1. CONSCIOUSNESS AND PREDICTIVE CODING FRAMEWORK

1.1. CONSCIOUS, PRECONSCIOUS, AND SUBLIMINAL PROCESSING

Dehaene, Changeux, Naccache, Sackur and Sergent (2006) have investigated the brain bases of conscious and non-conscious perception in the light of global neuronal workspace hypothesis. This conceptualization (Dehaene, Kerszberg, & Changeux, 1998) discriminates two main computational spaces: a unique global workspace comprising distributed and strongly interconnected neurons with long-range axons, and a set of specialized and modular perceptual, motor, memory, evaluative, and attentional processors. Workspace neurons are activated in effortful tasks for which the specialized processors are not sufficient. They selectively switch on or off, through descending connections, specific processor neurons input. All along task performance, workspace neurons become spontaneously coactivated, creating discrete though variable spatio-temporal patterns that can be modulated by vigilance signals and selected by reward signals.

More recently, Dehaene et al. (2006) have suggested that conscious perception founds its associated neural mechanism into spikes of parieto-frontal activity leading to top-down amplification. Different authors have tried to explain the brain bases of conscious processing, but a coherent picture from these studies is hardly emerging (Zeki, 2003; Dehaene & Changeux, 2005). Dehaene et al. (2006) have suggested that these apparent contradictions can be solved through a theory of the physiological conditions of consciousness. The authors constructed a taxonomy of brain activity states associated with conscious and non-conscious processing, and within the latter one they identified a transient "preconscious" state of activity, indicating that information is only potentially accessible. Consciousness has several meanings and, in particular, the expression "states of vigilance" indicates the non-transitive nuance, i.e. a continuum of states which encompasses wakefulness, sleep, coma, anesthesia etc. In a nutshell, vigilance represents a graded variable, and a minimum level is necessary to place thalamo-cortical systems into a receptive state. The second meaning of consciousness is the transitive one, and it refers to the experience of consciously perceiving a (visual) stimulus or to the access to conscious report. Hence, it could be stated that the transitive meaning of consciousness indicates the state, while the intransitive something more dynamic. The authors suggest that early sensory activation is necessary but not sufficient for conscious access, because the activity in the extrastriate visual areas is often observed when participants deny having seen the stimulus (Moutoussis & Zeki, 2002). Besides vigilance and bottom-up activation, Dehaene et al. (2006) suggest a third factor underlying conscious access: the spread of brain activation to higher association cortices interconnected by long-distance connections and creating a reverberating neuronal population with distant perceptual areas. This brain state results in two main changes: since the activation reverberates, the information is retained for a long period of time and can be propagated to many others brain systems. Furthermore, considerable evidence indicates that without attention, conscious perception cannot occur (Mack & Rock, 1998). Both bottom-up stimulus strength (e.g. emotional stimuli) and top-down attention amplification are jointly needed for conscious perception, but they might not always be sufficient for a stimulus to cross the threshold for conscious perception. In conclusion, this latter has to be measured through subjective report (Dehaene et al., 2006).

The above-described distinctions lead the authors to suggest a tripartite conceptualization of two non-conscious processes and a conscious one. Firstly, subliminal processing ("below the threshold") indicates a condition of information inaccessibility where bottom-up activation is not sufficient to trigger a large-scale reverberating state in a global network with long range connections. In this case, the activation spreads but remains weak and quickly dissipating. Secondly, preconscious processing has been conceptualized by Freud (1940) as a process that involves information that are "unconscious but capable of entering the consciousness", i.e. potential conscious information. There is enough activation for conscious access, but it is temporarily buffered in a non-conscious store because of a lack of top-down attention, so that even strong stimuli can remain in this state. If the central workspace is freed, a preconscious stimulus might achieve conscious access, whereas this is impeded if the preconscious buffer is erased before orienting top-down attention. In conclusion, during this kind of processing activation can be strong and spreadable, but it requires top-down attention to reach parieto-frontal areas through long-distance connections. Finally, conscious processing represents a process where activation invades parieto-frontal areas, can be maintained, and guides intentional actions, like verbal reports.

