

The neural codes of conscious perception and working memory

Los códigos neurales de la percepción consciente y la memoria de trabajo

Os códigos neurais da percepção consciente e da memória de trabalho

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Abstract: Working Memory (WM) and conscious cognition are intimately related neurocognitive functions. If conscious processing interacts with the information stored and available in WM, and if access to consciousness is a necessary condition for certain information to be able to be retained in WM, then certain correlates, mechanisms and neural codes could be shared. In this review and opinion article, the role in conscious perception and WM of a distributed activity in a fronto-parietal cortical network and the synchronized oscillatory activity of neuronal populations in different frequency bands and at different spatial scales is examined. Although conscious access and the first phases of information encoding share part of their neural codes, the retention of information in WM in a particular state could involve additional codes. At the end of the article it is suggested that a neural phase code, the theta-gamma code, could be the mechanism implemented by a global neuronal workspace to encode conscious contents and retain information in WM.

Key Words: conscious access; conscious processing; working memory; synchrony; cognitive control; neural correlates.

Resumen: La Memoria de Trabajo (MT) y la cognición consciente constituyen funciones neurocognitivas íntimamente relacionadas. Si el procesamiento consciente interactúa con la información almacenada y disponible en la MT, y si el acceso a la conciencia es una condición necesaria para que cierta información sea capaz de ser retenida en la MT, entonces ciertos correlatos, mecanismos y códigos neurales podrían ser compartidos. En el presente artículo de revisión y opinión se examina de manera particular el rol en la percepción consciente y en la MT de una actividad distribuida en una red cortical fronto-parietal y la actividad oscilatoria sincronizada de poblaciones neuronales en diferentes bandas de frecuencia y en diferentes escalas espaciales. Si bien el acceso consciente y las primeras fases de codificación de información comparten parte de sus códigos neurales, la retención de información en la MT en un estado particular podría involucrar códigos adicionales. Al final del artículo se sugiere que un código neural de fase, el código theta-gamma, podría ser el mecanismo utilizado por un espacio de trabajo neuronal global para

codificar contenidos conscientes y retener información en la MT.

Palabras clave: acceso consciente; procesamiento consciente; memoria de trabajo; control cognitivo; sincronía; correlatos neurales.

Resumo: A Memória de Trabalho (MT) e a cognição consciente constituem funções neurocognitivas intimamente relacionadas. Se o processamento consciente interage com a informação armazenada e disponível na MT, e se o acesso à consciência é uma condição necessária para que certa informação seja capaz de ser retida na MT, então certos correlatos, mecanismos e códigos neurais poderiam ser compartilhados. No presente artigo de revisão e opinião se examina de maneira particular o rol na percepção consciente e na MT de uma atividade distribuída numa rede cortical fronto-parietal e a atividade oscilatória sincronizada de populações neuronais em diferentes bandas de frequência e em diferentes escalas espaciais. Se bino acesso consciente e as primeiras fases de codificação de informação compartilham parte de seus códigos neurais, a retenção de informação na MT num estado particular poderia envolver códigos adicionais. No final do artigo sugere-se que um código neural de fase, o código theta-gamma, poderia ser o mecanismo implementado por um espaço de trabalho neuronal global para codificar conteúdos conscientes e reter informação na MT.

Palavras-chave: acesso consciente; processamento consciente; memória de trabalho; controle cognitivo; sincronia; correlatos neurais.

1. Introduction.

WM is traditionally defined as a limited capacity system that allows us to retain and manipulate information in the short term and in an online fashion, whether it be information that comes from our sensory inputs or from our long-term memory. Far from being a simple store of our recent sensory experiences, it is a mechanism through which certain information can be actively and volitionally used to control our thoughts, strategies and actions. As such, WM is a core component of higher cognition. Such a system constitutes from an evolutionary and ethological perspective an extremely valuable device, through which the organism is capable of processing in a reflexive mode certain information to deploy strategies or plans that

include the intervention of multiple decision-making steps, accumulation of evidence, and conservation of results of singular operations to be used in future additional computations.

In brief, WM is fundamental to perform a cognitive control, i.e., to adjust cognition and behavior in view of our intentions and goals. For these reasons, it is not surprising to corroborate that since its appearance in the field of Cognitive Psychology, the concept of Working Memory (WM) has been linked to operations and complex cognitive processes that require the intervention of conscious cognition and conscious processing of information (Miller, Galanter, & Pribram, 1960; Atkinson & Shiffrin, 1971; Baddeley & Hitch, 1974).

For Miller, Galanter and Pribram, who coined the term, WM is a type of quick access memory that we use to execute plans or programs (which may be composed of multiple parts or sub-plans) and a distinctive feature of these plans is their "special access to consciousness" (Miller, Galanter & Pribram, 1960: 65). On the other hand, for Atkinson and Shiffrin the representations contained in short-term memory are conscious by definition, and this fact is precisely what makes this memory function as a WM (Atkinson & Shiffrin, 1971). Finally, in the framework of the hierarchical and multi-componential cognitive model of WM proposed by Baddeley and Hitch (Baddeley & Hitch, 1974) the representations contained in the temporary buffers are, at least in principle, accessible to consciousness. According to Baddeley's model, WM constitutes an interface between perception, long-term memory and action, through which consciousness operates: in its own terms, consciousness "operates through working memory" (Baddeley, 1993: 21).

Now, if we are interested in clarifying the links at the neural level between WM and conscious cognition, we must first clarify what we understand by the expression or concept

of "consciousness". An epistemic operation of conceptual definition was indeed necessary for consciousness to become a well-defined problem in experimental psychology and neurosciences. Following the theoretical and conceptual framework of the global workspace model, the expression content of consciousness designates the information or representations of which I am aware at a given moment, information that is subject to volitional control and susceptible of being used in an active manner; Conscious access refers to the process or processes by which certain information becomes a conscious content, that is, the entry of certain information into a special information processing stage, thanks to which it can be included in additional cognitive processes. Finally, conscious processing refers to the set of controlled and special operations that can be applied to the contents of consciousness. These concepts must be distinguished from the concept of level of vigilance, which defines a set of different states that include coma, anesthesia, sleep, wakefulness, etc. Conscious access has its prerequisites, as a particular vigilance state, namely, being awake instead of asleep or under anesthesia, and also the participation of other cognitive mechanisms and functions such as attention. However, these prerequisites are necessary conditions for conscious access, although not sufficient conditions: we can be awake and attentive and yet not have conscious access to certain perceptual information due, for example, to the fact that the stimulus or object was only presented in the environment during a too short time interval.

Based on these definitions, WM can be conceived as the workspace of consciousness: once certain information has gained its conscious access and has therefore become a content of consciousness, we can evaluate it and decide if it is relevant from the point of view of our current purposes, and depending on this decision discard it or

on the contrary retain it to be used in any of our next operations. In other words, WM is the system in which a finite set of representations is maintained in a particular state thanks to which these representations are susceptible of becoming a content of consciousness and being the object of a conscious processing subject to volitional control.

