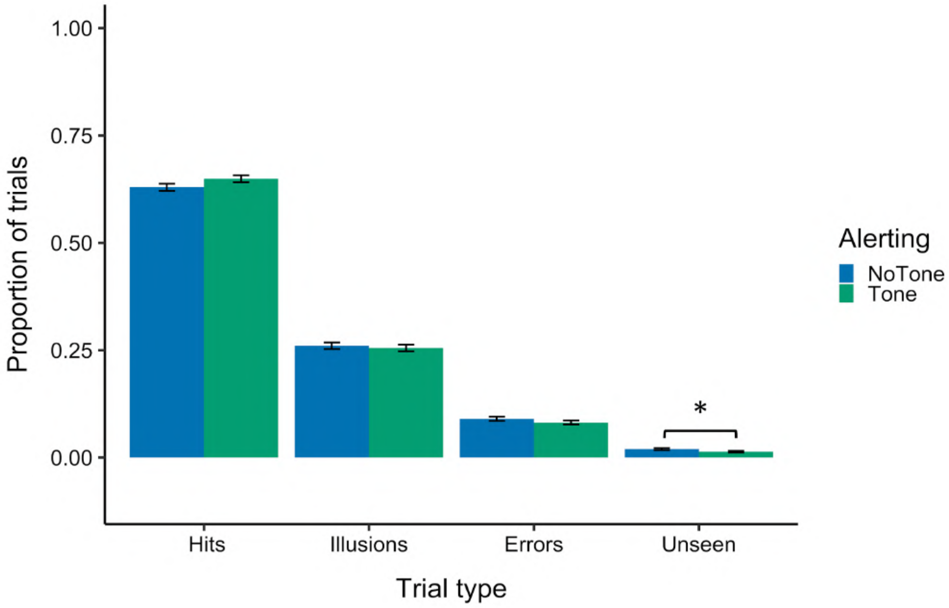

Figure 9.2: Proportion of hits, illusions, errors, and unseen responses for each Alerting condition (no tone vs. tone). This figure shows no significant differences in the proportion of hits, illusions, and errors in relation to the alerting condition. However, the proportion of unseen trials was reduced in the tone as compared to the no tone condition. Bars represent the standard error of the mean; asterisks represent statistically significant comparisons (*p<.05)

In order to explore whether aware and unaware participants differed in their performance during the expected bocks, Awareness was introduced as an additional factor in the analysis, although no significant main effect or interactions were observed (all ps>.122).

In the RT analysis, trials in which anticipatory responses (<200 ms) or slow responses (>2000 ms) occurred were eliminated from the analysis (5.83% of the trials). Responses were faster for hits, compared to illusions (X^2 (1) = 12.361, p<.001, η^2 =2.09^{-3}), and for tone vs. no tone conditions (X^2 (1) = 10.191, p<.001, η^2 =2.01^{-3}).

The interaction between Trial Type and Alerting was not significant (X^2 (1) = 1.615, p=.204, η^2 =2.76^{-4}) (see figure 9.3).

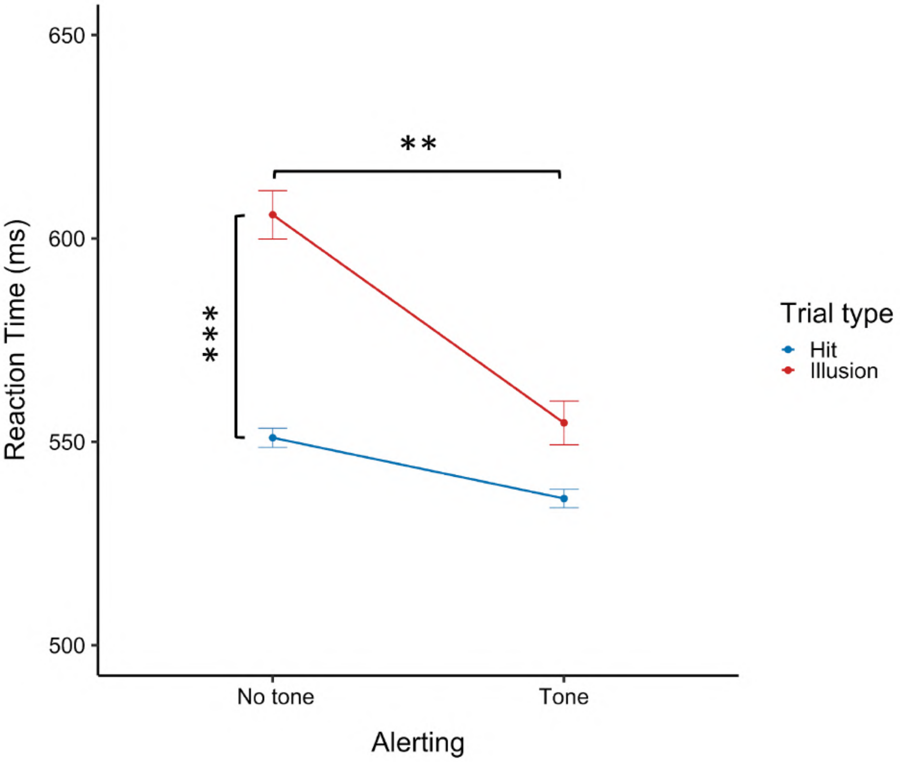

Figure 9.3: RT (in ms) for each condition of Alerting and Trial Type. This figure shows the main effects of Alerting and Trial type. Bars represent standard error of the mean; asterisks indicate significant effects (**p<.001; ***p<.0001).

When the Awareness factor was introduced in the analysis, no main effect of Awareness or its interactions were observed (all ps>.072).

9.4.1.2 Non-expected blocks results

The proportion of illusions (X^2 (1) = 488.933, p<.001, odds ratio =3.10, confidence interval = 2.68-3.59), errors (X^2 (1) = 508.884, p<.001, odds ratio =4.36, confidence interval = 3.62-5.26), and unseen trials (X^2 (1) = 444.716, p<.001, odds ratio =12.89, confidence interval = 9.35-17.77) increased in the unexpected blocks as compared to the expected blocks. Moreover, unseen responses were more likely in no tone as compared to tone conditions (main effect of Alerting, X^2 (1) = 5.554, p=.018, odds ratio =0.66, confidence interval = 0.44-0.98). No other main effects or interactions were significant (all ps>.209) (see figure 9.4).

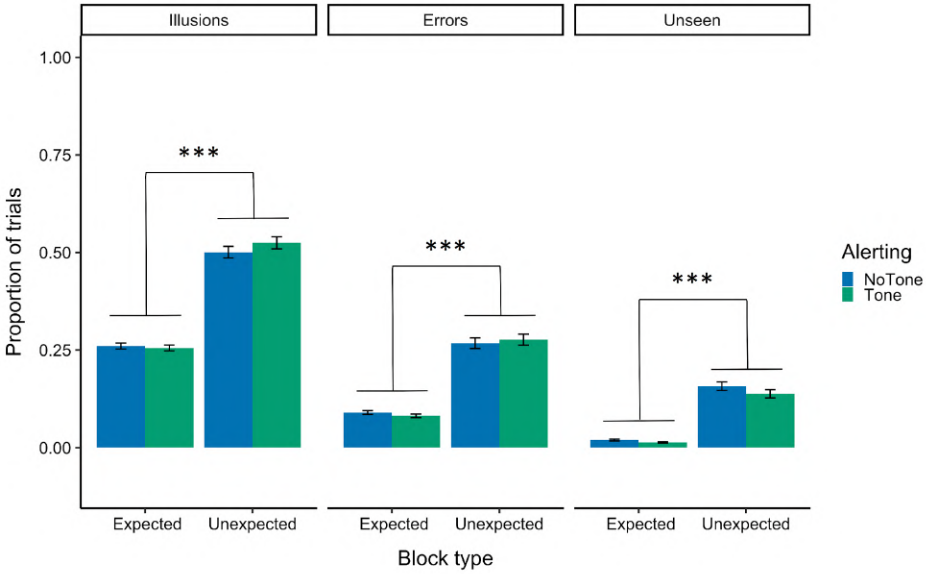

Figure 9.4: Proportion of illusions, errors, and unseen trials for each alerting condition in expected and unexpected blocks. In unexpected blocks, only trials with white targets were analyzed. The figure shows the main effect of Block type

for illusions, errors, and unseen trials. Bars represent the standard error; asterisks represent significant results (***p<.0001).

When the factor Awareness was introduced in the analysis, a significant interaction Awareness x Block type was observed in the proportion of illusions (X^2 (1) = 5.219, p=.022, odds ratio =1.40, confidence interval = 1.04-1.90). As shown in Figure 9.5, unaware participants tended to have more illusions than aware participants in both blocks, although the difference in the proportion of illusions in each block between groups did not achieve significance (expected: X^2 (1) = 2.319, p=.128; unexpected: X^2 (1) = 0.254, p=.614).

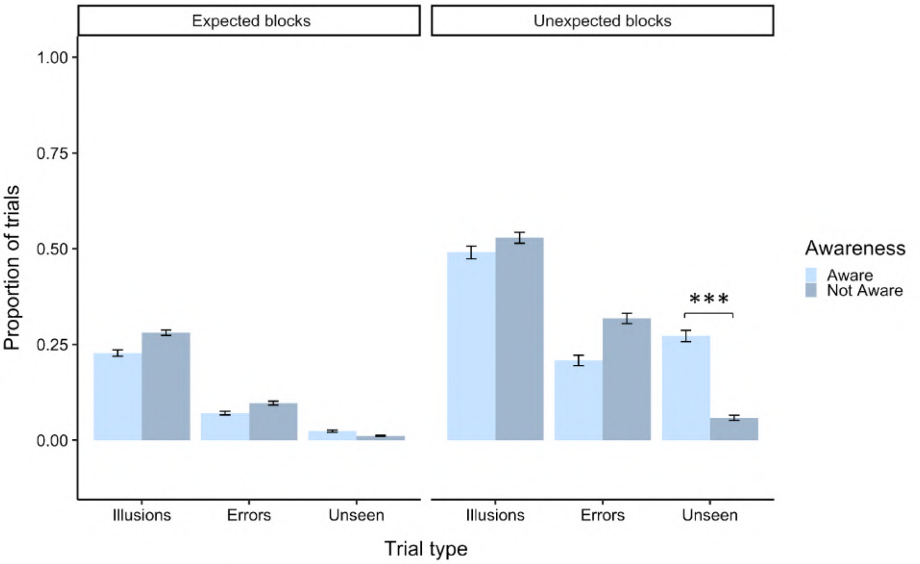

Figure 9.5: Proportion of illusions, errors, and unseen trials for aware and not aware participants in expected and unexpected blocks. The figure shows the interaction between Block type and Awareness in the proportion of unseen responses, with more unseen trials for aware than unaware participants in the

unexpected block. Bars represent the standard error; the asterisks represent significant results (***p<.0001).

For unseen responses, there was a main effect of Awareness (X^2 (1) = 4.530, p=.033, odds ratio =8.33, confidence interval = 0.51-136.80) and a significant interaction between Block type and Awareness (X^2 (1) = 24.383, p>.001, odds ratio =3.32, confidence interval = 1.72-6.40). The proportion of unseen responses for aware and unaware participants was comparable in the expected block (X^2 (1) = 2.319, p=.128), but more unseen responses were provided for aware than unaware participants in the unexpected block (X^2 (1) = 6.005, p=.014). No other main effects or interactions were significant (all ps>.056).

9.4.2 HR results

The analysis demonstrated a main effect of Time (X^2 (1) = 3475.571, p<.001, η^2 =0.01), showing the traditional deceleration pattern. There was a main effect of Trial Type (X^2 (1) = 3.872, p=.049, η^2 =1.43^{-5}) and an interaction between Trial Type and Alerting (X^2 (1) = 15.209, p<.001, η^2 =6.10^{-5}). This interaction showed an increased deceleration for hits compared to illusions, but only in the no tone condition (X^2 (1) = 16.931, p>.001; tone condition: X^2 (1) = 1.832, p=.176) (figure 9.6). No other main effects or interactions were significant (all ps>.143).

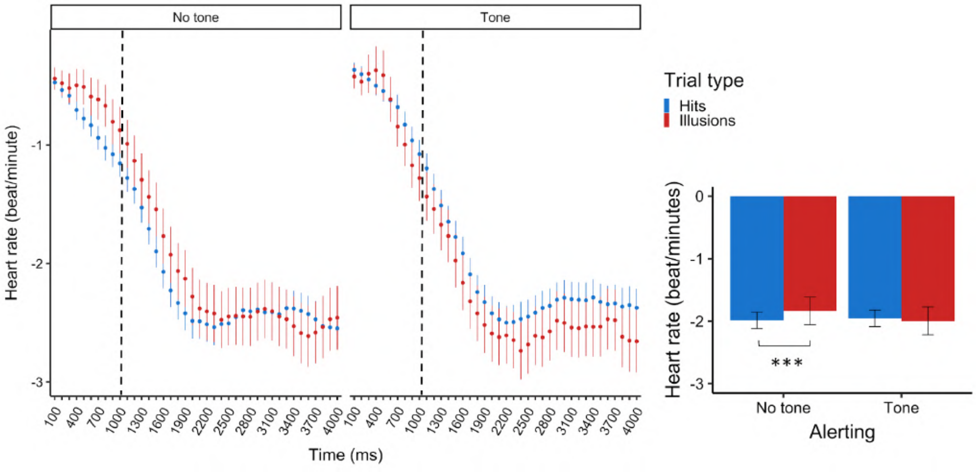

Figure 9.6: Left panel: Changes in HR (relative to baseline) for hits and illusions in No tone and Tone alerting conditions. The 0 value in the x-axis represents the fixation onset. The striped lines represent the moment in which the alerting tone could be presented. In both no tone and tone conditions, the deceleration HR pattern is observed. A significant interaction between Alerting and Trial type was observed. On the right, mean HR response (averaged over time) for each experimental condition of Alerting and Trial type. The main effect of trial type was only significant when no alerting tone was presented. Bars represent the standard error of the mean; the asterisks represent significant results of planned comparisons (***p<.0001)

When the Awareness factor was added to the analysis, the results demonstrated an interaction between Awareness and Alerting (X^2 (1) = 13.701, p<.001, η^2 = 5.81^{-7}) and between Awareness and Trial type (X^2 (1) = 41.841, p<.001, η^2 = 1.73^{-4}). The three-way interaction between Trial type, Alerting, and Awareness was also significant (X^2 (1) = 36.914, p<.001, η^2 = 6.94^{-3}). Exploring the three-way interaction, we found that aware participants demonstrated an enhanced deceleration HR pattern for hits compared to illusions for no tone (X^2 (1) = 47.607, p<.001) and tone conditions (X^2 (1) = 49.434, p<.001). For not aware participants, the deceleration pattern was comparable for hit and illusions in the no tone condition (X^2 (1) = 0.193, p=.660), but it was reversed (increased deceleration for illusions than hits) in the tone condition (X^2 (1) = 66.023, p<.001) (see figure 9.7).

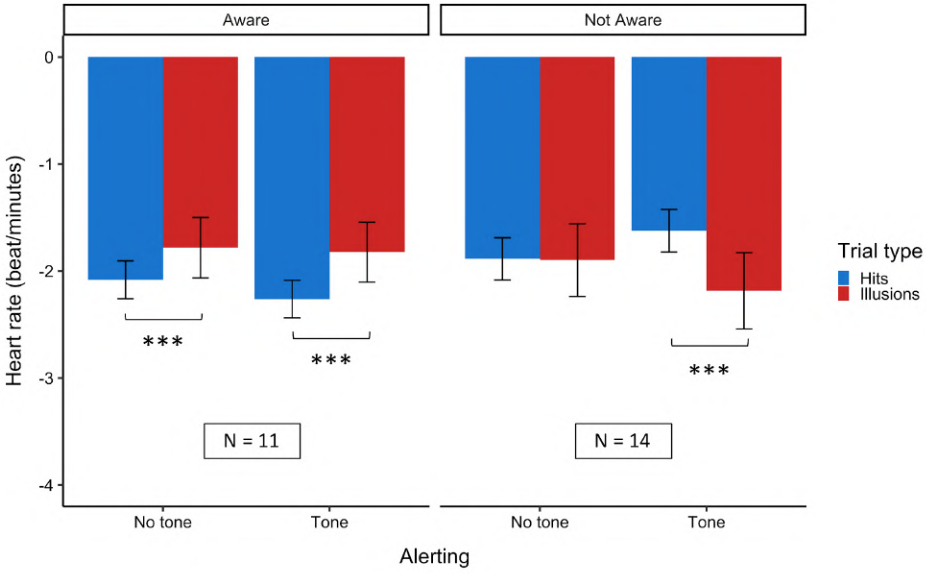

Figure 9.7: Mean HR response (averaged over time) for each experimental condition of Alerting and Trial type, for participants who were aware of the white target (left) and for those who were not aware (right). Bars represent the standard error of the mean; the asterisks represent significant results of planned comparisons (***p<.0001).

9.5 Discussion

The aim of this study was to explore the modulations in the PNS produced by the interaction of the attentional alerting system and phenomenological consciousness. At the behavioral level, we explored whether phasic alertness enhances the feature integration process. Likewise, we aim to replicate previously found effects of top-down expectancies on feature integration (Cobos et al., 2023; Cobos & Chica, 2022).

We used a feature integration task in which the shape and color features of a string of briefly-masked characters had to be correctly integrated. This integration could occur correctly (hits) if the color of the target letter was reported, or incorrectly (perceptual illusion) if the color of the distractor was reported. An alerting tone was randomly included in 50% of the trials to manipulate phasic alertness. To manipulate top-down expectancies, at the end of the experiment (unexpected blocks), the target letter was unexpectedly presented in white in half of the trials.

Behavioral results showed that the alerting tone did not modulate the feature integration process, i.e. the presence of the alerting tone did not increase the number of hits nor did it reduce the number of illusions (compared to the no-alerting tone condition). However, responses were faster in the presence of the alerting tone (compared to the no-alerting tone condition) and when integration occurred correctly (hits vs. illusions). Faster responses in the presence of alerting signals are associated to an increased preparation of the general activation system that allows faster responses, but that may come at a cost at the perceptual processing level (Briand & Klein, 1987; Petersen & Posner, 2012; Posner et al., 1973). Consistent with these observations, we observed faster responses to the alerting tone, but this did not imply modulations in the feature integration process. On the other hand, faster responses for hits vs. illusions is a result that has been previously reported with this paradigms (Cobos et al., 2023; Cobos & Chica, 2022; Rodríguez-San Esteban et al., 2022), and which has been interpreted as a better attentional preparation (Cobos et al., accepted; Mathewson et al., 2009; van den Berg et al., 2016). This preparation process has also been observed in alpha modulations at early stages of processing (Cobos et al., accepted; Ergenoglu et al., 2004; van den Berg et al., 2016; van Dijk et al., 2008; Wutz et al., 2018).

Regarding the top-down expectancy effect, the results observed in previous studies were replicated (Cobos et al., 2023; Cobos & Chica, 2022). The proportion of perceptual illusions, errors, and unseen trials increased in unexpected blocks compared to expected blocks. These results reaffirm the importance of top-down expectancy in the feature integration process (Aru et al., 2018; Aru & Bachmann, 2017; Cobos et al., 2023; Cobos & Chica, 2022; de Gardelle et al., 2009; Kuhn & Rensink, 2016; Mack et al., 2016). Some participants were aware of the expectancy manipulation, whereas others were not. Overall, aware participants had better integration ability (fewer perceptual illusions) throughout the experiment (expected and non-expected blocks) compared to those participants who were not aware. In addition, aware participants showed a higher proportion of unseen responses in the unexpected blocks as compared to not aware participants. Although these results are expected, they have not been observed in our previous studies using exactly the same manipulation (Cobos et al., 2023; Cobos & Chica, 2022). Future studies could improve the final interview by asking a more specific question about the color change, and by giving participants a choice between different colors to see if aware participants are more likely to choose the correct answer.

HR results showed a greater cardiac deceleration when correct integration occurred (hits), but only in trials in which the alerting tone was not presented. HR deceleration has been associated with stimulus detection processes (Barry & Tremayne, 1987; Cobos et al., 2019; Motyka et al., 2019; Park et al., 2014) or even with response efficiency (i.e., greater deceleration for faster responses) (Graham & Clifton, 1966; Jennings et al., 2009; Jennings & van der Molen, 2005; Lacey & Lacey, 1977; Lacey, 1970; Skora et al., 2022). In our study, responses were faster, and the decelerative response was also greater, for hits compared to illusions, consistent with the idea that cardiac deceleration is associated with more efficient responses.

Based on a previous study from our laboratory (Cobos et al., 2019), we hypothesized that the modulation of heart rate as a function of trial type would occur mainly in trials with alerting tone. This is what we observed in the previous study, although both tasks present notable differences. In Cobos et al. (2019) the targets were stimuli at the threshold of consciousness, which were perceived about ~50% of the trials. In these results, the alerting tone produced an effect on the percentage of correctly reported targets, whereas in the present study, alerting tone did not affect the perceptual quality (hits or illusions), only the reaction time. These methodological differences could explain the differences in HR in relation to the alerting tone for the different types of trials.

When we separated participants as aware or not aware of the expectancy manipulation, we observed that the modulations in HR were clearly different for both groups of participants. In aware participants, a greater deceleration pattern was observed for hits than for illusions both when the alerting tone was presented and when it was not presented. This could indicate a more efficient detection and preparation process by these aware participants. However, for not aware participants, the deceleration pattern was greater for illusions than for hits in the presence of the alerting tone. There is a large literature linking cardiac deceleration to error perception (Crone et al., 2003; Danev & de Winter, 1971; Fiehler et al., 2004; van der Veen et al., 2004; Wessel et al., 2011). This cardiac deceleration is most salient when receiving negative feedback about the error or when being aware of it (O'Connell et al., 2007; Wessel et al., 2011). In our study, we did not provide any feedback after response, and it is not possible to know if aware and unaware participants had different metacognitive awareness about their performance. Future studies will include a subjective response confidence scale in order to explore the role of metacognitive consciousness in perceptual illusions. The autonomic nervous system (ANS) involuntarily monitors performance and is responsible for sending negative feedback about errors. Errors active the saliency network (Notebaert et al., 2009), composed of areas such as the anterior insular cortex (AIC) (Seeley et al., 2007; Uddin, 2015), which is well known as a "hub" of interoception (subjective perception of bodily response) (Craig, 2009; Craig, 2002), and is directly related to autonomic responses such as heart rate (Critchley et al., 2003; Mutschler et al., 2009; Oppenheimer et al., 1992). Another relevant area in the salience network is the posterior medial frontal posterior cortex (pMFC) (Seeley et al., 2007), which also monitors performance in order to adapt the response to the external environment (Danielmeier et al., 2011). The AIC and pMFC regions increase their activity after perceiving an error (Wessel et al., 2011), and this activation is greater if the error is consciously perceived. The HR differences in aware and unaware participants suggest that these two groups of participants might present differences in their sensitivity to error detection and monitoring, which is associated to CNS-PNS interactions (Graham & Clifton, 1966; Hajcak et al., 2003; Notebaert et al., 2009; Obrist, 2012; Sokolov, 1963; Ullsperger et al., 2014; Vila et al., 2007). Our previous EEG results also showed differences in the gamma band between both groups, which we interpreted as better attentional selection (Gruber et al., 1999; Herrmann, Lenz, et al., 2004) or capacity to attend to multiple items (Rouhinen et al., 2013) in aware as compared to not aware participants. Future research will explore HR modulations in relation to brain responses (EEG signals) to further explore the functional role of HR modulations in cognitive processing.

To summarize the findings of this study, it was observed that the alerting system does not enhance feature integration. However, top-down expectancies have a significant influence on this process. HR responses for correct and incorrect feature integration trials were markedly different for aware and unaware participants, highlighting the role of CNS-PNS interactions in performance monitoring. These results underscore the importance of accounting for the peripheral, not just the central, nervous system response in perceptual processing, which recent theories propose as an essential mechanism for first-person awareness (Azzalini et al., 2019; Tallon-Baudry et al., 2018). Remarkably, the literature on heart rate modulations during feature integration is scarce or absent. Looking ahead to future studies, it would be relevant to analyze heart rate in conjunction with EEG, since there is literature associating higher alpha power with higher cardiac deceleration (Lechinger et al., 2015), which would reflect an optimal attentional state. In addition, it would be interesting to analyze the HEP, a type of potential that is closely related to cardiac activity in terms of sensory processing (Kern et al., 2013), attention (Petzschner et al., 2019) or access awareness (Park et al., 2014).

