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Elaborato finale

Neural correlates of visual awareness

Correlati neurali della consapevolezza visiva

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Abstract: l'elaborato si propone di esporre le attuali evidenze riguardanti il modo in cui i contenuti soggettivi di consapevolezza visiva sono codificati a livello neurale. Sebbene i meccanismi neurali della percezione visiva siano ampiamente conosciuti, rimane ancora da chiarire come l'informazione visiva entri a far parte dei contenuti della coscienza. Per identificare i correlati neurali della coscienza (CNC), che rappresentano la minima attività neurale per una specifica esperienza conscia, vengono messe in relazione misure comportamentali di consapevolezza, limitatamente a stimoli presentati in un contesto sperimentale, con i sottostanti meccanismi neurali. Attraverso paradigmi sperimentali come la rivalità binoculare e tecniche di mascheramento visivo è possibile provare ad identificare i CNC contenuto-specifici utilizzando misure neurofisiologiche e tecniche di neuroimaging. Tali tecniche forniscono infatti utili informazioni circa le basi neuroanatomiche e funzionali dell'esperienza sotto esame. Sebbene i meccanismi che sottendono l'attenzione siano spesso associati all'esperienza cosciente, evidenze sperimentali suggeriscono una separazione tra i due processi. Le ricerche sui correlati neurali della consapevolezza visiva indicano come l'attività di una singola area cerebrale non possa essere necessaria e sufficiente a spiegare le qualità dei contenuti coscienti. Sembrerebbe invece essere necessaria una rappresentazione della scena visiva distribuita nella corteccia visiva primaria (V1) e nelle aree visive ventrali con attivazione di regioni temporo-parietali. Misure elettrofisiologiche come la visual awareness negativity (VAN) sono state correlate alla consapevolezza visiva mentre altri indicatori sembrerebbero essere maggiormente legati a processi attentivi. Diversi modelli teorici offrono spiegazioni empiriche sull'emergenza della coscienza dall'attività cerebrale. Nel caso della consapevolezza visiva, alcuni modelli teorici rilevanti sono la teoria dello spazio di lavoro neurale globale, la quale sottolinea la necessità di condivisione dell'informazione tra ampie aree cerebrali e la teoria dell'elaborazione ricorrente che si concentra invece sul feedback proveniente a V1 dalle aree extrastriate. Inoltre, il modello dell'"elaborazione predittiva" descrive la percezione cosciente come il risultato di un processo attivo in cui il cervello crea costantemente previsioni sull'ambiente circostante. Allo stato attuale, la ricerca sui correlati neurali della consapevolezza visiva evidenzia dunque come un *network* di regioni cerebrali posteriori sia fondamentale per avere esperienze visive coscienti. Inoltre, i segnali di feedback sembrano svolgere un ruolo cruciale, evidenziando le complesse interazioni tra dinamiche neurali e percezione cosciente.

Chapter 1: Introduction

Consciousness has always been a mystery since the first philosophers began to question the nature of the human mind and its relationship with matter. This enigma is exemplified by the various definitions ascribed to consciousness. Rosenthal (2009) characterizes it as “a condition of people and other creatures when they are awake and responsive to sensory stimulation.” In contrast, philosopher John R. Searle (2002) described consciousness as “those subjective states of sentience or awareness that begin when one awakes in the morning from a dreamless sleep and continue throughout one day until one goes to sleep at night, or fall into a coma, or dies, or otherwise become, as one would say, ‘unconscious’.” However, a general definition of consciousness remains unsettled, continually shaped by the influence of theoretical and philosophical assumptions (Vimal & Sansthana, 2010). In modern times, Descartes (1596-1650) proposed the idea of mind and matter being made of two distinct substances. This philosophical notion gave rise to dualism which posits that the mind is immaterial and responsible for consciousness, thoughts, and mental processes while the body is instead material and governed by the laws of physics. While some consider Descartes to be the first to place the study of consciousness outside the domain of science, it is important to note that he was an interactive dualist (Frith & Rees, 2017), in the sense that he suggested a possible interaction between mind and body. Thus, he might have addressed the concept of the neural correlates of consciousness before anyone else, recognizing that the brain has a key role in linking the mind with matter, even though he conceptualized it as an unconscious organ (Frith & Rees, 2017). Descartes explored the relationship between the mind and the physical realm, for instance, hypothesizing that sensory stimuli could elicit brain activity and in this way lead to specific sensations. Yet, he attributed consciousness solely to the pineal gland, considering it the only structure engaged in enabling interactions between the soul and the body (Frith & Rees, 2017).

Later on, Immanuel Kant (1724-1804) denied psychological experimentation to be possible because scientific methods require the use of experimental manipulations that are not available in strictly private mental phenomena (Frith & Rees, 2017). Because of this position, psychological investigations were slowed while other scientific domains developed much faster. Even when psychology started being acknowledged as a scientific discipline during the nineteenth century, thanks to the development of the methods of psychophysics, consciousness was studied only in its phenomenological aspects, mainly because of the lack of many methodological tools that are available nowadays. Behaviourism, a psychological school of thought that arose in the USA during the 1920s and 1930s, proposed the rejection of consciousness from scientific investigations, as it was regarded as part of the "black box." In this context, the black box stands as a metaphor for a hypothetical internal representation that cannot be directly observed and investigated through external observation. Because of this position, behaviourists focused solely on observable behaviour and stimuli-response associations. It was with the advent of cognitive psychology that researchers began to address the topic of consciousness, although they tended not to use this term, referring to it by using the concept of working memory instead. Working memory refers to a system responsible for temporarily holding and manipulating information that is needed for cognitive tasks, which could be equated to the contents of consciousness (Frith & Rees, 2017). The cognitivists focused on working memory as it was more easily quantifiable with behavioural experiments, avoiding the complexities of introspection (Frith & Rees, 2017). While behaviourism was taking root in America, the Gestalt movement was concurrently growing in Europe. This movement's interest lied in understanding the mechanisms that underlie perception, and with this aim it proposed the exploitation of a subset of perceptual illusions that would later be used to investigate some peculiarities of the human visual system. Notably, this movement brought attention to phenomena like bistable perception, which could be evoked by visual stimuli such as the Necker cube and the Rubin face/vase illusion (Figure 1.1) (Fisher, 1967). This particular phenomenon will be discussed later.

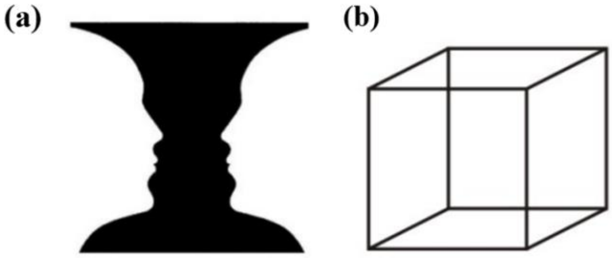

Figure 1.1 Contradictory interpretations in the Rubin Face/Vase **(a)** and Necker Cube **(b)** images (Rodriguez-Martìnez & Castillo-Parra. 2018)

Only in the late 80s has the topic of human consciousness begun to be taken seriously by neuroscientists, especially after Baars introduced the Global Workspace Theory (Baars, 1988). This theory suggests that the coordinated activity of a widespread brain network allows information to be integrated thanks to various cognitive processes, giving rise to conscious awareness. Since then, the main approach has been that to identify the "Neural Correlates of Consciousness" (NCCs), defined by Crick & Koch (1990a) as "the minimum neural activity necessary for the rise of a conscious experience." The NCCs are still under investigation, but upon their identification, the next step should be to better understand the causal relationship between neural events and subjective feelings, in order to finally shed light on the philosophical problem of *qualia* (Koch & Krick, 2002). The concept of *qualia* was introduced by C.I. Lewis in 1929, and it refers to the instances of a subjective experience, such as the *redness* of the colour red or the *pain* of a headache. Unfortunately, the concept of qualia is strictly related to the so-called "hard problem of consciousness" (Chalmers, 1995). The hard problem of consciousness refers to the question of why some physical processes in the brain give rise to distinctive subjective experiences while others do not. It also seeks to understand the connections between the qualities of subjective experiences and the underlying neural processes. For instance, it questions how the neural firing associated with pain does not lead to other feelings, such as joy, or why the neural impulses triggered by the sight of a red apple do not create a different experience like the smell of a rose fragrance (Chalmers, 1995). This issue raised the epistemological problem of explaining why and how humans (and presumably other species) have qualia.

The scientific quest to explain how brain activity generates the subjective mind turned out to be much more compelling than expected. This is significant as the most influential philosophy since the beginning of the research of the NCCs was a materialist reductionism. This philosophy posits that consciousness and subjective experience could be explained entirely through physical and neural processes in the brain. Since the 1990s, dozens of theories of consciousness have been put forth, yet the explanatory gaps seem to still be present. Some have argued that, in order to solve the "hard problem", a non-local theory of consciousness may be needed (Wahbeh, Radin, Cannard, & Delorme, 2022). Unlike perspectives that address consciousness as an emergent phenomenon of the brain, this approach extends beyond cerebral confines. Within this context, some theoretical frameworks, such as Kastrup's "analytic idealism" (Kastrup, 2021) or the increasingly considered panpsychism (Goff, 2017), regards consciousness as being fundamental, meaning that it precedes the physical substrates. These philosophical positions overlap to some extend but they differ in some features. Idealism posits that the physical world is not fundamental but rather entirely mental, suggesting that an object's existence relies on it being perceived by a mind. On the other hand, panpsychism views the world as both mental and physical, implying that an object could exist independently of perception because it is made up of particles that possess some degree of consciousness (Goff, 2017). However, these philosophical frameworks, although conceptualizing some elegant explanations for the hard problem, lack conceptual and empirical research programs. This deficiency hinders the development of new insights and experiments that might contribute to resolving the mind-body problem (Seth, 2022). Instead, Seth proposes to focus on what he calls the "real problem" which consists of trying to explain, predict, and control the properties of consciousness through the lens of physiological processes in the brain (Seth, 2022). Although not trying to solve the hard problem, this approach seeks to expand our comprehension of how conscious experiences can align and be regulated by neural mechanisms.

The importance of the term "minimum" in the definition of the NCCs is often stressed: if the aim is to identify NCCs, it is necessary to differentiate between neural activity that is a prerequisite for the conscious experience, like sensory processing and sufficient excitability to respond to incoming input, and the activity that is instead a consequence of the conscious experience, such as attentive states. To effectively identify the NCCs, researchers' focus should be on the core mechanisms that underlie conscious awareness itself. By doing so, they could pinpoint the neural processes necessary for conscious experience while avoiding the inclusion of secondary processes that are not directly related to the fundamental aspects of consciousness. Some authors (Koch, Massimini, Boly, & Tononi, 2016) have proposed to distinguish the NCCs into two main categories: the full NCC and the content-specific NCC, the first refers to the neural structures and mechanisms involved in supporting the conscious experience as a whole while the latter refers to the neuronal mechanisms that determine a particular experience.