The links between conscious cognition and WM are so deep that a great part of the neural correlates and signatures of conscious perception are generally associated in the literature with the neural correlates of WM. The hypothesis of the existence of an intimate relationship between WM and conscious perception is therefore not only raised in theory, but also seems to be supported by a significant amount of empirical evidence. Even though we still ignore at present a great part of the details about the mechanisms that support both aspects of higher cognition, the neuroscience of consciousness and WM has begun to allow us to understand the ways in which conscious perception or conscious awareness of certain perceptual information and the contents that are stored in WM are linked at the level of its neural substrates.

In the present article we will expose and analyze some of the tentative neural signatures and neural correlates of both conscious perception and WM. Particularly, we will examine the role in conscious perception and WM of a distributed activity in a cortical fronto-parietal network, the oscillatory activity in the gamma frequency band, and the long-range synchronized activity of neural ensembles at different frequency bands.

If conscious processing and cognition interacts with the information stored and available from WM, and if conscious access is a necessary condition (although maybe not a sufficient condition) for certain information to be able to be stored in WM, then we could expect to find some mechanisms, neural codes and processes to be shared.

In favor of this argument, the evidence available to date suggests that while conscious perception is characterized by a distributed, reverberant and synchronized activity in a fronto-parietal network that configures a global neuronal workspace, the processes in which WM is involved seem to use this same workspace and involve processes of synchronization and large-scale cross-frequency coupling to accomplish their different functions. However, we will also review a set of recent experimental results that suggest that although conscious access and the first instances of information encoding in WM could share their neural codes, the retention of information in WM in a state accessible to the conscience could additionally involve its own special codes.

Based on the analyzed evidence, at the end of the article it is suggested that a specific neural code, the theta-gamma code, could be implemented by a fronto-parietal workspace to encode conscious contents, allow the transition between contents of consciousness, and to retain information in WM.

2. Some signatures of conscious access and perception

Most of the knowledge we currently have about the neurobiology of conscious perception comes from studies that systematically compared temporal and spatial patterns of brain activity by manipulating the stimulus or stimuli that are presented to the experimental subjects in a controlled manner, in a way that in some cases they are accessible to consciousness while in some other cases they are not accessible to consciousness. Indeed, using different experimental paradigms it is possible to establish minimum contrasts between situations in which conscious perception or conscious access takes place and situations in which it is absent. This contrastive method, promulgated by B. Baars (1988), allows us to differentiate brain activity patterns in those

cases in which stimuli are processed, gains access to consciousness and become contents of consciousness and those cases in which, on the contrary, stimuli only evoke a non-conscious activity and treatment of information.

A fundamental task is to distinguish between mere neural correlates of a certain cognitive process and their markers or genuine neural signatures. When we speak about signatures we refer specifically to markers that are always and systematically present when conscious perception takes place, and absent otherwise (Sergent & Naccache, 2012; Dehaene, 2014). What differences in mental and neural treatment distinguish the cases in which perceptual information about a stimulus has accessed to consciousness from those cases in which it has not? Are there in the brain neural markers of the conscious awareness of a certain piece of information? What mechanisms are implemented to encode contents of consciousness?

2. 1. Distributed activity in a fronto-parietal network

A significant amount of research and experiments through electro-encephalography (EGG) and magneto-encephalography (MEG) show that around 270 milliseconds there is a fundamental divergence in brain activity between the cases in which presented visual stimuli are seen and consciously perceived and the cases in which they are not (Del Cul, Baillet & Dehaene, 2007; Gross et al., 2004; Sergent, Baillet & Dehaene, 2005; Salti, Monto, Charles, King, Parkkonen & Dehaene, 2015). In the cases in which the subjects report having seen the presented stimulus, it is observed that a sudden activation emerges that expands beyond local occipital sensory regions towards inferior bilateral frontal and dorsolateral regions, to the anterior cingulate cortex, and to the posterior parietal cortex. In those cases in which the stimulus never becomes a content of consciousness, this

activity is drastically reduced, and only a confined activation is observed in certain local brain regions that quickly begins to fade. In functional magnetic resonance imaging (fMRI), this activation of prefrontal and parietal associative cortical regions systematically distinguishes masked versus unmasked presentation of words (Dehaene et al., 2001) and images (Haynes, Driver & Rees, 2005), as well as lost stimuli versus perceived stimuli during the attentional blink (Marois & Ivanoff, 2005; Marois, Yi & Chun, 2004; Sergent, Baillet & Dehaene, 2005; Gross et al., 2004; Kranczioch, Debener, Schwarzbach, Goebel & Engel, 2005). For example, in a study in which the masking technique was used, the researchers observed that masked visual words evoked a brain activity confined to the Visual Word Form Area, while the perceived words involve primarily a sudden and massive activation of a fronto-parietal cortical network (Dehaene et al., 2001). In another fMRI experiment in which the researchers analyzed the brain activity of a group of healthy individuals in conditions in which their objective performances remained identical in the task they had to perform (determine if the stimulus presented was a square or diamond), varying only the subjective visibility of the stimulus presented, it was observed that only consciously perceived stimuli were associated with a spatially specific activity in dorsolateral and medial prefrontal cortex (Lau & Passingham, 2006). In other words, despite the fact that the objective performance of the participants remained identical whether they reported having consciously perceived the stimulus or not (a phenomenon called "blindsight"), only in the first case was an activity in prefrontal cortical regions observed.

Similarly, in another study in which a multivariate pattern analysis was applied to the data collected through EEG and MEG while the subjects had to locate and report the spatial position of a briefly presented visual

stimulus, this analysis revealed that even when the objective performance remained identical despite the subjective report of visibility, only in cases where stimuli had been reported as consciously perceived was it possible to decode specific spatial information of the stimulus in superior parietal and superior frontal regions, information that emerged in these regions from 270 ms. approximately (Salti et al., 2015).

These findings support the idea that conscious perception and conscious access mobilizes several cortical regions to distribute information about stimuli, that we can only experience certain information as a conscious content if it climbs up to prefrontal and parietal regions, and that conscious access and perception constitutes a late phenomenon that emerges almost a third of a second after the appearance of the stimulus in the environment.

According to one of the most prominent theoretical models of consciousness, the Global Neuronal Workspace Hypothesis (Dehaene & Naccache, 2001; Dehaene & Changeux, 2011; Dehaene, 2014), while the brain comprises multiple functionally specialized processors that treat information in a non-conscious and modular manner, what we call conscious access is the entry of certain information in a different neuronal system and computational space: the global neuronal workspace, a system of pyramidal neurons in prefrontal and parietal cortical regions whose axons and long-distance connections distribute information globally in the brain. The large pyramidal neurons that are situated in the II and III layers of the prefrontal cortex project their axons to multiple distant regions, in the same way that they receive messages thanks to their large dendritic trees, which exceed the size of those of other regions. Furthermore, neurons of parietal and prefrontal cortices, unlike other neurons, are characterized by they mixed-selectivity (Rigotti et al., 2013; Fusi, Miller &

Rigotti, 2016), which could underlie the flexibility that characterizes conscious cognition and complex behavior. From the perspective of the global neuronal workspace model there is therefore no single brain center or region responsible for conscious access and conscious processing, but rather they involve a distributed and at the same time integrated brain activity.