9.6 Acknowledges

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9.7 Author contributions

MIC: María I. Cobos

PMG: Pedro M. Guerra

ABC: Ana B. Chica

Conceptualization: MIC, ABC

Investigation: MIC,

Data analysis: MIC, PMG

Writing original draft: MIC, ABC

Review & Editing: MIC, PMG, ABC

Supervision and funding: ABC

General discussion

Chapter 10: General discussion and conclusions

The general aim of this doctoral thesis is to explore the relationship between attention and perceptual consciousness and how brain-body dynamics can modulate this relationship. Following the classification proposed by Block (2011), we can distinguish between access or phenomenological consciousness, which could have different brain and cardiac dynamics. In this thesis, we further explore the role of some attentional systems in both access consciousness and phenomenological consciousness. The evidence found throughout this dissertation is described below. The discussion of this evidence is divided into 4 blocks. The first block summarizes the general results found during this thesis. The second block discusses the behavioral results observed through the studies. In the third block, the brain (EEG study), and organism dynamics (EKG study) results and presented and discussed. In addition, this third block ends with an integrative discussion of brain-body dynamics. Finally, in the fourth block we highlight the limitations and future perspectives of this line of research.

10.1 Summary of empirical found in this thesis

In order to achieve the general objective of this thesis, four studies have been carried out. In these studies, different attentional systems (alerting, orienting, executive system, and expectancies) were manipulated to explore their effect in either access consciousness or phenomenological consciousness. In the study of access consciousness, near-threshold Gabor stimuli were used as targets. Previous literature has extensively explored the role of spatial and executive attention using this paradigm. We explored the role of alerting by presenting an alerting signal on half of the trials, while we recorded the activity of the PNS (heart rate). In the study of phenomenological consciousness, a feature integration paradigm was used allowing partial consciousness of a string of characters with different shapes and colors. The role of spatial attention, divided attention, expectancies, and phasic alerting in feature integration was explored. In different chapters, we explored the modulations of the CNS (brain oscillations) and the PNS (heart rate) when integration occurred correctly or incorrectly.

In the first study (Chapter 6), we replicated the behavioral effects of alerting on access consciousness (faster responses and increased perceptual sensitivity in the presence of alerting signal as compared to no alerting trials). In addition, EKG measurements were recorded to explore modulations in the PNS between phasic alerting and access consciousness. HR results showed a deceleration-acceleration pattern (Lacey & Lacey, 1978). This pattern was especially pronounced when the alerting tone was presented and the Gabor stimulus consciousness seen as compared to unseen trials.

In a complementary way, the SC was recorded and analyzed. The SC signal also showed different modulations between the alerting system and access consciousness. SC increased when the stimulus was not perceived as compared to perceived stimuli, especially when the alerting signal was not presented. These results were relevant as they showed subliminal processing of the stimulus, although at the behavioral level, we found no evidence of this subliminal processing (accuracy above chance in trials reported as unseen).

In the second study (chapter 7) we started a new experimental line that allowed us to explore phenomenological consciousness. The paradigm was adapted from Esterman et al. (2004). The stimuli chosen were a string of characters (e.g., **SLOS**) of different shapes and color. Participants were tasked to report the color of the target stimulus "L". Stimulus features (size, eccentricity, and duration) were manipulated to produce approximately 30% perceptual illusions.

In *experiment 1* of Chapter 7, the executive system (divided attention) was manipulated, by using a dual task. Before the response to the main task, participants were required to solve a numerical task that varied in difficulty or attentional demand (see Section 7.3.3 and Figure 7.1). The results showed that the calibration procedure worked, producing about 30% perceptual illusions. The results of the central task showed more efficient responses in the task with less attentional demands as compared to the conditions with more attentional demand, which demonstrated a successful manipulation of the attentional overload of the executive system. Furthermore, the efficiency of the response to the central task was better when a hit vs. an illusion occurred afterwards. However, contrary to our hypotheses, the attentional system overload did not modulate the feature integration process. That is, the proportion of hits and perceptual illusions were not affected by the different demands of the central task.

In *experiment 2*, we studied how the endogenous orienting and top-down expectancies modulated feature integration. Endogenous orienting was manipulated by instructing, in each block of trials, about the probability of target appearance in a given spatial location (e.g., "in this block, the target stimulus will appear with a higher probability on the right"). Expectancies were manipulated by unexpectedly including the target stimulus in an unexpected color at the end of the experiment on 50% of the trials (unexpected blocks). At the end of the experiment, a structured interview was conducted to classify participants as aware or not aware of this manipulation. The central task results demonstrated a more efficient response when a less demanding condition appeared compared to a more demanding condition. As in experiment 1, overloading the executive system did not modulate the integration process. However, the proportion of hits was increased and the proportion of illusions decreased in spatially attended as compared to unattended trials. Regarding the expectancy manipulation, half of the participants were not aware of the presence of the unexpected target. In this unexpected block, the proportion of perceptual illusions and errors increased as compared to the unexpected blocks.

In *experiment 3*, the response efficiency of the central task was greater in the less demanding compared to the more demanding conditions. This pattern held for both hits and illusions. In particular, the response efficiency of the central task was significantly higher for hits than for illusions, especially in the more demanding conditions. The exogenous attentional orienting was manipulated by a non-informative peripheral cue. We replicated again that feature integration was not modulated by the executive system manipulation. In the case of exogenous orienting, modulations in the proportion of hits and perceptual illusions were shown, but only when the central task was less demanding. I.e., exogenous attention increased the number of hits and decreased the proportion of illusions only on trials with low attentional demands. As in experiment 2, we observed a higher proportion of illusions and errors in the unexpected as compared to the expected blocks. In summary, we observed that divided attention did not modulate feature integration, but we did find effects of spatial attention (endogenous and exogenous) and expectancies.

In the third study (Chapter 8), we explored the brain dynamics of feature integration using a high-density EEG. In this study, we analyzed different brain oscillations (theta, alpha, beta, and gamma) found the feature integration task. The experimental paradigm used was the same as in experiments 2 and 3 of the second study (chapter 7), but without including the manipulation of the attentional orienting system.

At the behavioral level, results were replicated: for the central task, we observed more efficient responses for the less demanding condition as compared with the more demanding condition; again, this central task did not modulate responses in the feature integration task. Regarding expectancies, participants presented a higher proportion of illusions, errors, and unseen trials in the unexpected as compared to the expected blocks.

Brain oscillations results demonstrated no modulations in the theta power. However, significant modulations were found in the alpha band at both early and late processing times. Beta-band power also showed a larger decrease for hits than for illusions. Finally, a cross-frequency power-power correlation analysis was performed, showing different patterns for hits and illusions between the early theta-alpha, early-late alpha, and theta-beta bands.

Finally, in the fourth study (Chapter 9), EKG measurements were recorded to explore modulations in the PNS between phasic alerting and phenomenal consciousness. SC measurements were also obtained, but they have not been analyzed due to lack of time. Behavioral results showed faster responses when the alerting tone was presented compared to no-tone conditions. Faster responses were also recorded when a hit as compared to a perceptual illusion occurred. However, the alerting tone did not modulate the integration process. I.e. the proportion of hits and illusions was similar when the alerting signal was present vs. absent. Similar results to previous studies, a higher proportion of illusions, errors, and unseen responses were observed in the unexpected as compared with the expected block.

The HR was modulated during the integration process, but this only occurred in the absence of the alerting signal. This modulation consisted of an increased cardiac deceleration for hits compared to illusions. However, the pattern of HR modulations was different for aware and not aware participants. Whereas aware participants showed greater cardiac deceleration for hits vs.

illusions both in the presence of the alerting signal and in its absence, not aware participants showed increased cardiac deceleration for illusions compared to hits, although only in the presence of the alerting signal.

In summary, this set of studies has allowed us to explore the brain and cardiac responses related to access and phenomenological consciousness, as well as to better delineate the relationship between different attentional systems and both forms of perceptual consciousness. In the following, the results will be discussed in relation to the relevant literature.

10.2 Unlocking the role of attention in perceptual consciousness: a behavioral perspective

The study of how different attentional networks modulate access consciousness is extensive. Although it has not been the subject of study in this thesis, other research has shown that endogenous orienting does not improve access consciousness (Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012) and that although executive attention can influence access consciousness, this modulation is less consistent. Some studies have observed that the executive system can modulate perceptual sensitivity (Martín-Signes et al., 2018), and others have reported modulations in response criterion (Colás et al., 2017). More consistent modulations have been observed when exogenous orienting (Botta et al., 2014, 2017; Chica, Lasaponara, et al., 2011; Chica & Bartolomeo, 2012; Hein et al., 2006), and phasic alerting (Botta et al., 2017; Chica et al., 2010; Chica, Paz-Alonso, et al., 2013; Chica et al., 2016, 2018; Chica & Bartolomeo, 2012; Cobos et al., 2019;

Kusnir et al., 2011) have been manipulated. Both facilitate access consciousness. In this thesis, the facilitatory effects of phasic alerting were replicated. Responses were faster and more targets were detected when alerting signals were presented (as compared to trials with no alerting signals) (Botta et al., 2017; Cobos et al., 2019; Kusnir et al., 2011; Petersen et al., 2017). This evidence suggests that attention plays an important role in making information consciously accessible. One of the theories supporting this premise is GNWT (Dehaene & Changeux, 2011). According to this proposal, attention is necessary but not sufficient for consciousness. Attention helps amplifying the sensory signal travelling to parietal-frontal regions, which allow the maintenance of information throughout working memory. This maintenance of information would enable an intentional response to the perceived stimulus, such as a verbal report (Dehaene et al., 2006). The evidence described above addresses "the easy problem" of the study of consciousness (the mechanisms necessary for conscious processing), but does not explain "the hard problem", which is related to the subjective experience that emerges from such conscious processing.

Phenomenological consciousness tries to address "the hard problem" in the field of consciousness (Seth & Bayne, 2022). In the literature, GNWT indicates that the subjective nature of consciousness occurs at the unconscious level, and if this subjective nature is reportable, then this experience will, by definition, be part of access consciousness (Naccache, 2018). In contrast, Block (2011) suggests that access consciousness is not rich, as the information that accesses consciousness is limited. However, phenomenological consciousness would overflow access consciousness, creating a richer subjective experience of our environment, although this may be partially erroneous (producing for example perceptual illusions) (Kouider et al., 2010). In this thesis, we have explored the role of attention in this subjective experience. To explore this relationship between phenomenological consciousness and attention, a feature integration paradigm has been used. According to the Feature Integration Theory proposed by Treisman & Gelade (1980), the perception of simple features (e.g., shape or color) can occur without the need for attention, but the integration of features (e.g., shape and color), would require attentional resources (Kristjánsson & Egeth, 2020; Treisman, 1996; Treisman & Schmidt, 1982; Wolfe & Robertson, 2012). When these attentional resources are overloaded (due to limited attention), integration failures occur, resulting in perceptual illusions. In fact, perceptual failures/illusions during the integration process are more likely in patients with damage to the parietal lobe (an area related to attentional processing) (Bernstein & Robertson, 1998; Friedman-Hill et al., 1995; Gillebert & Humphreys, 2010; Robertson, 2003). By exploring how different attentional systems modulate feature integration, the role of attention in phenomenological consciousness can be clarified.

The results of this thesis show that some types of attention improve the integration process while other types do not. While executive attention or the alerting system (chapter 9) did not alter feature integration, spatial orienting improved this process (Cobos & Chica, 2022). If the stimulus to be integrated appears in an attended location (valid trials), the probability of correctly integrating its features increases and the probability of incorrectly integrating its features decreases. It should be noted, however, that other studies have demonstrated that the integration process can correctly occur without the need for attention (Gillebert & Humphreys, 2010; Henderson, 2014; Humphreys, 2016; Li et al., 2002; Pelli & Tillman, 2008; Whitney & Levi, 2011), but the attentional orienting system appears to amplify/enhance the integration process, mitigating the production of perceptual illusions (Briand, 1998; Briand & Klein, 1987; Grubb et al., 2013; Henderickx et al., 2010; Kewan-Khalayly et al., 2022; Yeshurun & Rashal, 2010).

Alternatively to the Feature Integration Theory, Humphreys' (2016) Feature Confirmation account emerged. This theory redefines the role of attention during the integration process, stating that attention is not necessary for the integration process to occur. However, this theory highlights the role of top-down feedback signals. Initially, sensory information would provide a weak signal in sensory regions that would require top-down feedback signals (e.g. from expectancies) coming from parietal regions. This top-down processing would be responsible for stabilizing the sensory signal for feature integration to occur. In this thesis, the brain areas involved in the integration process have not been explored (for more information see Rodríguez-San Esteban et al., 2022). However, our behavioral results show the importance of expectancies during the integration process. These results reveal that the proportion of perceptual illusions, as well as other perceptual failures (errors and unseen trials), significantly increase when expectancies about target features were violated (Cobos et al., accepted; Cobos & Chica, 2022). In the literature, it has been shown that when expectancies are matched, detection or recognition of certain stimuli improves (Sherman et al., 2015; Stefanics et al., 2010; Wyart et al., 2012), and violation of expectancies alters perceptual processing (Aru et al., 2018; Aru & Bachmann, 2017; Cobos & Chica, 2022; Summerfield & Egner, 2009; Summerfield et al., 2006).

In summary, both access consciousness and phenomenological consciousness are influenced by some attentional systems. While bottom-up processes, such as exogenous orienting and phasic alerting, modulate access consciousness, phenomenological consciousness, as measured through feature integration paradigms, undergoes more remarkable enhancements by top-down processes, such as endogenous orienting and expectancies. The exogenous (bottom-up) orienting system can also modulate phenomenological consciousness, as long as the attentional system is not overloaded (see experiment 3 in Cobos & Chica, 2022).

10.3 The brain-body dynamic duting conscious processing

For several decades, scientists interested in the study of consciousness have wondered how our subjective experience is generated from brain activity (the so-called "hard problem" of consciousness). However, it is undisputed that the brain does not act in isolation, rather it is in contact interaction with the environment and with the rest of the organism (e.g., heart, Park & Tallon-Baudry, 2014 or digestive system, Azzalini et al., 2019). Indeed, the study of the organism and the PNS has been focused for years on the study of emotions (for a review see Pace-Schott et al., 2019). But how important is the PNS and its relation to the brain in other complex cognitive processes such as consciousness? The studies in this thesis, presented in Chapters 6, 8, and 9, examined the interactions between attention and perceptual consciousness, both in terms of brain dynamics (brain oscillations) and organism dynamics (PNS measures via EKG), separately. While performing analyses that link CNS and PNS measures would have been ideal, the separate results are necessary steps that can aid in forming clearer hypotheses for future studies. Next, we will present and discuss the interpretation of the results from each system separately. Finally, we will include a section reviewing studies that have linked the two systems.

10.3.1 Brain dynamics during conscious processing

Studying brain dynamics throughout the behavior of brain oscillations can shed some light about different theories of consciousness, as well as to infere which cognitive processes are necessary and sufficient for consciousness. Some models of consciousness hypothesize a role of attention or WM in consciousness, implemented throughout long-range connections between brain regions (Dehaene & Changeux, 2011); re-entrant theories highlight the need for feedforward signals in sensory regions and top-down feedback signals coming from parietal regions (Lamme, 2003, 2006); higher-order theories emphasize the role of meta-representations, as well as coherence between low-order and higher-order representations; the information integration theory proposes that conscious experience in generated in sensory, temporal, and parietal regions, without a crucial role of frontal regions. However, this theory does propose attention as necessary for consciousness (Tononi, 2004, 2008; Tononi et al., 2016).

Previous studies have explored the role of some brain oscillations in phenomenological consciousness and feature integration. However, these studies have always explored a single frequency in isolation. In Chapter 8, we explored different frequency bands and their relationship to feature integration. The alpha-band has shown modulations at early and late moments of the integration process. At early moments, alpha power was higher for illusions compared to hits. It has been suggested that pre-stimulus alpha activity may predict the level of perceptual consciousness (Benwell et al., 2022). Other studies have shown that the alpha-band is related to attentional preparation processes and cortical excitability, which enhances subsequent perception (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Limbach & Corballis, 2016; van den Berg et al., 2016; van Dijk et al., 2008). These pre-stimulus alpha results are consistent with the results of our study. The behavioral results concerning response efficiency in the central task in Chapters 7 and 8 already pointed in an indirect way to the possibility that preparatory processes were involved in the integration process. When responding to the central task, we observed more efficient responses for trials later classified as hits as compared to illusions. The early alpha results confirmed that preparatory processes are important for feature integration. *Later alpha modulations* have been usually related to spatial attention. Contralateral modulations are commonly associated with the selection of spatial locations (Busch & VanRullen, 2010; Capilla et al., 2014; Kelly et al., 2006; Sauseng et al., 2006; Schroeder et al., 2018; Thut, 2006), whereas ipsilateral modulations are related to the inhibition of irrelevant stimuli (Capilla et al., 2014; Klimesch, 2012; Klimesch et al., 2007; Lange et al., 2014; Min et al., 2008; Min & Herrmann, 2007; Schroeder et al., 2018). In our study, an ipsilateral modulation was observed, indicating the importance of effective distractor inhibitory processes in feature integration.

The beta-band, commonly associated with motor responses (Engel & Fries, 2010; Khanna & Carmena, 2015), exhibited a more pronounced decrease for hits than illusions in our study. In tasks involving attention and working memory, the beta band has been related to top-down processes (Antzoulatos & Miller, 2016; Buschman et al., 2012; Buschman & Miller, 2007; Dubey et al., 2023; Fiebelkorn & Kastner, 2021; Miller et al., 2018). Alpha and beta have also been related to the reliability of perceptual representation in the cerebral cortex (Griffiths et al., 2016; Griffiths et al., 2019; Hanslmayr et al., 2009), inhibition processes (Jensen & Mazaheri, 2010; Klimesch et al., 2007) and the propagation of top-down feedback signals that facilitate feedforward communication (Bastos et al., 2014; Michalareas et al., 2016; Richter, Thompson, et al., 2017; Veniero et al., 2021). The role of the beta-band seems to be relevant during the feature integration process, which is associated with the transmission of feedback signals. Humphreys' (2016) FCA theory would support these findings by highlighting the role of parietal lobe feedback signals in the stabilization of sensory signals.

The results found for gamma do not seem entirely consistent with the literature on feature integration or conscious processing. In this literature, gamma power is enhanced when features are correctly as compared to incorrectly integrated (Bertrand & Tallon-baudry, 2000; Buschman & Miller, 2007; Phillips et al., 2012; Phillips & Takeda, 2009), when the number of features to integrate is larger (Honkanen et al., 2015; Keil & Müller, 2010; Morgan et al., 2011; Vidal et al., 2006) and when information accesses consciousness as compared to unconsciously perceived information (Burgess & Ali, 2002; Crick & Koch, 1990; Melloni et al., 2007; Panagiotaropoulos et al., 2012; Rieder et al., 2011; Schurger et al., 2006). However, in our study, we found that gamma power significantly increased at ipsilateral electrodes and but there was no significant modulation for correct vs. incorrect feature integration. EEG studies are not well-suited to study the gamma-band, as there are important confounds related to e.g. muscle activity (Goncharova et al., 2003) or microsaccades (Yuval-Greenberg et al., 2008). Studies showing gamma modulations require magnetoencephalography or intracranial electroencephalography techniques.

In summary, the results obtained in the EEG study demonstrate that different cognitive processes are crucial during feature integration, including preparation (early alpha), perceptual representation (late alpha and beta), and distractor inhibition (late alpha). It should be noted that we are inferring cognitive processes from brain oscillations, which is a reverse inference (Poldrack, 2006) that must be approached with caution. However, it is indisputable that errors in feature integration are linked to various cognitive processes that occur at different stages of information processing.

10.3.2 Coherence in brain dynamic and its link to consciousness theories

Contrary to our predictions, based on the revised literature (Cavanagh et al., 2009; Cohen, 2011; Fusco et al., 2018; Kalfaoğlu et al., 2018; Mathes et al., 2014), we did not find theta-band modulations related to correct or incorrect feature integration. We decided to carry out a power trial-by-trial correlation analysis (see section 8.3.6.4 and section 8.4.2.2). We observed a higher correlation in illusions compared to hits between theta-early alpha, early-late alpha, and between theta-beta. These correlations between frequencies may be related to perceptual quality (Busch et al., 2009; Busch & VanRullen, 2010; van Es et al., 2022) or to a failure between bottom-up and top-down communications (Angelidis et al., 2018; Knyazev, 2007; Putman et al., 2010; Schutter & Van Honk, 2005; van Son et al., 2018). All the theories explaining consciousness described in Chapter 1 of this thesis refer to these mechanisms of brain intercommunication that can occur either within the close or distant brain regions.

The GNWT proposes that conscious access requires the reverberation of information from high-order regions to low-order regions (Dehaene & Changeux, 2011b); according to the recurrent theory of Lamme & Roelfsema (2000) feedforward (bottom-up) and feedback (top-down) signals from parietal regions to sensory regions represent a crucial aspect for conscious perception; the higher-order theories underline the importance of coherence between low-order and higher-order representations (Cleeremans et al., 2020; Fleming, 2020; Lau, 2019); the IIT (Tononi et al., 2016) also propose the intercommunication between occipital, temporal, and parietal areas, as a necessary mechanism for consciousness. In other words, all theories agree on the necessity of intercommunication between brain regions for creating a conscious percept. The theta and gamma bands have been related to bottom-up signals, while the alpha and beta have been related to top-down signals (Bastos et al., 2014; Buschman & Miller, 2007; Michalareas et al., 2016; Richter et al., 2017, 2018; von Stein & Sarnthein, 2000). In our results, the correlation between early alpha and theta could be related to the quality of perceptual processing (Busch et al., 2009; Busch & VanRullen, 2010; van Es et al., 2022), whereas the correlation between theta and beta could be reflecting bottom-up and top-down intercommunication (Angelidis et al., 2018; Knyazev, 2007; Putman et al., 2010; Schutter & Van Honk, 2005; van Son et al., 2018).

In addition to the comparison between theories of consciousness, we can establish strong similarities between Lamme & Roelfsema's (2000) recurrent theory and Humphreys' (2016) FCA. Both theories state that sensory information needs top-down feedback signals from parietal regions to the visual cortex during perceptual processing. Lamme & Roelfsema (2000) indicate that top-down signals collaborate in conscious perception, while Humphreys (2016) proposes that feedback signals are necessary to stabilize the sensory signal.

In summary, brain oscillations and their relation to theories of consciousness reveal the importance of intercommunication in the brain. Correlations between frequencies suggest a complex coordination between bottom-up and top-down processes. These connections could support the idea that conscious perception depends on effective communication between different brain regions and that when this communication fails, information may not gain access to consciousness or may gain access incorrectly.

10.3.3 Expectancies in conscious perception

In the behavioral studies of feature integration, we have consistently reported the effects of expectancy violation in perception. These results show a higher number of integration errors when an unexpected stimulus appears. I.e., when participants perceived an unexpected feature, they tended to complete the information with other adjacent features in the scene. In all studies, about half of the sample was aware of this manipulation, while the other half was unaware. In the EEG study, we explored whether during the experiment (before the presentation of the unexpected stimulus), aware and not aware participants could present different strategies which could be reflected in their brain oscillations.

Without a prior hypothesis, we found that participants aware of the manipulation showed higher levels of gamma power compared to those participants who were not aware of this manipulation. Previous studies have observed that expectancies increased spatial resolution (Carrasco & Yeshurun, 2009; Yeshurun & Carrasco, 1998), contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2000), as well as stimulus detection or recognition (Summerfield & Egner, 2009; Summerfield et al., 2006). The gamma-band is related to numerous complex cognitive processes (Engel et al., 2001). Increased gamma is related to attentional selection (Bauer et al., 2009; Bauer et al., 2014), feature integration (Bertrand & Tallon-baudry, 2000; Buschman & Miller, 2007; Phillips et al., 2012; Vidal et al., 2006), consciousness (A. P. Burgess & Ali, 2002; Crick & Koch, 1990; Melloni et al., 2007; Panagiotaropoulos et al., 2012; Rieder et al., 2011; Schurger et al., 2006), or memory (Bastos et al., 2018; Honkanen et al., 2015; Howard, 2003; Lundqvist et al., 2011; Miller et al., 2018; Roux & Uhlhaas, 2014), among other cognitive processes. A study with monkeys by Lima et al. (2011) showed a relationship between temporal expectancies and the gamma-band in occipital regions. What is interesting about this study is that in addition to expectancies being associated with an increase in gamma power, they were also associated with a suppression of alpha. This trade-off between gamma and alpha has been related to the control of information flow in the brain (Jokisch & Jensen, 2007).