For example, the NCCs for the content-specific perception of a house could be a neuronal assembly responding in a synchronized manner and placed in the parahippocampal place area, a brain region that activates when we observe places. Another author, Block (1996) provides a valuable functional distinction between two aspects of consciousness: phenomenal consciousness and access consciousness. The former is associated with the concept of qualia and can be described as "what it is like to have an experience." On the other hand, access consciousness pertains to the cognitive availability of information (Block, 1996). Phenomenally conscious states may not always be fully cognitively accessible, meaning individuals can experience them but might be unable to verbally report them. For instance, in the classic Sperling test (Sperling, 1960), subjects can perceive all the letters presented briefly, but they can only report a portion of them. In this example, the entire letter field reflects phenomenal consciousness, while the letters that can be accurately recalled and reported demonstrate access consciousness.

The majority of the studies concerning content-specific NCCs have focused on changes in visual awareness, also referred to as visual consciousness, mainly because the visual system has been studied deeply both anatomically and functionally. Indeed, having a comprehensive understanding of the organization of the visual system helps psychologists design experiments and interpret the findings related to visual perception. This allows them to investigate how the structure and function of the visual system influence the generation of conscious visual experiences, including the content and the overall quality of visual awareness. This can be accomplished through self-report measures, psychophysical experiments, or qualitative interviews that assess the clarity and level of detail perceived. Moreover, vision neuroscientists had developed different techniques that allow experimental manipulation of the contents of visual consciousness while maintaining constant stimulation (Kim & Blake, 2005). These approaches will be discussed in greater detail in the second Chapter. In a situation where sensory informational inputs remain constant, neural activity patterns recorded through neuroimaging methods like functional Magnetic Resonance Imaging (fMRI), electroencephalography (EEG), or magnetoencephalography (MEG) could be attributed to the NCCs rather than sensory processing. For example, consider an experiment where the stimuli are rendered invisible by a masking image. In such a scenario, the neural response pattern elicited during this condition is related to sensory processing alone. This recorded activation can be contrasted with the response from the overall neural activity linked to the perception of the stimulus. This comparison can be facilitated thanks to the "subtractive method" employed in neuroimaging studies. The subtractive method involves the comparison of neural activity patterns elicited across different experimental conditions. For instance, it allows researchers to subtract the neural responses elicited by the masked task (related to sensory processing alone) from the overall neural activity recorded during the comprehensive task (in this case, when the stimulus is consciously perceived). This methodological approach enables the extraction of neural responses that are attributed to conscious awareness. The coupling of psychophysical methods with neuroimaging and neurophysiological techniques permits the proper investigation of NCCs by observing which area becomes active using Positron Emission Tomography (PET) or fMRI or by better understanding the neural dynamics using EEG, MEG, and invasive electrophysiological techniques in non-human subjects. Both neuroimaging techniques and EEG-related methods have some advantages and disadvantages: spatial resolution using fMRI is optimal and is constantly improving by reducing the voxel size. A voxel is the three-dimensional counterpart to the two-dimensional pixel, containing information about the strength signal in a small volume of brain tissue. On the downside, temporal resolution is delayed. fMRI techniques rely on BOLD (Blood Oxygenation Level Dependent) signals as an indirect measure of neural activity. The BOLD signal changes in relation to blood oxygenation levels, reflecting the increased oxygen demand in active areas compared to inactive ones. Some authors have raised the question of whether the BOLD signal is actually a good measure of neuronal activation since it infers it only indirectly (Pike, 2012). EEG offers valuable temporal information, providing precise timing of neural activity. However, it presents challenges in localizing the specific brain areas involved in the observed activity. On the other hand, MEG surpasses EEG in terms of spatial resolution, allowing for more accurate identification of the brain regions responsible for the recorded neural signals. Transcranial Magnetic Stimulation (TMS) is also an important tool, as it is extremely useful for understanding the causal relationships between brain activity and visual perception by temporarily and selectively modulating cortical areas. In addition to these methods, lesion studies of neuropsychological cases could also be extremely informative about the role of specific brain areas, and therefore, are also examined in the search for NCCs. Before discussing NCCs in more detail, it is worth to provide a brief overview on the organization of the visual system.

1.1 – The visual system

Visual information coming from the external world in the form of light, which can have different intensities and wavelengths, reaches the retina by entering the eye through the pupil. The retina is a layered tissue containing different types of cells such as photoreceptors, bipolar cells, horizontal and amacrine cells, and ganglion cells (Wolfe et al., 2006). Photoreceptors, namely cons and rods, are respectively responsible for photic vision which provides high visual acuity and colour perception, and for scotopic vision which instead enables us to see even in dimly lit environments (Wolfe et al., 2006). Of particular interest are ganglion cells: the information coming from the photoreceptors converges into bipolar cells and then flows to a ganglion cell providing excitatory or inhibitory inputs. Each ganglion cell represents a receptive field, that is, a region on the retina and in the corresponding visual space (Wolfe et al., 2006). These regions can be either center-on or center-off. In the center-on receptive field, light stimulation in the central region elicits excitation of the cell, while the stimulation of the surrounding region inhibits it; the opposite is true for center-off cells (Hubel & Wiesel, 1961; Wolfe et al., 2006). The fovea is a retinal region that corresponds to the central visual field and is characterized by a high concentration of cone cells, indeed, the receptive fields in the fovea are smaller compared to the periphery, which is congruent with the differences in visual acuity on different parts of the retina: a stimulus in the fovea is viewed in detail, while this ability falls off with increasing eccentricity (Hubel & Wiesel, 1961; Wolfe et al., 2006).

Ganglion cells can be divided into two main categories: parvocellular (P) and magnocellular (M) cells. These two types of cells differ in some important features: the size of the receptive fields of P cells is much smaller and they tend to respond at sustained firing rates, whereas M cells have larger receptive fields and respond more transiently (Wolfe et al., 2006). Considering the different properties of P and M cells, we can infer that P cells provide information about the details of objects, while M cells analyze their spatiotemporal characteristics. All the axons of the ganglion cells converge into the "blind spot" of the retina, and the nerve bundles form the optic nerve that travels to the optic chiasm. This structure is where the fibers coming from nasal hemiretina of each eye decussate and constitute the optic tract. The optic tract is connected to the Lateral Geniculate Nucleus (LGN), although a small portion of its fibers project to some other structures: the Superior Colliculus (SC) in the midbrain, a structure that is thought to be important for guiding visuomotor behaviour (Cerkevich, Lyon, Balaram, & Kaas, 2014); the pretectal area, which is responsible for the pupillary light reflex (Carpenter & Pierson, 1973) and for the optokinetic reflex (Lázár, 1972); the suprachiasmatic nucleus of the hypothalamus, which regulates circadian rhythms (Hastings, Maywood, & Brancaccio, 2018). The LGN is a bilateral six-layered structure located in the thalamus, characterized by four dorsal layers containing parvocellular neurons and two ventral magnocellular layers. The first, fourth, and sixth layers receive their input from the contralateral eye, whereas the other three layers receive information from the ipsilateral eye (Minkowski, 1920; Wolfe et al., 2006). As a result of the decussation of optic nerve fibers at the optic chiasm, the left and the right LGN represent each the contralateral visual field and their receptive fields are similar to those of the retina. The signals then flow into the V1 via the optic radiation.

It is interesting to observe that the feedback projections from the visual cortex to the LGN exceed in great numbers the LGN projections: it seems that the feedback is an important component of the cortico-thalamic circuitry that sustains many cognitive functions such as attention. Moreover, this mechanism plays a significant role in contour discrimination, and movement detection (Cudeiro & Sillito, 2006). The primary visual cortex (V1) is the first cortical visual structure that receives the signals from the optic radiation. V1 is located in the occipital lobe in correspondence with the calcarine fissure, a sulcus located in the medial surface of the occipital lobe. Just like the LGN, each V1 hemisphere receives information from the contralateral visual hemifield. V1 is divided into six layers: neurons in the fourth layer synapse with axons originating from the LGN. In more detail, sub-layer IVCα receives magnocellular inputs, while layer IVCβ processes information coming from the parvocellular pathway (Callaway, 1998; Hubel & Wiesel, 1972). Retinotopic organization and cortical magnification are two important features of V1: the organization of the primary visual cortex reflects that of the retina but the most central portion, where the receptive fields are smaller, occupies a much larger cortical area compared to the peripheral retina (Fox, Miezin, Allan, Essen, & Raichle, 1987). Importantly, the receptive fields coming from ganglion cells become increasingly complex along the visual cortex. The receptive field of V1 simple cells are the result of the partial fusion of classical receptive fields, which can detect lines or edges in a specific orientation with a tuning curve, a graphical representation of the neuron's preferred stimuli and its corresponding firing strength in response to stimuli presented at different orientation (Hubel & Wiesel, 1962; Ringach, Hawken, & Shapley, 1997; Olshausen & Field, 2005). Complex cells also exist in V1; they lack well-defined excitatory and inhibitory positions and respond to stimuli in a specific orientation like simple cells but are also able to detect motion. Hubel and Wiesel suspected that the receptive fields of these cells are created by spatial summation of simple cells' receptive fields, whose inputs are integrated into a single unit (Hubel & Wiesel, 1962; Olshausen & Field, 2005). Lastly, hypercomplex cells, also known as end-stopped cells, are a kind of complex cells that are also sensitive to stimulus length (Hubel & Wiesel, 1962; Olshausen & Field, 2005). Hubel and Wiesel observed that the primary visual cortex has a columnar organization: neurons that detect a particular orientation are placed in the cortex next to other neurons that detect a slightly different orientation. An ocular dominance column is a unit involved in processing the visual information of one eye only; left-eye and right-eye columns are always placed next to each other so that binocular vision is possible. One hypercolumn is made up of two ocular dominance columns, one for each eye, that allow the processing of all the information coming from a small portion of the visual field (Hubel, 1982; Olshausen & Field, 2005).

Once visual stimuli are processed in V1, which is also known as "striate cortex" due to the striped pattern on its surface, information on their different features is conveyed to extrastriate visual areas. Underleider and Mishkin (1982) distinguished a ventral and a dorsal stream of information, with the first reaching the inferotemporal cortex and the second reaching the posterior parietal region (Ungerleider & Mishkin, 1982). Roughly speaking, the two systems are thought to specialize in object recognition and spatial perception respectively. However, more recent findings challenge the distinction of these functions. Notably, Freud, Behrmann, and Snow, (2020) indicates that the dorsal stream, traditionally associated with spatial perception and to guide actions (Goodale & Milner, 1992), also plays a role in some aspects of perception such as shape processing. This suggests that the dorsal pathway is not exclusively dedicated to the mentioned processes but is also involved in object perception (Freud, Behrmann, & Snow, 2020). The two streams can be traced back to the parvocellular pathway for the ventral system and the magnocellular pathway for the dorsal system (Livingstone & Hubel, 1988); however, it seems that both streams receive signals from both the parvo and magno pathways (Maunsell, Sclar, & Nealy, 1991). In the vicinity just after area V1, we find that V2 area receives a strong feedforward connection from V1, but it also sends feedback signals to it (Rockland & Virga, 1989). In this region, the information regarding colour and texture is further processed (Perrett & Oram, 1993; Conway, 2003) before being sent to the V3 area, where the motion characteristics of the visual scene are further processed (Braddick et al., 2001). Area V4 sets the way for the ventral stream by further analyzing object features, while the middle temporal visual area (V5 or MT) processes motion and sends input to the MST region, and ultimately to the Posterior Parietal Cortex (PPC), the destination of the dorsal pathway where spatial perception and guidance of actions based on visual stimulation occur (Goodale & Milner, 1992). Area V4 is involved in color and shape feature processing, and signals flow to the inferotemporal cortex (ITC), whose neurons respond to specific objects or complex stimuli (Gross, 2008). Within the ITC, we can find some specialized regions such as the Fusiform Face Area (FFA), which has been linked to the recognition of faces, the Parahippocampal Place Area (PPA), which responds to places (Epstein & Kanwisher, 1988), and some other areas like the Extrastriate Body Area and the Lateral Occipital Complex (LOC) that respond to body parts and objects, respectively (Grill-Spector, Kourtzi, & Kanwisher, 2001; Kanwisher, 2010).

