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From brain-body function to conscious interactions

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ABSTRACT

In this review, we discuss empirical results inspiring the introduction of a formal mathematical multilayer model for the biological neuroscience of conscious experience. First, we motivate the discussion through evidence regarding the dynamic brain. Second, we review different brain-body couplings associated with conscious experience and its potential role in driving brain dynamics. Third, we introduce the machinery of multilayer networks to account for several types of interactions in brain-body systems. Then, a multilayer structure consists of two main generalisations: a formal semantic to study biological systems, and an integrative account for several signatures and models of consciousness. Finally, under this framework, we define composition of layers to account for entangled features of brain-body systems related to conscious experience. As such, a multilayer mathematical framework is highly integrative and thus may be more complete than other models.

1. Introduction

We shortly review an integrative multilayer framework for biological structures of consciousness (Kivela et al., 2014; Signorelli and Boils, 2021). Mathematically, a layer corresponds to a graph or network with intra-edges representing internal connectivity. Operationally, layers may constitute biological brain and bodily networks connected by metabolic and anatomical means. In this framework, the interplay of *intra* and *inter* interactions drives the coupling and decoupling of the whole brain-body system. Intra-interactions are the internal network interactions across nodes within a network, while inter-interaction corresponds to in-between networks exchanges. More abstractly, interactions are any relevant biological exchange for these biological networks and commonly represented by functional, metabolic or anatomical connections (Signorelli and Meling, 2021).

In light of increasing discussions about models of consciousness (Doerig et al., 2020; Melloni et al., 2021; Northoff and Lamme, 2020; Pin et al., 2021; Rosenthal, 2020; Sattin et al., 2021; Signorelli et al., 2021a; Wiese, 2020), we aim to introduce formal mathematical definitions and discuss how mathematical multilayers, together with their intra and inter interactions, may help to describe better the connection between the dynamic brain-body and human conscious experience (Signorelli and Boils, 2021; Signorelli and Meling, 2021). Our review points out the explicit framework of multilayer networks in combination with brain-body interactions related to conscious experience. In next sections we construct a conceptual framework and discuss how biological layers interacting may become the causal forces driving the dynamic of the whole brain-body system Werner (Werner, 2013). The conceptual model is based on recent developments inspired by the enactive approach and radical embodiment applied to conscious experience (Signorelli and Boils, 2021; Signorelli and Meling, 2021; Signorelli et al., 2021a; Thompson and Varela, 2001; Thompson, 2007; Varela et al., 2016). In short, multilayer networks are relevant because they can integrate multiple dimensions of interaction, better describe brain-body systems and the embodiment of conscious experience. Therefore, we can study, both conceptually and mathematically, the coupling of biological system via intra and inter interactions. Eventually, this framework may better serve to reason about the biology of conscious experience, becoming a more appropriate framework to explore the intertwined living features and the physics arising from living layers interacting (see below).

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2. The dynamic brain

In this section, we review dynamical insights from brain resting-state to bifurcation points, particularly criticality.

2.1. Resting states networks

Brain networks are the informative unit at the whole-brain scale (Pessoa, 2014). Brain networks are thought as groups of non-overlapping brain regions following organized patterns of function and/or structure. One example is the resting-state networks (RSNs), discovered by Biswal et al. (1995). RSNs appear from the spontaneous brain activity at rest, i.e., without performing any particular task. The default mode network (DMN) is one concrete example. DMN is an anatomical well-defined network associated with resting states and introspective tasks Buckner et al. (2008). Another example is the dorsal attention network (DAN), mostly activated by tasks requiring spatial attention.

In resting state, the brain seems organized into dynamical anti-correlated functional networks (Buckner et al., 2008; Fox et al., 2005; Fransson, 2006). In other words, the high functional correlation between areas of one network corresponds to the low correlation between areas of the other network (Fig. 1A). For instance, the relationship between DMN and DAN is anticorrelated. These results extend to task-related activity, such as the suggested anticorrelation for cingulated-operculum and frontal-parietal network in goal-directed executive control (Dosenbach et al., 2008). Currently, anticorrelated brain networks are also obtained from independent component analysis (ICA). These analyses better describe the statistically independence of brain networks (Zuo et al., 2010; Calhoun and de Lacy, 2017). Other techniques also aim to extract independent brain network organization (e.g., innovation-driven co-activation patterns (iCAPs) (Karahanoglu and Van De Ville, 2015) and decompositional eigenvector analyses such as in Atasoy et al. (2016); Luppi et al. (2020) and Preti and Van De Ville (2019). The main goal is to find the minimal brain organization through decompositional techniques.

To give a causal explanation of anticorrelated networks, instead of an statistical one, we propose that anticorrelated networks are the product of more basic metabolic and anatomical networks interacting (Figure 1A). Anticorrelations between networks suggest competing systems (Deco and Corbetta, 2011). Nevertheless, this competition is not a direct antagonism between networks, but triggered by inner spatio-temporal structure (Deco et al., 2011). This brain spatiotemporal structure partially relays on anatomical structure (Vincent et al., 2007), yet, spontaneous functional activity is not fully explained by anatomy (Deco et al., 2009),(Deco et al., 2013; Ghosh et al., 2008; Honey et al., 2009). RSNs are not explained by simple random noise either (Deco and Corbetta, 2011), despite noise-driven-transitions playing an important role in the underlying mechanisms of spontaneous activity (Deco et al., 2009; Ghosh et al., 2008).

Therefore, an alternative explanation is to disentangle RSNs by invoking more basic independent or semi-independent *networks*. These