To summarize, a stimulus is consciously perceived when it activates in a synchronized, long-lasting manner, a set of "central workspace" neurons, particularly present in parietal, prefrontal and cingulate cortices, and whose long-distance connections enable propagation to many distant areas. On the other hand, a stimulus could fail to become conscious for two reasons: it might not have enough bottom-up strength (subliminal stimulus), or a temporary withdrawal of attention (preconscious stimulus). The authors' proposal could integrate other two theories of consciousness. The first one is Lamme's hypothesis (2003) of a progressive construction of interactions, first locally (visual system) and second more globally (parieto-frontal regions). The second one is Zeki's proposal (2003) of an asynchronous build-up of perception in different sites before leading to a macro-consciousness. The only difference is the conception of pre-conscious processing, that they have attributed to micro-consciousness or phenomenal consciousness. For the present authors, the only reason for attributing phenomenal consciousness to preconscious processing is the insight that perception of reality involves experiences that we are not always able to report fully (Dehaene et al., 2006).

1.2 THEORIES OF CONSCIOUSNESS: A PERSPECTIVE OF INTEGRATION

Northoff and Lamme (2020) have reviewed and discussed different theories regarding the neural basis of consciousness. They suggest that they might be related to distinct aspects of neural activity and consciousness, which can in some way be integrated. Some of the most outstanding and broadly discussed neuroscientific theories of consciousness encompass: Recurrent Processing Theory (RPT) (Lamme, 2010), Synchrony Theory (ST) (Engel and Singer, 2001), Integrated Information Theory (IIT) (Tononi, Boly, Massimini, Koch, 2016), Global Neuronal Workspace Theory (GNWT) (Dehaene, Changeux, & Naccache, 2011), Temporo-spatial Theory of Consciousness (TTC) (Northoff and Huang, 2017), Predictive Coding Theory (PCT) (Hohwy, 2013), Higher-Order Thought theory (HOT) (Brown, Lau, & LeDoux, 2019), Operational Space-time theory (OST) (Fingelkurts & Neves, 2010), Entropy theory of consciousness (Carhart-Harris, 2018), and Embodied Theory (ET) (Park & Tallon-Baudry, 2014).

The differences between these theories can be categorized with respect to various characteristics (Northoff & Lamme, 2020). For instance, each of them aims at explaining a different target of consciousness. For example, phenomenal consciousness is the explanandum in RPT, IIT, ST, and TTC, whereas GNWT and HOT investigate more cognitive aspects of consciousness (e.g. awareness or access to consciousness) associated to functions like top-down attention. Other theories address more general processes of perception (content of consciousness in perception and cognition), such as PCT, or the relationship between perceptual states and action, body, emotions, or the self. Another characteristic which differentiates these theories regards the technical aspects concerning the studies. These are related to the targeted neural measure (stimulus/task evoked activity or resting state activity), the subjects included in the study (healthy or pathological groups), and the experimental paradigm used to test the theory. With respect to the latter, report paradigms are required to investigate cognitive consciousness aspects (e.g. access or awareness), whereas phenomenal features can be studied through non-report paradigms. In addition, perceptual aspects can be tested through masking or rivalry, while visual attention and memory are preferentially investigated through attentional blink or change blindness (cognitive designs). Finally, other authors indicate that emotion and affect represent the best “ground” to study consciousness (Damasio, 2010; Solms, 2019).