The results observed in the gamma-band suggest that participants who were aware or not aware of the manipulation developed different strategies throughout the experiment, and these strategies could influence the conscious perception of unexpected features. These different strategies could relate to better attentional capacity (Gruber et al., 1999; Herrmann, Lenz, et al., 2004; Tiitinen et al., 1993), perceptual processing of multiple stimuli (Rouhinen et al., 2013), integration ability (Bertrand & Tallon-baudry, 2000; Buschman & Miller, 2007a; Phillips et al., 2012; Phillips & Takeda, 2009; Vidal et al., 2006), conscious processing (Burgess & Ali, 2002; Crick & Koch, 1990; Panagiotaropoulos et al., 2012; Rieder et al., 2011; Schurger et al., 2006) or memory (Bastos et al., 2018; Honkanen et al., 2015; Howard, 2003; Lundqvist et al., 2011; Miller et al., 2018; Roux & Uhlhaas, 2014).

10.3.4 The body dynamic in conscious perception

Access consciousness has been associated to pre-stimulus alpha power and gamma power (Benwell et al., 2022; Gallotto et al., 2017; Panagiotaropoulos et al., 2012). Studies exploring phenomenological consciousness has shown either gamma-band (Keil & Müller, 2010; Morgan et al., 2011) or alpha-band (Müller et al., 2015; Zhang et al., 2019) modulations. The results of our study highlight the involvement of the alpha-band (early and late modulations) and beta (Cobos et al., 2023) bands in feature integration. However, the brain does not work in isolation; rather, the state of the organism, in particular the activity of the PNS, influences cognitive processing (Craig, 2009; Critchley et al., 2004; Critchley & Harrison, 2013; Lang et al., 1990; Park et al., 2014). One way to explore the activity of the PNS is to study cardiac patterns (Pollatos & Schandry, 2004; Skora et al., 2022). Chapters 6 and 9 explored the interaction between phasic alerting and access and phenomenal consciousness while HR was recorded.

In Chapter 6, we observed the typical deceleration-aceleration response, which was enhanced for consciously seen as compared to unseen targets, especially in the presence of the alerting signal. In contrast, the HR results in the feature integration paradigm (Chapter 9) showed a larger decrement in HR for correct as compared to incorrect responses, but especially in the absence of alerting signal. Although the cardiac patterns in access and phenomenal consciousness paradigms showed different modulations in relation to alerting signals, both demonstrated increased cardiac deceleration when a correct response occurs (seen vs. unseen and hits vs. illusions). In the literature, cardiac deceleration has been related to processes of detection (Barry & Tremayne, 1987; Cobos et al., 2019; Motyka et al., 2019; Park et al., 2014), response efficiency (Graham & Clifton, 1966; Jennings et al., 2009; Jennings & van der Molen, 2005; Lacey & Lacey, 1977; Lacey, 1970; Skora et al., 2022), preparatory processes (Graham & Clifton, 1966; Jennings et al., 2009; Jennings & van der Molen, 2005; Lacey & Lacey, 1977; Lacey, 1970; Skora et al., 2022) and conscious detection (Park et al., 2014). Behaviorally, phasic alerting enhanced access to consciousness, but not its content (measured as feature integration), while cardiac activity demonstrated significant decelerations associated to correct as compared to incorrect responses.

In the feature integration paradigm, the modulations in HR were significantly different when participants were classified as aware or unaware of the expectancy manipulation. During the expected blocks, aware participants presented a larger deceleration for hits as compared to illusions, both in the presence and absence of the alerting signal. For the not aware participants, the cardiac pattern was different. Only in the presence of the alerting signal did HR decelerate more for illusions vs. hits. The increased cardiac deceleration for hits as compared to illusions observed for aware participants seem to have can be related to better preparatory and/or detection strategies for feature integration (regardless of the alerting signal) (O'Connell et al., 2007; Wessel et al., 2011). For not aware participants, the increased cardiac deceleration for illusions as compared to hits can be related to the internal error feedback coming from the salience network (Danielmeier et al., 2011; Notebaert et al., 2009; Seeley et al., 2007). Errors often generate a greater response in the salience network (Notebaert et al., 2009), a network composed of areas such as the anterior insular cortex (Seeley et al., 2007; Uddin, 2015) (interoceptive "hub", see Craig, 2009) and the medial prefrontal cortex (Seeley et al., 2007). Both areas are related to the monitoring of cardiac activity and increase their activity after detecting an error (Wessel et al., 2011). In our study, aware and not aware participants would present differences in error detection as well as monitoring (Graham & Clifton, 1966; Hajcak et al., 2003; Notebaert et al., 2009; Obrist, 2012; Sokolov, 1963; Ullsperger et al., 2014; Vila et al., 2007).

The results of Chapters 6 and 9 highlight the importance of studying the PNS in complex cognitive processes such as perceptual consciousness. In both access and phenomenological consciousness paradigms, increased cardiac deceleration is observed when correct as compared to incorrect responses occurred. However, access consciousness improves when alerting signals are presented, whereas in phenomenological consciousness does not.

10.3.5 Brain-body dynamic interpretations and inferences

Although the measures obtained at the brain level (EEG) and at the PNS level (HR) have not been analyzed together, the results obtained in this thesis may help to formulate their joint interpretation based on the literature. In the study by Lechinger et al. (2015), they found a correlation between alpha-band and heart rate. This correlation showed that in the attentional optimal state, alpha power decreased and HR decelerated (de Munck et al., 2008; Lechinger et al., 2015). Both alpha decrement and cardiac deceleration have been related to optimal preparatory states for responding to a task (Ergenoglu et al., 2004; Jennings & van der Molen, 2005; Skora et al., 2022; van den Berg et al., 2016). In Chapters 8 and 9, we also observed alpha decrement and cardiac decelerations associated to correct responses. Both results, despite measuring different systems, might be reflecting partially similar processes that influence conscious processing.

A study with Parkinson's patients and healthy participants (Candia-Rivera, 2022) showed a coupling between cardiac activity and alpha and gamma frequencies. These modulations were weaker in Parkinson's patients than in healthy participants. Among the variability of symptoms presented by Parkinson patients, attention and executive functions are often impaired (Lawson et al., 2016). These findings of reduced coupling between cardiac activity and gamma and alpha bands could reflect attentional impairments in these patients. Furthermore, Fiebelkorn & Kastner (2020) have also indicated that the optimal attentional state is related to an increase in gamma activity and suppression of alpha activity, which usually translates into an efficient response to a given task. On the contrary, a smaller suppression of alpha and a decrease in gamma activity is related to impaired performance (non-optimal attentional state). Gamma activity has been associated to prefrontal cortex activity (Alekseichuk et al., 2016; Roux et al., 2012). The neurovisceral integration model of Thayer & Lane (2009) highlights the role of the prefrontal cortex as an inhibitory modulator of the amygdala, which interacts with changes in heart rate via the vagus nerve. Specifically, the prefrontal cortex sends inhibitory signals to the amygdala, which in turn also inhibits cardiac activity, together with the intervention of the vagus nerve, resulting in a deceleration of the heart rate. The neurovisceral integration theory associates this cardiac deceleration with cortical excitability, and thus with improved accuracy of perceptual processing of stimuli. The baroreceptor reflex hypothesis also supports this association although it justifies it using the concept of neural gain (Kolasinski et al., 2017; Skora et al., 2022; Smith et al., 2017; Thayer & Lane, 2009).

This description of studies and inferences between oscillatory activity and cardiac activity highlights the importance of the relationship between the CNS and PNS. This evidence underscores the importance of continually updating information between the organism and the brain for complex cognitive processes like perceptual consciousness, or at the very least, it highlights a significant influence between both systems. As Park & Tallon-Baudry (2014) highlight in their model called "subjective neural framework", for conscious experience to occur, both systems must communicate with each other efficiently.

In summary, this section attempts to establish a connection between the results obtained from the study of brain and organism dynamics. The interpretations provided place special emphasis on the involvement of preparatory attentional processes during conscious processing. Depending on the study, other cognitive processes may also come into play, but optimal preparation and effective communication between the brain and the organism appear to be crucial factors for gaining access to consciousness and establishing a conscious experience.

10.4 Limitations and future perspectives

The results of this thesis are broad and rich but also contain different limitations. In the feature integration paradigm, we tried to simplify the number of conditions in order to acquire more trials for each participant. When reporting the color of the target letter, participants must integrate shape and color. But it could be argued that what we called illusions in the current paradigm are not actually feature integration errors but simply errors. In some paradigms, shape and color must be reported (presenting for example an L and an inverted L as targets). In this case, both color and shape are reported, so the errors can be divided into simple errors (color error with the correct shape or shape error with the correct color) or integration errors. We are currently developing a follow-up study incorporating this improvement to replicate and extend our data. In this same study, a scale of response security has also been incorporated to explore metacognition.

Another limitation is not having analyzed the combined data of the CNS and PNS. I.e. the absence of HEP analysis or correlations between brain oscillations and HR. In the experiment presented in Chapter 8, cardiac measurements were recorded in order to achieve this goal. However, due to lack of time, such analyses could not be presented. Nevertheless, the results presented and the literature reviewed will allow us to establish clear hypotheses when these analyses will be performed in the near future.

Another future proposal is the application of multivariate pattern analysis (MVPA) to the EEG data. The new paradigm under development has also been adapted to perform MVPA, which will allow us to explore what information is represented in each frequency band. Also, by means of temporal generalization matrices, it will be explored how the feature integration process develops over time and how it interacts with other cognitive processes. In addition, multivariate analyses will allow the characterization of the brain responses of aware and not aware participants.

10.5 Highlights

- The relationship between attention and consciousness is complex and depends on how consciousness is measured and how attention is manipulated.
- Temporal brain dynamics show the involvement of different cognitive processes during feature integration.
- Peripheral dynamics, using HR measures, reflect partially distinct modulations in access and phenomenological consciousness.
- The results of this thesis emphasize the need to integrate CNS and PNS information in the study of perceptual consciousness.

Scientific disclosure

11. Resumen divulgativo para el público general

11.1 Percibir es un proceso complejo

A diario nos encontramos rodeados de una gran cantidad de estímulos. Estudiar cómo percibimos estos estímulos de manera consciente es de especial relevancia en el ámbito de la Neurociencia Cognitiva. Imagina que te encuentras conduciendo rumbo a tu trabajo, que se encuentra a las afueras de tu ciudad. Durante la conducción, tienes la impresión de percibir de manera muy detallada la escena que te rodea: diferentes carriles de conducción, carriles de incorporación, coches o motos a un lado u otro, diferentes señales lumínicas o carteles, etc. Sin embargo, si tuvieras que reportar si hay o no un vehículo detrás de ti, dirigirías tu atención al espejo retrovisor, lo que te permitiría acceder a esa información. En este caso, hablamos de consciencia de acceso, ya que puedes reportar lo que percibes conscientemente. Sin embargo, si tuvieras que indicar cuántos o qué vehículos se encuentran en tu campo de visión, esta tarea sería casi imposible de completar, y en caso de hacerlo, tu percepción estaría llena de errores. En este caso, hablamos de consciencia fenomenológica. Este tipo de consciencia se refiere a una experiencia subjetiva rica de la escena, pero que a menudo está llena de imprecisiones.

11.2¿Necesitamos atener para ser consicientes?

Ya que nuestra capacidad perceptual es limitada (no podemos percibir todo lo que llega a nuestros sentidos), necesitamos mecanismos de selección de la información. Uno de estos mecanismos es la atención, que nos permite seleccionar el espejo retrovisor para comprobar si hay un coche detrás de nosotros. Por ello, estudiar cómo se relaciona la atención con la consciencia es relevante. Existen diferentes tipos de atención: la alerta (activación producida por el claxon de un coche), la orientación en el espacio (como cuando ves un cartel con una flecha que te señala la entrada a una ciudad o cuando se cruza un peatón por el lado derecho), y el sistema ejecutivo (que permite hablar mientras conduces, planificar cómo cambiar de carril o dejar espacio cuando aparece una ambulancia). Otro aspecto relevante en este contexto es la experiencia previa, que hace que siempre que percibamos tengamos ciertas expectativas sobre qué encontraremos en esa situación. Si una expectativa no se cumple, aumenta la probabilidad de percibir el entorno de manera errónea. Por ejemplo, un conductor europeo espera que los coches que vienen de frente aparezcan por la izquierda, por lo que, si un coche aparece por la derecha, violando la expectativa, la probabilidad de percibirlo y responder de manera eficiente disminuirá.

Los diferentes modelos teóricos que intentan estudiar la consciencia cuestionan el papel de la atención en el procesamiento consciente. Estos modelos generalmente se centran en lo que ocurre a nivel cerebral. Sin embargo, el cerebro no trabaja de manera aislada, sino que se encuentra en constante comunicación con el estado del organismo. Dado el cuestionamiento del papel de la atención en la consciencia y la falta de exploración sobre cómo ocurre esta relación en la dinámica cerebro-organismo, surgen las preguntas y estudios de esta tesis doctoral.

11.3 Hallazgos comportamentales de la tesis doctoral

Los resultados de esta tesis muestran que los diferentes tipos de atención interactúan de manera diferente en la consciencia de acceso y en la consciencia fenomenológica. La alerta amplifica el acceso consciente a la información (como cuando el sonido de un claxon te ayuda a percibir un coche que se acerca), mientras que no influye en la consciencia fenomenológica (la percepción subjetiva y más detallada de la escena). Orientarse en el espacio beneficia tanto la consciencia de acceso como la consciencia fenomenológica (percibimos mejor a un peatón si sabemos que va a aparecer por la derecha y hay menos errores en la percepción si cuentas con un cartel que señala la entrada a una ciudad). En el caso del sistema ejecutivo, no se han encontrado efectos tan claros ni sobre la consciencia de acceso ni sobre la consciencia fenomenológica (hacer una doble tarea, por ejemplo, hablar por teléfono mientras conduces, no siempre afecta a la percepción –¡aunque se recomienda no hacerlo porque sí afecta a la velocidad de reacción!) Por otro lado, violar las expectativas tiene un claro efecto en la consciencia fenomenológica, ya que aumenta la cantidad de errores cuando aparece un estímulo inesperado. En este sentido hemos encontrado que cuando aparece información inesperada los observadores suelen "rellenar" esta información con otra información del ambiente como, por ejemplo: si te encuentras en una biblioteca, lo esperable es encontrar libros en las mesas y estanterías. Sin embargo, si de manera inesperada hay un portátil bajo algunos libros, es probable que ese portátil sea percibido como un libro, ya que los estímulos de alrededor son principalmente libros.

11.4 Hallazgos en la dinamica cerebro-organismo

El estudio de la dinámica cerebral mostró cómo las neuronas del cerebro se comunican mediante diferentes oscilaciones cuando percibimos de manera correcta e incorrecta. Estas oscilaciones cerebrales son cambios en el ritmo de la actividad eléctrica cerebral, y sus cambios en frecuencia, amplitud o fase reflejan diferentes procesos cognitivos. Nuestros resultados indican que oscilaciones alfa aumentaban en momentos previos a la presentación del estímulo. Este aumento de alfa parece indicar si la atención se encuentra en un estado óptimo de preparación, lo que puede influir en la percepción consciente posterior. Tras la presentación del estímulo, alfa disminuía, relacionándose esta disminución con procesos de inhibición de información distractora o no relevante. La banda beta, después de la presentación del estímulo, disminuye en la misma dirección que alfa, relacionándose ambas frecuencias con una representación precisa de los estímulos. La frecuencia gamma, por otro lado, fue mayor en las personas que se dieron cuenta de la violación de las expectativas (cuando un estímulo cambió inesperadamente al final del experimento) que en las personas que no se dieron cuenta. La frecuencia gamma se ha relacionado ampliamente con procesos cognitivos complejos como la consciencia, la selección atencional, la integración de rasgos y la memoria. Estos resultados sugieren que las personas conscientes de la violación de las expectativas emplean estrategias diferentes a aquellas que no fueron conscientes de la violación de las expectativas.

En las medidas cardíacas se encontraron los patrones esperados de desaceleración cardiaca durante la preparación y aceleración tras la presentación del estímulo. Esto quiere decir que el corazón, ante la presentación de un estímulo, late más lento que durante su estado basal, y tras la percepción del estímulo, late más rápido. A su vez, estas deceleraciones y aceleraciones cardiacas se han relacionado con diferentes procesos cognitivos. En nuestro caso, tanto en consciencia de acceso como en consciencia fenomenológica el corazón latía más lentamente cuando se percibía de manera correcta el estímulo. En la literatura, esta deceleración cardíaca se relaciona con procesos preparatorios atencionales óptimos, así como con la posterior detección de un estímulo que se percibe de manera consciente. Esta interpretación cardíaca apunta en la misma dirección que los resultados encontrados en la oscilación cerebral de alfa en momentos previos a la presentación del estímulo. Lo cual parece indicar que tanto las modulaciones a nivel cerebral como a nivel del organismo apuntan al papel que puede tener los procesos preparatorios en la percepción consciente.

En conclusión, los estudios de esta tesis exploran la relación entre los diferentes tipos de atención y la consciencia, y cómo esta relación se manifiesta de manera diferente en la consciencia de acceso y la consciencia fenomenológica. Además, esta interacción se refleja tanto en las señales cerebrales como en las señales del organismo.

12. Summary for the general public

12.1 Perceiving is a complex process

Every day we are surrounded by a large number of stimuli. Studying how we consciously perceive these stimuli is of special relevance in the field of Cognitive Neuroscience. Imagine that you are driving to work, which is located on the outskirts of your city. While driving, you have the impression of perceiving the scene around you in a very detailed way: different driving lanes, merging lanes, cars or motorcycles on one side or the other, different light signals or signs, and so on. However, if you had to report whether or not there is a vehicle behind you, you would direct your attention to the rearview mirror, which would allow you to access that information. In this case, we are talking about access consciousness, since you can report what you consciously perceive. However, if you were to indicate how many or which vehicles are in your field of vision, this task would be almost impossible to complete, and if you did, your perception would be full of errors. In this case, we speak of phenomenological consciousness. This type of consciousness refers to a rich subjective experience of the scene, but one that is often full of inaccuracies.

12.2 Do we need to attend to be conscious?

Since our perceptual capacity is limited (we cannot perceive everything that comes to our senses), we need mechanisms for selecting information. One of these mechanisms is attention, which allows us to select the rearview mirror to check if there is a car behind us. Therefore, studying how attention is related to consciousness is relevant. There are different types of attention: alerting (activation produced by the horn of a car), orienting in space (such as when you see a sign with an arrow pointing to the entrance to a city or when a pedestrian crosses on the right side), and the executive system (which allows you to talk while driving, to plan how to change lanes or to leave space when an ambulance appears). Another relevant aspect in this context is prior experience, which means that whenever we perceive we have certain expectations about what we will find in that situation. If an expectation is not fulfilled, the probability of wrongly perceiving the environment increases. For example, a European driver expects oncoming cars to appear from the left, so if a car appears from the right, violating the expectation, the probability of perceiving it and responding efficiently will decrease.

Different theoretical models that attempt to study consciousness question the role of attention in conscious processing. These models generally focus on what happens at the brain level. However, the brain does not work in isolation, rather it is in constant communication with the state of the organism. Given the questionable of the role of attention in consciousness and the lack of exploration of how this relationship occurs in brain-organism dunamics, the questions and studies of this doctoral thesis arise.

12.3 Behavioral findings of the doctoral thesis

The results of this thesis show that different types of attention interact differently in access consciousness and phenomenological consciousness. Alerting amplifies conscious access to information (as when the sound of a claxon helps you perceive an approaching car), whereas it does not influence phenomenological consciousness (the subjective and more detailed perception of the scene). Orienting oneself in space benefits both access consciousness and phenomenological consciousness (we perceive a pedestrian better if we know that he will appear on the right and there are fewer errors in perception if you have a sign pointing to the entrance of a city). In the case of the executive system, we have not found such clear effects on either access consciousness or phenomenological consciousness (doing a double task, for example, talking on the phone while driving, does not always affect perception -although it is recommended not to do so because it does affect reaction speed!) On the other hand, violating expectations has a clear effect on phenomenological consciousness, since it increases the number of errors when an unexpected stimulus appears. In this sense, we have found that when unexpected information appears observers tend to "fill in" this information with other information from the environment, for example: if you are in a library, you would expect to find books on the tables and shelves. However, if unexpectedly there is a laptop under some books, that laptop is likely to be perceived as a book, since the surrounding stimuli are mainly books.

12.4 Findings on the brain-body dynamic

The study of brain dynamics showed how neurons in the brain communicate through different oscillations when we perceive correctly and incorrectly. These brain oscillations are changes in the rhythm of the brain’s electrical activity, and their changes in frequency, amplitude or phase reflect different cognitive processes. Our results indicate that alpha oscillations increased at times prior to stimulus presentation. This increase in alpha seems to indicate whether attention is in an optimal state of preparation, which may influence subsequent conscious perception. After stimulus presentation, alpha decreased, and this decrease was related to processes of inhibition of distracting or irrelevant information. The beta band, after stimulus presentation, decreases in the same direction as alpha, both frequencies being related to an accurate representation of stimuli. The gamma frequency, on the other hand, was higher in people who were aware of the expectancy violation (when a stimulus changed unexpectedly at the end of the experiment) than in people who were not aware. Gamma frequency has been widely related to complex cognitive processes such as consciousness, attentional selection, feature integration, and memory. These results suggest that people aware of the expectancy violation employ different strategies than those who were not aware of the expectancy violation.

For cardiac measures, the expected patterns of cardiac deceleration during preparation and acceleration after stimulus presentation were found. This means that the heart, on stimulus presentation, beats slower on stimulus presentation than basal state, and it beats faster after stimulus perception. In turn, these cardiac decelerations and accelerations have been related to different cognitive processes. In our case, in both access consciousness and phenomenological consciousness, the heart beat slower when the stimulus was correctly perceived. In the literature, this cardiac deceleration is related to optimal attentional preparatory processes, as well as to the subsequent detection of a stimulus that is consciously perceived. This cardiac interpretation points in the same direction as the results found for alpha brain oscillations at times prior to stimulus presentation. This seems to indicate that both brain and body level modulations point to the role that preparatory processes may play in conscious perception.

In conclusion, the studies in this thesis explore the relationship between different types of attention and consciousness, and how this relationship manifests itself differently in access consciousness and phenomenological consciousness. Interstingly, this interaction is reflected in both brain signals and body signals.

Abreviations

Abreviations

AI: Anterior Insula
AIC: Anterior Insular Cortex
ACC: Anterior Cingulate Cortex
ANS: Autonomic Nervous System
BF: Bayes Factor
CNS: Central Nervous System
EEG: electroencephalography
EKG: Electrocardiogram
FA: False Alarm
FCA: Feature Confirmation Account
FIT: Feature Integration Theory
fMRI: functional magnetic resonance imaging
GWT: Global Workspace Theory
GNWT: Global Neural Workspace Theory
HEP: Heart-Evoked Potential
HR: Heart Rate
HRV: Heart Rate Variability
IIT: Integrated Information Theory
MEG: magnetoencephalography
NTS: Nucleus of the Solitary Tract
OSF: Orbitofrontal Cortex
PCI: Perturbative complexity index
PFC: Prefrontal Cortex
PI: Posterior Insula
PNS: Peripheral Nervous System

pMFC: Posterior Medial Frontal Cortex

PVT: Psychomotor Vigilance Task

RT: Reaction Time

SAM: Synaptic Attractor Model

SC: Skin Conductance

SDT: Signal Detection Theory

SMA: Supplementary Motor Area

SNS: Somatic Nervous System

TBR: Theta-to-Beta ratio

TF: Time - Frequency

References

References

Abdi, H. (2007). *Signal Detection Theory (SDT)*.