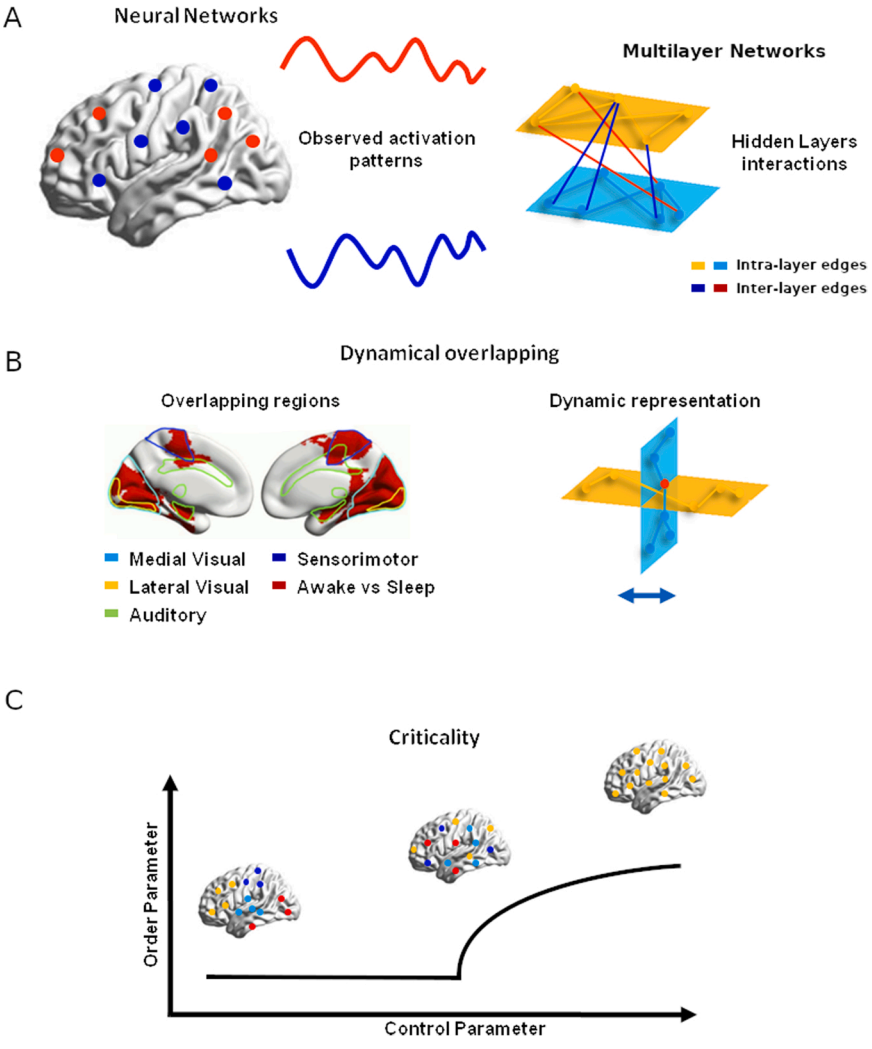


Fig. 1. The dynamic brain. (A) Anticorrelated networks. Each node represents a region of interest and each colour one family of observed anticorrelated networks. Colour lines are their hypothetical activities. These observed anticorrelated networks may be the result of more basic networks (yellow and light blue layers). These layers are abstractions to visualize physical brain and body structures. (B) Example of overlapping regions. The contrast between awake and sleep conditions (right). Different layers of a multilayer network may share nodes across their dynamical evolution. Here, a dynamical overlapping representation in the form of rotation layers interacting (left). Orange dot corresponds to one overlapping region. (C) Criticality is the transition point where a system presents fluctuations between order and disorder patterns. In our conceptual model, regions before a critical phase transition (disorder) represent uncoupled layers (given by coloured dots). Critically then emerges through the couplings of these layers generating the functional patterns observed in resting-state. If regions continue interacting beyond criticality (order), they become extremely coupled layers, such that their intrinsic layer dynamic is lost in favour of a homogeneous global dynamics. Here, the control parameter (i.e. the strength of interactions) mirrors the global interactions between layers (inter-interactions), while the order parameter (i.e. the degree of order) represents the degree of disruption of internal layer interactions (intra-interactions).
(a) Adapted from Signorelli and Boils (Signorelli and Boils, 2021) and Fox et al. (Fox et al., 2005). (b) Adapted from Signorelli and Meling (Signorelli and Meling, 2021) and Tagliazucchi et al. (Tagliazucchi et al., 2016a). (c) Reinterpreted and adapted from Cocchi et al. (Cocchi et al., 2017).

networks may interact according to specific contexts, giving rise to the dynamical organization observed RSNs during awake and other global conditions (e.g., by neurotransmitters release). Assuming these networks correspond to more fundamental biological structures (e.g., metabolism), they may also admit nodes that correspond to bodily systems, such as the heart, lungs, gut and others; together with brain regions. One example could be the recently defined brain-stomach functional network (Rebollo et al., 2021). Another example is the extension of the serotonergic system, including the gastrointestinal tract (Shine et al., 2022). Then, resting-state networks may be the result of more fundamental brain-body layers that either interact (e.g. during awake states) or do not interact (e.g., during deep sleep). Mathematically, we can simulate these transitions allowing new inter-interactions between layers that otherwise would remain disconnected in the model.

These hypothetical biological networks will be called *native layers* as a particular instance of mathematical layers in a multilayer structure (see next sections). These networks may entail more general structures representing different types of biological interactions (Signorelli and Meling, 2021; Signorelli and Boils, 2021). As such, the resulting co-dependent networks become multi-faced dynamical networks with overlapping regions (Mesulam, 1990; Pessoa, 2014) (Figure 1B). To describe this overlapping, we allow virtual/abstract rotation networks (for visual purpose), such that different regions dynamically overlap (see details in (Signorelli and Boils, 2021) and section 4). It allows the same and different areas to participate in the same and different behaviours. Then, emergent dynamical networks become contextual, namely, the region affiliation varies according to the time and task (Cole et al., 2013; McIntosh, 2000). One brain region is part of a different process according to its network affiliation at a given time (Pessoa, 2014).

2.2. At the edge of criticality

Another relevant aspect of brain organization is that structure-function relationships are not static but dynamic (Kiverstein and Miller, 2015; Varela et al., 2001; Allen et al., 2014; Valk et al., 2022). The observed brain functional patterns may mirror the dynamical organization of different overlapping layers in a more general multilayer structure.

For example, conscious experience seems to underlay rich temporal and dynamical brain organization (Barttfeld et al., 2015; Demertzi et al., 2019). Brain states associated with awake condition are characterised by a richer repertoire of functional configurations, while disruptions of this dynamic exploration seem to imply loss of consciousness (Signorelli et al., 2021b). Interestingly, transient lapses of awareness are also present during healthy wakefulness (Demertzi et al., 2019; Naccache, 2018; Mortaheb et al., 2022), emphasising the need for dynamical descriptions that might be addressed by empirical and theoretical models. Therefore, the neuroscience of consciousness requires dynamical frameworks to reconcile different aspects of conscious states and brain function (Tagliazucchi, 2017).