The last diversity tackled by Northoff and Lamme (2020) concerns the different aspects of neural activity addressed by each of the theories mentioned above: stimulus-related activity, pre-stimulus activity and spontaneous activity. Various conceptualizations identify different neural correlates of consciousness and, consequently, they rely on different measures targeting distinct aspects of it. The first aspect of neural activity taken into consideration is stimulus-related activation, which is the activity evoked after the presentation of the stimulus and represents the conscious percept of it (Neural Correlate of Consciousness, NCC). This activation can be viewed in spatial and temporal terms: respectively, elicited in specific regions of the brain and occurring in early or subsequent time intervals. Regarding the first dimension, different theories assume different areas of the brain to be important for consciousness, which depends on the explanandum. Some theories (like IIT and RPT; Lamme, 2006; Tononi et al., 2016) hypothesize that posterior regions are important for consciousness, which in this case is conceptualized as phenomenal/experiential, or "integrated information" (i.e. binding of features of the object and perceptual organization). So, from this perspective, the key feature of conscious percepts is their unity or "wholeness", and the amount of integrated information is referred to as "Phi". The so-called "posterior hot zone" (i.e. the combination of visual, other sensory and parietal cortices) is considered prone to have high Phi and consequently should be sufficient to construct a conscious sensory experience (Boly et al., 2017). Other theories (like GNWT and HOT; Dehaene et al., 2011; Brown et al., 2019) postulate that frontal regions are necessary for consciousness. The GNWT targets specifically the dorsolateral prefrontal cortex (DLPFC), that is considered the basis of the conscious "access" to the contents. It is a core region of the Global Neuronal Workspace, which is the area where sensory information is made globally "accessible" to other cognitive functions (Northoff & Lamme, 2020). In this process a key role is assigned to top-down attention. In HOT, sensory information is considered a "first order" representation, not sufficient for conscious experience. Then, a "second order" re-representation is necessary for the transition of this information to consciousness. In addition, thalamo-cortical connections are assumed to be important in the integration of two aspects of consciousness, state and content (Sanchez-Vives, Barbero-Castillo, Perez-Zabalza, Reig, 2020). Eventually, consciousness featured by both content and state/level is constructed from subcortical-cortical interaction, but the exact process underneath is still not known. On the other hand, when investigating the temporal dynamics of stimulus-related activity, it is important to define two kind of visual input processing (Northoff & Lamme, 2020): the feedforward and the recurrent. The feedforward sweep of information processing represents an early stimulus-related activity, as measured by the N100, and is not related to consciousness. It encompasses the extraction of various features of the stimuli by all parts of the visual brain. Afterwards, recurrent processing occurs, with feedback connections between higher and lower-level areas of the brain (Lamme, Super, & Spekreijse, 1998). The notion of recurrent interactions is complex, involving cortical and subcortical information integration. Giving these conceptualizations, it can be stated that the explanandum is the variable that has to be considered when investigating the timing of conscious perception after stimulus presentation. For instance, RPT theory (which refers to phenomenal consciousness) hypothesizes that conscious perception starts after 100-200 ms, which corresponds to the moment where recurrent processing sets in (Northoff & Lamme, 2020). Whereas GNWT, that considers conscious access, points to the later activity (P300), which refers to the moment when sensory information becomes available for different parts of the brain (Dehaene & Changeux, 2011). There are other characteristics of stimulus-related activity that may be relevant to consciousness (Northoff & Lamme, 2020), for example the degree of activity synchronicity between different neuronal populations. Synchronous activity between neurons in a population refers to "perceptual binding", which may not necessarily represent consciousness (Hermes, Miller, Wandell, Winawer, 2015). Nonetheless, especially for high frequency synchrony (i.e. gamma band oscillations), some theories link this process to consciousness (Fingelkurts & Neves, 2010), taking into consideration the specific explanandum (i.e. perceptual organization). Another aspect of stimulus induced activity is the complexity of the signal evoked, which measure is the "perturbational complexity index" (PCI) and reflects our brain capacity to integrate information (D'Andola, Rebollo, Casali, Weinert, Pigorini, Villa, Massimini, Sanchez-Vives, 2018). A further feature of stimulus-evoked activity is the "trial to trial variability" (TTV). Reduced TTV after stimulus onset (i.e. TTV quenching; Churchland et al., 2010) indicates that the variability in the amplitude of responses to the same stimulus is also reduced, thus enhancing the stability of the signal. TTV quenching has been related to consciousness because it has been hypothesized that this represents a suppression of the brain's intrinsic noise by the external stimulus. The possible mechanism underneath may be that a conscious stimulus evokes more synchronous/recurrent activity, thus stabilizing the signal (Northoff & Lamme, 2020).

The second aspect of neural activation tackled by the authors (2020) is pre-stimulus activity. Pre-stimulus activity provides a dual role: mediating content of consciousness and its associated level of arousal. In addition, the degree of change during post-stimulus activity with respect to the ongoing dynamics of the pre-stimulus activity is central for the conscious processing of the external stimuli.

Therefore, there has to be a specific interaction between pre- and post-stimulus activity in order to associate consciousness to contents: that is, strong TTV quenching (i.e. stimulus-related suppression of the ongoing pre-stimulus variability; Churchland et al., 2010). Starting from these findings about the relevance of pre-stimulus activity for consciousness, Northoff (2013) has proposed the Temporo-Spatial Theory of Consciousness (TTC). It concentrates on how the impact of the external stimulus on the brain depends on the brain's pre-stimulus activity: an external stimulus has to interact with ongoing activity such that the two become integrated into the current stream of consciousness. Thus, this theory focuses on the importance of pre-stimulus activity's spatiotemporal dynamics: the pre-stimulus activity can expand the stimulus's actual points in time and space beyond themselves (i.e. "going beyond", Buszaki, 2006). The last characteristic is spontaneous activity, which has two dimensions: a spatial and a temporal one (Northoff & Lamme, 2020). This kind of activation is reflected in various networks organized in a small-world way, and it shows an oscillatory pattern (measured in frequencies). Taking these two features together, it can be observed that the spontaneous activity's structure is not static but dynamic (i.e. it continuously changes its configurations). The relation between different frequencies of neuronal activity can be described as scale-free, scale invariant or self-similarity (i.e. the relationship between the power of the frequencies is the same irrespective of the spectrum of frequencies considered). Related to these concepts (Huang, Obara, Davis, Hap, Pokorny, & Northoff, 2016), different measures of spontaneous activity can be introduced, that are connected to consciousness. The first two are "power law exponent" (PLE) and "detrended fluctuation analysis" (DFA), which indicate the degree of self-similarity or scale-free activity and have been associated with different aspects of consciousness (Northoff and Lamme, 2020). Another measure is entropy, where a higher degree of it may lead to extended consciousness (Carhart-Harris, 2018). Finally, the last index considered by Northoff and Lamme (2020) is complexity, measured through the Lempel Zev Complexity (LZC) index.