Akyürek, E. G., Hommel, B., & Jolicoeur, P. (2007). Direct evidence for a role of working memory in the attentional blink. *Memory & Cognition*, *35*(4), 621-627. https://doi.org/10.3758/BF03193300

Alekseichuk, I., Turi, Z., de Lara, G. A., Antal, A., & Paulus, W. (2016). Spatial Working Memory in Humans Depends on Theta and High Gamma Synchronization in the Prefrontal Cortex. *Current Biology*, *26*, 1-9. https://www.researchgate.net/profile/Andrea-Antal/publication/303633709_Spatial_Working_Memory_in_Humans_Depends_on_Theta_and_High_Gamma_Synchronization_in_the_Prefrontal_Cortex/links/5a7d5636458515dea40f9028/Spatial-Working-Memory-in-Humans-Depends-on-Theta-and-High-Gamma-Synchronization-in-the-Prefrontal-Cortex.pdf

Andreassi, J. L. (1980). Human behavior and physiological response. *Psychophysiology*. https://cir.nii.ac.jp/crid/1574231875408847104

Angelidis, A., Hagenaars, M., van Son, D., van der Does, W., & Putman, P. (2018). Do not look away! Spontaneous frontal EEG theta/beta ratio as a marker for cognitive control over attention to mild and high threat. *Biological Psychology*, *135*, 8-17. https://doi.org/10.1016/j.biopsycho.2018.03.002

Angelidis, A., van der Does, W., Schakel, L., & Putman, P. (2016). Frontal EEG theta/beta ratio as an electrophysiological marker for attentional control and its test-retest reliability. *Biological Psychology*, *121*, 49-52. https://doi.org/10.1016/j.biopsycho.2016.09.008

Antzoulatos, E. G., & Miller, E. K. (2016). Synchronous beta rhythms of frontoparietal networks support only behaviorally relevant representations. *eLife*, *5*, e17822. https://doi.org/10.7554/eLife.17822

Arend, I., Naparstek, S., & Henik, A. (2013). Numerical-spatial representation affects spatial coding: Binding errors across the numerical distance effect. *Psychonomic Bulletin & Review*, *20*(6), 1181-1186. https://doi.org/10.3758/s13423-013-0428-x

Armour, J. A., & Ardell, J. L. (2004). *Basic and Clinical Neurocardiology*. Oxford University Press.

Arns, M., Conners, C. K., & Kraemer, H. C. (2013). A Decade of EEG Theta/Beta Ratio Research in ADHD: A Meta-Analysis. *Journal of Attention Disorders*, *17*(5), 374-383. https://doi.org/10.1177/1087054712460087

Aru, J., & Bachmann, T. (2017). Expectation creates something out of nothing: The role of attention in iconic memory reconsidered. *Consciousness and Cognition*, *53*, 203-210. https://doi.org/10.1016/j.concog.2017.06.017

Aru, J., Tulver, K., & Bachmann, T. (2018). It's all in your head: Expectations create illusory perception in a dual-task setup. *Consciousness and Cognition*, *65*, 197-208. https://doi.org/10.1016/j.concog.2018.09.001

Awh, E., Barton, B., & Vogel, E. K. (2007). *Visual Working Memory Represents a Fixed Number of Items Regardless of Complexity*.

18(7), 7.

Azzalini, D., Rebollo, I., & Tallon-Baudry, C. (2019). Visceral Signals Shape Brain Dynamics and Cognition. *Trends in Cognitive Sciences*, *23*(6), 488-509. https://doi.org/10.1016/j.tics.2019.03.007

Baars, B. J. (1997). *In the Theater of Consciousness: The Workspace of the Mind*. https://doi.org/10.1093/acprof:oso/9780195102659.001.1

Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, *6*(1), 47-52. https://doi.org/10.1016/S1364-6613(00)01819-2

Babo-Rebelo, M., Richter, C. G., & Tallon-Baudry, C. (2016). Neural Responses to Heartbeats in the Default Network Encode the Self in Spontaneous Thoughts. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *36*(30), 7829-7840.

Babo-Rebelo, M., Wolpert, N., Adam, C., Hasboun, D., & Tallon-Baudry, C. (2016). Is the cardiac monitoring function related to the self in both the default network and right anterior insula? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160004. https://doi.org/10.1098/rstb.2016.0004

Backs, R. W., & Seljos, K. A. (1994). Metabolic and cardiorespiratory measures of mental effort: The effects of level of difficulty in a working memory task. *International journal of psychophysiology*, *16*(1), 57-68.

Baddeley, A. (2020). Working memory. En *Memory* (3.ª ed.).

Routledge.

Baddeley, A. D., & Hitch, G. J. (1994). Developments in the concept of working memory. *Neuropsychology*, *8*(4), 485.

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., Hämäläinen, M. S., Marinkovic, K., Schacter, D. L., Rosen, B. R., & Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences*, *103*(2), 449-454. https://doi.org/10.1073/pnas.0507062103

Barry, R. J., & Tremayne, P. (1987). Separation of components in the evoked cardiac response under processing load. *Journal of Psychophysiology*, *1*, 259-264.

Bartolomeo, P. (2008). *Varieties of attention and of consciousness: Evidence from neuropsychology*.

Bartolomeo, P., Thiebaut De Schotten, M., & Doricchi, F. (2007). Left Unilateral Neglect as a Disconnection Syndrome. *Cerebral Cortex*, *17*(11), 2479-2490. https://doi.org/10.1093/cercor/bhl181

Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *International Journal of Psychophysiology*, *39*(2-3), 241-248. https://doi.org/10.1016/S0167-8760(00)00145-8

Başar-Eroglu, C., Başar, E., Demiralp, T., & Schürmann, M. (1992). P300-response: Possible psychophysiological correlates in delta and theta frequency channels. A review. *International Journal of Psychophysiology*, *13*(2), 161-179. https://doi.org/10.1016/0167-8760(92)90055-g

Bastos, A. M., Loonis, R., Kornblith, S., Lundqvist, M., & Miller, E. K. (2018). Laminar recordings in frontal cortex suggest distinct layers for maintenance and control of working memory. *Proceedings of the National Academy of Sciences*, *115*(5), 1117-1122. https://doi.org/10.1073/pnas.1710323115

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2014). *Visual areas exert feedforward and feedback influences through distinct frequency channels* [Preprint]. Neuroscience. https://doi.org/10.1101/004804

Bauer, F., Cheadle, S. W., Parton, A., Müller, H. J., & Usher, M. (2009). Gamma flicker triggers attentional selection without awareness. *Proceedings of the National Academy of Sciences*, *106*(5), 1666-1671. https://doi.org/10.1073/pnas.0810496106

Bauer, M., Stenner, M.-P., Friston, K. J., & Dolan, R. J. (2014). Attentional Modulation of Alpha/Beta and Gamma Oscillations Reflect Functionally Distinct Processes. *Journal of Neuroscience*, *34*(48), 16117-16125. https://doi.org/10.1523/JNEUROSCI.3474-13.2014

Baumgartner, F., Hanke, M., Geringswald, F., Zinke, W., Speck, O., & Pollmann, S. (2013). Evidence for feature binding in the superior parietal lobule. *NeuroImage*, *68*, 173-180. https://doi.org/10.1016/j.neuroimage.2012.12.002

Bayne, T., Hohwy, J., & Owen, A. M. (2016). Are There Levels of Consciousness? *Trends in Cognitive Sciences*, *20*(6), 405-413. https://doi.org/10.1016/j.tics.2016.03.009

Beissner, F., Meissner, K., Bär, K.-J., & Napadow, V. (2013). The autonomic brain: An activation likelihood estimation meta-analysis for central processing of autonomic function. *The*

Journal of neuroscience: the official journal of the Society for Neuroscience, *33*(25), 10503-10511.

Bengson, J. J., Mangun, G. R., & Mazaheri, A. (2012). The neural markers of an imminent failure of response inhibition. *NeuroImage*, *59*(2), 1534-1539. https://doi.org/10.1016/j.neuroimage.2011.08.034

Benwell, C. S. Y., Coldea, A., Harvey, M., & Thut, G. (2022). Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity. *European Journal of Neuroscience*, *55*(11-12), 3125-3140. https://doi.org/10.1111/ejn.15166

Berger, H. (1929). Über das elektroenkephalogramm des menschen. *Archiv für psychiatrie und nervenkrankheiten*, *87*(1), 527-570.

Bernstein, L. J., & Robertson, L. C. (1998). Illusory Conjunctions of Color and Motion with Shape Following Bilateral Parietal Lesions. *Psychological Science*, *9*(3), 167-175. https://www.jstor.org/stable/40063274

Bertrand, O., & Tallon-baudry, C. (2000). *Oscillatory gamma activity in humans: A possible role for object representation*.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, *13*(8), Article 8. https://doi.org/10.1038/nrn3292

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioral and Brain Sciences*, *30*(5-6), 481-499. https://doi.org/10.1017/S0140525X07002786

Block, N. (2011). Perceptual consciousness overflows cognitive access. *Trends in Cognitive Sciences*, *15*(12), 567-575.

https://doi.org/10.1016/j.tics.2011.11.001

Block, N. (2019). What Is Wrong with the No-Report Paradigm and How to Fix It. *Trends in Cognitive Sciences*, *23*(12), 1003-1013. https://doi.org/10.1016/j.tics.2019.10.001

Boehler, C. N., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences*, *105*(25), 8742-8747. https://doi.org/10.1073/pnas.0801999105

Boly, M., Massimini, M., & Tononi, G. (2009). Theoretical approaches to the diagnosis of altered states of consciousness. En *Progress in Brain Research* (Vol. 177, pp. 383-398). Elsevier. https://doi.org/10.1016/S0079-6123(09)17727-0

Boly, M., Massimini, M., Tsuchiya, N., Postle, B. R., Koch, C., & Tononi, G. (2017). Are the Neural Correlates of Consciousness in the Front or in the Back of the Cerebral Cortex? Clinical and Neuroimaging Evidence. *The Journal of Neuroscience*, *37*(40), 9603-9613. https://doi.org/10.1523/JNEUROSCI.3218-16.2017

Bor, D., & Seth, A. K. (2012). Consciousness and the prefrontal parietal network: Insights from attention, working memory, and chunking. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00063

Börger, N., & van der Meere, J. (2000). Motor control and state regulation in children with ADHD: A cardiac response study. *Biological Psychology*, *51*(2), 247-267. https://doi.org/10.1016/S0301-0511(99)00040-X

Botta, F., Lupiáñez, J., & Chica, A. B. (2014). When endogenous spatial attention improves conscious perception: Effects of alerting and bottom-up activation. *Consciousness and Cognition*, *23*, 63-73. https://doi.org/10.1016/j.concog.2013.12.003

Botta, F., Ródenas, E., & Chica, A. B. (2017). Target bottom-up strength determines the extent of attentional modulations on conscious perception. *Experimental Brain Research*, *235*(7), 2109-2124. https://doi.org/10.1007/s00221-017-4954-z

Braet, W., & Humphreys, G. W. (2009). The role of reentrant processes in feature binding: Evidence from neuropsychology and TMS on late onset illusory conjunctions. *Visual Cognition*, *17*(1-2), 25-47. https://doi.org/10.1080/13506280802193318

Breakspear, M., Heitmann, S., & Daffertshofer, A. (2010). Generative models of cortical oscillations: Neurobiological implications of the Kuramoto model. *Frontiers in human neuroscience*, *4*, 190. https://www.frontiersin.org/articles/10.3389/fnhum.2010.00190/full

Breitmeyer, B., & Ogmen, H. (2006). *Visual Masking: Time slices through conscious and unconscious vision*. OUP Oxford.

Briand, K. A. (1998). Feature integration and spatial attention: More evidence of a dissociation between endogenous and exogenous orienting. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(4), 1243-1256. https://doi.org/10.1037/0096-1523.24.4.1243

Briand, K. A., & Klein, R. M. (1987a). Is Posner’s «beam» the same as Treisman’s «glue»?: On the relation between visual orienting and feature integration theory. *Journal of Experimental Psychology: Human Perception and Performance*, *13*(2), 228-241. https://doi.org/10.1037/0096-1523.13.2.228

Briand, K. A., & Klein, R. M. (1987b). Is Posner's «beam» the same as Treisman's «glue»?: On the relation between visual orienting and feature integration theory. *Journal of Experimental Psychology. Human Perception and Performance*, *13*(2), 228-241. https://doi.org/10.1037//0096-1523.13.2.228

Broadbent, D. E. (1958). *Perception and communication*.

Burgess, A. P., & Ali, L. (2002). Functional connectivity of gamma EEG activity is modulated at low frequency during conscious recollection. *International Journal of Psychophysiology*, *46*(2), 91-100. https://doi.org/10.1016/S0167-8760(02)00108-3

Burgess, P., & Simons, J. (2005). Theories of frontal lobe executive function: Clinical applications. *Effectiveness of Rehabilitation for Cognitive Deficits*, 211-231. https://doi.org/10.1093/acprof:oso/9780198526544.003.0018

Busch, N. A., Dubois, J., & VanRullen, R. (2009). The Phase of Ongoing EEG Oscillations Predicts Visual Perception. *Journal of Neuroscience*, *29*(24), 7869-7876. https://doi.org/10.1523/JNEUROSCI.0113-09.2009

Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences*, *107*(37), 16048-16053. https://doi.org/10.1073/pnas.1004801107

Buschman, T. J., Denovellis, E. L., Diogo, C., Bullock, D., & Miller, E. K. (2012). Synchronous Oscillatory Neural Ensembles for Rules in the Prefrontal Cortex. *Neuron*, *76*(4), 838-846. https://doi.org/10.1016/j.neuron.2012.09.029

Buschman, T. J., & Miller, E. K. (2007a). Top-Down Versus

Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science*, *315*(5820), 1860-1862. https://doi.org/10.1126/science.1138071

Buschman, T. J., & Miller, E. K. (2007b). Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. *Science*, *315*(5820), 1860-1862. https://doi.org/10.1126/science.1138071

Buschman, T. J., Siegel, M., Roy, J. E., & Miller, E. K. (2011). Neural substrates of cognitive capacity limitations. *Proceedings of the National Academy of Sciences*, *108*(27), 11252-11255. https://doi.org/10.1073/pnas.1104666108

Buzsáki, G. (2006). *Rhythms of the Brain*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195301069.001.0001

Buzsáki, G., & Draguhn, A. (2004). Neuronal Oscillations in Cortical Networks. *Science*, *304*(5679), 1926-1929. https://doi.org/10.1126/science.1099745

Buzsáki, G., & Watson, B. O. (2012). Brain rhythms and neural syntax: Implications for efficient coding of cognitive content and neuropsychiatric disease. *Dialogues in Clinical Neuroscience*, *14*(4), 345-367. https://doi.org/10.31887/DCNS.2012.14.4/gbuzsaki

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research*, *42*(8), 949-967. https://cir.nii.ac.jp/crid/1360292619016017536

Canales-Johnson, A., Silva, C., Huepe, D., Rivera-Rei, Á., Noreika, V., Garcia, M. del C., Silva, W., Ciraolo, C., Vaucheret, E., & Sedeño, L.

(2015). Auditory feedback differentially modulates behavioral and neural markers of objective and subjective performance when tapping to your heartbeat. *Cerebral Cortex*, *25*(11), 4490-4503.

Candia-Rivera, D. (2022). Brain-heart interactions in the neurobiology of consciousness. *Current Research in Neurobiology*, *3*, 100050. https://doi.org/10.1016/j.crneur.2022.100050

Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2006). High Gamma Power Is Phase-Locked to Theta Oscillations in Human Neocortex. *Science*, *313*(5793), 1626-1628. https://doi.org/10.1126/science.1128115

Capilla, A., Schoffelen, J.-M., Paterson, G., Thut, G., & Gross, J. (2014). Dissociated α-Band Modulations in the Dorsal and Ventral Visual Pathways in Visuospatial Attention and Perception. *Cerebral Cortex (New York, NY)*, *24*(2), 550-561. https://doi.org/10.1093/cercor/bhs343

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484-1525. https://doi.org/10.1016/j.visres.2011.04.012

Carrasco, M., & Barbot, A. (2014). How Attention Affects Spatial Resolution. *Cold Spring Harbor Symposia on Quantitative Biology*, *79*, 149-160. https://doi.org/10.1101/sqb.2014.79.024687

Carrasco, M., & Barbot, A. (2019). Spatial attention alters visual appearance. *Current Opinion in Psychology*, *29*, 56-64. https://doi.org/10.1016/j.copsyc.2018.10.010

Carrasco, M., Fuller, S., & Ling, S. (2008). Transient attention does increase perceived contrast of suprathreshold stimuli: A reply to Prinzmetal, Long, and Leonhardt (2008). *Perception & Psychophysics*, *70*(7), 1151-1164. https://doi.org/10.3758/PP.70.7.1151

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*(3), 308-313. https://doi.org/10.1038/nn1194

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research*, *40*(10-12), 1203-1215. https://cir.nii.ac.jp/crid/1360292620569348224

Carrasco, M., & Yeshurun, Y. (2009). Covert attention effects on spatial resolution. *Progress in Brain Research*, 65-86. https://cir.nii.ac.jp/crid/1362825895558569728

Cavanagh, J., Cohen, M., & Allen, J. (2009). Prelude to and Resolution of an Error: EEG Phase Synchrony Reveals Cognitive Control Dynamics during Action Monitoring. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *29*, 98-105. https://doi.org/10.1523/JNEUROSCI.4137-08.2009

Chang, Y.-C., & Huang, S.-L. (2012). The influence of attention levels on psychophysiological responses. *International journal of psychophysiology: official journal of the International Organization of Psychophysiology*, *86*(1), 39-47.

Chechlacz, M. (2018). Bilateral parietal dysfunctions and disconnections in simultanagnosia and Bálint syndrome. *Handbook of Clinical Neurology*, *151*, 249-267.

https://doi.org/10.1016/B978-0-444-63622-5.00012-7

Chen, N., & Watanabe, K. (2021). Color–shape associations affect feature binding. *Psychonomic Bulletin & Review*, *28*(1), 169-177. https://doi.org/10.3758/s13423-020-01799-4

Chennu, S., Noreika, V., Gueorguiev, D., Blenkmann, A., Kochen, S., Ibanez, A., Owen, A. M., & Bekinschtein, T. A. (2013). Expectation and Attention in Hierarchical Auditory Prediction. *Journal of Neuroscience*, *33*(27), 11194-11205. https://doi.org/10.1523/JNEUROSCI.0114-13.2013

Chica, A. B., & Bartolomeo, P. (2012). Attentional Routes to Conscious Perception. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00001

Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research*, *237*, 107-123. https://doi.org/10.1016/j.bbr.2012.09.027

Chica, A. B., Bartolomeo, P., & Valero-Cabré, A. (2011). Dorsal and Ventral Parietal Contributions to Spatial Orienting in the Human Brain. *Journal of Neuroscience*, *31*(22), 8143-8149. https://doi.org/10.1523/JNEUROSCI.5463-10.2010

Chica, A. B., Bayle, D. J., Botta, F., Bartolomeo, P., & Paz-Alonso, P. M. (2016a). Interactions between phasic alerting and consciousness in the fronto-striatal network. *Scientific Reports*, *6*(1), Article 1. https://doi.org/10.1038/srep31868

Chica, A. B., Bayle, D. J., Botta, F., Bartolomeo, P., & Paz-Alonso, P. M. (2016b). Interactions between phasic alerting and consciousness in the fronto-striatal network. *Scientific Reports*, *6*(1), 31868. https://doi.org/10.1038/srep31868

Chica, A. B., Bayle, D. J., Botta, F., Bartolomeo, P., & Paz-Alonso, P. M. (2016c). Interactions between phasic alerting and consciousness in the fronto-striatal network. *Scientific Reports*, *6*(1), 31868. https://doi.org/10.1038/srep31868

Chica, A. B., Botta, F., Lupiáñez, J., & Bartolomeo, P. (2012). Spatial attention and conscious perception: Interactions and dissociations between and within endogenous and exogenous processes. *Neuropsychologia*, *50*(5), 621-629. https://doi.org/10.1016/j.neuropsychologia.2011.12.020

Chica, A. B., Lasaponara, S., Chanes, L., Valero-Cabré, A., Doricchi, F., Lupiáñez, J., & Bartolomeo, P. (2011). Spatial attention and conscious perception: The role of endogenous and exogenous orienting. *Attention, Perception, & Psychophysics*, *73*(4), 1065-1081. https://doi.org/10.3758/s13414-010-0082-6

Chica, A. B., Lasaponara, S., Lupiáñez, J., Doricchi, F., & Bartolomeo, P. (2010). Exogenous attention can capture perceptual consciousness: ERP and behavioural evidence. *NeuroImage*, *51*(3), 1205-1212. https://doi.org/10.1016/j.neuroimage.2010.03.002

Chica, A. B., Martín-Arévalo, E., Botta, F., & Lupiáñez, J. (2014). The Spatial Orienting paradigm: How to design and interpret spatial attention experiments. *Neuroscience & Biobehavioral Reviews*, *40*, 35-51. https://doi.org/10.1016/j.neubiorev.2014.01.002

Chica, A. B., Paz-Alonso, P. M., Valero-Cabre, A., & Bartolomeo, P. (2013). Neural Bases of the Interactions between Spatial Attention and Conscious Perception. *Cerebral Cortex*, *23*(6), 1269-1279. https://doi.org/10.1093/cercor/bhs087

Chica, A. B., Thiebaut de Schotten, M., Bartolomeo, P., & Paz-Alonso, P. M. (2018). White matter microstructure of attentional networks predicts attention and consciousness functional interactions. *Brain Structure and Function*, *223*(2), 653-668. https://doi.org/10.1007/s00429-017-1511-2

Chica, A. B., Thiebaut De Schotten, M., Toba, M., Malhotra, P., Lupiáñez, J., & Bartolomeo, P. (2012). Attention networks and their interactions after right-hemisphere damage. *Cortex*, *48*(6), 654-663. https://doi.org/10.1016/j.cortex.2011.01.009

Chica, A. B., Valero-Cabre, A., Paz-Alonso, P. M., & Bartolomeo, P. (2014). Causal Contributions of the Left Frontal Eye Field to Conscious Perception. *Cerebral Cortex*, *24*(3), 745-753. https://doi.org/10.1093/cercor/bhs357

Cleeremans, A. (2007). Consciousness: The radical plasticity thesis. En *Progress in Brain Research* (Vol. 168, pp. 19-33). Elsevier. https://doi.org/10.1016/S0079-6123(07)68003-0

Cleeremans, A., Achoui, D., Beauny, A., Keuninckx, L., Martin, J.-R., Muñoz-Moldes, S., Vuillaume, L., & De Heering, A. (2020). Learning to Be Conscious. *Trends in Cognitive Sciences*, *24*(2), 112-123. https://doi.org/10.1016/j.tics.2019.11.011

Cobos, M. I., & Chica, A. B. (2022). Attention does not always help: The role of expectancy, divided, and spatial attention on illusory conjunctions. *Quarterly Journal of Experimental Psychology*, 174702182210896. https://doi.org/10.1177/17470218221089625

Cobos, M. I., Guerra, P. M., Vila, J., & Chica, A. B. (2019a). Heart-rate modulations reveal attention and consciousness interactions. *Psychophysiology*, *56*(3), e13295. https://doi.org/10.1111/psyp.13295

Cobos, M. I., Guerra, P. M., Vila, J., & Chica, A. B. (2019b). Heart-rate modulations reveal attention and consciousness interactions: COBOS ET AL. *Psychophysiology*, *56*(3), e13295. https://doi.org/10.1111/psyp.13295

Cobos, M. I., Melcón, M., Esteban, P. R.-S., Capilla, A., & Chica, A. B. (2023). The role of brain oscillations in feature integration. *Psychophysiology*, e14467. https:// doi.org/10.1111/psyp.14467

Cobos, M. I., Melcón, M., Rodríguez San-Esteban, P., Capilla, A., & Chica, A. B. (accepted). *The role of brain oscillations in feature integration* [Preprint]. Preprints. https://doi.org/10.22541/au.167407914.47930383/v1

Cohen, A., & Ivry, R. (1989). Illusory conjunctions inside and outside the focus of attention. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(4), 650-663. https://doi.org/10.1037/0096-1523.15.4.650

Cohen, A., & Rafal, R. D. (1991). Attention and Feature Integration: Illusory Conjunctions in a Patient with a Parietal Lobe Lesion. *Psychological Science*, *2*(2), 106-110. https://doi.org/10.1111/j.1467-9280.1991.tb00109.x

Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*(1), 155-159. https://doi.org/10.1037/0033-2909.112.1.155

Cohen, M. A., & Dennett, D. C. (2011). Consciousness cannot be separated from function. *Trends in Cognitive Sciences*, *15*(8), 358-364. https://doi.org/10.1016/j.tics.2011.06.008

Cohen, M. A., Ortego, K., Kyroudis, A., & Pitts, M. (2020). Distinguishing the Neural Correlates of Perceptual Awareness and Postperceptual Processing. *The Journal of Neuroscience*, *40*(25), 4925-4935. https://doi.org/10.1523/JNEUROSCI.0120-20.2020

Cohen, M. X. (2011). Error-related medial frontal theta activity predicts cingulate-related structural connectivity. *NeuroImage*, *55*(3), 1373-1383. https://doi.org/10.1016/j.neuroimage.2010.12.072

Cohen, M. X. (2015). Cycles in mind: How brain rhythms control perception and action. *Sinc (x) press, E-Book Ausgabe*.