It is to be noted that a salient characteristic of visual physiology in the study of NCCs is the consistent amount of re-entrant neural activity. As mentioned above, feedback from V1 to the LGN is considerable, but it seems that this kind of circuitry also applies to higher areas in the visual hierarchy, such as in the ITC. The prefrontal cortex is a structure involved in executive functions such as working memory, selective attention, planning, and decision-making (Gazzaley et al., 2007, Coutlee & Huettel, 2012). Top-down signals from the prefrontal cortex to the ITC might be important for object recognition and cognitive processing, and feedback to V1 coming from frontal areas is thought to modulate visual attention and can influence the selection and prioritization of visual information (Lamme & Roelfsema, 2000; Kveraga, Ghuman, & Bar, 2007). These feedback interconnections spanning across distant brain areas highlight the important role of interconnectivity within the neural mechanisms that sustain visual processing and the emergence of conscious awareness. In Chapter 3, feedback activity will be delved in greater detail. However, before examining the neural substrate of visual consciousness, it is worth understanding the main experimental paradigms as well as the confounding variables in research.

Chapter 2: Theoretical Foundations

This Chapter is dedicated to an in-depth exploration of the experimental paradigms used in the quest to uncover the Neural Correlates of Consciousness (NCCs), delving into the intricate relationship between attention and consciousness. The initial section will focus on a review of the main psychophysical paradigms applied in the investigation of visual awareness. Special attention will be given to elucidating the advantages and limitations of each technique, while highlighting how the integration of these methods with neuroimaging and neurophysiological techniques yields valuable insights into the neural basis of visual consciousness. Furthermore, an essential aspect of this exploration involves differentiating attention from consciousness, given their complex interplay and profound influence on our perceptual experiences. Substantial evidence supporting the dissociation of these two processes will be presented, and the candidate neural mechanisms underlying some features of attention will be explicated. Through this synthesis of experimental paradigms and the examination of attention-consciousness interactions, I aim to provide a comprehensive overview for approaching the complexities of NCCs research.

2.1 – Experimental paradigms

If the aim is to empirically study the neural correlates of visual awareness, it is advisable to employ an experimental setting where stimulation is constant but the content of visual consciousness is not: the NCCs could then be identified based on whether the presence or absence of a conscious experience is the only variable between conditions. By contrasting the neural activity registered when a stimulus gets access to awareness with the neural correlates of a stimulus processed unconsciously the result would be a reliable content-specific NCC (Kim & Blake, 2005). For instance, the previously mentioned "subtractive method" in neuroimaging is widely employed as it allows researchers to look for differences in brain activity between two tasks in order to highlight the specific brain areas that activate solely during the main task. Measuring visual awareness using psychophysical methods typically requires the subject to respond in a dichotomous manner, with yes/no judgments. Among psychophysical techniques, visual masking has been widely used to study visual awareness. Visual masking exists in two variants, backward and forward masking. In forward masking, a target is rapidly followed by a mask that renders it invisible, whereas in backward masking, the mask precedes the target, making it invisible. Backward masking produces target undetectability by disrupting central processing, whereas forward masking interferes with early sensory processing. However, this method has some limitations: the mask must appear in close spatial and temporal proximity to the target, and it cannot make the target invisible for sustained periods; moreover, sometimes the target can still be detectable, yet unidentifiable (Kim & Blake, 2005).

Bistable perception is another commonly exploited phenomenon in the context of visual consciousness research. This phenomenon arises from the observation of bistable figures and binocular rivalry. Bistable figures induce bistable perception by virtue of them offering mutually exclusive interpretations pertaining figure-ground segregation, such as Rubin's face/vase illusion, or depth relations, as in the case of the Necker cube (Figure 1.1, pp. 5). In these conditions, the stimulation is constant despite the changes in awareness that follow one perceptual interpretation or the other, and these changes reflect the neural underpinnings of visual awareness (Leopold, D.A. & Logothetis, N.K., 1999). The perceptual reversals favouring one or the other interpretation occur over time and must reflect changes in the activity of neural assemblies that support either of the two possible visual states. Signal Detection Theory (SDT) serves as a powerful tool for investigating interindividual differences in perceptual thresholds, which refers to the minimum intensity needed to detect a stimulus. SDT allows the measurement of two key parameters: discriminability (d'), also known as detection sensitivity, assesses the ability of the participant to distinguish between the presence and absence of the stimulus, with a higher d' value indicating greater perceptual sensitivity. Additionally, the response criterion (c) represents the threshold an observer sets to decide whether the stimulus is present or absent. These measurements enable an investigation into the influence of weak or uncertain stimuli on perceptual thresholds and help reveal any response bias participants might exhibit. However, in the context of bistable perception triggered by bistable images, because the possible interpretations are mutually exclusive, the criterion problems are minimized (Kim & Blake, 2005). Unfortunately, the unpredictable timing of perceptual reversals does not allow a precise coupling of each state with external events, such as the onset of fMRI scans or the delivery of stimulation at the appropriate timepoint using TMS or tDCS (transcranial Direct Current Stimulation). On the other hand, binocular rivalry is a widespread technique that produces bistable perception by presenting two different images to the two eyes. Here, the perceptual fluctuations result from visual conflict, where the brain struggles with the processing of two stimuli because it receives two conflicting information. This occurs when the two eyes are exposed to different images, a situation distinct from the ambiguity typically associated with bistable figures. An important feature of binocular rivalry is that it is possible to use a wide variety of stimuli that can elicit responses in some specific brain areas (Kim & Blake, 2005). Tong & others (1998) used a face and a house as stimuli and observed that the FFA area was active when the face was seen while PPA response grew when the house was perceived (Tong, Nakayama, Vaughan, & Kanwisher, 1998). It seems that perceptual changes occur as consequences of both bottom-up mechanisms (such as neural fatigue) and top-down processes like expectation and attention (Long & Toppino, 2004). Bottom-up processes refers to the effects attributed to the physical characteristics of the stimulus. For instance, when individuals are exposed to an unambiguous version of a bistable image before being presented with the standard bistable image (Figure 2.1), they subsequently tend to report perceiving the alternative version of the image (Long & Toppino, 2004). This phenomenon, known as adaptation effect, is the result of neuronal fatigue of the assembly responsible for perceiving the adapted version of the image. However, in order to experience the adaptation effect, prolonged stimulation time is required as well as the retinal correspondence between the adapted stimulus and the bistable image. A similar effect might occur during the perception of a possible stimulus during binocular rivalry. On the other hand, top-down processes involve actions like shifting attention towards one possible interpretation. This might bias perception towards that particular interpretation, implying the presence of volitional effects on figure reversals (Long & Toppino, 2004). Moreover, acknowledging the two potential interpretations of a bistable figure is crucial in reporting its reversibility (Long & Toppino, 2004). Binocular rivalry and bistable figures share a common challenge: the timing of the switches from one precept to the other is mostly unpredictable. Although voluntary control is somewhat limited, it can influence both the percept duration and the frequency of perceptual reversals. However voluntary control appears to be more manageable with bistable images compared to binocular rivalry (van Ee, van Dam, & Brouwer, 2005). Flash suppression comes to aid by providing a methodological advantage: flashing an image to one eye causes the suppression of the percept in the other eye, even if the retinal stimulation is constant (Wolfe, 1984). By combining flash suppression with binocular rivalry, researchers can exert external control over perception, effectively making the stimulus invisible for a specific duration. This controlled manipulation offers a way to bias conscious perception, influencing which stimulus dominates the viewer's awareness during rivalry. A similar useful technique is Continuous Flash Suppression (CFS): a sequence of flickering patterns flashed at around 10 Hz to one eye can suppress the image shown to the other eye for several seconds (Tsuchiya & Koch, 2005) providing a great method for studying unconscious visual processes. Although binocular rivalry provides an excellent method for studying NCCs, it also has a disadvantage: when the two rival targets are large, they might produce periods of perceptual overlapping, making the forced-choice procedure less reliable (Kim & Blake, 2005).

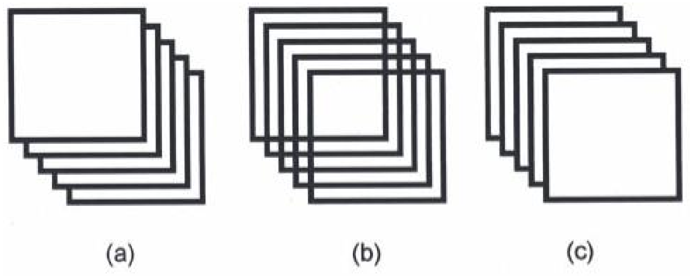

Figure 2.1 The unambiguous variation **(a)** and **(c)** of the primary ambiguous figure **(b)** are employed as stimuli to induce adaptation (Long & Toppino, 2004)

Attentional blink is yet another phenomenon that impacts the awareness of a stimulus: when a subject is instructed to search for two visual targets rapidly succeeding, when the second target follows the first one, it is highly likely that it will not enter the awareness of the participant. If the appearance of the first target is unpredictable, attention enters a brief refractory period that prevents the perception of the second target if it falls within this time range. Attentional blink offers the opportunity to work with different kinds of stimuli with the only condition to fall on that narrow temporal window (Kim & Blake, 2005). Other psychophysical methods that could be used in visual consciousness research include visual crowding, motion-induced blindness (MIB), inattentional blindness (IB), and change blindness (CB). Each of these paradigms poses issues that complicate the interpretation of findings about visual awareness. Visual crowding occurs when a figure becomes unrecognizable when flanked by nearby stimuli, but it remains detectable, thus blurring the boundaries between awareness and unawareness. MIB consists of the disappearance of the awareness of stimuli embedded in a moving field; the problems of MIB are that the fluctuations are unpredictable, stable fixation is needed, and the phenomena do not occur when the stimuli are foveally viewed or large, or when complex such as faces (Kim & Blake, 2005). When a subject fails to notice a change in an image, we call it change blindness, while inattentional blindness refers to the failure in the detection of an unexpected, yet salient, element of the visual scene. Neither CB nor IB can be considered cases in which there is no awareness *per se*, but rather circumstances during which subjects may still retain some level of awareness of the unattended changes or stimuli, but they fail to report their conscious experience due to constraints posed by the availability attentional resources (Kim & Blake, 2005). The relationship between attention and awareness will be explored in the following section.