To date, there haven't been found functional connectivity patterns and neural networks specifically associated with consciousness. Thus, researchers have been studying alternative measures of the spontaneous activity spatiotemporal dynamics during altered states of consciousness. They have found that the difference between the presence and the absence of consciousness is essentially represented by the relative differences in spatial dynamics (i.e. frequency of particular spatial patterns). In addition, it has been discovered that both a decrease of spatial dynamics and of temporal dynamics signals the absence of consciousness. On the other hand, studies on drug-induced psychosis demonstrated increased spatiotemporal dynamics of the spontaneous activity (e.g. entropy and complexity measures) while using different psychedelic drugs (Atasoy, Roseman, Kaelen, Kringelbach, Deco, Carhart-Harris, 2017). Along with its spatiotemporal dynamic, another aspect of the brain's spontaneous activity is the constant interoceptive input from the own body (Northoff & Lamme, 2020). The interoceptive processing and hence the body is the focus of researchers who posit that embodiment, including subcortical-cortical brain-body relation, is fundamental to consciousness (Azzalini, Rebollo, Tallon-Baudry, 2019; Park & Blanke, 2019). On the other hand, it has to be considered that these theories refer more to the potential neural correlates of the first-person perspective, which may consequently be the heart of consciousness to which phenomenal experience is integrated (Park & Tallon-Baudry, 2014).

Northoff and Lamme (2020) have observed that theories of consciousness agree on what is the role of the operational architecture underlying consciousness: the transition from independent to mutually interdependent (i.e. integrated and distributed) neural activity, reflecting the dynamic/temporospatial basis of consciousness. The integration refers to the fact that neurons are sharing the information with other neurons. Another point of convergence between theories is that they hypothesize that different conscious contents and levels of consciousness are processed in different parts of the brain at different points in time, reflecting a heterogeneous process. Posterior regions may mediate the phenomenal aspects of sensory contents, and then neural activity may be spread to anterior regions that allow for cognitive processing of the same contents, leading to their access, report, knowledge, and meta-cognition related processes (Baars, Franklin & Ramsoy, 2013). A more recent theory to go beyond dichotomies is the Global Brain Activity (GBA), that is related to global effects (Liu & Luo, 2019). This theory posits that, in the pre-stimulus phase, the neural context for the following processing and perception of the visual stimuli is already set. GS (Global Signal) is a measure of GBA, and its level of decrease is related to the level/state of consciousness. Furthermore, it has been observed that there are diverse topographical distributions of GS in different states and in different forms of consciousness (Tanabe, Huang, Zhang, Chen, Fogel, Doyon, Wu, Xu, Zhang, Qin, P, Wu, Mao, Mashour, Hudetz, Northoff, 2020). In summary, GBA reconciles different locations and different dimensions of consciousness, i.e. level and content. Hence, different contents of consciousness (sensory, cognitive, affective, etc.) are all associated with phenomenal experience but are processed in different regions of the brain (Northoff & Lamme, 2020). Furthermore, it may exist a common neural mechanism which leads to phenomenal consciousness. Different theories have tried to explain the nature of this common mechanism.