Cohen, M. X. (2017). Where Does EEG Come From and What Does It Mean? *Trends in Neurosciences*, *40*(4), 208-218. https://doi.org/10.1016/j.tins.2017.02.004

Cohen-Dallal, H., Soroker, N., & Pertzov, Y. (2021). Working Memory in Unilateral Spatial Neglect: Evidence for Impaired Binding of Object Identity and Object Location. *Journal of Cognitive Neuroscience*, *33*(1), 46-62. https://doi.org/10.1162/jocn_a_01631

Colás, I., Capilla, A., & Chica, A. B. (2018). Neural modulations of interference control over conscious perception. *Neuropsychologia*, *112*, 40-49. https://doi.org/10.1016/j.neuropsychologia.2018.02.027

Colás, I., Chica, A. B., Ródenas, E., Busquier, H., Olivares, G., & Triviño, M. (2019). Conscious perception in patients with prefrontal damage. *Neuropsychologia*, *129*, 284-293. https://doi.org/10.1016/j.neuropsychologia.2019.03.002

Colás, I., Triviño, M., & Chica, A. B. (2017). Interference Control Modulations Over Conscious Perception. *Frontiers in Psychology*, *8*, 712. https://doi.org/10.3389/fpsyg.2017.00712

Colzato, L. S., Spapé, M. M. A., Pannebakker, M. M., & Hommel, B. (2007). Working memory and the attentional blink: Blink size is predicted by individual differences in operation span. *Psychonomic Bulletin & Review*, *14*(6), 1051-1057. https://doi.org/10.3758/BF03193090

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The Reorienting System of the Human Brain: From Environment to Theory of Mind. *Neuron*, *58*(3), 306-324. https://doi.org/10.1016/j.neuron.2008.04.017

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201-215. https://doi.org/10.1038/nrn755

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology*, *1*(1), 42-45. https://doi.org/10.20982/tqmp.01.1.p042

Cowan, N. (2010). The Magical Mystery Four: How Is Working Memory Capacity Limited, and Why? *Current Directions in Psychological Science*, *19*(1), 51-57. https://doi.org/10.1177/0963721409359277

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655-666. https://doi.org/10.1038/nrn894

Craig, A. D. (2003). Interoception: The sense of the physiological condition of the body. *Current opinion in neurobiology*, *13*(4), 500-505.

Craig, A. D. (2009). How do you feel — now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*(1), 59-70. https://doi.org/10.1038/nrn2555

Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, *2*, 263-275. https://resolver.caltech.edu/CaltechAUTHORS:20130816-103136937

Critchley, H. D., & Harrison, N. A. (2013). Visceral Influences on Brain and Behavior. *Neuron*, *77*(4), 624-638. https://doi.org/10.1016/j.neuron.2013.02.008

Critchley, H. D., Mathias, C. J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B., Cipolotti, L., Shallice, T., & Dolan, R. J. (2003). Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. *Brain*, *126*(10), 2139-2152. https://doi.org/10.1093/brain/awg216

Critchley, H. D., Rotshtein, P., Nagai, Y., O'Doherty, J., Mathias, C. J., & Dolan, R. J. (2005). Activity in the human brain predicting differential heart rate responses to emotional facial expressions. *NeuroImage*, *24*(3), 751-762. https://doi.org/10.1016/j.neuroimage.2004.10.013

Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*(2), 189-195. https://doi.org/10.1038/nn1176

Crone, E. A., Bunge, S. A., de Klerk, P., & van der Molen, M. W. (2005).

Cardiac concomitants of performance monitoring: Context dependence and individual differences. *Cognitive Brain Research*, *23*(1), 93-106. https://doi.org/10.1016/j.cogbrainres.2005.01.009

Crone, E. A., Van Der Veen, F. M., Van Der Molen, M. W., Somsen, R. J. M., Van Beek, B., & Jennings, J. R. (2003). Cardiac concomitants of feedback processing. *Biological Psychology*, *64*(1-2), 143-156. https://doi.org/10.1016/S0301-0511(03)00106-6

Crone, N. E., Sinai, A., & Korzeniewska, A. (2006). High-frequency gamma oscillations and human brain mapping with electrocorticography. En *Progress in Brain Research* (Vol. 159, pp. 275-295). Elsevier. https://doi.org/10.1016/S0079-6123(06)59019-3

Damasio, A. (2010). Self Comes to Mind: Constructing the Conscious. *brain*.

Damasio, A., & Carvalho, G. B. (2013). The nature of feelings: Evolutionary and neurobiological origins. *Nature Reviews Neuroscience*, *14*(2), Article 2. https://doi.org/10.1038/nrn3403

Danev, S. G., & de Winter, C. R. (1971a). Heart rate deceleration after erroneous responses. *Psychologische Forschung*, *35*(1), 27-34. https://doi.org/10.1007/BF00424472

Danev, S. G., & de Winter, C. R. (1971b). Heart rate deceleration after erroneous responses. A phenomenon complicating the use of heart rate variability for assessing mental load. *Psychologische Forschung*, *35*(1), 27-34. https://doi.org/10.1007/bf00424472

Danielmeier, C., Eichele, T., Forstmann, B. U., Tittgemeyer, M., & Ullsperger, M. (2011). Posterior Medial Frontal Cortex Activity

Predicts Post-Error Adaptations in Task-Related Visual and Motor Areas. *The Journal of Neuroscience*, *31*(5), 1780-1789. https://doi.org/10.1523/JNEUROSCI.4299-10.2011

de Gardelle, V., Sackur, J., & Kouider, S. (2009). Perceptual illusions in brief visual presentations. *Consciousness and Cognition*, *18*(3), 569-577. https://doi.org/10.1016/j.concog.2009.03.002

De Loof, E., Verguts, T., Fias, W., & Van Opstal, F. (2013). Opposite effects of working memory on subjective visibility and priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *39*(6), 1959-1965. https://doi.org/10.1037/a0033093

de Munck, J. C., Gonçalves, S. I., Faes, Th. J. C., Kuijer, J. P. A., Pouwels, P. J. W., Heethaar, R. M., & Lopes da Silva, F. H. (2008). A study of the brain's resting state based on alpha band power, heart rate and fMRI. *NeuroImage*, *42*(1), 112-121. https://doi.org/10.1016/j.neuroimage.2008.04.244

De Pascalis, V., Barry, R. J., & Sparita, A. (1995a). Decelerative changes in heart rate during recognition of visual stimuli: Effects of psychological stress. *International Journal of Psychophysiology*, *20*(1), 21-31. https://doi.org/10.1016/0167-8760(95)00023-L

De Pascalis, V., Barry, R. J., & Sparita, A. (1995b). Decelerative changes in heart rate during recognition of visual stimuli: Effects of psychological stress. *International Journal of Psychophysiology*, *20*(1), 21-31. https://doi.org/10.1016/0167-8760(95)00023-L

Dehaene, S., Bossini, S., & Giraux, P. (1993). The Mental Representation of Parity and Number Magnitude. *Journal of Experimental Psychology: General*, *122*(3), 371-396.

insights.ovid.com

Dehaene, S., & Changeux, J.-P. (2011a). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200-227.

Dehaene, S., & Changeux, J.-P. (2011b). Experimental and Theoretical Approaches to Conscious Processing. *Neuron*, *70*(2), 200-227. https://doi.org/10.1016/j.neuron.2011.03.018

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204-211. https://doi.org/10.1016/j.tics.2006.03.007

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*(1), 1-37. https://doi.org/10.1016/S0010-0277(00)00123-2

Dehaene, S., Sergent, C., & Changeux, J.-P. (2003). A neuronal network model linking subjective reports and objective physiological data during conscious perception. *Proceedings of the National Academy of Sciences*, *100*(14), 8520-8525. https://doi.org/10.1073/pnas.1332574100

Dehais, F., Causse, M., & Tremblay, S. (2011). Mitigation of Conflicts with Automation: Use of Cognitive Countermeasures. *Human Factors*, *53*(5), 448-460. https://doi.org/10.1177/0018720811418635

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain Dynamics Underlying the Nonlinear Threshold for Access to Consciousness. *PLoS biology*, *5*, e260. https://doi.org/10.1371/journal.pbio.0050260

Delacour, J. (1995). An introduction to the biology of consciousness. *Neuropsychologia*, *33*(9), 1061-1074. https://doi.org/10.1016/0028-3932(95)00048-8

Della Sala, S., Baddeley, A., Papagno, C., & Spinnler, H. (1995). Dual-task paradigm: A means to examine the central executive. En *Structure and functions of the human prefrontal cortex* (pp. 161-171). New York Academy of Sciences.

Dennett, D. (2001). *Are we explaining consciousness yet?*

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, *18*(1), 193-222.

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology*, *64*(1), 135-168. https://doi.org/10.1146/annurev-psych-113011-143750

Donner, T., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A., & Brandt, S. A. (2000). Involvement of the human frontal eye ®eld and multiple parietal areas in covert visual selection during conjunction search. *European Journal of Neuroscience*, 8.

Drummond, S. P., Bischoff-Grethe, A., Dinges, D. F., Ayalon, L., Mednick, S. C., & Meloy, M. J. (2005). The neural basis of the psychomotor vigilance task. *Sleep*, *28*(9), 1059-1068.

Dubey, A., Markowitz, D. A., & Pesaran, B. (2023). Top-down control of exogenous attentional selection is mediated by beta coherence in prefrontal cortex. *Neuron*, S0896627323005068. https://doi.org/10.1016/j.neuron.2023.06.025

Duschek, S., Muckenthaler, M., Werner, N., & del Paso, G. A. R. (2009). Relationships between features of autonomic cardiovascular control and cognitive performance. *Biological* *psychology*, *81*(2), 110-117.

Duschek, S., Werner, N. S., & Reyes Del Paso, G. A. (2013). The behavioral impact of baroreflex function: A review. *Psychophysiology*, *50*(12), 1183-1193.

Duschek, S., Wörsching, J., & Reyes del Paso, G. A. (2015). Autonomic cardiovascular regulation and cortical tone. *Clinical physiology and functional imaging*, *35*(5), 383-392.

Dux, P. E., & Marois, R. (2009). The attentional blink: A review of data and theory. *Attention, Perception & Psychophysics*, *71*(8), 1683-1700. https://doi.org/10.3758/APP.71.8.1683

Egner, T., & Hirsch, J. (2005). The neural correlates and functional integration of cognitive control in a Stroop task. *NeuroImage*, *24*(2), 539-547. https://doi.org/10.1016/j.neuroimage.2004.09.007

Elbert, T., & Rau, H. (1995a). *What goes up (from heart to brain) must calm down (from brain to heart)!: Studies on the interaction between baroreceptor activity and cortical excitability*.

Elbert, T., & Rau, H. (1995b). *What goes up (from heart to brain) must calm down (from brain to heart)!: Studies on the interaction between baroreceptor activity and cortical excitability*.

Eldar, E., Cohen, J. D., & Niv, Y. (2013). The effects of neural gain on attention and learning. *Nature Neuroscience*.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156-165. https://doi.org/10.1016/j.conb.2010.02.015

Engel, A. K., Fries, P., & Singer, W. (2001a). Dynamic predictions: Oscillations and synchrony in top–down processing. *Nature*

Reviews Neuroscience, *2*(10), 704-716. https://doi.org/10.1038/35094565

Engel, A. K., Fries, P., & Singer, W. (2001b). Dynamic predictions: Oscillations and synchrony in top–down processing. *Nature Reviews Neuroscience*, *2*(10), Article 10. https://doi.org/10.1038/35094565

Engel, A. K., König, P., Kreiter, A. K., Schillen, T. B., & Singer, W. (1992). Temporal coding in the visual cortex: New vistas on integration in the nervous system. *Trends in Neurosciences*, *15*(6), 218-226. https://doi.org/10.1016/0166-2236(92)90039-B

Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Cognitive Brain Research*, *20*(3), 376-383. https://doi.org/10.1016/j.cogbrainres.2004.03.009

Eriksen, B. A., & Eriksen, C. W. (1974). *Effects of noise letters upon the identification of a target letter in a nonsearch task*.

Espy, K. A. (2004). Using developmental, cognitive, and neuroscience approaches to understand executive control in young children. *Developmental neuropsychology*, *26*(1), 379-384.

Esterman, M., Prinzmetal, W., & Robertson, L. (2004). Categorization influences illusory conjunctions. *Psychonomic Bulletin & Review*, *11*(4), 681-686. https://doi.org/10.3758/BF03196620

Esterman, M., Verstynen, T., & Robertson, L. C. (2007). Attenuating illusory binding with TMS of the right parietal cortex.

NeuroImage, *35*(3), 1247-1255. https://doi.org/10.1016/j.neuroimage.2006.10.039

Fan, J., Mccandliss, B., Fossella, J., Flombaum, J., & Posner, M. (2005). The activation of attentional networks. *NeuroImage*, *26*(2), 471-479. https://doi.org/10.1016/j.neuroimage.2005.02.004

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149-1160. https://doi.org/10.3758/BRM.41.4.1149

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175-191. https://doi.org/10.3758/BF03193146

Feldman, H., & Friston, K. (2010). Attention, Uncertainty, and Free-Energy. *Frontiers in human neuroscience*, *4*, 215. https://doi.org/10.3389/fnhum.2010.00215

Fenske, M. J., Aminoff, E., Gronau, N., & Bar, M. (2006). Top-down facilitation of visual object recognition: Object-based and context-based contributions. En *Progress in Brain Research* (Vol. 155, pp. 3-21). Elsevier. https://doi.org/10.1016/S0079-6123(06)55001-0

Ferguson, K. A., & Cardin, J. A. (2020). Mechanisms underlying gain modulation in the cortex. *Nature reviews. Neuroscience*, *21*(2), 80-92.

Fiebelkorn, I. C., & Kastner, S. (2019). A Rhythmic Theory of Attention. *Trends in Cognitive Sciences*, *23*(2), 87-101. https://doi.org/10.1016/j.tics.2018.11.009

Fiebelkorn, I. C., & Kastner, S. (2020). Functional Specialization in the Attention Network. *Annual Review of Psychology*, *71*(1), 221-249. https://doi.org/10.1146/annurev-psych-010418-103429

Fiebelkorn, I. C., & Kastner, S. (2021). Spike Timing in the Attention Network Predicts Behavioral Outcome Prior to Target Selection. *Neuron*, *109*(1), 177-188.e4. https://doi.org/10.1016/j.neuron.2020.09.039

Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron*, *99*(4), 842-853.e8. https://doi.org/10.1016/j.neuron.2018.07.038

Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic Sampling within and between Objects despite Sustained Attention at a Cued Location. *Current Biology*, *23*(24), 2553-2558. https://doi.org/10.1016/j.cub.2013.10.063

Fiehler, K., Ullsperger, M., Grigutsch, M., & Cramon, D. (2004). Cardiac responses to error processing and response conflict. *Errors, conflicts, and the brain : current opinions on performance monitoring, 135-140 (2004)*.

Finke, K., Matthias, E., Keller, I., Müller, H. J., Schneider, W. X., & Bublak, P. (2012). How does phasic alerting improve performance in patients with unilateral neglect? A systematic analysis of attentional processing capacity and spatial weighting mechanisms. *Neuropsychologia*, *50*(6), 1178-1189. https://doi.org/10.1016/j.neuropsychologia.2012.02.008

Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience*, *6*(6), 555-556. https://doi.org/10.1038/nn1066

Fischer, M. H., & Shaki, S. (2014). Spatial Associations in Numerical Cognition—From Single Digits to Arithmetic. *Quarterly Journal of Experimental Psychology*, *67*(8), 1461-1483. https://doi.org/10.1080/17470218.2014.927515

Fleming, S. M. (2020). Awareness as inference in a higher-order state space. *Neuroscience of Consciousness*, *2020*(1), niz020. https://doi.org/10.1093/nc/niz020

Foxe, J. J., & Snyder, A. C. (2011). The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00154

Friedman-Hill, S., Robertson, L., & Treisman, A. (1995). Parietal Contributions to Visual Feature Binding: Evidence from a Patient with Bilateral Lesions. *Science (New York, N.Y.)*, *269*, 853-855. https://doi.org/10.1126/science.7638604

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474-480. https://doi.org/10.1016/j.tics.2005.08.011

Fries, P. (2009). Neuronal Gamma-Band Synchronization as a Fundamental Process in Cortical Computation. *Annual Review of Neuroscience*, *32*(1), 209-224. https://doi.org/10.1146/annurev.neuro.051508.135603

Friese, U., Köster, M., Hassler, U., Martens, U., Trujillo-Barreto, N., & Gruber, T. (2013). Successful memory encoding is associated with increased cross-frequency coupling between frontal theta and posterior gamma oscillations in human scalp-recorded EEG. *NeuroImage*, *66*, 642-647. https://doi.org/10.1016/j.neuroimage.2012.11.002

Friston, K. (2005). A theory of cortical responses. *Philosophical transactions of the Royal Society B: Biological sciences*, *360*(1456), 815-836.

Fritz, C. O., Morris, P. E., & Richler, J. J. (2012). Effect size estimates: Current use, calculations, and interpretation. *Journal of Experimental Psychology: General*, *141*(1), 2-18. https://doi.org/10.1037/a0024338

Fuller, S., Park, Y., & Carrasco, M. (2009). Cue contrast modulates the effects of exogenous attention on appearance. *Vision Research*, *49*(14), 1825-1837. https://www.sciencedirect.com/science/article/pii/S0042698909001977

Fuller, S., Rodriguez, R. Z., & Carrasco, M. (2008). Apparent contrast differs across the vertical meridian: Visual and attentional factors. *Journal of Vision*, *8*(1), 16. https://doi.org/10.1167/8.1.16

Funes, M. J., & Lupiáñez, J. (2003). *La teoría atencional de Posner: Una tarea para medir las funciones atencionales de Orientación, Alerta y Control Cognitivo y la interacción entre ellas*.

Fusco, G., Scandola, M., Feurra, M., Pavone, E. F., Rossi, S., & Aglioti, S. M. (2018). Midfrontal theta transcranial alternating current stimulation modulates behavioural adjustment after error execution. *European Journal of Neuroscience*, *48*(10), 3159-3170.

https://doi.org/10.1111/ejn.14174

Gabor, D. (1946). Theory of communication. *J. Inst. Elect. Engr.*, *93*, 429-457. https://cir.nii.ac.jp/crid/1572824500490990976

Gaillard, R., Dehaene, S., Adam, C., Clémenceau, S., Hasboun, D., Baulac, M., Cohen, L., & Naccache, L. (2009). Converging Intracranial Markers of Conscious Access. *PLoS Biology*, *7*(3), e1000061. https://doi.org/10.1371/journal.pbio.1000061

Gaillard, R., Del Cul, A., Naccache, L., Vinckier, F., Cohen, L., & Dehaene, S. (2006). Nonconscious semantic processing of emotional words modulates conscious access. *Proceedings of the National Academy of Sciences*, *103*(19), 7524-7529. https://doi.org/10.1073/pnas.0600584103

Gallotto, S., Sack, A. T., Schuhmann, T., & De Graaf, T. A. (2017). Oscillatory Correlates of Visual Consciousness. *Frontiers in Psychology*, *8*, 1147. https://doi.org/10.3389/fpsyg.2017.01147

Gershman, S. J. (2019). The Generative Adversarial Brain. *Frontiers in Artificial Intelligence*, *2*, 18. https://doi.org/10.3389/frai.2019.00018

Ghiani, A., Maniglia, M., Battaglini, L., Melcher, D., & Ronconi, L. (2021). Binding Mechanisms in Visual Perception and Their Link With Neural Oscillations: A Review of Evidence From tACS. *Frontiers in Psychology*, *12*. https://doi.org/10.3389/fpsyg.2021.643677

Gillebert, C. R., & Humphreys, G. W. (2010). The decomposition of visual binding over time: Neuropsychological evidence from illusory conjunctions after posterior parietal damage. *Visual Cognition*, *18*(7), 954-980.

https://doi.org/10.1080/13506280903356764

Goldstein, E. B. (2013). *Sensation & Perception (Book Only)*. Cengage Learning.

Goncharova, I. I., McFarland, D. J., Vaughan, T. M., & Wolpaw, J. R. (2003). EMG contamination of EEG: Spectral and topographical characteristics. *Clinical Neurophysiology*, *114*(9), 1580-1593. https://cir.nii.ac.jp/crid/1363670320150473216

Goss-Sampson, M. (2019). *Statistical analysis in JASP: A guide for students*. JASP. https://jasp-stats.org/jasp-materials/

Graham, F. K., & Clifton, R. K. (1966). Heart-rate change as a component of the orienting response. *Psychological Bulletin*, *65*, 305-320. https://doi.org/10.1037/h0023258

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus-specific information. *eLife*, *8*, e49562. https://doi.org/10.7554/eLife.49562

Griffiths, B., Mazaheri, A., Debener, S., & Hanslmayr, S. (2016). Brain oscillations track the formation of episodic memories in the real world. *NeuroImage*, *143*, 256-266. https://doi.org/10.1016/j.neuroimage.2016.09.021

Groen, I. I., Silson, E. H., & Baker, C. I. (2017). Contributions of low-and high-level properties to neural processing of visual scenes in the human brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1714), 20160102.

Grubb, M. A., Behrmann, M., Egan, R., Minshew, N. J., Heeger, D. J., & Carrasco, M. (2013). Exogenous spatial attention: Evidence for intact functioning in adults with autism spectrum disorder.

Journal of Vision, *13*(14), 9-9. https://doi.org/10.1167/13.14.9

Gruber, T., Müller, M. M., Keil, A., & Elbert, T. (1999). Selective visual-spatial attention alters induced gamma band responses in the human EEG. *Clinical Neurophysiology*, *110*(12), 2074-2085. https://doi.org/10.1016/S1388-2457(99)00176-5

Hajcak, G., McDonald, N., & Simons, R. F. (2003). To err is autonomic: Error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology*, *40*(6), 895-903.

Hall, J. E. (2021). *Guyton & Hall. Tratado de fisiología médica*. Elsevier Health Sciences.

Han, S., & Humphreys, G. W. (2007). The Fronto-Parietal Network and Top-Down Modulation of Perceptual Grouping. *Neurocase*, *13*(4), 278-289. https://doi.org/10.1080/13554790701649930

Hansen, A. L., Johnsen, B. H., & Thayer, J. F. (2003). Vagal influence on working memory and attention. *International Journal of Psychophysiology*.

Hansen, T., Pracejus, L., & Gegenfurtner, K. R. (2009). Color perception in the intermediate periphery of the visual field. *Journal of Vision*, *9*(4), 26-26. https://doi.org/10.1167/9.4.26

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465-1473. https://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Spitzer, B., & Bäuml, K.-H. (2009). Brain Oscillations Dissociate between Semantic and Nonsemantic Encoding of

Episodic Memories. *Cerebral Cortex*, *19*(7), 1631-1640. https://doi.org/10.1093/cercor/bhn197

Harris, J. J., Schwarzkopf, D. S., Song, C., Bahrami, B., & Rees, G. (2011). Contextual Illusions Reveal the Limit of Unconscious Visual Processing. *Psychological Science*, *22*(3), 399-405. https://doi.org/10.1177/0956797611399293

Haynes, J.-D. (2009). Decoding visual consciousness from human brain signals. *Trends in Cognitive Sciences*, *13*(5), 194-202. https://doi.org/10.1016/j.tics.2009.02.004

Hein, E., Rolke, B., & Ulrich, R. (2006). Visual attention and temporal discrimination: Differential effects of automatic and voluntary cueing. *Visual Cognition - VIS COGN*, *13*, 29-50. https://doi.org/10.1080/13506280500143524

Helfrich, R. F., Fiebelkorn, I. C., Szczepanski, S. M., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S. (2018). Neural Mechanisms of Sustained Attention Are Rhythmic. *Neuron*, *99*(4), 854-865.e5. https://doi.org/10.1016/j.neuron.2018.07.032

Helmholtz, H. L. F. von, & Southall, J. P. C. (2000). Helmholtz’s treatise on physiological optics. *(No Title)*. https://cir.nii.ac.jp/crid/1130000798046487424

Henderickx, D., Maetens, K., & Soetens, E. (2010). Feature integration and spatial attention: Common processes for endogenous and exogenous orienting. *Psychological Research PRPF*, *74*(3), 239-254. https://doi.org/10.1007/s00426-009-0251-1

Henderson, C. M. (2014). *The binding problem and the perception of multiple stimuli*. Doctoral dissertation, Standford University.

https:// searchworks.stanford.edu/view/10608091.