The architecture of this global neuronal workspace allows breaking the parallelism and modularity of the unconscious computations, and that certain information can be retained in time, distributed among different modules, incorporated in our decision-making, and become the object of additional processes and computations. Particularly, only the information that has accessed this global workspace can be used to carry out a series of strategies and serial and recursive operations (such as calculating $4 \times 2 + 7$) (De Lange, van Gaal, Lamme & Dehaene, 2011; Sackur & Dehaene, 2009). Thanks to this global neuronal workspace, it is possible to select, amplify and treat in a flexible and reflexive manner certain piece of information, functions that define the computational role of consciousness in the brain.

When a piece of information gains access to consciousness and becomes a content of consciousness, the neurons in the prefrontal cortex receive information about the stimulus according to a bottom-up modality, at the same time that these regions send projections in the opposite direction and towards several distributed areas, configuring a synchronized brain network of exchange of information, a network that does not become active when the wave of activity fails to overcome the threshold for conscious access. Gaillard et al. (2009) showed through a Granger Causality analysis of the data collected through intracranial electrodes that the increase of bidirectionality in the brain in conscious trials occurs precisely around 300 milliseconds, at

the precise moment when the ignition of the global neuronal workspace takes place, i.e., a sudden non-linear transition towards a meta-stable state of globally distributed brain activity. These observations support the hypothesis that conscious perception is supported not merely by a wave of bottom-up or feedforward activity, but by a reentrant, recurrent, or reverberant activity (Lamme & Roelfsema, 2000; Dehaene & Naccache, 2001; Dehaene, Changeux, Naccache, Sackur & Sergent, 2006; Tononi & Koch, 2008).

The close relationship between the global integration of information in a global neuronal workspace distributed in a fronto-parietal network and conscious perception or conscious access can also be appreciated through the examination of certain psychopathological disorders such as schizophrenia. Studies show that although the unconscious processing of information remains intact in schizophrenics, the threshold for conscious perception is altered, and they need more sensory evidence than healthy subjects to perceive a stimulus (Dehaene et al., 2003; Del Cul, Dehaene, & Leboyer, 2006), possibly due to deficits in top-down attentional mechanisms (Berkovitch, Dehaene & Gaillard, 2017). In other words, the ignition of the global neuronal workspace is reduced, and for that reason we find a disruption of conscious access (Berkovitch et al., 2017; Berkovitch, Del Cul, Maheu & Dehaene, 2018).

Finally, there is evidence about the causal role of the prefrontal cortex in processes that involve conscious cognition. Transcranial magnetic stimulation or damage in these regions can interfere with conscious perception, limiting the ability to perceive and reflect, for example, about a simple image (Rounis, Maniscalco, Rothwell, Passingham & Lau, 2010), or shifting the threshold for access to consciousness (Del Cul, Dehaene, Reyes, Bravo & Slachevsky, 2009). For

example, Rounis et al. (2010) have shown that theta-burst transcranial magnetic stimulation to the prefrontal cortex impairs metacognitive visual awareness. Furthermore, repetitive transcranial magnetic stimulation on the right dorsolateral prefrontal cortex (Turatto, Sandrini & Miniussi, 2004) or on regions of the right parietal cortex (Beck, Muggleton, Walsh & Lavie, 2005) impair conscious access to visual change, i. e., increase change blindness.

To be precise, activity in prefrontal regions seems to be a necessary condition for conscious perception but not a sufficient condition, since there is evidence that even unconscious processing of information can be deployed in these regions (Lau & Passingham, 2007; van Gaal, Ridderinkhof, Fahrenfort, Scholte & Lamme, 2008). According to the Global Neuronal Workspace model, even when the phases or perceptual stages could be displayed in an identical way in conscious and non-conscious trials, only when certain piece of information obtains its access to consciousness does this information become amplified and recoded in areas of a fronto-parietal network. This model predicts, therefore, that additional information about a stimulus must be present in these regions only in conscious trials. Some experimental results seem to confirm this prediction (Salti et al., 2015).

In summary, contrary to certain hypotheses of conscious access that postulate that the latter takes place when local recurrent loops in sensory regions are established (Lamme, 2006; 2010), studies using fMRI, iEEG, EEG and MEG, together with evidence from studies of brain injuries, certain neuropsychiatric disorders and transcranial stimulation experiments, indicate that prefrontal and parietal cortices play a central role in conscious access and conscious processing.

2. 2. Late and sustained amplification of gamma-band activity

Studies through EEG, iEEG and MEG allow us to examine in detail the evolution of cortical activity over time. The oscillations generated by active neuronal tissue often exhibit rhythmic characteristics. Traditionally, neural oscillations are divided into different frequency bands, including slow oscillations (< 1 Hz), delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-30 Hz), and gamma (> 30 Hz) bands. When information of a presented stimulus accesses the brain, there is a disturbance of the fluctuations that were taking place until then, and also new frequencies are imposed. Although brain oscillations have been known for decades, only recently have serious attempts begun to take place to understand how different brain rhythms support different cognitive functions and operations.

In a study in which was combined the data of ten clinical patients to which intracranial electrodes were implanted across the visual pathway, researchers obtained information about the step by step advancement across the cortex of a visually presented word, and they observed a pattern of differentiated activity in the cases in which the subjects reported having seen the stimulus with respect to the cases in which they reported not having seen it (Gaillard et al., 2009). In all cases (whether the word was reported as seen or not seen), a wave of increased activity in the gamma band was observed within the first 200 milliseconds after the presentation of the word. However, the eruption of gamma rhythms in the cases in which words were not seen quickly disappeared around this time interval. Only a brief burst of high frequency activity in the gamma band was observed crossing the ventral visual cortex. On the contrary, for the words seen an all-or-non difference was found around 300 milliseconds: a sustained and huge increase in the gamma-band power. In another experiment in which the masking technique was used, the ECoG recordings

revealed a similar increase in the gamma-band power (30-70 Hz) in the ventral pathway of the visual cortex of the subjects, specifically associated with satisfactory recognition of certain presented visual information (Fisch et al., 2009), results from which the researchers suggested that this increase in neural activity of higher visual areas in the cortical hierarchy plays a critical role in the emergence of a "conscious visual percept".

The repeated observation of a similar pattern of activity has led to the proposal according to which this increase and sustainment in the gamma-band power that starts around 300 milliseconds after stimulus onset constitutes a marker of conscious perception (Dehaene, 2014). In the last decade of the twentieth century, Crick and Koch had already discussed the possible role of oscillations at 40 Hz in conscious cognition (Crick & Koch, 1990a; 1990b). The evidence available to date suggests that although high-frequency activity is present in certain instances of unconscious information processing (Gaillard et al., 2009, Fisch et al., 2009; Aru et al., 2012), it is not this mere presence but the increase and sustainment in the gamma-band power what constitutes a marker of conscious perception.