One relevant dynamic description is criticality (Figure 1C). For dynamical systems, criticality is a transition point, or bifurcation between stable equilibrium and multistable states with coexisting multiple attractors (Deco and Jirsa, 2012; Cocchi et al., 2017). Dynamical systems at criticality help us to model large scale brain activity. Large-scale dynamical models use different neural signals and combinations of structural (SC) and functional connectivity (FC) to search for links between spatial (anatomy) and temporal (functional) brain dynamics (Deco et al., 2013; Cabral et al., 2017; Breakspear, 2017). These models teach us that spontaneous brain activity presents deviations from equilibrium trajectories, resulting in rapid switching between a discrete number of functional states (Hansen et al., 2015; Lynn et al., 2020). Functional activity evolves through multiple and recurrent discrete functional states (Allen et al., 2014; Cabral et al., 2017), lasting around 100–200 ms (Vidaurre et al., 2016; Deco et al., 2019). These deviations from equilibrium suggest that brains maximize their possible microstates at the edge of criticality (Cocchi et al., 2017). In fact, RSNs are described by critical points (Deco et al., 2009; Ghosh et al., 2008) and different models find their optimal fitting points at the edge of the critical instability (Cabral et al., 2017).

Criticality seems to underlay a fundamental principle of brain self-organization (Aguilera and Di Paolo, 2021). At criticality, small extrinsic perturbations can trigger the dynamic of task-related networks, while intrinsic perturbations may generate the exploration of functional resting states (Deco et al., 2013). Therefore, the brain at criticality is maximally sensitive to internal and external fluctuations. Evidence for criticality, however, does not exclude alternative interpretations and mechanisms involved. One example is how criticality seems supported by scale-free dynamics.

2.3. Criticality and consciousness

Criticality may also unify different group of evidence regarding conscious experience (Werner, 2013; Tagliazucchi, 2017; Aguilera and Di Paolo, 2021). For instance, departure of criticality is reported in conditions of general anaesthesia (Scott et al., 2014; Tagliazucchi et al., 2016b; Zhang et al., 2018), deep sleep (Priesemann et al., 2013; Tagliazucchi et al., 2013; Zilio et al., 2021) and epileptic seizures (Meisel et al., 2012). In deep sleep, the dynamic of the whole brain presents an increase of stability and decrease of effective interactions (Jobst et al., 2017). Contrary, perturbations in computational simulations showed that recovery of integration properties at the whole-brain scale are associated with shifts in the model operation point (Deco et al., 2018a; Jobst et al., 2021). From information theory, the concepts of integration and differentiation have been postulated as relevant to describe conscious interactions (Tononi and Koch, 2008; Aguilera and Di Paolo, 2021). In dynamical system theory, systems before a critical point present noisy dynamic associated with high differentiation and low integration, while system after critical points are highly integrated and poorly differentiated. It is at the critical point of dynamic transition where the optimal balance between these measures is found. For example, several works have shown that metrics of consciousness based on neural activity peak at phase transitions of the system (Tagliazucchi et al., 2012;Tagliazucchi et al., 2016b; Tagliazucchi, 2017; Mediano et al., 2019). This indicates that awake brains activity seems to operate far from a stable equilibrium.

Criticality also helps to reinterpret current evidence. For instance, in awake condition, complex patterns appear after transcranial magnetic stimulation (TMS), but they disappear in non-conscious conditions (Casali et al., 2013). One dynamical reinterpretation of these results convey criticality: in non-conscious conditions, the brain moves away from the edge of criticality and therefore becomes only locally responsive. The disruption of criticality might be due to the switch of different systems from coupled to uncoupled intrinsic dynamical modes that disconnect functional correlations (see section 5).

Criticality, however, is only a description of the dynamic evolution of a system. It is not a mechanism by itself and does not explain how such a system reaches this dynamical behaviour. Criticality is more general than a mechanism and applies to different types of phenomena. To answer the mechanistic question we need to focus on the causal forces driving the dynamics of the system (Werner, 2013), i.e. consider physiological sources in the brain as well as the rest of the body.

Consequently, the question about *mechanisms* of conscious experience might turn into the question about driven forces of criticality (see (Aguilera and Di Paolo, 2019; Aguilera and Di Paolo, 2021). Then, network integration becomes a consequence of this critical dynamic scenario (Werner, 2013), instead of the other way around.

3. The brain-body coupling

If criticality and/or bifurcation points play a role in functional brain organization, what makes the brain work at these critical points?

(Cocchi et al., 2017). Although one would expect only neural activity involved (e.g. action potentials), more complex physiological signals also seem to participate (Breakspear, 2017). Diffuse neurotransmitter release, for example, likely play a key role by modifying excitatory and inhibitory balance. If this is the case, the brain activity alone is not enough to explain this type of diffusion. We might also consider production centres of such substances, which are located in the rest of the body (Shine et al., 2022). As such, the brain and the rest of the body form an entangled metabolic system. Moreover, removing physiological confounds have an enormous impact on neural signals (Laumann et al., 2017), decreasing non-stationarities. Physiological fluctuations also have subtle but important cognitive effects (Allen et al., 2016), such as effects that co-vary with brain regions in anticipation tasks (Nguyen et al., 2016; Skora et al., 2022). This forces us to distinguish between the confounding role of first-order physiological signal (e.g. heart rate, respiration), and the second-order effects (e.g., heart rate variability) in BOLD and/or EEG signals, among others.

3.1. Physiological coupling

One example of brain-body interaction is the gut's influence in neurological conditions like anxiety, depression, and autism spectrum disorder (Critchley and Harrison, 2013; Mayer, 2011; Sharon et al., 2016). The bi-directional signalling between the gut and the central nervous system include different paths: the vagus nerve, the enteric nervous system (ENS), sympathetic and parasympathetic branches of the autonomic nervous system (ANS), gut hormone signalling, the immune system, neuroendocrine signalling, tryptophan metabolism, and microbial metabolites such as short-chain fatty acids (Foster et al., 2017; Grenham et al., 2011). These paths ensure the coordination of gastrointestinal functions to support behaviour, as well as feedback from the gut to influence motivated behaviour and high cognitive functions (Foster et al., 2017; Mayer et al., 2015; Rhee et al., 2009). For instance, the vagus nerve targets the nucleus of the solitary tract in the caudal brainstem, which mediates polysynaptic inputs to higher brain regions, such as the hypothalamus, limbic forebrain, ventromedial basal nucleus of the thalamus (Saper, 2002) and the ventral anterior cingulate cortex (Vogt and Derbyshire, 2009). While descending neural projections from cingulate and insular cortices, amygdala, bed nucleus of stria terminalis and hypothalamus provides a bi-directional control (O'Mahony et al., 2011). Recently, a novel resting state network coupled with low frequency stomach activity has been discovered (Rebollo et al., 2018; Rebollo et al., 2021; Azzalini et al., 2019), supporting the future connection between brain-stomach interactions and cognition. Other examples of visceral interactions also include the heart and lungs (Candia-Rivera, 2022; Criscuolo et al., 2022).