Henderson, C. M., & McClelland, J. L. (2020a). Intrusions into the shadow of attention: A new take on illusory conjunctions. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-019-01893-3

Henderson, C. M., & McClelland, J. L. (2020b). Intrusions into the shadow of attention: A new take on illusory conjunctions. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-019-01893-3

Herrmann, C. S., Lenz, D., Junge, S., Busch, N. A., Maess, B., Junge, S., Busch, N. A., & Maess, B. (2004). *Memory-matches evoke human gamma-responses*.

Herrmann, C. S., Munk, M. H. J., & Engel, A. K. (2004). Cognitive functions of gamma-band activity: Memory match and utilization. *Trends in Cognitive Sciences*, *8*(8), 347-355. https://doi.org/10.1016/j.tics.2004.06.006

Heusser, A. C., Poeppel, D., Ezzyat, Y., & Davachi, L. (2016). Episodic sequence memory is supported by a theta-gamma phase code. *Nature neuroscience*, *19*(10), 1374-1380. https://doi.org/10.1038/nn.4374

Hochstein, S., & Ahissar, M. (2002). View from the Top: Hierarchies and Reverse Hierarchies in the Visual System. *Neuron*, *36*(5), 791-804. https://doi.org/10.1016/S0896-6273(02)01091-7

Hommel, B. (2011). The Simon effect as tool and heuristic. *Acta psychologica*, *136*(2), 189-202.

Honkanen, R., Rouhinen, S., Wang, S. H., Palva, J. M., & Palva, S. (2015). Gamma Oscillations Underlie the Maintenance of

Feature-Specific Information and the Contents of Visual Working Memory. *Cerebral Cortex*, *25*(10), 3788-3801. https://doi.org/10.1093/cercor/bhu263

Howard, M. W. (2003). Gamma Oscillations Correlate with Working Memory Load in Humans. *Cerebral Cortex*, *13*(12), 1369-1374. https://doi.org/10.1093/cercor/bhg084

Huang, Y., Pollick, F., Liu, M., & Zhang, D. (2023). Gabor and Non-Gabor Neural Representations Are Shared between Visual Perception and Mental Imagery. *Journal of Cognitive Neuroscience*, *35*(6), 1045-1060. https://doi.org/10.1162/jocn_a_01992

Humphreys, G. W. (2016). Feature Confirmation in Object Perception: Feature Integration Theory 26 Years on from the Treisman Bartlett Lecture. *Quarterly Journal of Experimental Psychology*, *69*(10), 1910-1940. https://doi.org/10.1080/17470218.2014.988736

Humphreys, G. W., Cinel, C., Wolfe, J., Olson, A., & Klempen, N. (2000). Fractionating the binding process: Neuropsychological evidence distinguishing binding of form from binding of surface features. *Vision Research*, *40*, 1569-1596. https://search.bwh.harvard.edu/new/pubs/VRneglect.pdf

Ivry, R. B., & Prinzmetal, W. (1991). Effect of feature similarity on illusory conjunctions. *Perception & Psychophysics*, *49*(2), 105-116. https://doi.org/10.3758/BF03205032

James, W. (1890). The Principles of Psychology. *THE PRINCIPLES OF PSYCHOLOGY*, 919.

Jennings, J. R., Van Der Molen, M. W., & Tanase, C. (2009). Preparing hearts and minds: Cardiac slowing and a cortical inhibitory network. *Psychophysiology*, *46*(6), 1170-1178. https://doi.org/10.1111/j.1469-8986.2009.00866.x

Jennings, J. R., & Wood, C. C. (1977). Cardiac cycle time effects on performance, phasic cardiac responses, and their intercorrelation in choice reaction time. *Psychophysiology*, *14*(3), 297-307.

Jennings, J., & van der Molen, M. (2005). Preparation for Speeded Action as a Psychophysiological Concept. *Psychological bulletin*, *131*, 434-459. https://doi.org/10.1037/0033-2909.131.3.434

Jensen, O., Kaiser, J., & Lachaux, J.-P. (2007). Human gamma-frequency oscillations associated with attention and memory. *Trends in Neurosciences*, *30*(7), 317-324. https://doi.org/10.1016/j.tins.2007.05.001

Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00186

Jiang, J., Summerfield, C., & Egner, T. (2013). Attention Sharpens the Distinction between Expected and Unexpected Percepts in the Visual Brain. *Journal of Neuroscience*, *33*(47), 18438-18447. https://doi.org/10.1523/JNEUROSCI.3308-13.2013

Jiang, Y., & Chun, M. M. (2001). Selective attention modulates implicit learning. *The Quarterly Journal of Experimental Psychology Section A*, *54*(4), 1105-1124. https://doi.org/10.1080/713756001

Jokisch, D., & Jensen, O. (2007). Modulation of Gamma and Alpha

Activity during a Working Memory Task Engaging the Dorsal or Ventral Stream. *The Journal of Neuroscience*, *27*(12), 3244-3251. https://doi.org/10.1523/JNEUROSCI.5399-06.2007

Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movements. *Attention and performance*.

Kalfaoğlu, Ç., Stafford, T., & Milne, E. (2018). Frontal theta band oscillations predict error correction and posterror slowing in typing. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(1), 69-88. https://doi.org/10.1037/xhp0000417

Kapoor, V., Dwarakanath, A., Safavi, S., Werner, J., Besserve, M., Panagiotaropoulos, T. I., & Logothetis, N. K. (2020). *Decoding the contents of consciousness from prefrontal ensembles* [Preprint]. Neuroscience. https://doi.org/10.1101/2020.01.28.921841

Kastner, S., & Ungerleider, L. G. (2000). MECHANISMS OF VISUAL ATTENTION IN THE HUMAN CORTEX. *Annu. Rev. Neurosci*, *23*, 315-341.

Kayser, C., Ince, R. A. A., & Panzeri, S. (2012). Analysis of Slow (Theta) Oscillations as a Potential Temporal Reference Frame for Information Coding in Sensory Cortices. *PLOS Computational Biology*, *8*(10), e1002717. https://doi.org/10.1371/journal.pcbi.1002717

Keil, A., & Müller, M. M. (2010). Feature selection in the human brain: Electrophysiological correlates of sensory enhancement and feature integration. *Brain Research*, *1313*, 172-184. https://doi.org/10.1016/j.brainres.2009.12.006

Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in

Alpha Oscillatory Power Reflect an Active Retinotopic Mechanism for Distracter Suppression During Sustained Visuospatial Attention. *Journal of Neurophysiology*, *95*(6), 3844-3851. https://doi.org/10.1152/jn.01234.2005

Kentridge, R. (2004). Spatial attention speeds discrimination without awareness in blindsight. *Neuropsychologia*, *42*(6), 831-835. https://doi.org/10.1016/j.neuropsychologia.2003.11.001

Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1430), 1805-1811. https://doi.org/10.1098/rspb.1999.0850

Kentridge, R. W., Nijboer, T. C. W., & Heywood, C. A. (2008). Attended but unseen: Visual attention is not sufficient for visual awareness. *Neuropsychologia*, *46*(3), 864-869. https://doi.org/10.1016/j.neuropsychologia.2007.11.036

Kern, M., Aertsen, A., Schulze-Bonhage, A., & Ball, T. (2013). Heart cycle-related effects on event-related potentials, spectral power changes, and connectivity patterns in the human ECoG. *NeuroImage*, *81*, 178-190. https://doi.org/10.1016/j.neuroimage.2013.05.042

Kewan-Khalayly, B., Migó, M., & Yashar, A. (2022). Transient attention equally reduces visual crowding in radial and tangential axes. *Journal of Vision*, *22*(9), 3. https://doi.org/10.1167/jov.22.9.3

Khanna, P., & Carmena, J. M. (2015). Neural oscillations: Beta band activity across motor networks. *Current Opinion in Neurobiology*, *32*, 60-67. https://doi.org/10.1016/j.conb.2014.11.010

King, J.-R., Pescetelli, N., & Dehaene, S. (2016). Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron*, *92*(5), 1122-1134. https://www.cell.com/neuron/pdf/S0896-6273(16)30801-7.pdf

Klausberger, T., Magill, P. J., Márton, L. F., Roberts, J. D. B., Cobden, P. M., Buzsáki, G., & Somogyi, P. (2003). Brain-state-and cell-type-specific firing of hippocampal interneurons in vivo. *Nature*, *421*(6925), 844-848. https://idp.nature.com/authorize/casa?redirect_uri=https://www.nature.com/articles/nature01374&casa_token=wTh685_Y8F0AAAAA:QAuzNBYEPuB4IU6G-jBiNTYFmNZAm461ed2Y4CvKWLL__aFm2cBZNGA9PlSeXNXhHoLeWThhfv7AhvOu

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*(4), 138-147. https://doi.org/10.1016/S1364-6613(00)01452-2

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606-617. https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1002-1014. https://doi.org/10.1016/j.neubiorev.2009.10.004

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007a). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research*

Reviews, *53*(1), 63-88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007b). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63-88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience and Biobehavioral Reviews*, *3*(31), 377-395. https://doi.org/10.1016/j.neubiorev.2006.10.004

Koch, C., & Tsuchiya, N. (2007a). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, *11*(1), 16-22. https://doi.org/10.1016/j.tics.2006.10.012

Koch, C., & Tsuchiya, N. (2007b). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, *11*(1), 16-22. https://doi.org/10.1016/j.tics.2006.10.012

Kok, P., Mostert, P., & de Lange, F. P. (2017). Prior expectations induce prestimulus sensory templates. *Proceedings of the National Academy of Sciences*, *114*(39), 10473-10478. https://doi.org/10.1073/pnas.1705652114

Kolasinski, J., Logan, J. P., Hinson, E. L., Manners, D., AP, D. Z., Makin, T. R., Emir, U. E., & Stagg, C. J. (2017). A Mechanistic Link from GABA to Cortical Architecture and Perception. *Current Biology: CB*, *27*(11), 1685-1691.

Köster, M., Finger, H., Graetz, S., Kater, M., & Gruber, T. (2018). Theta-gamma coupling binds visual perceptual features in an associative memory task. *Scientific Reports*, *8*(1), 17688.

https://doi.org/10.1038/s41598-018-35812-7

Kouider, S., de Gardelle, V., & Dupoux, E. (2007). Partial awareness and the illusion of phenomenal consciousness. *Behavioral and Brain Sciences*, *30*, 510-511. https://doi.org/10.1017/S0140525X07002919

Kouider, S., de Gardelle, V., Sackur, J., & Dupoux, E. (2010). How rich is consciousness? The partial awareness hypothesis. *Trends in Cognitive Sciences*, *14*(7), 301-307. https://doi.org/10.1016/j.tics.2010.04.006

Kovács, I., Papathomas, T. V., Yang, M., & Fehér, Á. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences*, *93*(26), 15508-15511. https://doi.org/10.1073/pnas.93.26.15508

Krajcsi, A., & Kojouharova, P. (2017). Symbolic Numerical Distance Effect Does Not Reflect the Difference between Numbers. *Frontiers in Psychology*, *8*, 2013. https://doi.org/10.3389/fpsyg.2017.02013

Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. *NeuroImage*, *24*, 704-714. http://www.andreas-engel.com/kranczioch_2005.pdf

Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F., & Baker, C. I. (2009). Circular analysis in systems neuroscience: The dangers of double dipping. *Nature Neuroscience*, *12*(5), 535-540. https://doi.org/10.1038/nn.2303

Kristjánsson, Á., & Egeth, H. (2020). How feature integration theory integrated cognitive psychology, neurophysiology, and psychophysics. *Attention, Perception, & Psychophysics*, *82*(1), 7-23. https://doi.org/10.3758/s13414-019-01803-7

Kuhn, G., & Rensink, R. A. (2016). The Vanishing Ball Illusion: A new perspective on the perception of dynamic events. *Cognition*, *148*, 64-70. https://doi.org/10.1016/j.cognition.2015.12.003

Kusnir, F., Chica, A. B., Mitsumasu, M. A., & Bartolomeo, P. (2011). Phasic auditory alerting improves visual conscious perception. *Consciousness and Cognition*, *20*(4), 1201-1210. https://doi.org/10.1016/j.concog.2011.01.012

LaBerge, D. (1995). *Attentional processing: The brain's art of mindfulness*. Harvard University Press.

Lacey, B. C., & Lacey, J. I. (1977). Change in heart period: A function of sensorimotor event timing within the cardiac cycle. *Physiological Psychology*, *5*, 383-393. https://doi.org/10.3758/BF03335349

Lacey, B. C., & Lacey, J. I. (1978). Two-way communication between the heart and the brain: Significance of time within the cardiac cycle. *American Psychologist*, *33*, 99-113. https://doi.org/10.1037/0003-066X.33.2.99

Lacey, J. (1967). Somatic response patterning and stress: Some revisions of activation theory. *Psychological stress: Issues in research*. https://cir.nii.ac.jp/crid/1571135650010479232

Lacey, J. I. (1972). Some cardiovascular correlates of sensorimotor behavior: Examples of visceral afferent feedback. *Limbic system mechanisms and autonomic function*, 175-201.

Lacey, J. I., & Lacey, B. C. (1958). The relationship of resting autonomic activity to motor impulsivity. *Research Publications of the Association for Research in Nervous & Mental Disease*.

Lacey, P. J. (1970). Some autonomic-central nervous system inter-relations. *Physiological Correlates of Emotion.*, 205-227.

Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, *7*(1), 12-18. https://doi.org/10.1016/S1364-6613(02)00013-X

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494-501. https://doi.org/10.1016/j.tics.2006.09.001

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, *1*(3), 204-220. https://doi.org/10.1080/17588921003731586

Lamme, V. A. F., & Roelfsema, P. (2000). The Distinct Modes of Vision Offered by Feedforward and Recurrent Processing. *Trends in neurosciences*, *23*, 571-579. https://doi.org/10.1016/S0166-2236(00)01657-X

Lamme, V. A. F., Supèr, H., Landman, R., Roelfsema, P. R., & Spekreijse, H. (2000). The role of primary visual cortex (V1) in visual awareness. *Vision Research*, *40*(10-12), 1507-1521. https://doi.org/10.1016/S0042-6989(99)00243-6

Lamme, V. A. F., Supèr, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology*, *8*(4), 529-535. https://doi.org/10.1016/S0959-4388(98)80042-1

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological review*, *97*(3), 377.

Lange, J., Keil, J., Schnitzler, A., van Dijk, H., & Weisz, N. (2014). The role of alpha oscillations for illusory perception. *Behavioural Brain Research*, *271*, 294-301. https://doi.org/10.1016/j.bbr.2014.06.015

Lau, H. (2019). *Consciousness, metacognition, & perceptual reality monitoring*.

Lau, H. C., & Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proceedings of the National Academy of Sciences*, *103*(49), 18763-18768. https://doi.org/10.1073/pnas.0607716103

Lau, H., & Rosenthal, D. (2011). Empirical support for higher-order theories of conscious awareness. *Trends in Cognitive Sciences*, *15*(8), 365-373. https://doi.org/10.1016/j.tics.2011.05.009

Laureys, S., Owen, A. M., & Schiff, N. D. (2004). *Brain function in coma, vegetative state, and related disorders*. *3*, 537-546. http://neurology.thelancet.com

Laureys, S., & Schiff, N. D. (2012). Coma and consciousness: Paradigms (re)framed by neuroimaging. *NeuroImage*, *61*(2), 478-491. https://doi.org/10.1016/j.neuroimage.2011.12.041

Lavie, N. (2006). The role of perceptual load in visual awareness. *Brain Research*, *1080*(1), 91-100. https://doi.org/10.1016/j.brainres.2005.10.023

Lavie, N. (2010). Attention, Distraction, and Cognitive Control Under Load. *Current Directions in Psychological Science*, *19*(3), 143-148. https://doi.org/10.1177/0963721410370295

Lawson, R. A., Yarnall, A. J., Duncan, G. W., Breen, D. P., Khoo, T. K., Williams-Gray, C. H., Barker, R. A., Collerton, D., Taylor, J.-P., &

Burn, D. J. (2016). Cognitive decline and quality of life in incident Parkinson's disease: The role of attention. *Parkinsonism & Related Disorders*, *27*, 47-53. https://doi.org/10.1016/j.parkreldis.2016.04.009

Lechinger, J., Heib, D. P. J., Gruber, W., Schabus, M., & Klimesch, W. (2015). Heartbeat-related EEG amplitude and phase modulations from wakefulness to deep sleep: Interactions with sleep spindles and slow oscillations: Cardiac activity modulates brain oscillations. *Psychophysiology*, *52*(11), 1441-1450. https://doi.org/10.1111/psyp.12508

Lee, J. H., Whittington, M. A., & Kopell, N. J. (2013). Top-Down Beta Rhythms Support Selective Attention via Interlaminar Interaction: A Model. *PLoS Computational Biology*, *9*(8), e1003164. https://doi.org/10.1371/journal.pcbi.1003164

Lee, T. S., & Mumford, D. (2003). Hierarchical Bayesian inference in the visual cortex. *Journal of the Optical Society of America A*, *20*(7), 1434. https://doi.org/10.1364/JOSAA.20.001434

Leonards, U., Sunaert, S., Van Hecke, P., & Orban, G. A. (2000). Attention Mechanisms in Visual Search—An fMRI Study. *Journal of Cognitive Neuroscience*, *12*(Supplement 2), 61-75. https://doi.org/10.1162/089892900564073

Leopold, D. A., Logothetis, N. K., Leopold, D. A., Logothetis, N. K., Leopold, D. A., Logothetis, N. K., Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, *3*(7), 254-264. https://doi.org/10.1016/S1364-6613(99)01332-7

Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience*, *5*(6), 605-609. https://doi.org/10.1038/nn0602-851

Leske, S., & Dalal, S. S. (2019). Reducing power line noise in EEG and MEG data via spectrum interpolation. *NeuroImage*, *189*, 763-776. https://doi.org/10.1016/j.neuroimage.2019.01.026

Li, F. F., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. *Proceedings of the National Academy of Sciences*, *99*(14), 9596-9601. https://doi.org/10.1073/pnas.092277599

Lima, B., Singer, W., & Neuenschwander, S. (2011). Gamma Responses Correlate with Temporal Expectation in Monkey Primary Visual Cortex. *The Journal of Neuroscience*, *31*(44), 15919-15931. https://doi.org/10.1523/JNEUROSCI.0957-11.2011

Limbach, K., & Corballis, P. M. (2016). Prestimulus alpha power influences response criterion in a detection task. *Psychophysiology*, *53*(8), 1154-1164. https://doi.org/10.1111/psyp.12666

Liu, P., Yang, W., Chen, J., Huang, X., & Chen, A. (2013). Alertness Modulates Conflict Adaptation and Feature Integration in an Opposite Way. *PLoS ONE*, *8*(11), e79146. https://doi.org/10.1371/journal.pone.0079146

Liu, T., Abrams, J., & Carrasco, M. (2009). Voluntary Attention Enhances Contrast Appearance. *Psychological Science*, *20*(3), 354-362. https://doi.org/10.1111/j.1467-9280.2009.02300.x

Loh, S., Lamond, N., Dorrian, J., Roach, G., & Dawson, D. (2004). The validity of psychomotor vigilance tasks of less than 10-minute duration. *Behavior Research Methods, Instruments, & Computers*, *36*(2), 339-346. https://doi.org/10.3758/BF03195580

Lubar, J. F. (1991). Discourse on the development of EEG diagnostics and biofeedback for attention-deficit/hyperactivity disorders. *Biofeedback and Self-Regulation*, *16*(3), 201-225. https://doi.org/10.1007/BF01000016

Lundqvist, M., Herman, P., & Lansner, A. (2011). Theta and Gamma Power Increases and Alpha/Beta Power Decreases with Memory Load in an Attractor Network Model. *Journal of Cognitive Neuroscience*, *23*(10), 3008-3020. https://doi.org/10.1162/jocn_a_00029

Lupiáñez, J., Klein, R. M., & Bartolomeo, P. (2006). Inhibition of return: Twenty years after. *Cognitive Neuropsychology*, *23*(7), 1003-1014. https://doi.org/10.1080/02643290600588095

Luque-Casado, A., Perales, J. C., Cárdenas, D., & Sanabria, D. (2016). Heart rate variability and cognitive processing: The autonomic response to task demands. *Biological Psychology*, *113*, 83-90. https://doi.org/10.1016/j.biopsycho.2015.11.013

Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. *Clinical Neurophysiology*, *115*(8), 1821-1835. https://doi.org/10.1016/j.clinph.2004.03.031

Mack, A. (2003). Inattentional Blindness: Looking Without Seeing. *Current Directions in Psychological Science*, *12*(5), 180-184. https://doi.org/10.1111/1467-8721.01256

Mack, A., Erol, M., Clarke, J., & Bert, J. (2016). No iconic memory without attention. *Consciousness and Cognition*, *40*, 1-8.

https://doi.org/10.1016/j.concog.2015.12.006

Mack, A., & Rock, I. (1998). *Inattentional blindness: Perception without attention.*

Makovac, E., Garfinkel, S. N., Bassi, A., Basile, B., Macaluso, E., Cercignani, M., Calcagnini, G., Mattei, E., Agalliu, D., & Cortelli, P. (2015). Effect of Parasympathetic Stimulation on Brain Activity During Appraisal of Fearful Expressions. *NEUROPSYCHOPHARMACOLOGY*, *40*(7), 1649-1658.

Mapelli, I., & Özkurt, T. E. (2019). Brain Oscillatory Correlates of Visual Short-Term Memory Errors. *Frontiers in Human Neuroscience*, *13*, 33. https://doi.org/10.3389/fnhum.2019.00033

Martens, S., & Wyble, B. (2010). The attentional blink: Past, present, and future of a blind spot in perceptual awareness. *Neuroscience & Biobehavioral Reviews*, *34*(6), 947-957. https://doi.org/10.1016/j.neubiorev.2009.12.005

Martín-Signes, M., Cano-Melle, C., & Chica, A. B. (2021). Fronto-parietal networks underlie the interaction between executive control and conscious perception: Evidence from TMS and DWI. *Cortex*, *134*, 1-15. https://doi.org/10.1016/j.cortex.2020.09.027

Martín-Signes, M., Paz-Alonso, P. M., & Chica, A. B. (2018). Connectivity of Frontoparietal Regions Reveals Executive Attention and Consciousness Interactions. *Cerebral Cortex*, *29*(11), 4539-4550. https://doi.org/10.1093/cercor/bhy332

Martín-Signes, M., Pérez-Serrano, C., & Chica, A. B. (2019). Causal Contributions of the SMA to Alertness and Consciousness

Interactions. *Cerebral Cortex*, *29*(2), 648-656. https://doi.org/10.1093/cercor/bhx346

Mashour, G. A. (2013). Cognitive unbinding: A neuroscientific paradigm of general anesthesia and related states of unconsciousness. *Neuroscience & Biobehavioral Reviews*, *37*(10, Part 2), 2751-2759. https://doi.org/10.1016/j.neubiorev.2013.09.009

Mashour, G. A., Roelfsema, P., Changeux, J.-P., & Dehaene, S. (2020). Conscious Processing and the Global Neuronal Workspace Hypothesis. *Neuron*, *105*(5), 776-798. https://doi.org/10.1016/j.neuron.2020.01.026

Mathes, B., Khalaidovski, K., Schmiedt-Fehr, C., & Basar-Eroglu, C. (2014). Frontal theta activity is pronounced during illusory perception. *International Journal of Psychophysiology*, *94*(3), 445-454. https://doi.org/10.1016/j.ijpsycho.2014.08.585

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To See or Not to See: Prestimulus Phase Predicts Visual Awareness. *Journal of Neuroscience*, *29*(9), 2725-2732. https://doi.org/10.1523/JNEUROSCI.3963-08.2009

Mathewson, K. J., Jetha, M. K., Drmic, I. E., Bryson, S. E., Goldberg, J. O., Hall, G. B., Santesso, D. L., Segalowitz, S. J., & Schmidt, L. A. (2010). Autonomic predictors of Stroop performance in young and middle-aged adults. *International journal of psychophysiology: official journal of the International Organization of Psychophysiology*, *76*(3), 123-129.