2. 3. Large-Scale Synchronized Activity

In several empirical studies and theoretical proposals it has been observed and suggested that the synchronization of electromagnetic signals across distant regions could play a key role in conscious perception (Damasio, 1989; Crick & Koch, 1990a; 1990b; Rodriguez, George, Lachaux, Martinerie, Renault & Varela, 1999; Engel, Fries, König, Brecht & Singer, 1999; Varela, Lachaux, Rodriguez & Martinerie, 2001; Gross et al., 2004; Singer, 2007; Tononi, Srinivasan, Russell & Edelman, 1998; Tononi & Koch, 2008; Tononi, 2008; Melloni, Molina, Pena, Torres, Singer & Rodriguez, 2007; Melloni & Singer, 2010; 2011; Gaillard et al., 2009;

Dehaene, 2014; Dehaene et al., 2006; Dehaene & Changeux, 2011; Doesburg, Green, McDonald & Ward, 2009; Uhlhaas et al., 2009; Hipp, Engel & Siegel, 2011).

The role in conscious cognition and WM of synchronous/synchronized activity in the gamma-band has been the object of reflection of neuroscientists since the end of the last century (Crick & Koch, 1990a, 1990b). For example, Crick and Koch hypothesized that consciousness depends crucially on some form of short-term WM, and that the generation of synchronous oscillations in the gamma-band, which would reflect the integration of different characteristics of a stimulus, activate this memory (Crick & Koch, 1990b).

Singer and colleagues were the first to examine the role in perception of synchronous neuronal oscillations in the gamma-frequency band in the visual system (Singer & Gray, 1995), and at the end of the 20th century it was speculated that these synchronous oscillations in the visual system could be fundamental in the process of integrating different properties of a stimulus (such as color and shape) into a single and singular percept (Engel et al., 1999).

At present, some theoretical proposals argue that while unconscious processing of information would have as a neural signature the local coordination of neural activity and a restricted propagation, conscious perception would require the global coordination of widely distributed neural activity through large-scale synchronization (Dehaene et al., 2006; Melloni & Singer, 2010).

Why our brains generate synchronized oscillations of neuronal ensembles? What could be the advantages of this synchronized activity? The neuronal communication through neuronal coherence theory (Fries, 2005; 2015) postulates that the reason why the brain generates synchronized neuronal oscillations is because synchrony facilitates the transmission of information, not only

between nearby or closed regions, but also between distant regions. If two networks in two different brain regions oscillate in phase, they are in an advantageous position to share information (Engel, Fries & Singer, 2001). Rhythmic synchrony would constitute the mechanism that the brain uses to coordinate the interactions between neurons and to form neural ensembles and networks in a flexible way. In this way, neural synchrony could be the basis for the transient functional integration of different networks or modules in the brain that are involved in a certain cognitive process or function.

Ensembles of active neurons that oscillate in a synchronized way are in the same active and receptive state, and by combining their discharges they strategically send and receive information. There is evidence that the neural impulses (spikes) of two neurons that arrive simultaneously at a third neuron have a greater impact than if the impulses had arrived at different times (Aartsen, Gerstein, Habib & Palm, 1989; Salinas and Sejnowski, 2000; Fries, 2005; Engel et al., 2001). In brief, synchronized rhythms can regulate the interactions between networks. When neural ensembles oscillate together, they open a channel through which they transmit signals from one region to another (Womelsdorf et al., 2007; Fries, 2005; Varela et al., 2001). Furthermore, synchronized activity would allow to retain information in differentiated phases, protecting its possible loss due to interferences (Miller & Buschman, 2013). In order that different neuronal ensembles do not interfere with each other, our brain keeps them oscillate out of phase in relation to each other. New evidence seems to be emerging that indicates that highly complex aspects of cognition such as attention (Landau & Fries, 2012; Helfrich et al., 2018; Fiebelkorn & Kastner, 2018), WM, and consciousness, operate rhythmically.

Synchronized oscillations could help to form new functional networks between brain

regions during learning (Antzoulatos & Miller, 2011), and this dynamic formation of neural networks could be at the foundation of the cognitive flexibility that underlies the processes in which conscious information processing or higher cognition is involved.

Neural synchrony occurs at different temporal and spatial scales. Regarding consciousness or conscious cognition, the synchronization of oscillations between not only local regions, but also the synchronization between distant regions, seems to constitute an optimal state to share information on a large scale, configuring a network of exchange of information that typically occurs in the lower frequencies of the beta band (13-30 Hz) or the theta band (3-8 Hz). The formation of dynamic links between distant brain regions through synchronized activity in different frequency bands could be the mechanism capable of counterbalancing the anatomical nature of our brain, and the mechanism that allows different regions to coordinate to give rise to a "unified cognitive moment" (Varela et al., 2001).

In an experiment in which the researchers recorded cortical activity through MEG, they observed that the conscious perception and report of a weak somatosensory stimulus correlated with a sustained strengthening of synchrony in the delta/theta frequency bands (3-7 Hz) and the gamma band (40-60 Hz), and this synchronization dynamically connected fronto-parietal, sensory, and motor systems (Hirvonen, Monto, Wang, Palva & Palva, 2018). These data indicate that the brain regions that underlie perception, decision-making and actions are connected transiently through dynamic phase synchronization in these frequency bands. The neuronal activity that defines the pathway from perception to action could therefore be supported by a dynamic synchronization of a large-scale brain network.

On the other hand, in experiments in which invisible images are presented to the subjects

it is observed that these images that do not cross the threshold for conscious access present a synchrony that is only temporary, less intense, and confined in spatial terms to posterior regions of the brain. In a study in which brain activity recorded at 176 local sites was analyzed through intracortical depth electrodes, Gaillard et al. (2009) observed that visible words, in contrast to invisible words, elicited a cortico-cortical long-distance synchronization in the beta band between 300 and 500 milliseconds after stimulus onset. In other terms, coherent long-distance neural activity systematically differentiated trials in which words were seen and consciously perceived from those trials in which they did not reach the conscious access.

In a set of experiments specifically designed to explore the relationship between conscious perception and neural synchrony, Melloni et al. (2007) combined the masking technique and electroencephalographic recordings (EEG) to examine the differences in neuronal activity between words perceived and words not perceived, and they observed crucial differences in the electrophysiological responses in both conditions. While both perceived and non-perceived words produced a similar local increase and synchrony in the gamma frequency band in the EEG, only the perceived words induced a transient long-distance synchronization of gamma oscillations across frontal, parietal and occipital regions. In addition, they observed an increase in oscillatory activity in the theta frequency band in frontal regions while the subjects retained the perceived words in their memory. Based on these results the researchers suggested that this transient long-distance synchronization in the gamma band could not only allow for certain contents to get access to consciousness, but also that other additional processes, such as their retention in WM, can take place later.