Studies strengthen and extend the link between brain-body interactions to conscious perception (Fig. 2A). Neural spontaneous fluctuations locked to heartbeats seem to predict and shape visual detection, suggesting the influence of heartbeats in conscious perception (Park et al., 2014). These findings suggest that neural activity propagates from ventromedial prefrontal cortex and ventral anterior cingulate cortex (known to receive cardiac inputs) to the posterior right inferior parietal lobe (Park et al., 2014). Interoceptive heartbeats activity sent to the insula also has a systemic effect on conscious perception, modulating exteroceptive awareness (Salomon et al., 2016) and emotional experiences (Nguyen et al., 2016). Explicit cardiac perception also influences activity in regions such as the posterior and anterior insula, dorsal anterior cingulate, somatomotor cortices, among others, supporting interoceptive awareness (Critchley et al., 2004).

The breathing rhythms in mice, for example, have been linked with brain oscillations, suggesting that respiration-entrained oscillations facilitate long-range communication in the brain (Tort et al., 2018). Respiration may also have an unexpected influence on cognitive processes, by modulating neural coordination (Varga and Heck, 2017). These and other oscillatory couplings (e.g., brain and muscle activity) put forward the hypothesis of an organizational frequency structure between brain and body (Klimesch, 2018).

Visceral states, interoception and interactions thereof might shape the topology of functional brain states. Studies of anaesthesia and sleep also indicate the importance of brain-body couplings and its connection with awake states. In Stankovski et al. (2016), the authors demonstrated alterations on the coupling functions of cortical and cardio-respiratory oscillations under sevoflurane and propofol. Sevoflurane affects the respiratory-theta coupling more than propofol, while heart-theta coupling presents complex couplings forms. It suggests the influence from the heart to theta neural oscillations. Delta activity influences alpha oscillations (Stankovski et al., 2017), which are thought to play a key role in conscious perception. These couplings are significantly stronger in anaesthesia than awake condition, suggesting a reduction of the dynamic brain repertoire under anaesthesia (Stankovski et al., 2016).

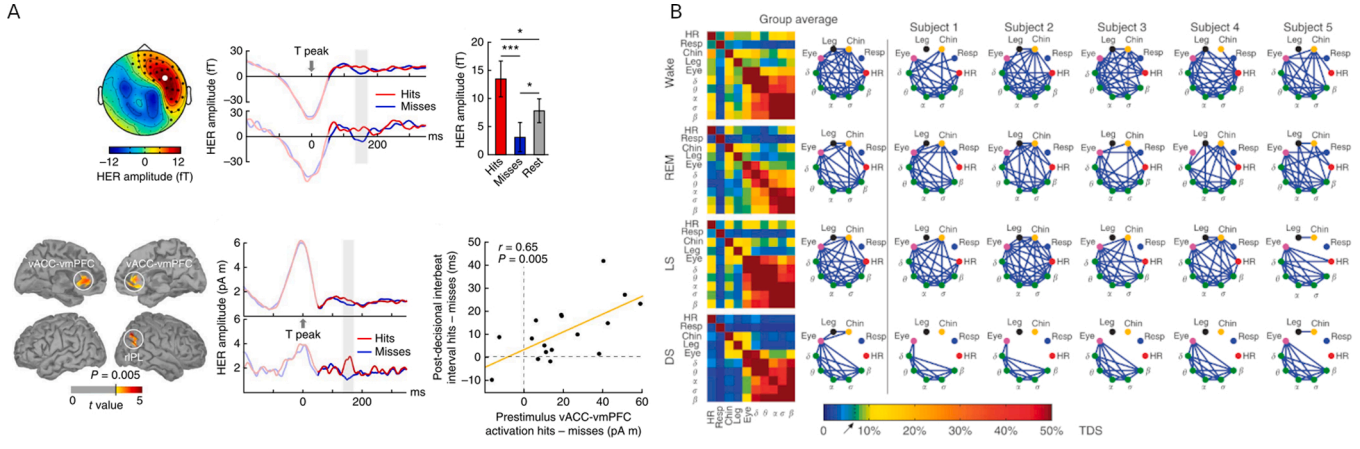


Fig. 2. Brain-body couplings. (A) Conscious perception is predicted by neural events locked to heartbeats. Upper, the average of heartbeat-evoked response (HER) is shown for all black dots, followed by the HER in a single node (white dot). The amplitude of HER (at 135–171 ms) changes for observed versus missed stimuli, also compared under open eye rest. Bottom, differential activation for bilateral vACC-vmPFC and rIPL regions, followed by their HER curves across hits and misses before stimulus onset. Correlation across subjects between the hit-miss difference in cardiac interbeat and the hit-miss difference in HER before stimulus onset in vACC-vmPFC. Shaded areas highlight the significant difference. (B) Brain-body couplings across different sleep stages: wake, rapid eye movement (REM, light sleep (LS) and deep sleep (DS).
(a) Adapted from Park et al. (Park et al., 2014). (b) Adapted from Bashan et al. (Bashan et al., 2012).

Other analytical coupling techniques reveal sleep-stage transitions correlated with changes in the topology of dynamical brain-body physiological networks (Bartsch et al., 2015; Bashan et al., 2012) (Fig. 2B). The coupling of cardiac, respiratory, cerebral, ocular and muscle signals exhibit higher network interactions in awake and light sleep, intermediate values in REM and much lower in deep sleep (Bashan et al., 2012). Moreover, brain couplings characterised by different oscillations exhibit a decoupling from the other physiological systems through different sleep-stages (i.e., decoupling of inter-connectivity). At the same time, the strength on intra-connectivity was stronger in light and deep sleep, intermediate in awake and low in REM.

In summary, data suggest that brain-body couplings, given by different means of interactions, have an effect in brain states related to conscious-awake conditions. The brain and physiological systems sometimes act connected, and other times disconnected. Interestingly, these couplings and interactions may be better modelled in a more integrative multilayer structure (see section 4).