Matthews, J., Schröder, P., Kaunitz, L., van Boxtel, J. J. A., & Tsuchiya, N. (2018). Conscious access in the near absence of attention:

Critical extensions on the dual-task paradigm. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1755), 20170352. https://doi.org/10.1098/rstb.2017.0352

Mayer, A., Schwiedrzik, C. M., Wibral, M., Singer, W., & Melloni, L. (2016). Expecting to See a Letter: Alpha Oscillations as Carriers of Top-Down Sensory Predictions. *Cerebral Cortex*, *26*(7), 3146-3160. https://doi.org/10.1093/cercor/bhv146

Mayer, E. A. (2011). Gut feelings: The emerging biology of gut-brain communication. *Nature reviews. Neuroscience*, *12*(8), 453-466.

Mazaheri, A., & Jensen, O. (2010). Rhythmic Pulsing: Linking Ongoing Brain Activity with Evoked Responses. *Frontiers in Human Neuroscience*, *4*. https://www.frontiersin.org/article/10.3389/fnhum.2010.00177

Mazaheri, A., Nieuwenhuis, I. L. C., van Dijk, H., & Jensen, O. (2009). Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human Brain Mapping*, *30*(6), 1791-1800. https://doi.org/10.1002/hbm.20763

Melloni, L., Ferrante, O., Gorska-Klimowska, U., Henin, S., Hirschhorn, R., Khalaf, A., Lepauvre, A., Liu, L., Richter, D., & Vidal, Y. (2023). *An adversarial collaboration to critically evaluate theories of consciousness*.

Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W., & Rodriguez, E. (2007). Synchronization of Neural Activity across Cortical Areas Correlates with Conscious Perception. *Journal of Neuroscience*, *27*(11), 2858-2865. https://doi.org/10.1523/JNEUROSCI.4623-06.2007

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain structure and function*, *214*, 655-667.

Mi, Y., Katkov, M., & Tsodyks, M. (2017). Synaptic Correlates of Working Memory Capacity. *Neuron*, *93*(2), 323-330. https://doi.org/10.1016/j.neuron.2016.12.004

Michalareas, G., Vezoli, J., van Pelt, S., Schoffelen, J.-M., Kennedy, H., & Fries, P. (2016). Alpha-Beta and Gamma Rhythms Subserve Feedback and Feedforward Influences among Human Visual Cortical Areas. *Neuron*, *89*(2), 384-397. https://doi.org/10.1016/j.neuron.2015.12.018

Michelmann, S., Bowman, H., & Hanslmayr, S. (2016). The Temporal Signature of Memories: Identification of a General Mechanism for Dynamic Memory Replay in Humans. *PLOS Biology*, *14*(8), e1002528. https://doi.org/10.1371/journal.pbio.1002528

Miller, E. K., & Cohen, J. D. (2001). An Integrative Theory of Prefrontal Cortex Function. *Annual Review of Neuroscience*, *24*(1), 167-202. https://doi.org/10.1146/annurev.neuro.24.1.167

Miller, E. K., Lundqvist, M., & Bastos, A. M. (2018). Working Memory 2.0. *Neuron*, *100*(2), 463-475. https://doi.org/10.1016/j.neuron.2018.09.023

Min, B.-K., & Herrmann, C. S. (2007). Prestimulus EEG alpha activity reflects prestimulus top-down processing. *Neuroscience Letters*, *422*(2), 131-135. https://doi.org/10.1016/j.neulet.2007.06.013

Min, B.-K., Park, J. Y., Kim, E. J., Kim, J. I., Kim, J.-J., & Park, H.-J. (2008). Prestimulus EEG alpha activity reflects temporal expectancy. *Neuroscience Letters*, *438*(3), 270-274. https://doi.org/10.1016/j.neulet.2008.04.067

Miyake, A., & Shah, P. (1999). *Models of working memory*. Citeseer.

Montaser-Kouhsari, L., & Rajimehr, R. (2005). Subliminal attentional modulation in crowding condition. *Vision Research*, *45*(7), 839-844. https://doi.org/10.1016/j.visres.2004.10.020

Montoya, P., Schandry, R., & Müller, A. (1993). Heartbeat evoked potentials (HEP): Topography and influence of cardiac awareness and focus of attention. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *88*(3), 163-172.

Moore, C. M., Yantis, S., & Vaughan, B. (1998). Object-Based Visual Selection: Evidence From Perceptual Completion. *Psychological Science*, *9*(2), 104-110. https://doi.org/10.1111/1467-9280.00019

Mordkoff, J. T., & Halterman, R. (2008). Feature integration without visual attention: Evidence from the correlated flankers task. *Psychonomic Bulletin & Review*, *15*(2), 385-389. https://doi.org/10.3758/PBR.15.2.385

Morey, R. D. (2008). Confidence Intervals from Normalized Data: A correction to Cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, *4*(2), 61-64. https://doi.org/10.20982/tqmp.04.2.p061

Morgan, H. M., Muthukumaraswamy, S. D., Hibbs, C. S., Shapiro, K. L., Bracewell, R. M., Singh, K. D., & Linden, D. E. J. (2011). Feature integration in visual working memory: Parietal gamma activity is related to cognitive coordination. *Journal of Neurophysiology*, *106*(6), 3185-3194. https://doi.org/10.1152/jn.00246.2011

Motyka, P., Grund, M., Forschack, N., Al, E., Villringer, A., & Gaebler, M. (2019). Interactions between cardiac activity and conscious somatosensory perception. *Psychophysiology*, *56*(10). https://doi.org/10.1111/psyp.13424

Müller, N. G., Vellage, A.-K., Heinze, H.-J., & Zaehle, T. (2015). Entrainment of Human Alpha Oscillations Selectively Enhances Visual Conjunction Search. *PLOS ONE*, *10*(11), e0143533. https://doi.org/10.1371/journal.pone.0143533

Murphy, G., Groeger, J. A., & Greene, C. M. (2016). Twenty years of load theory—Where are we now, and where should we go next? *Psychonomic Bulletin & Review*, *23*(5), 1316-1340. https://doi.org/10.3758/s13423-015-0982-5

Mutschler, I., Wieckhorst, B., Kowalevski, S., Derix, J., Wentlandt, J., Schulze-Bonhage, A., & Ball, T. (2009). Functional Organization of the Human Anterior Insular Cortex and its Relation to the Amygdala. *Neuroimage*, *47*. https://doi.org/10.1016/S1053-8119(09)70943-7

Naccache, L. (2018). Why and how access consciousness can account for phenomenal consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1755), 20170357. https://doi.org/10.1098/rstb.2017.0357

Niedermeyer, E. (2003). The Clinical Relevance of EEG Interpretation. *Clinical Electroencephalography*, *34*(3), 93-98. https://doi.org/10.1177/155005940303400303

Norman, D. A., & Shallice, T. (1986). Attention to Action: Willed and Automatic Control of Behavior. En R. J. Davidson, G. E. Schwartz,

& D. Shapiro (Eds.), *Consciousness and Self-Regulation* (pp. 1-18). Springer US. https://doi.org/10.1007/978-1-4757-0629-1_1

Notebaert, W., Houtman, F., Opstal, F. V., Gevers, W., Fias, W., & Verguts, T. (2009). Post-error slowing: An orienting account. *Cognition*, *111*(2), 275-279. https://doi.org/10.1016/j.cognition.2009.02.002

Obrist, P. A. (2012). *Cardiovascular Psychophysiology: A Perspective*. Springer Science & Business Media.

O'Connell, R. G., Dockree, P. M., Bellgrove, M. A., Kelly, S. P., Hester, R., Garavan, H., Robertson, I. H., & Foxe, J. J. (2007). The role of cingulate cortex in the detection of errors with and without awareness: A high-density electrical mapping study. *European Journal of Neuroscience*, *25*(8), 2571-2579.

Odegaard, B., Knight, R. T., & Lau, H. (2017). Should a Few Null Findings Falsify Prefrontal Theories of Conscious Perception? *The Journal of Neuroscience*, *37*(40), 9593-9602. https://doi.org/10.1523/JNEUROSCI.3217-16.2017

Oizumi, M., Albantakis, L., & Tononi, G. (2014). From the Phenomenology to the Mechanisms of Consciousness: Integrated Information Theory 3.0. *PLoS Computational Biology*, *10*(5), e1003588. https://doi.org/10.1371/journal.pcbi.1003588

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, 1-9. https://doi.org/10.1155/2011/156869

Oppenheimer, S. M., Gelb, A., Girvin, J. P., & Hachinski, V. C. (1992).

Cardiovascular effects of human insular cortex stimulation. *Neurology*, *42*(9), 1727-1727.

Oswal, A., Brown, P., & Litvak, V. (2013). Synchronized neural oscillations and the pathophysiology of Parkinson's disease. *Current opinion in neurology*, *26*(6), 662-670. https://journals.lww.com/co-neurology/FullText/2013/12000/Synchronized_neural_oscillations_and_the.12.aspx?casa_token=Xrhzok4KAWQAAAAA:7kooYBy8UBei7TEwtVR6AzehqMXCjvHpfi4pdpLrEBDFwp6VcnMdM57RYVXNaiGcmGC0HYbXeWR3Ue4QLeRNt67K5Ud3CkOjHVDI

Pace-Schott, E. F., Amole, M. C., Aue, T., Balconi, M., Bylsma, L. M., Critchley, H., Demaree, H. A., Friedman, B. H., Gooding, A. E. K., Gosseries, O., Jovanovic, T., Kirby, L. A. J., Kozlowska, K., Laureys, S., Lowe, L., Magee, K., Marin, M.-F., Merner, A. R., Robinson, J. L., … VanElzakker, M. B. (2019). Physiological feelings. *Neuroscience & Biobehavioral Reviews*, *103*, 267-304. https://doi.org/10.1016/j.neubiorev.2019.05.002

Palva, S., & Palva, J. M. (2007). New vistas for α-frequency band oscillations. *Trends in Neurosciences*, *30*(4), 150-158. https://doi.org/10.1016/j.tins.2007.02.001

Panagiotaropoulos, T. I., Deco, G., Kapoor, V., & Logothetis, N. K. (2012). Neuronal Discharges and Gamma Oscillations Explicitly Reflect Visual Consciousness in the Lateral Prefrontal Cortex. *Neuron*, *74*(5), 924-935. https://doi.org/10.1016/j.neuron.2012.04.013

Papaioannou, O., Crespo, L. P., Clark, K., Ogbuagu, N. N., Alliende, L. M., Silverstein, S. M., & Erickson, M. A. (2022). Is Cortical

Theta-Gamma Phase-Amplitude Coupling Memory-Specific? *Brain Sciences*, *12*(9), Article 9. https://doi.org/10.3390/brainsci12091131

Parasuraman, R., & Davies, D. R. (1984). *Varieties of attention*.

Pardo, J. V., Pardo, P. J., Janer, K. W., & Raichle, M. E. (1990). The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proceedings of the National Academy of Sciences*, *87*(1), 256-259.

Park, H.-D., Bernasconi, F., Salomon, R., Tallon-Baudry, C., Spinelli, L., Seeck, M., Schaller, K., & Blanke, O. (2018). Neural Sources and Underlying Mechanisms of Neural Responses to Heartbeats, and their Role in Bodily Self-consciousness: An Intracranial EEG Study. *Cerebral Cortex*, *28*(7), 2351-2364. https://doi.org/10.1093/cercor/bhx136

Park, H.-D., Correia, S., Ducorps, A., & Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. *Nature Neuroscience*, *17*(4), 612-618. https://doi.org/10.1038/nn.3671

Park, H.-D., & Tallon-Baudry, C. (2014). The neural subjective frame: From bodily signals to perceptual consciousness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130208. https://doi.org/10.1098/rstb.2013.0208

Pascual-Leone, A., & Walsh, V. (2001). Fast Backprojections from the Motion to the Primary Visual Area Necessary for Visual Awareness. *Science*, *292*(5516), 510-512. https://doi.org/10.1126/science.1057099

Paul, L., & Schyns, P. G. (2003). Attention enhances feature integration. *Vision Research*, *43*(17), 1793-1798. https://doi.org/10.1016/S0042-6989(03)00270-0

Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: Distinguishing feature integration from detection. *Journal of Vision*, *4*(12), 12. https://doi.org/10.1167/4.12.12

Pelli, D. G., & Tillman, K. A. (2008). The uncrowded window of object recognition. *Nature Neuroscience*, *11*(10), 1129-1135. https://doi.org/10.1038/nn.2187

Pelli, D. G., Tillman, K. A., Freeman, J., Su, M., Berger, T. D., & Majaj, N. J. (2007). Crowding and eccentricity determine reading rate. *Journal of Vision*, *7*(2), 20. https://doi.org/10.1167/7.2.20

Perakakis, P., Joffily, M., Taylor, M., Guerra, P., & Vila, J. (2010). KARDIA: A Matlab software for the analysis of cardiac interbeat intervals. *Computer Methods and Programs in Biomedicine*, *98*(1), 83-89. https://doi.org/10.1016/j.cmpb.2009.10.002

Percival, D. B., & Walden, A. T. (1993). Spectral Analysis for Physical Applications. *Spectral Analysis for Physical Applications*. https://ui.adsabs.harvard.edu/abs/1993sapa.book.....P/abstract

Peters, M. A. K., Kentridge, R. W., Phillips, I., & Block, N. (2017). Does unconscious perception really exist? Continuing the ASSC20 debate. *Neuroscience of Consciousness*, *2017*(1). https://doi.org/10.1093/nc/nix015

Petersen, A., Petersen, A. H., Bundesen, C., Vangkilde, S., & Habekost, T. (2017). The effect of phasic auditory alerting on visual perception. *Cognition*, *165*, 73-81. https://doi.org/10.1016/j.cognition.2017.04.004

Petersen, S. E., & Posner, M. I. (2012a). The Attention System of the Human Brain: 20 Years After. *Annual Review of Neuroscience*, *35*(1), 73-89. https://doi.org/10.1146/annurev-neuro-062111-150525

Petersen, S. E., & Posner, M. I. (2012b). The Attention System of the Human Brain: 20 Years After. *Annual Review of Neuroscience*, *35*(1), 73-89. https://doi.org/10.1146/annurev-neuro-062111-150525

Petzschner, F. H., Weber, L. A., Wellstein, K. V., Paolini, G., Do, C. T., & Stephan, K. E. (2019). Focus of attention modulates the heartbeat evoked potential. *NeuroImage*, *186,* 595-606. https://doi.org/10.1016/j.neuroimage.2018.11.037

Pfurtscheller, G., Stancák, A., & Neuper, Ch. (1996). Event-related synchronization (ERS) in the alpha band — an electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*(1), 39-46. https://doi.org/10.1016/S0167-8760(96)00066-9

Phillips, S., & Takeda, Y. (2009). Greater frontal-parietal synchrony at low gamma-band frequencies for inefficient than efficient visual search in human EEG. *International Journal of Psychophysiology*, *73*(3), 350-354. https://doi.org/10.1016/j.ijpsycho.2009.05.011

Phillips, S., Takeda, Y., & Singh, A. (2012). Visual Feature Integration Indicated by pHase-Locked Frontal-Parietal EEG Signals. *PLoS ONE*, *7*(3), e32502. https://doi.org/10.1371/journal.pone.0032502

Pins, D., & Ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral Cortex (New York, N.Y.*, *13*(5), 461-474. https://doi.org/10.1093/cercor/13.5.461

Poldrack, R. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*(2), 59-63. https://doi.org/10.1016/j.tics.2005.12.004

Pollatos, O., Herbert, B. M., Mai, S., & Kammer, T. (2016). Changes in interoceptive processes following brain stimulation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1708), 20160016. https://doi.org/10.1098/rstb.2016.0016

Pollatos, O., & Schandry, R. (2004). Accuracy of heartbeat perception is reflected in the amplitude of the heartbeat-evoked brain potential. *Psychophysiology*, *41*(3), 476-482.

Popov, T., Jensen, O., & Schoffelen, J.-M. (2018). Dorsal and ventral cortices are coupled by cross-frequency interactions during working memory. *NeuroImage*, *178*, 277-286. https://doi.org/10.1016/j.neuroimage.2018.05.054

Posner, M. I. (1978). *Chronometric explorations of mind.* Lawrence Erlbaum.

Posner, M. I. (1980). Orienting of attention. *Q J Exp Psychol*, *32*, 3-25.

Posner, M. I. (1994). Review Attention: The mechanisms of consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 7798-7403. https://doi.org/10.1073/pnas.91.16.7398

Posner, M. I., Klein, R., Summers, J., & Buggie, S. (1973). On the selection of signals. *Memory & cognition*, *1*, 2-12.

Posner, M. I., & Petersen, S. E. (1990). *The Attention System of the*

Human Brain.

Prinzmetal, W., Henderson, D., & Ivry, R. (1995). Loosening the Constraints on Illusory Conjunctions: Assessing the Roles of Exposure Duration and Attention. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(6), 1362-1375. https://doi.org/10.1037/0096-1523.21.6.1362

Prinzmetal, W., Presti, D. E., & Posner, M. I. (1986). Does attention affect visual feature integration? *Journal of Experimental Psychology: Human Perception and Performance*, *12*(3), 361-369. https://doi.org/10.1037/0096-1523.12.3.361

Putman, P., van Peer, J., Maimari, I., & van der Werff, S. (2010). EEG theta/beta ratio in relation to fear-modulated response-inhibition, attentional control, and affective traits. *Biological Psychology*, *83*(2), 73-78. https://doi.org/10.1016/j.biopsycho.2009.10.008

Putman, P., Verkuil, B., Arias-Garcia, E., Pantazi, I., & van Schie, C. (2014). EEG theta/beta ratio as a potential biomarker for attentional control and resilience against deleterious effects of stress on attention. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(2), 782-791. https://doi.org/10.3758/s13415-013-0238-7

Raccah, O., Block, N., & Fox, K. C. R. (2021). Does the Prefrontal Cortex Play an Essential Role in Consciousness? Insights from Intracranial Electrical Stimulation of the Human Brain. *The Journal of Neuroscience*, *41*(10), 2076-2087. https://doi.org/10.1523/JNEUROSCI.1141-20.2020

Rafal, R. D., Calabresi, P. A., Brennan, C. W., & Sciolto, T. K. (1989).

Saccade Preparation Inhibits Reorienting to Recently Attended Locations.

Rau, H., & Elbert, T. (2001). Psychophysiology of arterial baroreceptors and the etiology of hypertension. *Biological Psychology*, *57*(1-3), 179-201.

Rau, H., Pauli, P., Brody, S., Elbert, T., & Birbaumer, N. (1993). Baroreceptor stimulation alters cortical activity. *Psychophysiology*, *30*(3), 322-325.

Reisenzein, R., Meyer, W.-U., & Schützwohl, A. (1995). *James and the physical basis of emotion: A comment on Ellsworth.*

Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To See or not to See: The Need for Attention to Perceive Changes in Scenes. *Psychological Science*, *8*(5), 368-373. https://doi.org/10.1111/j.1467-9280.1997.tb00427.x

Reyes del Paso, G. A., Montoro, C. I., & Duschek, S. (2015). Reaction time, cerebral blood flow, and heart rate responses in fibromyalgia: Evidence of alterations in attentional control. *Journal of clinical and experimental neuropsychology*, *37*(4), 414-428.

Ribeiro, M. J., & Castelo-Branco, M. (2019). Neural correlates of anticipatory cardiac deceleration and its association with the speed of perceptual decision-making, in young and older adults. *NeuroImage*, *199*, 521-533. https://doi.org/10.1016/j.neuroimage.2019.06.004

Richter, C. G., Babo-Rebelo, M., Schwartz, D., & Tallon-Baudry, C. (2017). Phase-amplitude coupling at the organism level: The amplitude of spontaneous alpha rhythm fluctuations varies with the phase of the infra-slow gastric basal rhythm. *NeuroImage*, *146*, 951-958.

Richter, C. G., Coppola, R., & Bressler, S. L. (2018). Top-down beta oscillatory signaling conveys behavioral context in early visual cortex. *Scientific Reports*, *8*(1), 6991. https://doi.org/10.1038/s41598-018-25267-1

Richter, C. G., Thompson, W. H., Bosman, C. A., & Fries, P. (2017). Top-Down Beta Enhances Bottom-Up Gamma. *The Journal of Neuroscience*, *37*(28), 6698-6711. https://doi.org/10.1523/JNEUROSCI.3771-16.2017

Rieder, M. K., Rahm, B., Williams, J. D., & Kaiser, J. (2011). Human gamma-band activity and behavior. *International Journal of Psychophysiology*, *79*(1), 39-48. https://doi.org/10.1016/j.ijpsycho.2010.08.010

Ripoll, D. R. (2010). *Fundamentos de Psicobiología*. Editorial UOC.

Robertson, I. H., Mattingley, J. B., Rorden, C., & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature*, *395*(6698), Article 6698. https://doi.org/10.1038/25993

Robertson, L. C. (2003). Binding, spatial attention and perceptual awareness. *Nature Reviews Neuroscience*, *4*(2), 93-102. https://doi.org/10.1038/nrn1030

Rodríguez-San Esteban, P., Chica, A., & Paz-Alonso, P. (2022). Functional characterization of correct and incorrect feature integration. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhac147

Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face-related expectations in the brain. *PLOS ONE*, *16*(7), e0255116. https://doi.org/10.1371/journal.pone.0255116

Rohenkohl, G., Bosman, C. A., & Fries, P. (2018). Gamma Synchronization between V1 and V4 Improves Behavioral Performance. *Neuron*, *100*(4), 953-963.e3. https://doi.org/10.1016/j.neuron.2018.09.019

Rohenkohl, G., Gould, I. C., Pessoa, J., & Nobre, A. C. (2014). Combining spatial and temporal expectations to improve visual perception. *Journal of Vision*, *14*(4), 8-8. https://doi.org/10.1167/14.4.8

Romei, V., Driver, J., Schyns, P. G., & Thut, G. (2011). Rhythmic TMS over Parietal Cortex Links Distinct Brain Frequencies to Global versus Local Visual Processing. *Current Biology*, *21*(4), 334-337. https://doi.org/10.1016/j.cub.2011.01.035

Romei, V., Rihs, T., Brodbeck, V., & Thut, G. (2008). Resting electroencephalogram alpha-power over posterior sites indexes baseline visual cortex excitability. *NeuroReport*, *19*(2), 203-208. https://doi.org/10.1097/WNR.0b013e3282f454c4

Ronchi, R., Bello-Ruiz, J., Lukowska, M., Herbelin, B., Cabrilo, I., Schaller, K., & Blanke, O. (2015). Right insular damage decreases heartbeat awareness and alters cardio-visual effects on bodily self-consciousness. *Neuropsychologia*, *70*, 11-20. https://doi.org/10.1016/j.neuropsychologia.2015.02.010

Rouhinen, S., Panula, J., Palva, J. M., & Palva, S. (2013). Load Dependence of β and γ Oscillations Predicts Individual Capacity of Visual Attention. *Journal of Neuroscience*, *33*(48), 19023-19033. https://doi.org/10.1523/JNEUROSCI.1666-13.2013

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in Cognitive Sciences*, *18*(1), 16-25. https://doi.org/10.1016/j.tics.2013.10.010

Roux, F., Wibral, M., Mohr, H. M., Singer, W., & Uhlhaas, P. J. (2012). Gamma-Band Activity in Human Prefrontal Cortex Codes for the Number of Relevant Items Maintained in Working Memory. *Journal of Neuroscience*, *32*(36), 12411-12420. https://doi.org/10.1523/JNEUROSCI.0421-12.2012

Rungratsameetaweemana, N., & Serences, J. T. (2019). Dissociating the impact of attention and expectation on early sensory processing. *Current Opinion in Psychology*, *29*, 181-186. https://doi.org/10.1016/j.copsyc.2019.03.014

Salvia, E., Guillot, A., & Collet, C. (2012). Autonomic nervous system correlates to readiness state and negative outcome during visual discrimination tasks. *International Journal of Psychophysiology*, *84*(2), 211-218. https://doi.org/10.1016/j.ijpsycho.2012.02.010

Sammer, G., Blecker, C., Gebhardt, H., Bischoff, M., Stark, R., Morgen, K., & Vaitl, D. (2007). Relationship between regional hemodynamic activity and simultaneously recorded EEG-theta associated with mental arithmetic-induced workload. *Human Brain Mapping*, *28*(8), 793-803. https://doi.org/10.1002/hbm.20309

Saper, C. B. (2002). The central autonomic nervous system:

Conscious visceral perception and autonomic pattern generation. *Annual Review of Neuroscience*, *25*, 433-469. https://www.proquest.com/docview/198861111/abstract/9978D7884B964A5APQ/1

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1015-1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., Gruber, W., & Birbaumer, N. (2006). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *The European journal of neuroscience*, *22*, 2917-2926. https://doi.org/10.1111/j.1460-9568.2005.04482.x

Schandry, R., & Weitkunat, R. (1990). Enhancement of heartbeat-related brain potentials through cardiac awareness training. *International Journal of Neuroscience*, *53*(2-4), 243-253.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-Prime: User's guide*. Psychology Software Incorporated.