Short periods of long-distance synchronization between frontal and parietal

regions in the gamma-band were also observed in binocular rivalry experiments (Doesburg, Kitajo & Ward, 2005; Doesburg et al., 2009). For example, Doesburg et al. (2009) detected that a transient phase synchronization in the gamma band across prefrontal and parietal regions preceded the perceptual change between images, and that the amplitude was coupled to the phases of theta oscillations in those same cortical regions. Based on these results, the authors suggested that the emergence of consciousness contents is supported by a large-scale brain integration implemented through the synchronization of specific neuronal ensembles in the gamma band, a synchronization that is modulated by theta rhythms. Theta-gamma cross-frequency coupling between could therefore constitute a fundamental mechanism in the emergence and transitions between contents of consciousness. The dynamics of a fronto-parietal oscillatory network that alternates between gamma synchronization and desynchronization, adjusted to the phase of theta cortical rhythms, could according to the researchers provide the temporal structure that governs the emergence and dissolution of "discrete moments of experience".

Finally, the possible causal link between the large-scale synchronization of neural ensembles and conscious perception also seems to get support from the evidence collected in research on certain neuropsychiatric disorders. Indeed, some neuropsychiatric disorders such as schizophrenia and Autism Spectrum Disorder (ASD) present as one of their distinctive pathophysiological phenomena certain abnormalities in long-distance synchronized oscillatory activity (Uhlhaas & Singer, 2010; 2007; Berkovitch, Dehaene & Gaillard, 2017; Hirvonen et al., 2017). For example, in one study the MEG recordings of patients with chronic schizophrenia while performing a visual perceptual closure task showed,

compared to healthy individuals, a reduced long-range synchronization in the beta and gamma bands between visual regions, as well as between the visual cortex and the frontal cortex (Hirvonen, Wibral, Palva, Singer, Uhlhaas & Palva, 2017). According to these results, schizophrenia presents a deficit in the coordination of distributed neural activity (Tononi & Edelman, 2000), expressed in the disruption of transient large-scale synchronization.

In summary, research in the field of the neuroscience of consciousness indicates that some of the brain correlates and tentative markers or signatures of conscious access and conscious perception are the increase and sustainment of the gamma-band power, a distributed and reverberant activity of regions that mainly involve a fronto-parietal workspace, and the at least transient synchronization of the activity at different frequency bands, not only in local but also distant neural ensembles that are part of this fronto-parietal network. If WM constitutes the workspace of consciousness, i. e., the space in which certain information is stored after becoming a content of consciousness, information that is subject to volitional control and that can become the object of serial and recursive computations, then we might expect to find similar signatures and/or correlates between conscious perception and WM.

3. The Cognitive Neuroscience of WM

Given the profound links between conscious perception and WM it is not surprising to corroborate that a great part of the neural correlates and genuine signatures of conscious perception are generally associated in the literature with the neural correlates of WM.

Indeed, a distributed and synchronized activity in a fronto-parietal network and a particular type of activity in the gamma-band are also markers usually correlated to WM. In the following pages, we are going to expose

and examine a set of studies that provide us with both correlational and causal evidence about the role in WM of these brain activity patterns.

Regarding the neuroscience of consciousness, studies on WM can be interpreted as relevant experimental data that can inform us about conscious access, conscious processing, and the ways in which certain information can be maintained in a particular state thanks to which certain contents and representations can eventually become contents of consciousness once again.

3. 1. Sustained or persistent activity in prefrontal cortex

When we think about WM, the first question that emerges can be succinctly posed in the following way: How do groups of neurons represent and maintain information of sensory stimuli once these are no longer available in the environment?

A persistent spiking activity, especially in prefrontal cortex, a brain region particularly involved in the top-down cognitive control of complex behaviors (Miller & Cohen, 2001; Miller & Buschman, 2012), has been conceived for decades as the mechanism and neural correlate of WM par excellence (Fuster & Alexander, 1971; Funahashi, Bruce & Goldman-Rakic, 1989; Goldman-Rakic, 1995; Miller, Erickson & Desimone, 1996), and even neural attractor networks models based on such persistent activity have been proposed (Amit & Brunel, 1997; Wang, 1999; Compte, Brunel, Goldman-Rakic & Wang, 2000; Renart, Moreno-Bote, Wang & Parga, 2007; Barbieri & Brunel, 2008; Lundqvist, Compte & Lansner., 2010; Wimmer, Nykamp, Constantinidis & Compte, 2014).

In brief, the idea is that once activated by a stimulus, co-activated groups of neurons (ensembles) keep spiking, maintaining the representation of the stimulus during the delay period in which the subject retains the

information. This idea goes back to the work of D. O. Hebb (1949), for whom the short-term retention of information would have as a correlate a persistent and elevated neural activity. Hebb hypothesized that the reverberant activity between neurons involved in the perception of certain information is necessary to retain this information until it can eventually be encoded in long-term memory through a process of synaptic reorganization. Thanks to recordings of prefrontal cortex activity in non-human primates, from 1970 onwards evidence began to accumulate that seemed to support this idea about such a persistent activity.

Fuster's research showed that in delayed-response tasks individual neurons in the prefrontal cortex of non-human primates presented a persistent activity during the information retention period (Fuster, 1973; Fuster & Alexander, 1971), which seemed to suggest, according to a prediction put forward by Jacobsen (1936), that there would be an immediate memory whose location would be reserved, precisely, to prefrontal regions.

3. 2. Persistence vs sparseness

The presence and precise role of sustained activity during the period in which the brain retains information in WM is however at present the subject of controversy. While some groups of researchers support the hypothesis that the fundamental cellular mechanism underlying the maintenance of information in WM is based on persistent activity (see for example Constantinidis et al., 2018), others claim that this persistent activity is not necessary (Trübutschek et al., 2017; Lundqvist, Herman & Miller, 2018).

One of the objections that have been raised to the evidence supporting persistent activity is the fact that this evidence generally comes from studies that averaged spiking across time and across trials, a strategy that could hide the precise details of the dynamics of neural activity. For this reason, some

researchers have argued that the activity should be accurately examined as it is presented on single trials (Shafi, Zhou, Quintana, Chow, Fuster & Bodner, 2007; Stokes & Spaak, 2016; Lundqvist, Rose, Herman, Brincat, Buschman & Miller, 2016; Lundqvist, Herman & Miller, 2018). Another problem that arises is that the observation of a persistent activity comes mostly from investigations in which the subjects must perform a task that includes in some of its instances a motor component (for example, oculomotor delayed response tasks), for which the motor preparation could eventually contribute in the observed spiking activity.

Recent research in non-human primates shows that when spiking activity is examined on individual trials or in real time we don't find a persistent activity, but rather a spiking activity that occurs in sparse and transient synchronous bursts, both at the level of individual neurons and local networks (Lundqvist et al., 2016; Lundqvist, Herman, Warden, Brincat & Miller, 2018; Bastos, Loonis, Kornblith, Lundqvist & Miller, 2018). On the other hand, research carried out through the use of tasks that do not involve a motor component in the period in which the subject must retain the previously presented information, such as change-detection tasks (Lundqvist et al., 2016) and delayed-matching tasks (Shafi et al., 2007), found in the same way a less persistent and robust activity.