3.2. Within-brain couplings

Within the brain, it has been proposed an anatomical layer division. One relevant example for consciousness research is the role of pyramidal cortical layer L5 as a mediator mechanism between the influence of feedback connectivity in cortico-cortical loops and higher-order thalamocortical loops in mice (Suzuki and Larkum, 2020). In that work, the authors demonstrated that three different types of anaesthetics decouple the apical signalling between dendrites and cell body in layer L5 (Fig. 3A). Cortical layers are a group of layers given by anatomical considerations (e.g., cell morphology, location, axon connectivity). In a multilayer structure, these anatomical layers can be represented by mathematical layers/networks. More abstractly, thalamic and other sub-cortical regions can also be considered as another group of layers. Together, all cortical and sub-cortical layers may form a more general structure, where intra and inter interactions can model different types of signals.

Beyond the neurocentric approach of cognitive neuroscience, other types of cells such as astrocytes and glial cells also play an important role inside brain and body interactions. The hemodynamic functions of the heart partially determine the heart-brain coupling and the cardiac-theta coupling. This coupled system provides metabolic substances and oxygen through the blood flux. At the neural level, astrocytes and other glial cells are responsible for mediation of these processes (Haydon and Carmignoto, 2006; Zonta et al., 2003). For instance, mice with knockout of mitochondrial astrocyte-specific proteins take longer to recover from volatile anaesthetics than control (Ramadasan-Nair et al., 2019). It suggests that astrocytes' mitochondrial function modulates the recovery from anaesthesia. Astrocytes also seem to play a role in sleep-wake cycles, mechanisms and functions of sleep (Haydon, 2017; Petit and Magistretti, 2016). The interaction neuron-astrocytes is crucial to maintain neural energy consumption, making astrocytes the supplier of brain glucose (Bélanger et al., 2011; Jha and Morrison, 2018; Magistretti and Allaman, 2015). In fact, glia and astrocytes cells, as producers of glucose, may influence the whole-brain energy states and eventually impact conscious experiences (Velazquez, 2020). Astrocytes and other cells can also be modelled by specific layers in a multilayer network (Vaiana and Muldoon, 2020).

Another finding investigating the role of psychedelics points out to more general interactions thought the optimal coupling of neurotransmitter molecular system and cellular whole-brain system (Kringelbach et al., 2020). The brain is approached as a three-layer system where layers are defined by their types of interactions (Fig. 3B). Specifically, functional connectivity, anatomical connectivity and molecular diffusion. Then, the resting-state activity under psilocybin is fitted by coupling the systems, while decoupling systems produce a breakdown in the fitting of the empirical data (Kringelbach et al., 2020). This result, and particularly the addition of a third dynamical dimension (molecular density and diffusion), is crucial to understand how functional activity is modulated under a mostly unchangeable anatomical neural substrate. In this case, the neurotransmitter layer brings a new physical dimension not considered before. In other words, this new layer and its interactions

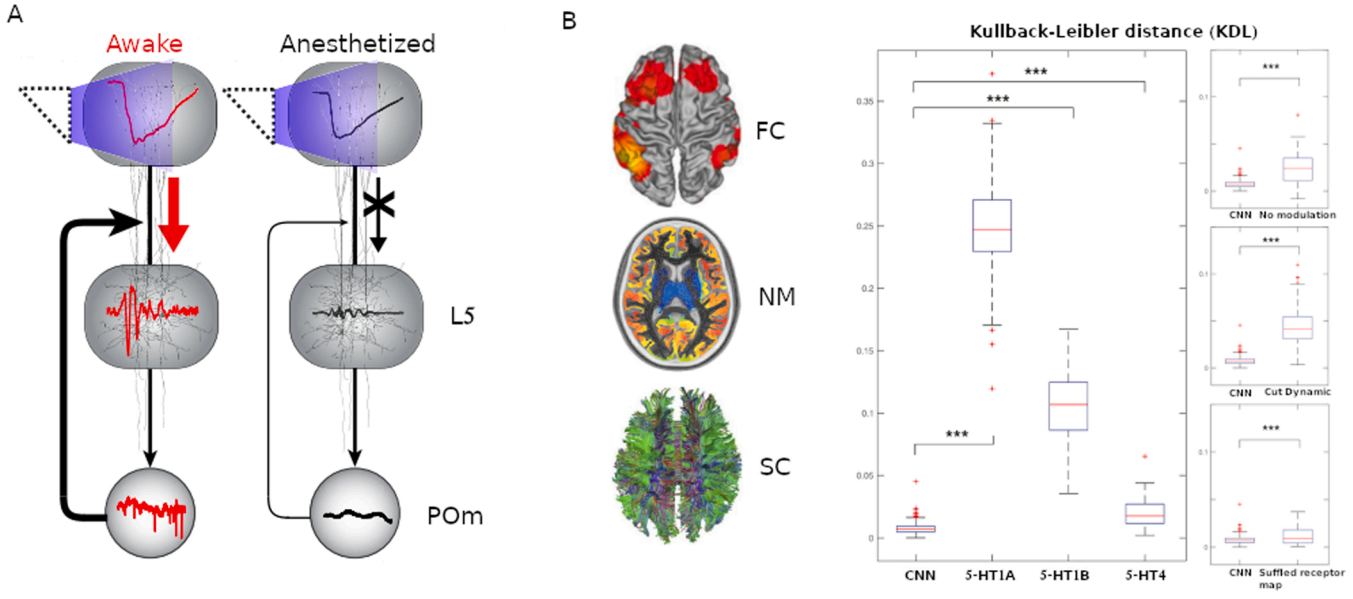


Fig. 3. Reinterpretation of empirical evidence from a multilayer perspective. (A) Neural activity in the posteromedial nucleus (POm) correlates with coupling activity of L5 pyramidal neurons during awake conditions, independently of optogenetic stimulation of distal apical dendrites. In turns, inactivation of POm impaired the coupling. In terms of multilayer descriptions, these results can be modelled by a group of cortical and thalamic anatomical layers. (B) Functional (FC), neuromodulatory (NM) and structural connectivity (SC) represent three interacting layers. The optimal dynamical coupled neuronal-neurotransmission (CNN) is measured by Kullback-Leibler distance (KLD). The coupling neural and neuromodulatory system of $5 - HT_{2A}$ fits the observed brain functional activity much better than other receptors maps, uncoupled neuromodulatory system, cutting the dynamic feedback dynamic between systems, as well as the result using shuffled receptors maps.
(a) Adapted from Suzuki and Larkum (Suzuki and Larkum, 2020). (b) Adapted from Kringelbach et al. (Kringelbach et al., 2020).

with other layers account for the modulation and dynamical switch of whole-brain repertoire.