Schroeder, S. C. Y., Ball, F., & Busch, N. A. (2018). The role of alpha oscillations in distractor inhibition during memory retention. *European Journal of Neuroscience*, *48*(7), 2516-2526. https://doi.org/10.1111/ejn.13852

Schurger, A., Cowey, A., & Tallon-Baudry, C. (2006). Induced gamma-band oscillations correlate with awareness in hemianopic patient GY. *Neuropsychologia*, *44*(10), 1796-1803. https://doi.org/10.1016/j.neuropsychologia.2006.03.015

Schutter, D. J. L. G., & Van Honk, J. (2005). Electrophysiological ratio markers for the balance between reward and punishment. *Cognitive Brain Research*, *24*(3), 685-690. https://doi.org/10.1016/j.cogbrainres.2005.04.002

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., Reiss, A. L., & Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, *27*(9), 2349-2356.

Sel, A., Azevedo, R. T., & Tsakiris, M. (2016). Heartfelt Self: Cardio-Visual Integration Affects Self-Face Recognition and Interoceptive Cortical Processing. *Cerebral Cortex*, cercor;bhw296v1. https://doi.org/10.1093/cercor/bhw296

Senkowski, D., & Herrmann, C. S. (2002). Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task. *Clinical Neurophysiology*, *113*(11), 1742-1753. https://doi.org/10.1016/S1388-2457(02)00266-3

Senkowski, D., Schneider, T. R., Foxe, J. J., & Engel, A. K. (2008). Crossmodal binding through neural coherence: Implications for multisensory processing. *Trends in Neurosciences*, *31*(8), 401-409. https://doi.org/10.1016/j.tins.2008.05.002

Sergeant, C., & Dehaene, S. (2004). Is consciousness a gradual phenomenon. *Psychological Science*, *15*, 11-19.

Seth, A. K. (2013). Interoceptive inference, emotion, and the embodied self. *Trends in Cognitive Sciences*, *11*(17), 565-573.

Seth, A. K., & Bayne, T. (2022). Theories of consciousness. *Nature Reviews Neuroscience*, *23*(7), Article 7. https://doi.org/10.1038/s41583-022-00587-4

Shafritz, K., Gore, J., & Marois, R. (2002a). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 10917-10922. https://doi.org/10.1073/pnas.152694799

Shafritz, K., Gore, J., & Marois, R. (2002b). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 10917-10922. https://doi.org/10.1073/pnas.152694799

Shapiro, K. L., Raymond, J. E., & Arnell, K. M. (1997). The attentional blink. *Trends in Cognitive Sciences*, *1*(8), 291-296.

Sherman, M. T., Seth, A. K., Barrett, A. B., & Kanai, R. (2015). Prior expectations facilitate metacognition for perceptual decision. *Consciousness and Cognition*, *35*, 53-65. https://doi.org/10.1016/j.concog.2015.04.015

Shore, D. I., McLaughlin, E. N., & Klein, R. M. (2001). Modulation of the attentional blink by differential resource allocation. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, *55*(4), 318-324. https://doi.org/10.1037/h0087379

Shu, N., Gao, Z., Chen, X., & Liu, H. (2015). Computational Model of Primary Visual Cortex Combining Visual Attention for Action Recognition. *PLOS ONE*, *10*(7), e0130569. https://doi.org/10.1371/journal.pone.0130569

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal Synchronization along the Dorsal Visual Pathway Reflects the Focus of Spatial Attention. *Neuron*, *60*(4), 709-719. https://doi.org/10.1016/j.neuron.2008.09.010

Simons, D. J., & Ambinder, M. S. (2005). Change Blindness: Theory and Consequences. *Current Directions in Psychological Science*, *14*(1), 44-48. https://doi.org/10.1111/j.0963-7214.2005.00332.x

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*(7), 261-267. https://doi.org/10.1016/S1364-6613(97)01080-2

Singer, W. (2013). Cortical dynamics revisited. *Trends in Cognitive Sciences*, *17*(12), 616-626. https://doi.org/10.1016/j.tics.2013.09.006

Singer, W., & Gray, C. M. (1995). Visual Feature Integration and the Temporal Correlation Hypothesis. *Annual Review of Neuroscience*, *18*(1), 555-586. https://doi.org/10.1146/annurev.ne.18.030195.003011

Sklar, A. Y., Levy, N., Goldstein, A., Mandel, R., Maril, A., & Hassin, R. R. (2012). Reading and doing arithmetic nonconsciously. *Proceedings of the National Academy of Sciences*, *109*(48), 19614-19619. https://doi.org/10.1073/pnas.1211645109

Skora, L. I., Livermore, J. J. A., & Roelofs, K. (2022). The functional role of cardiac activity in perception and action. *Neuroscience & Biobehavioral Reviews*, *137*, 104655. https://doi.org/10.1016/j.neubiorev.2022.104655

Smith, E. E., & Jonides, J. (1999). *Storage and Executive Processes in the Frontal Lobes. 283*.

Smith, M. L., Gosselin, F., & Schyns, P. G. (2006). Perceptual moments of conscious visual experience inferred from oscillatory brain activity. *Proceedings of the National Academy of Sciences*, *103*(14), 5626-5631. https://doi.org/10.1073/pnas.0508972103

Smith, R., Thayer, J. F., Khalsa, S. S., & Lane, R. D. (2017). The hierarchical basis of neurovisceral integration. *Neuroscience & Biobehavioral Reviews*, *75*, 274-296. https://doi.org/10.1016/j.neubiorev.2017.02.003

Snyder, S. M., & Hall, J. R. (2006). A Meta-analysis of Quantitative EEG Power Associated With Attention-Deficit Hyperactivity Disorder: *Journal of Clinical Neurophysiology*, *23*(5), 441-456. https://doi.org/10.1097/01.wnp.0000221363.12503.78

Sokolov, E. N. (1963). *Perception and the conditioned reflex*.

Somsen, R. J. M., Jennings, J. R., & Van der Molen, M. W. (2004). The cardiac cycle time effect revisited: Temporal dynamics of the central-vagal modulation of heart rate in human reaction time tasks. *Psychophysiology*, *41*(6), 941-953. https://doi.org/10.1111/j.1469-8986.2004.00241.x

Son, D., Rover, M., De Blasio, F. M., Does, W., Barry, R. J., & Putman, P. (2019). Electroencephalography theta/beta ratio covaries with mind wandering and functional connectivity in the executive control network. *Annals of the New York Academy of Sciences*, *1452*(1), 52-64. https://doi.org/10.1111/nyas.14180

Soto, D., & Humphreys, G. W. (2009). *Semantically induced distortions of visual awareness in a patient with Balint's syndrome*. 5.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*(11), 1-29. https://doi.org/10.1037/h0093759

Stankovski, T., Ticcinelli, V., McClintock, P. V. E., & Stefanovska, A. (2017). Neural Cross-Frequency Coupling Functions. *Frontiers in Systems Neuroscience*, *11*, 33. https://doi.org/10.3389/fnsys.2017.00033

Staudigl, T., & Hanslmayr, S. (2013). Theta Oscillations at Encoding Mediate the Context-Dependent Nature of Human Episodic Memory. *Current Biology*, *23*(12), 1101-1106. https://doi.org/10.1016/j.cub.2013.04.074

Stefanics, G., Hangya, B., Hernádi, I., Winkler, I., Lakatos, P., & Ulbert, I. (2010). Phase Entrainment of Human Delta Oscillations Can Mediate the Effects of Expectation on Reaction Speed. *Journal of Neuroscience*, *30*(41), 13578-13585. https://doi.org/10.1523/JNEUROSCI.0703-10.2010

Stein, T. (2019). *The Breaking Continuous Flash Suppression Paradigm* (pp. 1-38). https://doi.org/10.4324/9780429469688-1

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of experimental psychology*, *18*(6), 643.

Strüber, D., Basar-Eroglu, C., Hoff, E., & Stadler, M. (2000). Reversal-rate dependent differences in the EEG gamma-band during multistable visual perception. *International Journal of Psychophysiology*, *38*(3), 243-252. https://doi.org/10.1016/S0167-8760(00)00168-9

Sturm, W., & Willmes, K. (2001). On the Functional Neuroanatomy of Intrinsic and Phasic Alertness. *NeuroImage*, *14*(1), S76-S84. https://doi.org/10.1006/nimg.2001.0839

Summerfield, C., & De Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience*, *15*(11), 745-756. https://doi.org/10.1038/nrn3838

Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences*, *13*(9), 403-409. https://doi.org/10.1016/j.tics.2009.06.003

Summerfield, J. J., Lepsien, J., Gitelman, D. R., Mesulam, M. M., & Nobre, A. C. (2006). Orienting Attention Based on Long-Term Memory Experience. *Neuron*, *49*(6), 905-916. https://doi.org/10.1016/j.neuron.2006.01.021

Sweeney-Reed, C. M., Riddell, P. M., Ellis, J. A., Freeman, J. E., & Nasuto, S. J. (2012). Neural Correlates of True and False Memory in Mild Cognitive Impairment. *PLoS ONE*, *7*(10), e48357. https://doi.org/10.1371/journal.pone.0048357

Tallon-Baudry, C. (2009). The roles of gamma-band oscillatory synchrony in human visual cognition. *Frontiers in Bioscience (Landmark Edition)*, *14*, 321-332. https://doi.org/10.2741/3246

Tallon-Baudry, C. (2012). On the Neural Mechanisms Subserving Consciousness and Attention. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00397

Tallon-Baudry, C., & Bertrand, O. (1999). Activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*(4), 12.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus Specificity of Phase-Locked and Non-Phase-Locked 40 Hz Visual Responses in Human. *The Journal of Neuroscience*, *16*(13), 4240-4249.

https://doi.org/10.1523/JNEUROSCI.16-13-04240.1996

Tallon-Baudry, C., Campana, F., Park, H.-D., & Babo-Rebelo, M. (2018). The neural monitoring of visceral inputs, rather than attention, accounts for first-person perspective in conscious vision. *Cortex*, *102*, 139-149. https://doi.org/10.1016/j.cortex.2017.05.019

Tamura, M., Spellman, T. J., Rosen, A. M., Gogos, J. A., & Gordon, J. A. (2017). Hippocampal-prefrontal theta-gamma coupling during performance of a spatial working memory task. *Nature Communications*, *8*(1), 2182. https://doi.org/10.1038/s41467-017-02108-9

Thayer, J. F., Åhs, F., Fredrikson, M., Sollers, J. J., & Wager, T. D. (2012). A meta-analysis of heart rate variability and neuroimaging studies: Implications for heart rate variability as a marker of stress and health. *Neuroscience and Biobehavioral Reviews*, *36*(2), 747-756.

Thayer, J. F., & Lane, R. D. (2009). Claude Bernard and the heart–brain connection: Further elaboration of a model of neurovisceral integration. *Neuroscience & Biobehavioral Reviews*, *33*(2), 81-88. https://doi.org/10.1016/j.neubiorev.2008.08.004

Thut, G. (2006a). -Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *Journal of Neuroscience*, *26*(37), 9494-9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Thut, G. (2006b). -Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *Journal of Neuroscience*, *26*(37), 9494-9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Tiitinen, H. T., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., & Näätänen, R. (1993). Selective attention enhances the auditory 40-Hz transient response in humans. *Nature*, *364*(6432), Article 6432. https://doi.org/10.1038/364059a0

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular Rivalry and Visual Awareness in Human Extrastriate Cortex. *Neuron*, *21*(4), 753-759. https://doi.org/10.1016/S0896-6273(00)80592-9

Tononi, G. (2004). An information integration theory of consciousness. *BMC Neuroscience*, *5*(1), 42. https://doi.org/10.1186/1471-2202-5-42

Tononi, G. (2008). Consciousness as Integrated Information: A Provisional Manifesto. *The Biological Bulletin*, *215*(3), 216-242. https://doi.org/10.2307/25470707

Tononi, G. (2012). *Integrated information theory of consciousness: An updated account*. *150*, 290-326.

Tononi, G., Boly, M., Massimini, M., & Koch, C. (2016). Integrated information theory: From consciousness to its physical substrate. *Nature Reviews Neuroscience*, *17*(7), Article 7. https://doi.org/10.1038/nrn.2016.44

Tootell, R. B. H., Hadjikhani, N. K., Vanduffel, W., Liu, A. K., Mendola, J. D., Sereno, M. I., & Dale, A. M. (1998). Functional analysis of primary visual cortex (V1) in humans. *Proceedings of the National Academy of Sciences*, *95*(3), 811-817. https://doi.org/10.1073/pnas.95.3.811

Townsend, J. T., & Ashby, F. G. (1983). *The stochastic modeling of* *elementary psychological processes*. Cambridge University Press.

Traub, R. D., Whittington, M. A., Colling, S. B., Buzsáki, G., & Jefferys, J. G. (1996). Analysis of gamma rhythms in the rat hippocampus in vitro and in vivo. *The Journal of Physiology*, *493*(2), 471-484. https://doi.org/10.1113/jphysiol.1996.sp021397

Treisman, A. (1998). *Feature binding, attention and object perception*.

Treisman, A. M. (1996). The binding problem. *Current Opinion in Neurobiology*, *6*(2), 171-178. https://doi.org/10.1016/S0959-4388(96)80070-5

Treisman, A. M., & Gelade, G. (1980). A Feature-Integration Theory of Attention. *Cognitive Psychology*, *12*, 97-136. https://doi.org/OOlO-0285/80/010097-40$05.00/O

Treisman, A. M., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, *14*(1), 107-141. https://doi.org/10.1016/0010-0285(82)90006-8

Trujillo, L. T., & Allen, J. J. B. (2007). Theta EEG dynamics of the error-related negativity. *Clinical Neurophysiology*, *118*(3), 645-668. https://doi.org/10.1016/j.clinph.2006.11.009

Tsuchiya, N., & Adolphs, R. (2007). Emotion and consciousness. *Trends in Cognitive Sciences*, *11*(4), 158-167. https://doi.org/10.1016/j.tics.2007.01.005

Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, *8*(8), 1096-1101. https://doi.org/10.1038/nn1500

Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V. A. F. (2015). No-Report Paradigms: Extracting the True Neural Correlates of

Consciousness. *Trends in Cognitive Sciences*, *19*(12), 757-770. https://doi.org/10.1016/j.tics.2015.10.002

Tzagarakis, C., Ince, N., Leuthold, A., & Pellizzer, G. (2010). Beta-Band Activity during Motor Planning Reflects Response Uncertainty. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *30*, 11270-11277. https://doi.org/10.1523/JNEUROSCI.6026-09.2010

Uddin, L. Q. (2015). Salience processing and insular cortical function and dysfunction. *Nature Reviews Neuroscience*, *16*(1), Article 1. https://doi.org/10.1038/nrn3857

Ullsperger, M., Danielmeier, C., & Jocham, G. (2014). Neurophysiology of performance monitoring and adaptive behavior. *Physiological reviews*, *94*(1), 35-79.

van den Berg, B., Appelbaum, L. G., Clark, K., Lorist, M. M., & Woldorff, M. G. (2016). Visual search performance is predicted by both prestimulus and poststimulus electrical brain activity. *Scientific Reports*, *6*(1), 37718. https://doi.org/10.1038/srep37718

Van der Heijden, A. H. C. (1992). *Selective attention in vision.*

van der Veen, F. M., van der Molen, M. W., Crone, E. A., & Jennings, J. R. (2004). Phasic heart rate responses to performance feedback in a time production task: Effects of information versus valence. *Biological Psychology*, *65*(2), 147-161. https://doi.org/10.1016/j.biopsycho.2003.07.003

Van Diest, I., Bradley, M. M., Guerra, P., Van den Bergh, O., & Lang, P. J. (2009). Fear-conditioned respiration and its association to cardiac reactivity. *Biological Psychology*, *80*(2), 212-217.

https://doi.org/10.1016/j.biopsycho.2008.09.006

van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *Journal of Neuroscience*, *28*(8), 1816-1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008

van Es, M. W. J., Marshall, T. R., Spaak, E., Jensen, O., & Schoffelen, J. (2022). Phasic modulation of visual representations during sustained attention. *European Journal of Neuroscience*, *55*(11-12), 3191-3208. https://doi.org/10.1111/ejn.15084

Van Gaal, S., Lamme, V. A., & Ridderinkhof, K. R. (2010). Unconsciously triggered conflict adaptation. *PloS one*, *5*(7), e11508. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0011508

Van Gaal, S., Naccache, L., Meuwese, J. D. I., Van Loon, A. M., Leighton, A. H., Cohen, L., & Dehaene, S. (2014). Can the meaning of multiple words be integrated unconsciously? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130212. https://doi.org/10.1098/rstb.2013.0212

van Son, D., De Blasio, F. M., Fogarty, J. S., Angelidis, A., Barry, R. J., & Putman, P. (2019). Frontal EEG theta/beta ratio during mind wandering episodes. *Biological Psychology*, *140*, 19-27. https://doi.org/10.1016/j.biopsycho.2018.11.003

van Son, D., Schalbroeck, R., Angelidis, A., van der Wee, N. J. A., van der Does, W., & Putman, P. (2018). Acute effects of caffeine on threat-selective attention: Moderation by anxiety and EEG theta/beta ratio. *Biological Psychology*, *136*, 100-110.

https://doi.org/10.1016/j.biopsycho.2018.05.006

Van Vugt, B., Dagnino, B., Vartak, D., Safaai, H., Panzeri, S., Dehaene, S., & Roelfsema, P. R. (2018). The threshold for conscious report: Signal loss and response bias in visual and frontal cortex. *Science*, *360*(6388), 537-542. https://doi.org/10.1126/science.aar7186

Vandierendonck, A. (2017). A comparison of methods to combine speed and accuracy measures of performance: A rejoinder on the binning procedure. *Behavior Research Methods*, *49*(2), 653-673. https://doi.org/10.3758/s13428-016-0721-5

Vangkilde, S., Coull, J. T., & Bundesen, C. (2012). Great expectations: Temporal expectation modulates perceptual processing speed. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(5), 1183-1191. https://doi.org/10.1037/a0026343

VanRullen, R. (2016). Perceptual Cycles. *Trends in Cognitive Sciences*, *20*(10), 723-735. https://doi.org/10.1016/j.tics.2016.07.006

Varela, F., Lachaux, J.-P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, *2*(4), 229-239. https://doi.org/10.1038/35067550

Veniero, D., Gross, J., Morand, S., Duecker, F., Sack, A. T., & Thut, G. (2021). Top-down control of visual cortex by the frontal eye fields through oscillatory realignment. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-021-21979-7

Verguts, T., & Van Opstal, F. (2005). Dissociation of the distance effect and size effect in one-digit numbers. *Psychonomic Bulletin & Review*, *12*(5), 925-930. https://doi.org/10.3758/BF03196787

Vernet, M., Japee, S., Lokey, S., Ahmed, S., Zachariou, V., & Ungerleider, L. (2019). Endogenous visuospatial attention increases visual awareness independent of visual discrimination sensitivity. *Neuropsychologia*, *128*, 297-304. https://doi.org/10.1016/j.neuropsychologia.2017.08.015

Viarouge, A., Hubbard, E. M., & McCandliss, B. D. (2014). The Cognitive Mechanisms of the SNARC Effect: An Individual Differences Approach. *PLoS ONE*, *9*(4), e95756. https://doi.org/10.1371/journal.pone.0095756

Vicente, J., Johannesen, L., Galeotti, L., & Strauss, D. G. (2013). ECGlab: User friendly ECG/VCG analysis tool for research environments. En *Computing in Cardiology 2013*. https://www.infona.pl//resource/bwmeta1.element.ieee-art-000006713492

Vidal, J. R., Chaumon, M., O'Regan, J. K., & Tallon-Baudry, C. (2006). Visual Grouping and the Focusing of Attention Induce Gamma-band Oscillations at Different Frequencies in Human Magnetoencephalogram Signals. *Journal of Cognitive Neuroscience*, *18*(11), 1850-1862. https://doi.org/10.1162/jocn.2006.18.11.1850

Vila, J., & Guerra, P. (2010). Introducción a la psicofisiología clínica. *Psicothema*, 355-356.

Vila, J., Guerra, P., Munoz, M., Vico, C., Viedmadeljesus, M., Delgado, L., Perakakis, P., Kley, E., Mata, J., & Rodriguez, S. (2007). Cardiac defense: From attention to action☆. *International Journal of Psychophysiology*, *66*(3), 169-182. https://doi.org/10.1016/j.ijpsycho.2007.07.004

von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, *38*(3), 301-313. https://doi.org/10.1016/S0167-8760(00)00172-0

Wessel, J. R., Danielmeier, C., & Ullsperger, M. (2011). Error Awareness Revisited: Accumulation of Multimodal Evidence from Central and Autonomic Nervous Systems. *Journal of Cognitive Neuroscience*, *23*(10), 3021-3036. https://doi.org/10.1162/jocn.2011.21635

Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160-168. https://doi.org/10.1016/j.tics.2011.02.005

Wokke, M. E., Vandenbroucke, A. R. E., Scholte, H. S., & Lamme, V. A. F. (2013). Confuse Your Illusion: Feedback to Early Visual Cortex Contributes to Perceptual Completion. *Psychological Science*, *24*(1), 63-71. https://doi.org/10.1177/0956797612449175

Wolfe, J., & Robertson, L. (2012). *From Perception to Consciousness: Searching with Anne Treisman*. OUP USA.

Wutz, A., Melcher, D., & Samaha, J. (2018). Frequency modulation of neural oscillations according to visual task demands. *Proceedings of the National Academy of Sciences*, *115*(6), 1346-1351. https://doi.org/10.1073/pnas.1713318115

Wyart, V., Nobre, A. C., & Summerfield, C. (2012). Dissociable prior influences of signal probability and relevance on visual contrast sensitivity. *Proceedings of the National Academy of Sciences*, *109*(9), 3593-3598. https://doi.org/10.1073/pnas.1120118109

Wyart, V., & Tallon-Baudry, C. (2008). Neural Dissociation between Visual Awareness and Spatial Attention. *Journal of Neuroscience*, *28*(10), 2667-2679. https://doi.org/10.1523/JNEUROSCI.4748-07.2008

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*(6706), 72-75. https://doi.org/10.1038/23936

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision*, *10*(10), 16-16. https://doi.org/10.1167/10.10.16

Yuval-Greenberg, S., Tomer, O., Keren, A. S., Nelken, I., & Deouell, L. Y. (2008). Transient Induced Gamma-Band Response in EEG as a Manifestation of Miniature Saccades. *Neuron*, *58*(3), 429-441. https://cir.nii.ac.jp/crid/1363951796249125760

Zaretskaya, N., & Bartels, A. (2015). Gestalt perception is associated with reduced parietal beta oscillations. *NeuroImage*, *112*, 61-69. https://doi.org/10.1016/j.neuroimage.2015.02.049

Zeki, S., & Bartels, A. (1999). Toward a theory of visual consciousness. *Consciousness and cognition*, *8*(2), 225-259. https://www.sciencedirect.com/science/article/pii/S1053810099903902?casa_token=-kDuEB1PwIgAAAAA:xEAOQpVwH44iyf5eK_phAxXV1rlnxq-cgZ3vCFSl-hOrnxYRXGFhst7jfDTn3gWqqy3 up-FbAQ

Zeman, A. (2001). *Consciousness. Brain, 124 (Pt 7), 1263-1289*.

Zhang, Y., Zhang, X., Wang, Y., & Fang, F. (2016). Misbinding of color and motion in human early visual cortex: Evidence from event-related potentials. *Vision Research*, *122*, 51-59. https://doi.org/10.1016/j.visres.2015.12.010

Zhang, Y., Zhang, Y., Cai, P., Luo, H., & Fang, F. (2019). The causal role of α-oscillations in feature binding. *Proceedings of the National Academy of Sciences*, *116*(34), 17023-17028. https://doi.org/10.1073/pnas.1904160116

Zhang, Y., Zhang, Y.-Y., & Fang, F. (2020). Neural mechanisms of feature binding. *Science China Life Sciences*, *63*(6), 926-928. https://doi.org/10.1007/s11427-019-1615-4

Zimmer, H., Vossel, G., & Fröhlich, W. (1990). Individual differences in resting heart rate and spontaneous electrodermal activity as predictors of attentional processes. *International journal of psychophysiology : official journal of the International Organization of Psychophysiology*, *8*, 249-259. https://doi.org/10.1016/0167-8760(90)90016-7

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