Whatever methods are used in the research regarding NCCs, subjects are almost always required to report their current perception, whether verbally or by pushing buttons on a keyboard or button box. In recent years, several studies have shown that the candidate NCCs identified using the above-mentioned paradigms might have been conflated with the neural mechanisms necessary to report inner experience: in this sense, there would have been an entanglement of the *minimal* neural activity jointly sufficient for the conscious percept with neural activations underlying other functions, such as working memory, attention, and expectation (Tsuchiya, Wilke, Frässle, & Lamme, 2015). The no-report paradigm addresses this issue by excluding subjective reports, choosing to rely upon other measures that seem to correlate with reports of conscious perception, such as eye movements and pupil dilatation (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014). Most experiments employing no-report paradigms include trials with explicit reports. These serve a double purpose: explicit reports act as a control condition for eye movements and pupil dilatation, and they also enable to compare brain activation between these reported trials and those without reports (Tsuchiya & Koch, 2016). The aim is to identify more restricted NCCs. It has been demonstrated that content-specific NCCs obtained using this paradigm do not include activation of the prefrontal cortex during binocular rivalry, which was once thought to be necessary for conscious perception; rather, prefrontal activity is associated with introspection and self-monitoring (Koch et al., 2016; Tsuchiya et al., 2015). It is also important to bear in mind that even if the stimulus is suppressed by whatever techniques are used, conscious perception of the masking or distractor should be considered as a confounding variable (Pitts, Lydia, Lutsyshyna, & Hillard, 2018). Researchers must consider this by using control conditions to ensure accurate results. As an example, within a masking experiment, utilizing a control condition where participants are exclusively exposed to the mask stimulus serves to differentiate the neural activity associated with the mask itself from that linked to the stimulus. Given that one of the primary obstacles in research on NCCs lies in distinguishing them from concurrent processes, such as unconscious sensory processing, expectations, visual working memory, and attentive mechanisms (Tsuchiya et al., 2015), no-report paradigms and robust experimental designs are extremely useful in isolating the many confounding variables. However, the dissociation of attention from consciousness proves to be significantly more intricate due to their close interconnection, as will be shown in detail in the following section.

2.2 – Consciousness and attention are distinct processes

The question of whether attention and consciousness are equivalent has been a longstanding subject of debate, but recent evidence from psychophysical and neuropsychological studies leans toward a dissociation of these two processes. Attention can be divided into two modalities: top-down attention and bottom-up attention. Top-down attention is endogenously driven, therefore under voluntary control, and it allows us to focus on objects (object-based attention), features (feature-based attention), or regions in space (focal attention). Bottom-up attention, on the other hand, is stimulus-driven, therefore automatically triggered by a salient stimulus. While attention can be considered as the capacity of the mind to select information, consciousness can be viewed as a process capable of summarizing all the internal and external information regarding an organism and allowing the elaboration of information by making the summary accessible to brain areas involved in planning, error-detection, decision making, and rational thought (Koch & Tsuchiya, 2006). In this conceptual framework, attention could be seen as an analyzer while consciousness as a synthesizer (Van Boxtel, Tsuchiya, & Koch, 2010).

Authors who believe that attention and consciousness are the same process base their view on the strong connection between the two: when attention is focused on a particular task and unexpected stimuli are presented, inattentional blindness occurs (Mack & Rock, 1998). Similarly, when a major change between two static images goes unnoticed we call that, as mentioned before, change blindness (Simons & Ambinder, 2005). Attention is crucial in these phenomena as cueing of the items (i.e., informing the participants that something unusual might be displayed) prevents both IB and CB (Rensink, 2002). Moreover, when visual attention is divided between concurrent tasks in dual-task paradigms, there is a reduction in visual sensitivity, known as load-induced blindness (Macdonald & Lavie, 2008). Even cortical damage that results in the impairment of attentional resource allocation to a region of space, such as in visual neglect, leads to the invisibility of a stimulus (Driver & Mattingley, 1998). The close connection between attentive mechanisms and awareness is also highlighted by the phenomenon of “attentional blink”, where there’s a difficulty in perceiving a consecutive target when the first is presented unexpectedly. Moreover, attention is important in facilitating visual consciousness. When attention is directed towards an object, its attributes can be stored in working memory, enabling the subsequent conscious retrieval. Additionally, top-down attention enhances our ability to detect unexpected and unfamiliar stimuli. The presented scenarios showcase the tight interconnection between attention and visual awareness.

However, as a matter of fact, while focusing on a scene, our perception of it is not reduced to the tunnel that represents the focus of attention, as we are always aware of the essence of the scene, its gist. Some authors noticed that in cases where both attention and consciousness are absent, the stimuli are to some extent perceived, yet not in detail; in load-induced blindness, the detection sensitivity (d’) values are often greater than 0; therefore, the stimuli are eventually perceived (Macdonald & Lavie, 2008). Matt and Rock (1998) also noticed that when natural images are flashed unexpectedly for just 30 ms subjects can still describe the gist of it; in such a brief time frame, only bottom-up attention is engaged, as top-down activations require longer stimulus duration to occur (Van Boxtel et al., 2010). In dual-task paradigm, even if attention is drawn to the central attention-demanding task, subjects can still tell if a peripheral stimulus was a scene containing an animal (or a vehicle) or not while they struggle with more computationally simpler tasks, like distinguishing a bisected red-green disk from a green-red one (Li, VanRullen, Koch. & Perona, 2002). Similarly, subjects can tell if the peripheral stimulus is a male or a female face and even if it is a famous one or not but when they have to detect if a letter was a rotated “T” or an “L” they showed an inability to perform this task accurately (Reddy & Koch, 2006). These examples show how awareness of objects/features in /of the visual field/scene is possible in the near absence of attention. However, some authors argued that a limited amount of top-down attention can still be employed in these tasks (Pitts et al., 2018), nevertheless, it is also true that without a good amount of top-down attentional amplification, many tasks cannot be executed. It appears that the essential content of a scene typically enters phenomenal consciousness, whereas the limitations of our attentive mechanisms may prevent certain minor scene changes from being included in our access consciousness.

At this point, it is clear how visual awareness and attention, even if intimately bound, may not be as coupled as many authors thought. Additional evidence of a dissociation between the two processes comes from events in which there is attention without consciousness. Even if the attention of a subject is directed to an object, it could still not induce a conscious percept. In visual crowding, a tilted grating placed in the peripheral visual field with flanks is not discriminable; however, it can still induce an orientation-dependent aftereffect (He, Cavanagh, & Intriligator, 1996). In this context, priming experiments are also employed. Priming effect consist of the examination on how a stimulus (referred to as the priming stimulus) influences the processing of a subsequent stimulus (the target stimulus) without intention. For instance, the word “sun” might be detected quicker if it follows the word “moon”, in contrast to an unrelated word. Words suppressed by both forward and backward masking can still elicit a priming effect, but only if the subjects are attending to the prime stimuli (Naccache, Blandin, & Dehaene, 2002). Experiments using continuous flash suppression (CFS) demonstrated how invisible stimuli can attract bottom-up attention: Jiang and colleagues (2006) observed that male/female nude pictures rendered invisible by CFS increased the accuracy in a subsequent task involving orientation discrimination of a Gabor patch (Jiang, Costello, Fang, Huang, & He, 2006).

In 1997, Weiskrantz described the case of GY, a patient affected by a blindsight condition. Blindsight is a neurological condition arising from damage to the primary visual cortex leading to the inability to perceive stimuli, despite these individuals retaining the capacity to respond to them. Indeed, patients with blindsight which encompasses their entire visual field, are still able to avoid obstacles while moving (Weiskrantz, 1997). The extent of the impaired visual field can vary depending on the location and size of the brain lesions. In GY's case, only half of his visual field was affected. In short, GY could not consciously perceive stimuli in his blind vision field. Nevertheless, he demonstrated the ability to accurately detect and respond to visual stimuli in the blind visual region (Kentridge, Heywood, & Weiskrantz, 1999). GY abilities could be explained by considering the possibility that visual information might still be processed through alternative pathways. These pathways include extrastriate areas that receive input from V1 and the superior colliculus, which is involved in the detection and localization of objects in the visual field (Conway, 2010). Even a sleepwalking person can retain bottom-up attention and move in their environment without being conscious (Hughes, 2007). According to a study conducted by Tsushima et al. in 2006, sub-threshold stimuli, including random dot motion, can have a negative impact on attention. If the coherence of these stimuli is too low for participants to perceive, this can harm their ability to complete a central task. This was supported by an fMRI study that found that the lateral prefrontal cortex (LPFC), which is responsible for inhibiting distracting stimuli, is not activated by sub-threshold stimuli. Conversely, the MT area exhibited a stronger BOLD signal, and activation of this area impaired overall performance. However, if the coherence of the stimuli is above the perceptual threshold, the LPFC becomes active and can inhibit the MT area, known for its involvement in motion perception, ensuring that the execution of the central task is not impaired (Tsushima, Sasaki, & Watanabe, 2006). More support for a dissociation between attention and consciousness comes from situations in which these two processes have opposite effects. In MIB, the more salient the targets are, in the sense that they attract a consistent amount of bottom-up attention, the less time it will take for the target to disappear (Bonneh, Cooperman, & Sagi 2001). Similarly, in the Troxler fading effect, when attention is directed to the peripheral stimuli while maintaining a constant fixation, their disappearance will be much faster (Bonneh et al., 2001). Moreover, afterimages and motion after-effects fade faster when we direct our focal attention to them (Bachmann & Murd, 2010; Murd & Bachmann, 2011). During attentional blink experiments, if participants hear distracting noise or are asked to distract themselves during the task, the chances of detecting both the first and second targets increase (Olivers & Nieuwenhuis, 2005). In a more ecological study conducted by Beilock et al. (2002), athletes were asked to execute a trained behaviour while either focusing on it or being distracted by an unrelated task. Researchers discovered that athletes performed better when they did not pay direct attention to the trained behaviour (Beilock, Carr, MacMahon, & Starkes, 2002).

Before delving into the neural correlates of visual awareness, it is essential to first grasp the neural correlates of attention, as it represents the primary confounding factor in research on Neural Correlates of Consciousness (NCCs). A series of studies revealed a distributed network of cortical areas supporting attention, with activations in bilateral parietal and dorsolateral prefrontal cortices (Pessoa, Kastner, & Ungerleider, 2003). Corbetta and Shulman (2002) identified a series of multimodal brain areas that are activated independently of the sensory modality and that could be clustered into two main attentional networks: the dorsal attention network (DAN) and the ventral attention network (VAN). DAN consists of the superior parietal lobule (SPL), intraparietal sulcus (IPS), and frontal eye fields (FEF), which are involved in goal-directed stimulus-response selection and seem to support top-down attention. On the other hand, the VAN connects the temporoparietal junction and the middle and inferior frontal gyri; this network mediates shifts of attention when triggered by unattended or unexpected stimuli, thus supporting bottom-up attention (Figure 2.2) (Corbetta & Shulman, 2002). It appears that the VAN is more lateralized in the right hemisphere while the DAN has a bilateral organization (Corbetta, Patel, & Shulman, 2008).