Indeed, the activity of neural ensembles during intervals of information retention shows variability and dispersion rather than persistence. In the middle of the sparse spiking activity there are intervals of time where a relatively silent activity is observed rather than a persistent spiking activity (Lundqvist et al., 2016; Trübutschek et al., 2017). In an experiment with non-human primates, the analysis of the electrophysiological recordings of individual trials during a WM task revealed an absence of any kind of continuous activity, and instead

the researchers identified the presence of brief bursts of beta (~ 20-35 Hz) and gamma (~ 50-120 Hz) oscillations in prefrontal regions, and their dynamics suggested that these oscillations could have different roles in the maintenance and control of the elements contained in WM (Lundqvist et al., 2018). The data obtained by Earl K. Miller and colleagues suggest that the rapid transitions that are observed between high-power events in gamma and beta bands allow for the flexible coordination of multiple elements contained in WM (Lundqvist et al., 2018). The gamma bursts were correlated with the coding, maintenance and use of information stored in WM.

WM models have been developed to account for this variability and sparseness, such as the Dynamic Attractor Network model (Lundqvist, Herman & Lansler, 2011) and the Activity-Silent model (Stokes, 2015). Both models postulate that in order to retain information in WM no persistent activity is necessary, but rather temporary changes in the synaptic weights of the network could be sufficient. While in the Activity-Silent model the delayed spiking activity produces these changes, in the Dynamic Attractor Network model oscillatory dynamics is responsible for their production. In this latter model, multiple items can be maintained in WM without interfering with each other, because gamma bursts occurring at different times encode different items. In other words, different items are serially encoded and read out.

In both WM models, the neuronal impulses leave an "impression" in the network by modifying the synaptic weights, and this impression is able to retain the memories between the episodes of activity of these impulses. Briefly, in both models spiking would not be responsible for doing all the work that is required to maintain information in WM: the cerebral cortex could encode and retain the information in WM during the episodes of sparse activity by modifying the

synaptic weights. In addition to its functional implications, from an economic perspective this mechanism seems to provide our brains with certain advantages: instead of using a significant amount of energy producing a sustained and persistent spiking activity during the periods in which we retain certain information, the impressions that spiking activity leave in the network allow us to retain our memories using a smaller amount of it (Lundqvist, Herman & Miller, 2018).

A recent study in which a set of experiments were conducted to elucidate the relationships between the mere conscious access and perception of a stimulus and its eventual retention in WM indicates that there may be two successive mechanisms for the short-term maintenance of information: an initial and transient period of approximately 1 second, during which the representation of the stimuli is encoded by active firing with a slowly decaying amplitude, and then an instance of maintenance of the representation through a silent activity that takes place through short-term changes in synaptic weights, during which the activity intermittently resurfaces (Trübutschek et al., 2017). In other terms, after a transient encoding phase carried out through active firing, the representations in WM could be maintained by means of activity-silent changes in synaptic weights that do not imply any detectable neural activity, and a periodic update could stabilize the representations stored during the information retention period.

3. 3. Gamma-band activity and large-scale synchronization in WM

Neural oscillations at different frequencies and their dynamics play a central role in a vast repertoire of cognitive processes. For example, we have already seen that some theoretical proposals hold that conscious perception emerges as a product of a large-scale integration facilitated by the synchronization of neuronal ensembles in

different frequency bands, and that an increase and sustainment in the gamma-band power accompanies conscious access to perceptual information.

Gamma-band oscillations are associated not only with conscious perception, as we have already seen, but also with other aspects of cognition, such as attention and long-term memory (for a review see Jensen, Kaiser & Lachaux, 2007). It has even been suggested that neural gamma-band synchronization constitutes a fundamental process in cortical computations that supports multiple higher cognitive functions (Fries, 2009).

Regarding WM, gamma-band activity has been associated with different aspects such as the encoding (Howard et al., 2003; Sedenberg, Kahana, Howard, Donner & Madsen, 2003; Mainy, Kahane, Minotti, Hoffmann, Bertrand & Lachaux, 2007) and maintenance of sensory information (Pesaran, Pezaris, Sahani, Mitra & Andersen, 2002; Jensen et al., 2007; Honkanen, Rouhinen, Wang, Palva & Palva, 2015; Lundqvist et al., 2016; Wutz, Loonis, Roy, Donoghue & Miller, 2018). Tallon-Baudry and colleagues provided for the first-time evidence about a link between the maintenance of information in WM and gamma-band oscillatory activity. In a delayed-matching-to-sample task, they observed an increase and sustained activity in the gamma-band in occipito-temporal and frontal regions during the information retention period, an activity that was absent when the subjects performed a control task that did not involve any instance of memorization of information (Tallon-Baudry, Bertrand, Peronnet & Pernier, 1998). Since then, multiple investigations have found gamma-band activity related to different aspects of WM. A study through MEG identified a sustained activity in the gamma band while subjects retained for a period of 3 seconds the orientation of previously presented faces in a spatial delayed-match-to-sample task (Jokisch & Jensen, 2007), and the sources of

this activity were identified in early occipital sensory areas. There are also studies that provide evidence about a sustained activity in the gamma band outside these early sensory regions. For example, two studies using intracranial EEG (iEEG) reported an increase in gamma band activity outside visual cortical regions while subjects memorized visual letter sequences (Howard et al., 2003, Mainy et al., 2007). For example, Mainy et al. (2007) found this kind of activity in the auditory cortex and also in regions traditionally associated with the component of Baddeley's WM model called the phonological loop, i.e., Broca's area in the inferior frontal gyrus.

A gamma-band activity correlated with an increase in WM load has also been localized in key regions of the brain network of conscious cognition, i.e., in prefrontal and parietal cortical regions (Roux, Wibral, Mohr, Singer & Uhlhaas, 2012; Palva, Monto, Kulashekhar & Palva, 2010; Palva, Kulashekhar, Hamalainen & Palva, 2011). Some studies even show that there is a parametric relationship between WM load (i.e., the number of items or amount of information to be memorized) and the amplitude of gamma oscillations (Howard et al., 2003; van Vugt, Schulze-Bonhage, Litt, Brandt & Kahana, 2010; Palva et al., 2010; 2011; Honkanen et al., 2015). For example, in a study in which the researchers analyzed the intracranial recordings of epileptic patients while performing a WM task (Sternberg's task), spectral analyses revealed that the power of the gamma oscillations (30-60 Hz) increased approximately linearly with memory load, that it remained constant during the retention interval, and that it returned to a base level when the subjects no longer needed to keep the information in their memory (Howard et al., 2003). In another study, Roux et al. (2012) showed that gamma-band activity in prefrontal cortex codes for the number of relevant items maintained in WM. The researchers observed not only an

increase in gamma-band activity associated with the increase in WM load in prefrontal regions (Brodmann area 9), but also that this activity predicted the number of items retained in WM.