The cases above are examples of neuron-neuron and neuron-glial interactions within brains. These examples show at least two possible ways to define layers in a more general multilayer structure (i.e. cells types, including neural anatomy, and types of interactions). The interactions above cannot always be reduced to one single type of network communication (e.g. same type of neurons, electrical action potential, etc), showing that more general network structures may account better for such complexity.

3.3. Brain-body and consciousness

Unfortunately, consciousness research has paid little attention to brain-body interactions. The neuroscience of consciousness focuses on the cascade of neural events, taking for granted basic brain-body couplings (Revach and Salti, 2021; Perouansky et al., 2019).

Nevertheless, the previous findings are important because they add new complex dimensions on the understanding of conscious perception, anaesthesia, sleep mechanisms, and their relationship with conscious experience. We may pay attention to different types of within brain interactions, such as neuron-neuron and neuron-glia (Velazquez, 2020). Additionally, we may reconsider the role of complex molecular, metabolic and kinetic physiological brain-body systems interacting, such as gut, heart and lungs (Thompson and Varela, 2001; Merleau-Ponty, 2005; Steinman, 2004; Steinman, 2004; Dantzer, 2018; Criscuolo et al., 2022). All together, these interactions might be essential to support and describe better the richer phenomenology associated with conscious experiences.

Park and Tallon-Baudry (2014), for example, suggest a neural subjective frame made of a group of basic biological mechanisms responding to visceral inputs. This frame defines the subject as a biological entity, and this entity as the building blocks of first-person experience (Park and Tallon-Baudry, 2014). The intrinsic connection between body signals and higher brain areas would generate the seed of the -IJI-İ and subsequent subjective experiences through an interaction of neural responses to visceral inputs and stimuli responses. The enactive and radical embodiment model goes one step further and argues that these bodily interactions are the basis of any phenomenal experience (Thompson, 2007; Thompson, 2014). In such a model, conscious experience co-emerges with a large-scale and transient cascade of activity that cuts across brain-body-world processes (Thompson and Varela, 2001). Unfortunately, the modeling, description and integration of these processes is almost impossible when using dynamical system theory with only monoplex networks (i.e., a single network).

Bodily inputs seems to contribute by grounding conscious experience as well as bringing specificity to phenomenal experiences. For example, a particular body may feel and experience different than other body (Nagel, 1961). Moreover, the need to urinate feels quite different than the need to eat, both experiences arguable different. These aspects of subjective experience can rarely be explained by brain activity only. Recent works show how different types of non-neurocentric bodily interactions contribute to specific experiences such as time-flow experience (Ogden et al., 2022; Khoshnoud et al., 2022), emotions (Quadt et al., 2022), fear balance (Klein et al., 2021), hallucinogenic experiences (Ballentine et al., 2022) and conscious tactile perception (Grund et al., 2022), among others. In this line of thoughts, the evidence reviewed suggests that a sound explanation of the difference between unconscious (e.g., deep sleep) and the conscious brain (e.g., awake states) may involve bodily interactions (e.g., glucose release) together with the intrinsic cortical brain activity. There is nothing that structurally changes between an unconscious brain and a conscious one. However, brain-body couplings change in all unconscious states.

Furthermore, we hypothesize that bodily inputs drive brain repertoire through adding instability to the otherwise stable brain system (e.g. by releasing and diffusing hormones and neurotransmitters). One could imagine different networks/layers representing different dimensions of activity between brain-body systems. These systems could interact to account for different states of arousal, dreams, wakefulness, phenomenal states and ultimately, conscious perception (see (Signorelli and Meling, 2021). Evidence above, for example, suggests that heart variability, respiration rate and slower stomach activity may impact the dynamics of the brain, and therefore, also impact cognitive functions associated with conscious states (Candia-Rivera, 2022; Criscuolo et al., 2022). Additionally, these bodily inputs could impact the phenomenology of experience. For example, higher heart rates may be accompanied by feelings of fear or danger, while stomach pain could be related to feelings such as anxiety and depression. A multilayer framework with dynamical coupling and decoupling edges may allow a simpler, integrative and intuitive description of these processes (see examples below).

Taking together, an integrative approach to conscious experience and its relationship with brain-body functioning demands a switch from a neurocentric perspective to a more holistic view (Thompson and Varela, 2001; Merleau-Ponty, 2005; Signorelli and Meling, 2021). This integration justifies the introduction of multilayers networks as a mathematical structure to describe the coupled brain and body organization (Signorelli and Boils, 2021).

4. Multilayers and brain-body organization

The previous discussion lead us to formally define our intuitions from Section 2. Here, we will introduce a multilayer structure for brain and body organization, as well as interpretations for conscious processes. This mathematical structure appears extensively in physics, engineering and social sciences (Kivela et al., 2014; Boccaletti et al., 2014), while becoming a common analytical and modelling tool in neuroscience (Mucha et al., 2010; Domenico, 2017; Pedersen et al., 2018; Vaiana and Muldoon, 2020; Grazia Puxeddu et al., 2021). This is mainly because a multilayer structure allows us to describe complex interactions in simple terms, adding more details of the structure and function at multiple levels of interaction (as shown in examples below). This ultimately lead to the discovery of new phenomena that are not always present in monoplex networks.

4.1. Multilayer networks

Multilayer network is an extension of the widely used graph theory. A graph is a tuple $G = (V, E)$, where V is the set of nodes and $E \subseteq V \times V$ is the set of edges that connect pairs of nodes. A graph is a network of interactions, also called a *single-layer network* or *monoplex*. Then, a multilayer network is a quadruplet $M = (V_M, E_M, V, \mathbf{L})$, where $\mathbf{L} = \{L_k\}_{k=1}^{d}$ is a sequence of sets L_k of *elementary layers*, with d being the total number of aspects. These aspects are given by the colour of the edges and they represent the different types of interactions. $V_M \subseteq V \times L_1 \times \cdots \times L_d$ is the subset of all tuples containing mixed information about the node and the layer present in every case. Finally, $E_M \subseteq V_M \times V_M$ is the set of pairs of possible nodes and elementary layers (Kivela et al., 2014).