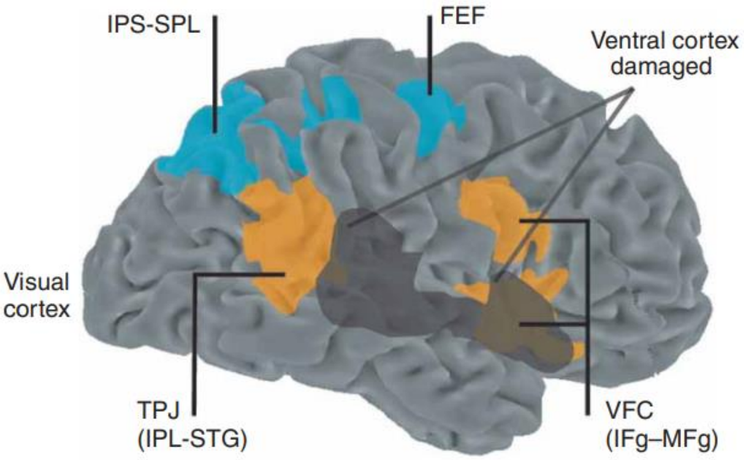

Figure 2.2 The dorsal (blue, top-down) and the ventral (orange, bottom-up) attentional systems. The dark region represents a theoretical cortical injury responsible for spatial neglect (Corbetta, Kincade, Lewis, Snyder & Sapir, 2005)

Chapter 3: Localization of neural correlates of visual awareness

This Chapter aims to provide an overview of the cortical areas involved in visual awareness by discussing various experiments that shed light on both the sufficiency and necessity of these cortical regions in shaping our perceptual experiences. The role of the primary visual cortex is discussed first, followed by an examination of the contributions of extrastriate areas. The functions of the frontal and parietal cortex supporting visual consciousness are also taken into consideration. Evidence sourced from psychophysical experiments coupled with fMRI and other techniques is presented along with lesion and stimulation studies.

3.1 – Neural correlates of visual awareness in visual areas

Visual perception appears effortless and reliable to us, as our visual brain unconsciously handles the complex computational work. However, delving into the underlying processes of visual perception reveals that it is essentially an interpretative act comprising two key components: information analysis and subjective awareness (Tong, 2003). Theories of visual awareness can be clustered into two models: hierarchical and interactive (Silvanto, 2014). According to hierarchical models, the primary visual cortex (V1) is not necessary for conscious perception, as its role is not different from that of the retina; it feeds information forward to the higher visual areas. This model proposes that extrastriate visual areas are the cortical areas supporting awareness. In fact, at this level, the receptive fields are much more complex and their role is to elaborate the raw visual information input coming from V1, making it eventually accessible to awareness. On the other hand, interactive models consider V1 a necessary area for subjective experiences because they are involved in recurrent processing with higher visual areas. Indeed, anatomical connections between V1 and many extrastriate areas, such as V2, V3, V4, and MT, are reciprocal (Figure 3.1); thus, visual awareness may be the result of sustained activity among these circuits. Moreover, feedback signals are important for attentional modulation and for confirming the reliability of information based on top-down knowledge (Di Gregorio, Ernst, & Steinhauser, 2019). Overall, the main difference between hierarchical and interactive models revolves around the role of V1: the former does not consider it a necessary area for visual awareness, while the latter does.

Alternative models have been proposed to consider a wider range of possible interactions between V1 and awareness. This relationship may not be as rigid as that suggested by the mentioned models. V1 may be necessary only in specific contexts, such as the perception of low-level features or during focal attention (Tong, 2003). However, in a study conducted by Haynes, Driver, and Rees (2005), it was observed that fMRI signals in the primary visual cortex (V1) elicited by a fundamental feature like brightness, which is typically processed in the early visual cortex, did not exhibit parametric changes related to stimulus visibility. In contrast, higher visual areas and the surrounding area of stimulated V1 showed significant parametric changes in response to changes in stimulus brightness, implying that dynamic interactions between the early and higher visual cortices play a crucial role in visual awareness. This finding suggests that the mechanisms responsible for visual perception extend beyond the early visual cortex and involve complex processes in higher visual areas to mediate our conscious experience of even primary features.

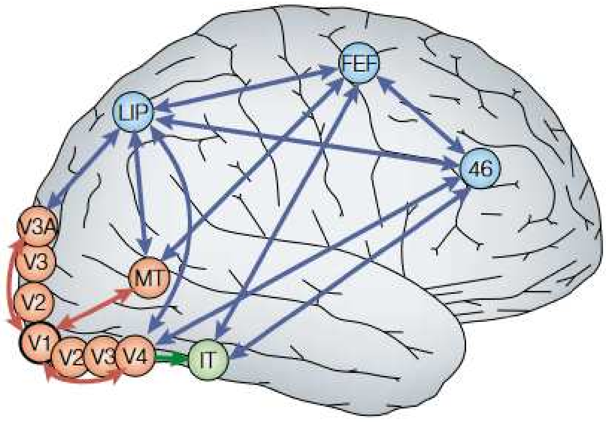

Figure 3.1 Reciprocal connections within and between cortical visual and frontal areas (Tong, 2003)

Several studies have provided supporting evidence for a relationship between V1 activity and visual awareness. These fMRI investigations have revealed that BOLD signals in V1 increase when a stimulus at a threshold level is consciously perceived by the subject, in contrast to when the same stimulus does not reach conscious awareness (Ress & Heeger, 2003). Moreover, Pins, and Ffyche (2003) detected early cortical signals in posterior occipital sites associated with conscious perception. Other studies reported activity in V1, related to the perception of illusory features, such as apparent motion and visual phantoms (Muckli, Kohler, Kriegeskorte, & Singer, 2005; Murray, Boyaci, &

Kersten, 2006). On the other hand, activity in the striate cortex often does not correlate with visual experience: during eye saccades and blinks made in complete darkness, activity in V1 is present yet the phenomenal content is absent (Bodies-Wollner, Bucher, & Seelos, 1999; Sylvester, Haynes, & Rees, 2005). V1 is known to be involved in tilt-aftereffects, a perceptual illusion caused by the adaptation of V1 neurons to a specific orientation that biases neutral stimuli to be perceived in the opposite direction. He and MacLeod (2001) demonstrated that even gratings presented at a spatial frequency so high to not be distinguished from a uniform field can produce tilt after-effects, suggesting that orientation-selective activity on V1 is associated with unconscious perception. Colour opponent cells in monkeys' V1 respond to a flickering colour grating even when the flickering rate exceeds heterochromatic fusion frequencies (Gur & Snodderly, 1997). This study is another example of dissociation between V1 activity and visual consciousness. In an influential study conducted by Haynes & Rees (2005), a technique called multivoxel pattern analysis (MVPA) was used to predict the oriented masked stimulus that subjects had been exposed to. MVPA is an fMRI technique that involves the analysis of patterns of neural activity across multiple voxels. This finding indicates that even if the subject is not aware of the stimulus, its orientation can be encoded in patterns of brain activity in the striate cortex.

The presented evidence shows that V1 activity is not sufficient for visual perception, while the question of whether this area is necessary is still a subject of ongoing debate. Supporters of the position that V1 is necessary for visual awareness point to evidence from patients with blindsight, where a lesioned V1 is linked to the loss of conscious visual perception in the specific retinotopic region of space corresponding to the damaged cortical area. Blindsight presents challenges for hierarchical models because it has been proven that high-level visual regions continue to receive feedforward inputs even in the absence of V1, as shown in recorded MT neural activity in monkeys with ablated striate cortex (Rodman, Gross, & Albright, 1989), and in fMRI responses in MT, V3A, V4, and LOC regions in patients with unilateral V1 lesions and stimuli presented to the blind hemifield (Goebel, Muckli, Zanella, Singer, & Stoering, 2001), meaning that this structure is important for reaching awareness. However, the necessity of V1 activation via feedback loops to support consciousness, as proposed in interactive frameworks, has also been questioned. When TMS impulses are applied in the visual areas of healthy subjects, they report perceiving phosphenes (brief flashes of light). However, in a study conducted by Mazzi, Mancini, and Savazzi (2014), TMS impulses on the parietal region of the damaged hemisphere of blindsight patients also caused them to perceive phosphenes. Such a situation would not be possible according to feedback models as there is no V1 area that can be activated by backward inputs. Moreover, hemianoptic completion, a phenomenon in which an entire image is perceived even when only half is presented in the intact visual hemifield, while the other half lies in the blind hemifield, can occur in the absence of parts of V1 (McCarhy, James-Galton, & Plant, 2006). Patients with blindsight are even able to perceive afterimages in their blind visual field despite seeing the inducing stimulus only in their sighted field (Bender & Kahn, 1949; Marcel, 1998). TMS-induced phosphenes, hemianoptic completion, and afterimages in blindsight provide evidence that visual qualia can occur even when the striate cortex is not functional (Mazzi, Savazzi, & Silvanto, 2017).

Methods that induce bistable perception coupled with fMRI have been proven to be informative about the role of both early and higher visual areas. Research has shown that fMRI BOLD signals in human V1 are correlated with perceptual fluctuations induced during binocular rivalry (Polonsky, Blake, Braun, & Heeger, 2000; Lee, Blake, & Heeger, 2005). Additionally, TMS over V1 has been observed to shift current perception to the other possible percept (Pearson, Tadin, & Blake, 2007), suggesting that V1 might be the structure involved in such fluctuations. A review carried out by Tong, Meng, and Blake (2006) presents evidence supporting the notion that early visual processing stages, such as the LGN and V1, are involved in the perceptual outcomes in binocular rivalry. For instance, when presenting high-contrast and low-contrast gratings during binocular rivalry, fMRI signals recorded from both the LGN and V1 reveal increased activity when the high-contrast grating is the dominant perceptual experience. (Wunderlich, Schneider, & Kastner, 2005). Some authors (Tong, 2003; Sterzer, Kleinschmidt, & Rees, 2009) have argued that V1's involvement in perceptual reversals is to regulate the flow of visual information. However, the precise mechanism behind this regulation remains unclear. It has been suggested that local competitive interaction or the influence of feedback signals coming from higher areas might be involved in the gating of information within V1.