There are also studies in humans that have also reported a sustained cortical activity in the theta band during the retention interval (Gevins, Smith, McEvoy & Yu, 1997; Jensen & Tesche 2002; Raghavachari et al., 2001; Scheeringa, Petersson, Oostenveld, Norris, Hagoort & Bastiaansen, 2009), results that have led to the suggestion that activity in this frequency band could also have a central role in the processes and mechanisms that underlie WM. For example, in a study in which the researchers examined theta-band activity during a WM task (Sternberg's task), they observed that in several cortical zones the amplitude of theta oscillations increased from the beginning of the trial, remained constant during the retention period, and finally decreased towards the end of the trial (Raghavachari et al., 2001).

On the other hand, large-scale synchronization of neuronal ensembles in different frequency bands, one of the markers of conscious perception that we have examined, has also been found in several WM studies (Sarnthein, Petsche, Rappelsberger, Shaw & von Stein, 1998; Palva, Palva & Kaila, 2005; Palva et al., 2010; Sauseng, Klimesch, Doppelmayr, Hanslmayr & Schabus, 2004; Sauseng, Klimesch, Doppelmayr, Pecherstorfer, Freunberger & Hanslmayr, 2005a; Sauseng, Klimesch, Schabus & Doppelmayr, 2005b; Crespo-Garcia, Pinal, Cantero, Díaz, Zurrón & Atienza, 2013; Salazar, Dotson, Bressler & Gray, 2012), and even certain theoretical proposals postulate this large-scale synchronized activity, especially in a fronto-parietal network, as a key mechanism for the retention of information in WM (Sarnthein et al., 1998; Tallon-Baudry, Bertrand & Fischer, 2001; Palva et al., 2010; Salazar et al., 2012).

For example, Sauseng et al. (2005b) showed that phase synchronization in the theta frequency band between frontal and parietal regions increased during complex manipulations of elements retained in WM. Other studies show that there is even a relationship between theta phase synchronization and WM load. Indeed, theta-band coherence between frontal, temporal and parietal regions increases with WM load (Payne & Kounios, 2009) and also varied with individual WM capacity (Kopp, Schröger & Lipka, 2006). Other studies have found a phase synchronization between the beta and gamma bands: in relation to a control condition, during the retention of information in WM the coherence between fronto-parietal areas is improved at these frequencies (Lutzenberger, Ripper, Busse, Birbaumer & Kaiser, 2002; Babiloni et al., 2004). Finally, in another study Palva et al. (2010) observed that during the periods in which the subjects had to retain the information in a visual WM task, interareal phase synchronization was stable and sustained among fronto-parietal and visual regions in the alpha (1-13 Hz), beta (18-24 Hz) and gamma (30-40 Hz) frequency bands. Furthermore, they observed that phase synchrony across fronto-parietal regions was strengthened as a function of the increase in memory load.

A recent additional analysis of data that had already been collected in a previous experiment in which the researchers studied the brain activity patterns of three different regions of monkeys' cortex while performing a WM task, seems to provide us with direct evidence about the precise functional role of long-range neural synchronization in the retention and control of information in WM. What happens in the brain when WM load capacity is exceeded? Is it possible to detect neurophysiological events that reflect or explain the limits of our ability to retain information in the workspace of consciousness? As suggested by the analysis

of the data, an overloaded WM could lead to a loss of synchrony (Pinotsis, Buschman & Miller, 2018). The researchers developed a theoretical model based on Predictive Coding theory and used this model to analyze Cross Spectral Density data obtained through local field potentials (LFP) from three brain regions (prefrontal cortex, frontal eye fields, and lateral intraparietal area), collected while the monkeys performed a visual change-detection task. By manipulating the number of objects that the monkeys had to remember (1-3 objects in each visual hemifield), they observed that the increase in memory load produced modifications in the connectivity of the three regions examined. The analysis of the data showed that the amount of information retained in WM modulates the neuronal coupling between areas and that an overloaded WM left them out of synchrony. In other terms, the overload of WM broke down the communication between different brain regions generally associated with the WM network.

3. 4. Large-scale cross-frequency phase-amplitude coupling

In addition to large-scale synchronized activity in a particular frequency band and phase-phase cross-frequency coupling (also called cross-frequency phase synchronization), some research and theoretical proposals have emphasized a particular type of coupling: phase-amplitude cross-frequency coupling. This type of phase-amplitude cross-frequency coupling occurs when the amplitude of a high-frequency oscillation is modulated as a function of the phase of an oscillation at a lower frequency. Following this approach, for Lisman, Idiart and Jensen (Lisman & Idiart, 1995; Jensen & Lisman, 1998; Jensen, 2006; Lisman & Jensen, 2013) the phase-amplitude coupling between theta and gamma frequency oscillations forms a neural code for representing multiple items in WM in a

sequential and ordered way: the theta-gamma code. According to this model (known as the LIJ model), the number of items capable of being memorized without interference in WM is limited by the number of gamma cycles that can fit into a theta cycle (4 to 8 cycles). According to the hypothesis of the researchers, each gamma cycle that occurs in different phases of a theta cycle expresses an active neuronal ensemble that represents a determined item. Thanks to this code, the elements stored in WM, each of them represented by a gamma subcycle, would be reactivated sequentially in different points of time in a theta cycle. In this way, the temporal segmentation implemented through a phase code could be the mechanism responsible for maintaining multiple representations in WM. Multiple neuronal ensembles, each one representing an item in WM, would avoid overlapping their activity by occurring in different times of a theta cycle.

A theta-gamma coupling has been observed in humans during the performance of WM tasks both in cortical regions (Canolty et al., 2006; Jacobs & Kahana, 2009; Rajji, Zomorróni, Barr, Blumberger, Mulsant & Daskalakis, 2016; Bahramisharif, Jensen, Jacobs & Lisman, 2018; Lara, Alekseiuk, Turi, Lehr, Antal & Paulus, 2018) and the hippocampus (Axmacher, Henseler, Jensen, Weinreich, Elger & Fell, 2010). In the hippocampus, gamma-band amplitude is modulated by the phase of theta oscillations during the retention of information in WM, and the strength of this cross-frequency coupling predicts the individual performance of the subjects (Axmacher et al., 2010). In another study, it was observed that the maximum number of gamma cycles in a theta cycle correlated with individual's memory span in a verbal WM task (Kaminski, Brzezicka & Wróbel, 2011). These results seem to be therefore consistent with the theoretical proposal according to which nested oscillations in the theta and gamma frequency

bands play a fundamental role in WM processes (Lisman & Jensen, 2013), and with the idea that cross-frequency coupling between different brain rhythms could be responsible for the coordination of the cortical areas required to perform complex cognitive operations in which conscious cognition intervenes.