TTC (Northoff & Huang, 2017) posits that this is represented by pre-post stimulus interaction with temporo-spatial expansion. In addition, GBA could represent another mechanism, where the same contents may undergo different levels of processing, allowing us to access them in different ways (Baars et al., 2013). To summarize, consciousness may be conceived as a heterogenous multifaceted neuronal process with different layers or levels of neuronal activity nesting with each other (Northoff & Huang, 2017). The concept of layers refers to nestedness: consciousness and the brain's neural activity are hypothesized to be characterized by layers that contain (i.e. nest with) each other. This means that both phenomenal and neuronal levels of consciousness are nested: there is a nested organization of the brain's neuronal activity and a nested organization of contents of consciousness. In summary, consciousness gestalt nature comprises a figure (local activity) and a background (global activity). Different theories have proposed different functions of consciousness, that is an integrated, distributed and interdependent kind of processing (Northoff & Lamme, 2020). The function may be sensory (perceptual organization), cognitive (access or prediction), bodily (neural monitoring of bodily input). A recent proposal by TTC theory, is that the function underlying consciousness is a temporo-spatial dynamic process, which mediates sensory, bodily and cognitive functions by operating across different regions, and it is content-unspecific.

The next question addressed by Northoff and Lamme (2020) is the nature of the interaction between the three forms of neural activity related to consciousness (stimulus-related, pre-stimulus, and resting state activity). In fact, the TTC suggests the existence of different temporo-spatial mechanisms that relate to different aspects of consciousness and different forms of neural activity (Northoff and Huang, 2017). The kind of interaction which is postulated by the TTC is reflected in the scale-free nature of consciousness: increased scale-free integration and, hence, temporo-spatial nestedness of the three forms of neural activity will produce consciousness. This must be tested empirically in future research. In addition, there are different dimensions of consciousness: state/level, content, form (Northoff, 2013) and they are related to three kinds of neural activity. The form is a new concept which refers to consciousness' structure or organization at a phenomenal level, like its complex gestalt with figure and background: it encompasses unconscioussness, phenomenal consciousness and reflective consciousness and it is mediated by the spontaneous activity's architecture (i.e. its temporo-spatial nestedness across subcortical and cortical regions). In addition, the content may be associated to post-stimulus and pre-stimulus activity (on the cortical level), and the state/level may be especially related to pre-stimulus activity. Furthermore, different neural activity is linked to different aspects of consciousness. Stimulus related activity is hypothesized to be sufficient for phenomenal consciousness (NCC proper; Koch, Massimini, Boly, Tononi, 2016) and its cognitive aspects or consequences of consciousness (NCCcon; Aru, Bachmann, Singer, Melloni, 2012). On the other hand, pre-stimulus activity is presumed to enable consciousness, so to be a neural prerequisite of it (preNCC). These are all neural correlates of consciousness, i.e. neural features that are present when there is consciousness, and they regard different time points of neural activity (Northoff & Lamme, 2020). PCT proposed a potential hypothesis for their relationship: according to this theory, pre-NCC is linked to NCC proper by the prediction error, that is a modification of the perception influenced by the top-down prediction through the bottom-up stimulus related activity. TCC theory explains this aspect through the presence of temporo-spatial dynamics, which can represent the connection between pre- and post-stimulus activity. In fact, becoming aware of the contents of consciousness requires both spontaneous activity and stimulus related activity. The first one represents the activity independent of specific stimuli or tasks, and it enables the neural capacity or predisposition of consciousness (NPC; Northoff & Huang, 2017). In extreme situations like anesthesia and coma, the basic shape of the spontaneous activity's power spectrum (i.e. its scale free nature) is not preserved, but it is replaced by low power values for both slow and fast frequencies. To summarize, the NPC represents a form of default activity (i.e. the brain's baseline) which, given that is necessary for consciousness, has been related to the brain's scale-freeness (Northoff & Lamme, 2020).

In conclusion the TTC, a novel approach to the study and understanding of consciousness, has hypothesized some basic similarity between neuronal and phenomenal states, that allows for a transformation of the former into the latter. Thus, the relevant innovation of this theory is that neuronal and phenomenal states are no longer conceived as different. This basic similarity has been called "common currency" (Northoff, Wainio-Theberge, Evers, 2019), and it represents the temporo-spatial dynamics of the brain's spontaneous activity, which in turn refers to the NPC: the neural predispositions of consciousness. The concept of "nestedness" can be included in this theorical framework by assuming that all the different types of neural activity related to consciousness are nested into each other, but the larger and overarching temporo-spatial frame is actually the NPC (Northoff & Lamme, 2020). In brief, NCCcon is nested in NCCproper that is in turn nested in pre-NCC, and all those are eventually spatio-temporally contained in the more inclusive NPC. Thus, the NPC provides a way to enable the phenomenal features of consciousness, that is the temporo-spatial dynamics of the brain's spontaneous activity. This