A large body of evidence from fMRI experiments and electrophysiological recordings shows a strong correlation between activation in functionally specialized extrastriate areas and conscious perception fluctuations, which are indicative of shifts in perception between competing stimuli. For instance, consider a scenario in which binocular rivalry involves a face and grating as presented stimuli. When the subject reports perceiving the face, there is a simultaneous observation of heightened BOLD activity in the Face Fusiform Area (FFA). Conversely, if the competing stimulus is an object instead of a face, the Later Occipital Complex (LOC) exhibits an increase in metabolic activity during the perception of the object. This points to these fluctuations in neural activity being closely related to the identity of the perceived stimulus during the phenomenon of binocular rivalry (Leopold & Logothetis, 1999; Blake & Logothetis, 2002). Bistable images evoke similar responses, indeed, during face perception in Rubin's face/vase illusion, activity in FFA is greater than during vase perception (Hasson, Hendler, Bashat, & Malach, 2001). An important consideration to be made is that, even if one stimulus is suppressed, activity in the specialized extrastriate areas can still be seen, only the amplitude of activation of this area is smaller than the activation of the specialized area corresponding to the current percept (Sterzer, Haynes, & Rees, 2008). Moreover, face images rendered invisible by continuous flash suppression (CFS) can still evoke category-specific responses using MEG, such as the M170 component which correlates with face perceptions (Sterzer, Jalkanen, & Rees, 2009). This evidence suggests that category-specific processing of objects in the ventral pathway is present despite stimuli being suppressed. Thus, activation of the ventral extrastriate areas alone does not lead to visual awareness, although their activation clearly reflects the current qualitative experience. In contrast, stimulus characteristics correlate better with early visual activity. Single-neuron recordings in monkeys during binocular rivalry appear to demonstrate these functional differences (Logothetis, 1998; Blake & Logothetis, 2002).

Different variables might influence which stimulus we are going to perceive during bistable vision tasks by influencing the state of the neuronal groups that represent potential percepts: perceptual memory appears to play a significant role in this phenomenon. Specifically, when an ambiguous stimulus is taken away briefly and then presented again, the prevailing perception tends to align with the one observed just before its removal (Pearson & Brascamp, 2008). An fMRI study suggests that extrastriate areas are the ones involved in perceptual memory as FFA presented greater activity after stimulus removal when the preceding percept was a face (Sterzer & Rees, 2008). Moreover, imagery can also influence the baseline activity of extrastriate areas (Pearson, Clifford, & Tong, 2008), thus biasing the perceptual conflict in one direction while viewing ambiguous stimuli. However, stochastic signal fluctuations around the inferotemporal cortex might strongly determine the first seen stimulus (Hesselmann, Kell, Eger, & Kleinschmidt, 2008).

Since Penfield's pioneering observations, direct cortical stimulation has been a valuable research method employed in both primates and humans during neurosurgical operations. Numerous authors have used this technique to investigate the causal role of different populations of cortical neurons in feature perception. Penfield was the first to use direct cortical stimulation on patients during brain surgeries, and his groundbreaking work laid the foundation for exploring how stimulating specific neurons in the cortex can elicit perceptual experiences and uncover the functional organization of the brain. Microstimulation of specific MT neurons causes monkeys to perceive motion in the direction represented by these neurons while observing an ambiguous random dot stimulus (Salzman & Newsome, 1994), suggesting that cortical activity in this region directly influences subjective experience. In a study conducted by Afraz, Kiani, and Esteky (2006), monkeys were trained to distinguish between noisy images of faces and other objects. When microstimulation was directed at regions in the inferotemporal cortex with a high concentration of face-selective cells, the monkeys showed an increased tendency to identify noisy images as faces. This suggests that stimulation of specific regions in the inferotemporal cortex can elicit distinct perceptions, influencing monkeys' judgments of visual stimuli.

Studies on various neuropsychological conditions have shown that damage to specific cortical areas results in the loss of perceptual characteristics supported by the lesioned areas. For instance, lesions in V4 area lead to achromatopsia (Bartolomeo, Bachoud-Lévi, & de Schotten, 2013), causing the loss of colour vision, while MT lesions lead to akinetopsia (Pelak & Hoyt, 2005) which is the loss of movement perception. Additionally, disruptions in the FFA and LOC areas lead to prosopagnosia (Barton, Press, Keenan, & O'Connor, 2002) and object agnosia (de-Wit, Kentridge, & Milner, 2009), respectively, in which individuals struggle to recognize faces and objects. Microstimulation studies, in which targeted neural activation influences perceptual experiences, have highlighted the functional roles of these areas. Meanwhile, lesion studies further underscore the necessity of extrastriate areas in various aspects of visual processing. Taken together, evidence from microstimulation and lesion studies strengthen the idea that extrastriate areas are essential for specific feature perception.

3.2 – Neural correlates of visual awareness in frontal and parietal regions

Unilateral spatial neglect is a condition caused by unilateral damage to parietal cortical regions. Patients cannot report being aware of a stimulus placed in the contralesional side of space and they have behavioural deficits towards that spatial region. They are unable to direct their attention and explore whatever is presented on the compromised side, which in most cases is the left one. However, neglect patients are not blind in the traditional sense. Often, when a single object is presented to the left side, they can see it and pick it up if they direct their attention to it, which is typically biased to the right side (Vallar, 1998). This effect is perhaps due to a bias in attention toward that side because of right parietal impairment (Rees, 2013). Indeed, it has been suggested that right parietal lesions might prejudice the correct functioning of the ventral attention network (VAN), which is in fact lateralized to the right side, leading to problems with vigilance and sustained attention, which are symptoms that are usually concomitant with neglect (Corbetta & Shulman, 2011, Corbetta, 2014). However, to explain hemispatial neglect we must consider that VAN is functionally connected to the right dorsal attention network (rDAN). Thus, impairment in VAN might indirectly cause malfunctioning in DAN, which sustains top-down attention, explaining the interhemispheric imbalance between the two spatial sides (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). Still, the neural basis underlying visual neglect is an area of active research, and multiple areas and brain networks may be involved. Importantly, neglect cases imply that even if the visual areas and pathways are not impaired, we can still lose the ability to consciously be aware of an object, suggesting that neural activity outside the visual cortex is important for visual awareness. Visual extinction is a variant of neglect conditions in which patients, despite being able to detect stimuli on the impaired side, exhibit a deficit when multiple stimuli are simultaneously presented to both the side of the brain with the lesion (ipsilesional) and the opposite side (contralesional). In this scenario, patients can only report the stimulus presented in the ipsilesional region of space, disregarding the contralesional stimulus. Indeed, Rees et al. (2000) demonstrated that a patient with profound extinction to his left visual side, during simultaneous presentation of two stimuli to both the functional and impaired visual hemifield could not perceive the left stimulus. However, in this patient, fMRI signals revealed metabolic activity in the right visual cortex, in both primary and extrastriate areas. This pattern of activity was very similar to that seen when a single stimulus was presented in the left field and perceived by the patient. Moreover, specialized extrastriate activity in the inferotemporal cortex is retained even after stimulus invisibility caused by parietal lesions (Rees et al., 2002).

Some researchers have proposed that frontal brain regions may play a crucial role in visual consciousness (Dehaene & Changeux, 2011). fMRI studies indicate that when participants see a stimulus, such as a word, there is an increase in activity within the fronto-parietal network, along with activity in the occipital regions responsible for visual processing. In contrast, when the same words were made invisible through masking, the activity in these frontal areas decreased, suggesting their involvement in the conscious perception of visual stimuli. (Dehaene et. al., 2001). Similarly, activity patterns in frontal and parietal regions are observed during perceptual reversals in binocular rivalry (Lumer, Friston & Rees, 1998) and perceptual fluctuations are impaired in patients with damaged prefrontal or parietal cortex (Windmann, Wehrmann, Calabrese, & Güntürkün, 2006). Dehaene, Kerszberg, and Changeux (1998) are proponents of the Global Neuronal Workspace Theory (GNWT), an evolution of Baars' first theory of consciousness. This theory proposes that specific groups of excitatory neurons with long-range axons sustain and broadcast representations to a widespread cognitive processing network, involving frontal cortical regions as a crucial component (Dehaene, Kerszberg, & Changeux, 1998). Recent findings challenge the assumption of GNWT that frontal activation is required for subjective experience, as discussed in the methodological sections. In experiments in which participants were not required to report their current perceptions, frontal activation was not detected, while activity in parietal and occipital regions remained, suggesting an involvement of frontal activation in working memory, decision-making, and reporting (Frässle, et al., 2014). Frontal activity observed during bistable perception might reflect top-down processes that aim to reorganize activity in the visual cortex (Weilnhammer, Ludwig, Hesselmann, & Sterzer, 2013). Further evidence that the frontal parts of the brain are not involved in consciousness comes from lesion cases such as patient KM, who remained fully conscious and even showed an improvement in his IQ after a near-complete bilateral resection of prefrontal cortical areas (Mettler, 1949; Boly, et al., 2017). In addition, direct electrical stimulation and TMS modulations of the frontal cortex do not elicit any experience. However, when other areas are stimulated, such as the middle and inferior frontal gyrus, hallucinations can occur (Blanke, Landis, & Seeck, 2000), likely because of indirect activation of other regions by network effects (Boly et al., 2017).

On the other hand, stimulation of parietal regions can lead to perceptual experiences ranging from phosphenes (Beauchamp, Sun, Baum, Tolias, & Yoshor, 2012; Schaeffner & Welchman, 2016) to even out-of-body experiences (Blanke, Ortigue, Landis, & Seeck, 2002). Recent studies employing no-task paradigms have pointed out a "posterior hot-zone" in parieto-occipital areas (Siclari, LaRocque, Bernardi, Postle, & Tononi, 2014). Activity in this region is related to conscious experiences during sleep, particularly dreams. Notably, EEG markers of arousal within temporo-parieto-occipital cortices have been able to predict when the subject was dreaming during NREM sleep with high accuracy (Siclari et al., 2017). Again, these recordings did not register activation in the broad fronto-parietal network, and the recorded localized activity in the frontal region was related to highly thought-like experiences. All things considered, lesion, recording, and stimulation studies provide evidence supporting the involvement of regions in the "back" of the cortex (Boly et al., 2017) specifically the "posterior cortical hot-zone," which is a suitable candidate for the neural correlates of visual awareness. On the other hand, it seems that areas in the frontal cortex are not essential for conscious experiences; however, they do work in conjunction with the core NCCs and can contribute to conscious access by supporting cognitive processes (Boly et al., 2016; Boly, et al., 2017).

Chapter 4: Neural Dynamics

The aim of this Chapter is to provide an overview of the neural dynamics underlying visual consciousness. To begin, we will delve into the crucial role of feedback signals which have given rise to theoretical explanations of consciousness such as the Recurrent Processing theory (RPT) and the Predictive Processing (PP) framework. Psychophysiological correlates will also be taken into consideration as neural oscillations like gamma and alpha band activity have shown connections with conscious experience. Additionally, event-related potentials like the P3b and VAN will be considered in this context. However, it is important to acknowledge that some of these correlates are closely intertwined with other cognitive processes, such as attention and task-related activities, which can often confound consciousness research. In conclusion, the chapter will explore the important role of both sustained and phasic neuronal activity in enabling perceptual experiences.