If the hypothesis about the role of theta-gamma cross-frequency coupling in WM is correct, then allowing more gamma cycles to fit into a theta cycle should increase WM capacity. Is there evidence that confirm this prediction? Some correlational studies provide indirect evidence that supports this hypothesis. For example, Axmacher and colleagues (Axmacher et al., 2010) showed that the increase in WM load results in a decreased frequency of theta oscillation. On the other hand, recent studies that used Transcranial Alternating Current Stimulation (tACS) seem to provide causal evidence that supports the hypothesis that WM capacity is determined by the number of gamma cycles that can fit in a theta cycle (Voskuhl, Huster & Hermann, 2015; Wolinski, Cooper, Sauseng & Romei, 2018). Two studies have shown that by slowing down theta rhythm, more gamma cycles could be nested in a theta cycle. For example, Wolinski et al. (2018) showed that modifying the theta rhythm at a slower frequency (4 Hz) enhanced WM capacity, while modifying the theta rhythm at a faster frequency (7 Hz) reduced it.

On the other hand, evidence has recently begun to be collected that seems to support the claim about the existence of a causal role of fronto-parietal synchronization in WM operations. By means of tACS, Polanía et al. (2012) provided causal evidence about the role of fronto-parietal theta phase-coupling in the performance of individuals during a delayed letter discrimination task. The modulation of fronto-parietal synchronization in the theta band improved reaction time in the task, while its desynchronization

deteriorated performance. On the other hand, using the same stimulation technique, Alekseichuk, Pabel, Antal and Paulus (2017) observed that the intrahemispheric theta rhythm desynchronization between prefrontal and posterior parietal cortex produced a decrease in the memory performance of the subjects and an increase in reaction time in a visuospatial MT task. Finally, Violante et al. (2017) have shown that the imposition of a synchronized activity in the theta band along the inferior parietal lobe and the medial frontal gyrus improved the performance in a verbal MT task and also increased the fronto-parietal activity and its functional connectivity. The external manipulation of oscillatory synchrony along the fronto-parietal network again showed an impact on the neural activity and the behavioral performance of the subjects.

Taken together, these results show that WM, in the same way that conscious perception, is supported by interactions in a large-scale network, and that synchronization of oscillatory activity could be the mechanism responsible for allowing these interactions and the flexible treatment of information in WM. Particularly, research in the field of WM shows the role that different interactions between frequency bands could have in different cognitive processes, especially cross-frequency coupling, both phase-phase coupling and phase-amplitude coupling.

4. Discussion

Conscious perception and WM are difficult to separate both conceptually and empirically. WM defines the set of information accessible to consciousness and conscious processing during transitory periods, i.e., the set of information that is currently available to be incorporated into our plans, strategies, decisions and actions. Given its role in conscious cognition and the operations it supports WM can be therefore conceived as the workspace of consciousness.

If conscious cognition interacts with the information stored and available from WM, and if access to consciousness is a necessary condition for certain information to be able to be stored in WM, then we could expect to find some correlates or markers, mechanisms and neural codes to be shared. We have seen that conscious access and perception seems to have as part of their neural markers a distributed and reverberant activity across a fronto-parietal network, a transient and sudden synchronization of oscillations in different frequency bands and between distant regions, and an increase and sustainment in the gamma-band power. Due to the complex processes that it supports and in which it is involved, WM operates through the same fronto-parietal network and global neuronal workspace as conscious cognition and is supported in the same way by synchronized activity of neural ensembles to carry out their different functions, such as encoding, maintenance, and manipulation of information.

The synchronic/synchronized activity of different neuronal ensembles could be found at the foundation of the cognitive flexibility that underlies the processes in which WM and conscious information processing are involved, by allowing the transient and dynamic functional integration of different modules and neural networks. Particularly, phase-synchronization and phase-amplitude and phase-phase cross-frequency coupling seem to play a fundamental role in both memory processes and conscious cognition. When the workspace of consciousness, i.e., WM, is overloaded, large-scale synchrony could break down, as observed in non-human primates (Pinotsis, Buschman & Miller, 2018).

With respect to the temporal evolution of the neural codes that are implemented both to give rise to a conscious content and to retain information in the MT, we have reviewed experimental results that suggest that after a first and transient encoding phase of

approximately 1 second through active firing, the representations in WM could be maintained by changes in the synaptic weights that do not imply any detectable neural activity, and a periodic update could stabilize the representations stored during the information retention period (Trübtschek et al., 2017). Regarding the conceptual framework of the Global Neuronal Workspace model, we interpret these phases or stages of information processing in the following way: while the active firing phase could correspond to instances or processes associated with conscious access and a first instance of information encoding, the activity-silent phase could correspond to the mechanisms that intervene to keep the representations in the workspace of consciousness, i. e., to maintain in WM and in a particular state those contents that have been consciously accessed, thanks to which they can be eventually retrieved as conscious contents and become the object of a conscious processing (a similar position is maintained in Sergent, 2018). The results obtained by Trübtschek et al. (2017) therefore indicate that conscious access and the cognitive processes involved in the retention of information in WM share the same neural codes and mechanisms during a first phase, but that the maintenance of information in WM in a state available for conscious access and conscious processing subsequently and additionally implies their own mechanisms, processes and neural codes.

Regarding gamma-band oscillatory activity, we have seen that certain theoretical frameworks and hypotheses postulate that the increase and sustainment of the power or amplitude at this frequency band constitutes a marker of conscious perception (Dehaene, 2014), and that synchronized activity in the gamma band could solve the problem of the integration of different characteristics of a stimulus into a single percept (the so-called binding-by-synchronization hypothesis). In the same way, other frameworks and hypotheses

regarding the role of gamma-band activity in WM have highlighted that it could play a fundamental role both in the encoding and maintenance of information, and even that each gamma cycle nested in a theta cycle could represent an active neuronal ensemble that codes and retains a particular item (Lisman & Jensen, 2013).

We suggest that the theta-gamma code could represent the oscillatory mechanism implemented in a fronto-parietal network by the "global neuronal workspace" to encode conscious contents, as well as to retain information in WM. In other words, the global workspace could achieve a functional integration and allow the emergence and transition between contents of consciousness through an oscillatory mechanism based on theta-gamma phase-amplitude cross-frequency coupling, as suggested by results in a binocular rivalry experiment (Doesburg et al., 2009).

A detailed knowledge of the mechanisms and neural processes that underlie both consciousness and WM could offer multiple tools for the clinical field. Even when additional studies that observe the same results are needed, we have seen that there are some special techniques to stimulate oscillations in specific frequency bands in a controlled manner, and that by modulating activity in certain bands we can produce a transient enhancement in WM and short-term memory capacity load. Given that there are some neuropsychiatric disorders such as schizophrenia and ASD that present certain physiopathological alterations at the level of oscillatory and synchronous activity across distant regions (Uhlhaas & Singer, 2010; 2007; Berkovitch et al., 2017), it is possible to conjecture that the development and improvement of currently available brain stimulation techniques can offer powerful tools to intervene in the clinic of these neuropsychiatric disorders. In this regard, more research and interventions in different

frequency bands that examine the long-term effects of the modulation of synchronization/desynchronization of oscillatory activity between local and distant brain regions are needed. In the same way, the observable behavioral effects that are a result of the controlled intervention at different frequencies offers an opportunity to obtain knowledge about the possible differentiated functional roles of oscillatory activity at different frequency bands in different aspects of conscious cognition and WM.

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