4.1 – Re-entrant activity and the Predictive Processing framework

The cerebral cortex presents an abundance of reciprocal connections. In fact, the majority of links between visual cortical areas are bidirectional, indicating the important role of interactive processing (Tong, 2003). Re-entrant activity, also referred to as feedback, recurrent, recursive, top-down, or reverberant activity, is not confined to the visual cortex because connections linking cortical visual areas with frontal areas, such as the frontal eye fields (FEF) and dorsolateral prefrontal cortex (DLPC), are also present. These connections appear to be involved in visual attention and motor planning (Tong, 2003). Moreover, there are feedback projections originating in the striate cortex (V1) that reach the LGN of the thalamus (Cudeiro & Sillito, 2006). The vast number of back-projections may be a direct result of the hierarchical organization of the visual stream of information. For example, the receptive fields in the LGN are not sensitive to orientation, in contrast to V1 cells. To achieve an unbiased output from V1 direction-sensitive cells to the LGN, it would require simultaneous activation of V1 cells representing all directions. This situation could explain the exceeding number of backpropagations compared to feedforward ones. However, the simultaneous activation of V1 cells is unlikely, and given that LGN cells do not exhibit orientation preferences, the feedback effect may not be robust (Tononi, Boly, Gosseiries, & Laureys, 2016). Top-down processing is a fundamental substrate for attentional modulation and imagery and might manipulate signals based on prior expectations. Moreover, one important purpose of this vast number of structures is to support conscious awareness (Tononi et al., 2016).

As previously discussed in the context of interactive models of V1, the experiment of Mazzi, Mancini, and Savazzi (2014) provided evidence that even with a damaged V1, TMS impulses still trigger phosphenes in patients with blindsight. This finding implies that the presence of intact back connections to V1 might not be an absolute requirement for visual awareness. However, it is plausible that alternative brain regions could potentially receive these re-entrant signals (as suggested by Tononi et al., 2016), thereby not definitively excluding the significance of recursive signals in the emergence of consciousness. Other TMS studies, such as those by Pascual-Leone and Walsh (2001), highlight the role of feedback in visual awareness: TMS over MT elicited moving phosphenes, but when a subsequent subthreshold TMS pulse over V1 was applied in a specific time interval (from +5 to +45 ms), the participants often did not perceive the phosphene, and if they saw one, it was not moving. In a second study by Boyer, Harrison, and Ro (2005), TMS pulses disrupted the visibility of a stimulus that was either an oriented bar or a colored patch. Nevertheless, they were still able to discriminate between stimuli, similar to the blindsight condition.

An alternative approach to distinguish between feed-forward sweep and re-entrant activity involves employing ultra-rapid categorization experiments. In this method, images are grouped into various clusters (e.g., images containing an animal vs. images with no animals) and then presented to participants for a short duration. This technique bears resemblance to masking experiments, as they share similar underlying neural mechanisms (Bacon-Macé, Macé, Fabre-Thorpe, & Thorpe, 2004). During this process, the images are displayed in a manner that allows the neural signals they elicit to reach high-level cortical areas responsible for the categorization process (Koivisto, Kastrati, & Revonsuo, 2014). However, the presentation of successive images disrupts feedback signals, thus preventing their conscious perception (Lamme & Roelfsema, 2000). It is important to note that spatiotemporal dynamics related to neural input latencies might also contribute significantly. In this regard, the presentation of a subsequent image can interfere with the neural offset discharges of the preceding image (Bacon-Macé et al., 2004). Additional research may be required to gain a clearer understanding of the underlying mechanisms at play. However, even though participants are not consciously aware of each individual image, the neural inputs appear to be adequate for generating nearly automatic categorization responses (VanRullen & Koch, 2003).

In front of the fact that recurrent signalling is strictly associated with conscious experience, Lamme has proposed a theory of consciousness that is based on this phenomenon called Recurrent Processing Theory (RPT) (Lamme & Roelfsema, 2000; Lamme, 2010). He argues that, given the necessary preconditions (e.g., an adequate level of oxygen and arousal in the brain, which is a consequence of brainstem activity), re-entrant processing is sufficient to give rise to phenomenal consciousness, while the frontal and parietal areas are involved in reporting percepts that are supported by other cognitive processes (Lamme, 2006). Other authors have proposed a more general framework than Lamme's theory, called predictive processing (PP), which aims to lay the foundations for explaining the properties of consciousness and bridging the gaps between its phenomenology and the underlying neural basis (Hohwy & Seth, 2020). Hohwy & Seth (2020) noticed that many theoretical explanations for consciousness have two common themes: *uncertainty reduction*, which refers to the tendency of a conscious system to settle in one unified and informative representational state, and *top-down signalling*, which has been discussed above. In the context of the Predictive Processing framework, the mechanism underlying perceptual inference is predictive coding. This process involves generating predictions of representations from higher visual levels to lower ones, allowing for a comparison between these top-down predictions and the sensory representations at the lower levels. These predictions are the result of expectations and learned patterns from past experiences. The discrepancies between predictions and the sensory input are the prediction errors that are then sent upward to the higher levels, allowing the updating of the internal model (Figure 4.1) (Hohwy & Seth, 2020). This process is the result of the brain's goal of minimizing prediction errors through these processes of Bayesian inference, which is a statistical framework that formalizes the updating of probabilities based on incoming new information. However, predictive coding of the brain is not an entirely passive process because we can actively interact with the environment via saccadic eye movements or by shifting our attention to some information rather than others, thus shaping the sensory input in a way that is consistent with our models and beliefs about the world. In this context, attention may be essential to changing conscious content (Seth & Bayne, 2022). This link between perception and action is explained in the active inference framework, which is an expression of the PP. Predictive processing explains binocular rivalry as two conflicting predictions generated in the brain. The brain's goal to minimize the prediction errors leads to a constant updating of the perceptual state as the suppressed image increases predictive errors until the brain adjusts its predictions making that image the dominant one, thus reducing the prediction errors. However, this results in a back-and-forth alternation between the images, as the brain continuously updates its internal predictions (Seth & Bayne, 2022).

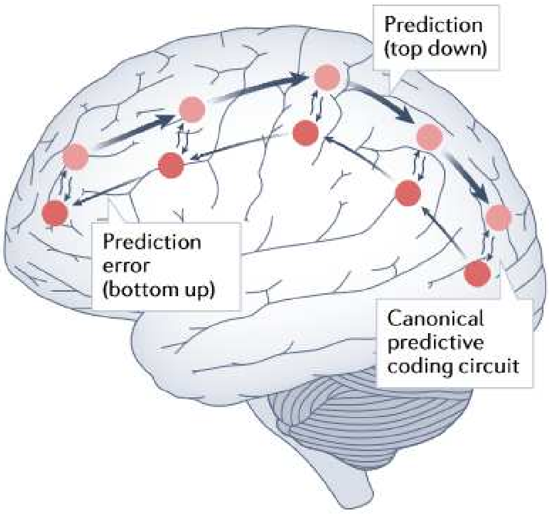

Figure 4.1 Predictive processing posits that conscious mental states are associated with top-down signalling (thick arrows) which convey predictions. The bottom-up prediction error (thin arrows) then flows back to higher areas to update the internal models (Seth & Bayne, 2022).

In summary, the minimization of surprise and uncertainty by means of predictive coding and active inference improves the brain's capacity to understand its environment. Therefore, the neural correlates of visual awareness can be functionally considered as the brain's "best guess" of the incoming input from the external world (Seth & Bayne, 2022).

4.2 – Oscillations and event-related potentials

As the neural activity that sustains various processes in the brain, including perceptual experiences, is structured not only in space but also in time, it might help to take into consideration the neural dynamics that occur over this dimension, such as synchronization and oscillations, might help to better comprehend the relationship between brain activity and conscious perception. Synchronous discharges of neurons have been proposed as a possible explanation of the "binding problem" which represents a challenge in understanding how different features of a scene are "bound" together given that the areas that represent each attribute are in different cortical regions (Singer, 1999). Synchronous firing patterns among neurons could also play a crucial role in preventing the misattribution of certain characteristics to an incorrect object. This is achieved through precise phase-locking between distinct attributes, which is a synchronization process that varies across different objects (Tononi, Sporns, & Edelman, 1992). However, many experiences are conscious, even if they do not require the binding of different features, for example, while experiencing a uniform-coloured wall (Tononi et al., 2016). Therefore, synchronous pattern discharges may not be necessary for visual awareness (Tononi et al., 2016). Moreover, hypersynchronizations due to generalized seizures are not followed by coherent perception with multiple features, but rather a loss of any conscious experience (Tononi et al., 2016).

Crick and Koch (1990b) were the first to point out gamma-band activity (30-100 Hz) as an NCC when they proposed the "40 Hz hypothesis", which stated that attentional mechanisms elicit neural synchronizations that correlate with conscious perception, as suggested by the finding that visual stimuli evoked oscillatory activity in the cat's visual cortex (Gray, Konig, Engel, & Singer, 1989). Evidence of a correlation between gamma band synchrony and visual consciousness also comes from animal studies conducted by Fries, Roelfsema, Engel, Konig, and Singer (1997). In this study, cats were subjected to binocular rivalry. The researchers noted that when the cats perceived the dominant stimulus, there was gamma-band synchronization in the early visual regions. Conversely, the suppressed stimuli exhibited a lack of coordinated neural activity. Gamma-band fluctuations have also been found in humans: words that are consciously perceived are related to gamma activity, while invisible words are not (Melloni et al., 2007), and long-distance gamma oscillations appear only when the participants see coherent faces in contrast to meaningless shapes (Rodriguez et al., 1999). However, most of these studies did not consider the role of attention as a confounding variable; in fact, attention seems to correlate with gamma-band activity (Wyart & Tallon-Baudry, 2008; Fries, Reynolds, Rorie, & Desimone, 2001). This oscillation pattern can even increase in conditions where consciousness is absent, such as during anaesthesia (Imas, Ropella, Ward, Wood, & Hudetz, 2005) and seizures (Pockett & Holmes, 2009), suggesting that gamma activity is not sufficient to allow visual awareness (Boly et al., 2016; Gallotto, Sack, Schuhmann, & Graaf, 2017).

Alpha rhythm, which falls within the frequency range of 7–13 Hz, is another neural oscillation pattern that has been related to visual awareness. Alpha activity is prominent in the occipital regions of the brain and has been associated with regulating the input of visual information, leading to the inhibition of perception. Indeed, when our eyes are closed, alpha power is enhanced (Berger, 1929; Uhlhaas, Haenschel, Nikolic, & Singer, 2008). Additionally, a higher alpha power is linked to decreased performance in a visual detection task (Hanslmayr et al., 2005). This connection is explained by the notion that a higher alpha power raises the threshold for visual excitability, thus inhibiting the brain's responsiveness to visual input (Lange, Oostenveld, & Fries, 2013). Besides the amplitude of alpha fluctuations, studies show that its phase covaries with visual detection performance (Busch, Dubois, & VanRullen, 2009) and that the probability to detect masked visual stimuli rises when they are presented at the peak of the EEG's recorded alpha oscillations (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Moreover, the probability of perceiving phosphenes elicited by TMS pulses at the threshold level, which reflects visual excitability, systematically covaries with the prepulse EEG phase of alpha oscillations (Dugué, Marque, & VanRullen, 2011). These results are in line with the theoretical assumption of periodic perception, which posits that perception is discrete rather than continuous, and its "rhythmic clock" consists of cyclic oscillations of neural waves in the alpha band (VanRullen & Koch, 2003; VanRullen, 2016). Indeed, individuals with slower alpha rhythms have a poorer temporal resolution when compared to observers with faster cyclic activity who are more likely to detect two stimuli presented in a short time frame (Samaha & Postle, 2015).

Further studies are required to gain a better understanding of the relationship between neural synchronization and visual consciousness and to dissociate attentional processes in the search for core NCCs. Employing entrainment approaches, such as rhythmic visual stimulation, or non-invasive brain stimulation techniques, such as TMS or tACS (transcranial Alternating Current Stimulation), is essential to gain knowledge on the causal relationship between neural oscillations and features of consciousness (Gallotto et al., 2017).

Moving on to the event-related potentials (ERPs) that correlate with visual awareness, several reviews have aimed to gather information about ERPs, focusing on two components that have been labelled as signatures of consciousness for decades: the P3/LP and VAN (Railo & Koivisto, 2009; Railo, Koivisto, & Revonsuo, 2011; Förster, Koivisto, & Revonsuo, 2020). P3 is a positive deflection that occurs approximately 300 ms after stimulus onset, also called "late positivity" (LP). This deflection is linked to discrepancies between trials in which the stimulus is consciously noticed and those in which it is not (Förster et al., 2020). These distinctions are observed in experimental approaches like masking, attentional blink, and manipulations of stimulus contrast. The P3 component exhibits distinct manifestations: one can be recorded in frontal sites (peaking at around 250 ms after stimulus onset), called P3a, while the other emerges in posterior regions, known as the P3b component, peaking at around 350 ms (Picton, 1992). However, the P3a component is now associated with bottom-up attentional mechanisms (Polich, 2007), which can occur even during unconscious trials. On the other hand, different literature reviews establish a connection between P3b and post-perceptual processes, such as the allocation of attentional resources toward task-relevant events and the updating of working memory (Förster et al., 2020). As a result, P3b reflects many cognitive processes that allow one to report a conscious experience. Moreover, many conscious patients with brain damage lack any P3b component (Kotchoubey, 2005; Boly et al., 2016) whereas around 40% of comatose patients, who are clearly unconscious, present the P3b (Tzovara, Simonin, Oddo, Rossetti, & De Lucia, 2016; Boly et al., 2016).

Conversely, the "visual awareness negativity" or VAN component is a negative deflection that begins 100 ms after stimulus presentation, while its peak can be seen at approximately 200-250 ms when the subjects are aware of the presented stimulus (Förster et al., 2020). However, later onset and peak latencies are observed when low-contrast stimuli are used (Wilenius & Rovonsuo, 2007), which reflects lower stimulus visibility. MEG studies suggest that VAN is generated along the ventral stream. In particular, the lateral-occipital complex (LOC) is quite certainly the source of this component (Liu, Paradis, Yahia-Cherif, & Tallon-Baudry, 2012; Pitts, Martínez, & Hillyard, 2011). The VAN also demonstrates lateralization towards the contralateral hemifield in relation to stimulus presentation (Eklund & Wiens, 2018). Different reviews that have examined results from different experimental paradigms, such as masking, manipulation of contrast level, attentional blink, bistable perception, and change blindness, have concluded that VAN is the ERP that has the stronger link with perceptual awareness (Koivisto & Rovonsuo, 2010; Railo et al., 2011; Förster et al., 2020).

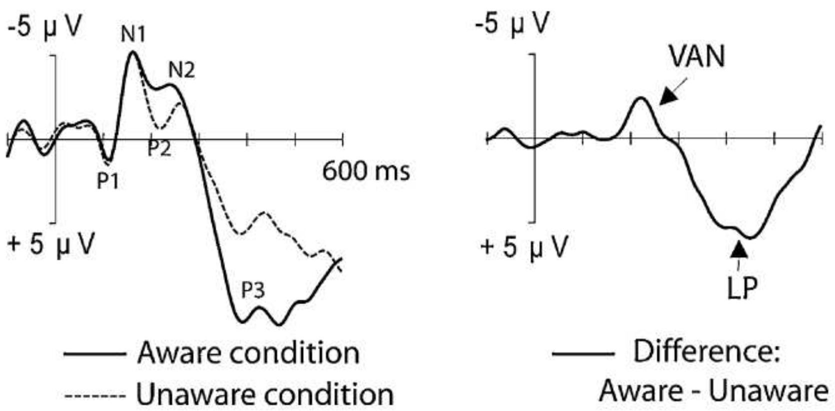

Figure 4.2 On the left the typical course of ERPs over occipital lobes in response to a visual stimulus. On the right the difference wave resulting from subtracting unaware from aware condition (Koivisto & Revonsuo, 2010)

A theoretical discussion in the field of conscious vision is the so-called "early vs. late debate" which refers to the question of whether neural processing of the stimuli leads to awareness in the early stages or involves high-order processing. In the "late" side of the controversy, a prominent theory is the Global Neuronal Workspace Theory (GNWT). This theory designates the P3b component as a hallmark of consciousness, potentially indicating the activation of the broadcast neural workspace. According to this theory, the workspace facilitates attention and other cognitive functions that are crucial for the emergence of conscious experiences (Dehaene & Changeux, 2011; Förster et al., 2020). On the other side of the spectrum, the Recurrent Processing theory (RPT) proposed by Lamme identifies early components such as VAN as indicative of conscious experience (Förster et al., 2020). Indeed, VAN has been hypothesized to reflect local recurrent processing in the visual cortex (Förster et al., 2020). Overall, as suggested in the review by Förster and colleagues (2020), later components such as P3/LP are related to access consciousness, while early ERPs such as VAN are, in fact, reliable neural correlates of visual awareness as they reflect phenomenal consciousness.

4.3 – Sustained and phasic activity

Visual information is processed in the brain by neurons that can have different patterns of activity. Sustained and phasic activities are involved in various aspects of visual processing. Sustained activity consists of an increase in the firing rate of neurons for a prolonged period of time in response to a stimulus. The orchestration of these dynamics is facilitated by the corticothalamic system. This system serves a dual role: it activates a select group of neurons while concurrently inhibiting another group of neurons. This interplay allows for the sustained activation necessary to sustain conscious perception, while enabling the interruption of this sustained firing when novel stimuli demand attention (Tononi et al. 2016). For instance, EEG and MEG studies revealed patterns of sustained activity lasting tens to hundreds of milliseconds, followed by a shorter period of decreased activity (Van De Ville, Britz, & Michel, 2010). This sequence of events reflects the brain's balance between maintaining ongoing perception and promptly shifting focus to new or salient stimuli.

On the other hand, masking experiments highlight the importance of the phasic activity of a stimulus; in both the onset and offset of an image, transient bursts of spikes in the primary visual cortex can be recorded. If a masked stimulus is introduced at the spatiotemporal edges of the target image, it can suppress spike bursts. Presumably, this inhibition is caused by the mechanisms of lateral inhibition that occur at multiple levels along the visual hierarchy (Macknik, 2006). Additional evidence corroborating the importance of phasic discharges comes from investigations of the Troxler illusion. This phenomenon occurs when, while maintaining a steady gaze, the surrounding images gradually vanish and fade from our visual experience (Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). When the subject fixates on a central point, the neurons responsible for processing the surrounding objects undergo adaptation, causing their firing rate to decrease. To counteract this effect, microsaccades are required, as they induce bursts of neural activity (Martinez-Conde, Macknik, & Hubel, 2002). These bursts prevent the visual objects from becoming invisible. However, phasic activity occurs in the early visual cortex, which, as explained in Chapter 3, is not likely to be a substrate of NCCs. As suggested by Tononi et al. (2016), phasic discharges may be important to activate cortical areas in the higher levels of the visual hierarchy, whereas in these regions, sustained firing might be necessary for visual consciousness.

Conclusions

Consciousness can be defined as “a condition of people and other creatures when they are awake and responsive to sensory stimulation” (Rosenthal, 2009). However, consciousness remains elusive, and there is not an agreement upon a common definition of this concept. An aspect of our conscious experience is vision, which involves the capacity to form meaningful mental representations of the world. This phenomenon is referred to as visual awareness, which Crick and Koch (2002) defined as the vivid and detailed experience of looking at a visual scene, as opposed to the less vivid and less detailed visual images produced by trying to remember the same scene. However, it is worth noting that even imagery and memory recollection are some forms of content-specific conscious experiences. The scientific effort to identify the Neural Correlates of Consciousness (NCCs), defined as “the minimum neural activity necessary for the rise of a conscious experience,” aims to expand our comprehension of consciousness. This exploration often delves into the well-understood visual system. Nowadays, different experimental approaches are used in the search for content-specific NCCs, all of which share some features: the stimulation is constant despite changes in the current conscious experience. Various experimental methods, such as visual masking and binocular rivalry, employ constant stimulation to change conscious experience. These approaches offer substantial experimental control and accommodate diverse stimuli. The quest to reveal the core NCCs involves uncovering the phenomenal correlates of consciousness while avoiding the confounds related to neural activity tied to access consciousness, such as attention, working memory, and the effort to report the experience. No-report paradigms are particularly useful in this regard. Attention is the primary confounding variable in NCCs’ research, as it is strictly interwoven with consciousness. However, situations where consciousness arises without attention (e.g., gist perception) and instances of attention without consciousness (e.g., visual priming and blindsight) suggest a dissociation between the two. Moreover, attention and consciousness can have opposing effects, with attention serving as an analyzer that selects information and consciousness as a synthesizer, integrating inputs into a coherent percept.

Efforts to locate the neural correlates of visual awareness have focused on visual areas and the fronto-parietal network. While the primary visual cortex is insufficient for conscious perception, debates persist regarding its necessity. Evidence from microstimulation and lesion studies suggests that extrastriate areas are necessary, but not sufficient, for conscious awareness. Activity in early visual cortices is linked to stimulus attributes, whereas higher-level visual regions are more closely associated with conscious contents. Although frontal areas were once thought to be crucial, recent experimental evidence suggests their involvement in conscious access rather than phenomenal awareness. Lesion and stimulation studies further cast further doubt on the necessity of the frontal regions. Conversely, parietal regions, particularly around the temporo-parietal-occipital cortices, host a "cortical hot-zone," a network that is thought to contribute to conscious experiences. This implies that the neural correlates of visual awareness are more likely to be situated in posterior brain regions.

Recurrent processing along the visual cortex has been proven to be essential for visual awareness. The Predictive Processing framework, not a consciousness theory *per se*, offers a promising avenue by conceptualizing visual consciousness as the brain's predictive inference of incoming stimuli, aimed at minimizing prediction errors. Visual Awareness Negativity (VAN) appears to reflect recurrent activity and serves as a reliable psychophysiological correlate of visual awareness. By contrast, the P3b component seems to be mostly associated with the cognitive processes responsible for conscious access. Contrary to previous beliefs, gamma-band activity is no longer unequivocally linked to consciousness. Regarding alpha band activity, its power does not uniformly correlate with visual awareness, whereas its phase might affect the temporal resolution of visual perception.

In conclusion, the pursuit of the Neural Correlates of Consciousness advances our understanding of consciousness by disentangling the fundamental neural processes underlying conscious experiences. While attention and consciousness share intricate connections, evidence suggests their distinct roles. The localization of NCCs primarily focuses on the posterior brain regions, with recurrent processing and predictive inference playing essential roles. These discoveries highlight the complex interactions between neural dynamics and conscious perception, driving the investigation of consciousness into promising uncharted realms.

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