If a node u is present on different layers (l_1, …, l_d), we can use the notation:

$$(u, \mathbf{l}) \equiv (u, l_1, \ldots, l_d)$$

The set of edges is partitioned into *intra-layer edges* as those belonging to sets

$$E_A = \{((u, \mathbf{l}), (v, \mathbf{h})) \in E_M | \mathbf{l} = \mathbf{h}\}$$

and *inter-layer edges* as those in $E_C = E_M - E_A$. Intra-layer edges correspond to the interactions inside layers (e.g., yellow and light blue edges, Fig. 1A), while inter-layer edges are those representing interactions among layers (e.g., red and blue edges, Fig. 1A). In neuroscience, the multilayer approach is used to analyse and model the human brain as a

group of different functional layers. One example is the decomposition of electroencephalogram (EEG) and magneto-encephalography (MEG) into layers defined by different frequency bandwidth (Domenico, 2017; Vaiana and Muldoon, 2020).

This simple extension, from networks to multilayer networks, allows us to incorporate more complex brain-body structure. For example, one group of elementary layers might represent types of neurotransmitters, while another represents cell types. In such cases, we might either speak about within brain interactions or extend the description taking other bodily systems (e.g., the gut as a node with high density of serotonin neurotransmitter (Shine et al., 2022). The general idea is that each colour edge in a multilayer represents a particular type of interaction, from electrical activity in the cortex to physiological, metabolic, kinesthetic, etc, activity from the body, and between the body and neural central system. The new layers of description add new dimensions to account for complex interactions.

One example, would be to treat the brain as one group of layers and bodily organs as another group of layers. Each of these elementary layers will have their own aspect, given by the specifications of their elements (nodes) and/or types of internal interactions (intra-edges). Additionally, nodes in different layers can interact between them via inter-layer interactions (inter-edges). For example, the gut seems to play a role in the stomach-brain gastric resting state network (Rebollo et al., 2018). This functional connection can be described by inter-connectivity between the stomach-gut as one layer and the cortical areas involved as another layer. In this example, the brain becomes one extra layer of the body, instead of the body becoming one new layer of the brain. As such we avoid brain centred explanations and expand them to more holistic brain-body interactions.

This framework brings new dimensions of analyses in one simple mathematical structure (Kivela et al., 2014). One example is a phenomenon called multiplexity: the overlap of roles, exchanges, or affiliations of nodes in a particular network. For instance, the relationships of a group of colleagues in their workplace generates a social network. The same group of colleagues using online communication (e.g., Slack), instead of in-person communication, may give rise to another social network of interactions. In this case, a monoplex, or single network, is not enough to study the aggregated dynamics of social influence. If some colleagues are more active on Slack than in-person, then we need to consider the inter-layer interactions between social networks to account for output parameters and internal influences.

The simulation of transportation networks is another example from engineering (Boccaletti et al., 2014). One layer corresponds to airplane transport networks, another corresponds to tracks transportation networks, while a third one can be a train transportation network, etc. Then, a supply chain of a city can be modelled more realistically by complex interactions between these layers.

Similarly, the brain is not an isolated system, and it cannot be reduced to only action potentials and electrical communication. The brain is embedded in a particular biological context (bodily, environmentally and socially). Therefore, to understand how brain regions influence each other, we might account for other ways of communication, as well as the influence of neglected bodily organs exert in the brain system.

In neuroscience, a familiar example of different types of interactions is the relationships between anatomical and functional brain connectivity (Vaiana and Muldoon, 2020). One might consider that anatomical connectivity between brain regions accounts for all the spatiotemporal complexity of the brain. This is the analysis of one-dimensional network, one layer given by only anatomical connections, and therefore only one type of intra-layer interaction. If we now turn to another dimension of interaction, the functional one, we realize that anatomy is not enough to explain the richness of the brain dynamic at resting state. Indeed, the functional network by itself is also insufficient to explain its own richness. Only the dynamical link between both dimensions of analyses, given by dynamical inter-interactions of two layers, brings a more compelling explanation (Cabral et al., 2017; Valk et al., 2022), i.e., the analysis of inter-connectivity between anatomy and function through global coupling parameters.

As mentioned in the examples above, each concrete application of multilayers needs to operationalize the definition of layers in terms of the phenomena being modelled. The same happens with graph theory and network theory. On one hand we have the mathematical definition of networks; and, on the other hand we have implementations of networks simulating social networks, transport networks, brain networks, among others. In the case of multilayers for conscious experience, we may assume layers correspond to biological systems. Nevertheless, we leave open the specifics of each layer, since the concrete definition will depend on the particular phenomena being modelled. For instance, someone would like to model the brain-heart interaction and its role in conscious perception. Until now, this has been done through statistical models and coupling functions. In terms of multilayers, we could consider certain regions of the brain (e.g., insula) as one network/layer and the heart as another network/layer. Then, the coupling between layers will be modelled by intra-layer edges as defined above. However, if someone would like to model more complex interactions, perhaps a better layer definition would correspond to one network/layer with all brain regions that show to correlate with the heart and the heart in the same layer, while other brain networks would form part of another set of layers. In this example, we would have one brain-heart layer interaction together with other brain-brain layer interaction. The particular definition of the layers depends on the phenomenon to model.

Consequently, the multilayer structure has the potential to become an integrative meta-framework to account for further empirical evidence on brain-body function, cognitive science and consciousness research (see Section 5).

4.2. Composition of layers

In order to specify layers for conscious experience, one may include particular definitions for brain-body multilayers interacting (i.e. its operationalization). To account for these particular complex interactions, we introduce one formal way to compound and combine different layers into multilayers. This is given by the commutative operation $\odot$. For an extended discussion, see (Signorelli and Boils, 2021; Baez et al., 2018).

First, we restrict our presentation to only one set of elementary layers, where aspects match a set of colours $\mathscr{C}$ of dimension d. Secondly, we extend the notion of graph to multigraph. A multigraph G with a set of *vertices* $V(G)$ is a multisubset of *edges* $E(G)$ that corresponds to pairs of elements of $V(G)$, together with a function $m : E(G) \to \mathbb{N}$ that calculates the multiplicity of every edge ($\mathbb{N}$ refers to natural numbers). A *network model* is then a nomenclature MG such that when inserting a number n into MG we obtain a set of multigraphs with n vertices $MG(n)$. We endow $MG(n)$ with an operation $+$ that corresponds to the addition of multiplicities of edges that share the same vertices. In short, every element of $(MG(n), +)$, or simply $MG(n)$, corresponds to our special case of *layers* discussed in this section. The edges into every layer have a single colour or aspect c_i from a set $\mathscr{C}$. Then, we can define:

Definition 1. Let $\mathscr{C}$ be a fixed set of colours representing different bodily interactions (such as heart, gut, brain networks, etc) and $\mathscr{C}_1$, $\mathscr{C}_2 \subseteq \mathscr{C}$ two disjoint sets (e.g. the set of heart interactions and gut interactions signified by $\mathscr{C}_1$, and heart and DMN interactions for $\mathscr{C}_2$). Then, consider s and q as the number of possible interactions (i.e. the number of colour edges in each network/layer), and n and m the number of nodes in two networks/layers called G and H. For every s-coloured layer G in a multilayer structure given by $MG^{\otimes \mathscr{C}_1}(n)$ and q-coloured layer H in $MG^{\otimes \mathscr{C}_2}(m)$, the distributive operation

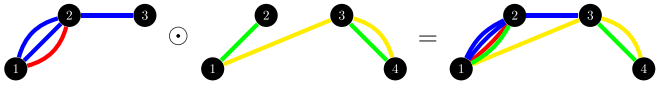
$$MG^{\otimes \mathscr{C}_1}(n) \times MG^{\otimes \mathscr{C}_2}(m) \xrightarrow[\odot]{} MG^{\otimes \mathscr{C}_1 \cup \mathscr{C}_2}(n+m-p)$$

produces a new $(s+q)$-coloured layer $G \odot H$ where $p = |V(G) \cap V(H)|$. The notation $MG^{\otimes_{\mathscr{C}}}(n)$ refers to a tensor product of sets. For example, let's define two types of interactions in $\mathscr{C}_1$. One for a single brain-heart interaction c_1 and another for a brain-gut interaction c_2. Then, we obtain:

$$MG^{c_1 \otimes c_2}(n) = MG^{c_1}(n) \times MG^{c_2}(n)$$

Each element into $MG^{c_1}(n)$ contains one single-coloured layer. In this instance, a tensor product is what we call *multilayer*. We can also have another set $\mathscr{C}_2$ with colours c_1 for brain-heart interactions and c_3 for brain-brain interactions (such as the ones given by DMN). In this case, we can compose all the interactions with the operation $\odot$ producing the multilayer structure $MG^{\otimes_{\mathscr{C}_1 \cup \mathscr{C}_2}}$, which is also a tensor product with a final set of colour given by $\mathscr{C} = \mathscr{C}_1 \cup C_2$. In other words, the final multilayer $\mathscr{C}$ corresponds to the set c_1, c_2, c_3 relating to *heart, gut, DMN* in a simplified form where colours represent types of layers interactions. After using the operator $\odot$, layers become many-coloured or multi-aspect, i.e. different types of interactions now take place. This becomes clear with the next example.

Example 1. For $n = 3$, $m = 4$, $s = q = 2$ and $p = 3$:



Note that in $t = 0$ we have $s = q = 1$. New colours appear in a layer after more applications of $\odot$.

Roughly speaking, $\odot$ shows the way by which one can combine biological layers (represented by different colours) into a multilayer. This is done by the process of *merging layers* whenever they interact (see 4.3).

Note that, in the sense of Kivela et al. (2014), $\odot$ does not generate any *inter-layer edge* among layers but rather the combination of *intra-layer edges* of a $(s+q)$-aspect layer from previous s-aspect and q-aspect. In other words, to describe the specific case where brain and body layers account for conscious experience, we consider only the *inter-layer edges* in one layer that become new *intra-layer edges* under composition of layers. As such, these interactions add up as new layers are incorporated (for mathematical details see (Signorelli and Boils, 2021).

To give an account of conscious experience, the above restriction seems important because it emphasises the irreducibility of brain and body processes (i.e., the difficulty to isolate brain-body interactions as independent interactions under awake condition). In our formal model, the conscious brain acts as an entangled system of layers that includes many biological systems and organs of the body (Pessoa, 2022). This prevents us from identifying these layers during awake states in a unequivocally manner. However, the fact that every layer contains a unique and different colour in an initial unconscious time ($t = 0$) ensures the empirical distinction of different layers, at least theoretically.

Beyond descriptive and operational layers, the distinction of independent optimal layers is an empirical task that needs to be done in the context of maximal natural decoupling (see Section 5.1 and 5.2). Therefore, our formalism predicts the existence of biological layers, as well as the optimal scenario to recognize them.

4.3. Interaction of layers

We can formalise the comments above adding another relevant feature for these particular multilayers: the time indexation. To formally describe these time-evolving interactions, we introduce a notion of a multigraph endowed with a rotation angle.

Definition 2. A *rotation layer* is a pair $[G, \alpha]$ where G is an edge-coloured multigraph and $\alpha \in [-\pi/2, \pi/2]$ is an angle.

Given an interval of positive numbers including 0, $T \subseteq \mathbb{R}^+ \cup \{0\}$, the angles considered are continuous functions α: $T \to [-\pi/2, \pi/2]$. Then:

Definition 3. Two rotation layers $[G, \alpha]$ and $[H, \beta]$ *interact in a time* $t \in T$ if $\alpha(t)$ and $\beta(t)$ have a different sign, and $|\alpha(t)| + |\beta(t)| \geq \pi/2$. We consider 0 as a sign in itself.

Then we define the sets $RMG^t(n)$, where every element is a *rotation layer* or simply a *layer*:

$$RMG^t(n) = \{\text{rotation graphs}\,[G, \alpha]\,\text{with}\,|V(G)| = n\}$$

We impose $RMG^0(n)$ to contain only 1-coloured multilayers when there is no interaction.

Finally, the $\odot$ operation in the non-rotation case is extended to the rotation. Fixing a set of systems represented by colours $\mathscr{C}$, we have the following:

$$[G, \alpha] \boldsymbol{\odot} [H, \beta] = [G \odot H, min(\alpha(t), \beta(t))]$$

Note that $\boldsymbol{\odot}$ is now bold. According to this extension, every rotation layer mixes colours as in the previous subsection. In addition, the angles bring another formal notion of *coupling*: the $\boldsymbol{\odot}$ operator preserves the individuality of layers' colours at the cost of losing their angle independence. This coupling allows us to define *coupling edges*, such as edges whose constituent nodes appear in more than one layer end up in a *coupling graph* for conscious experience (Signorelli and Boils, 2021). In other words, *coupling edges* admit an underlying *coupling graph* containing the basic configuration of the system. These nodes might correspond to observed brain-body regions whose contribution to the conscious experience is diverse. In the extreme case that a coupling edge is coloured with all colours into $\mathscr{C}$, we have a pair of nodes that participate in every conscious operation that the system could or may have. They should be seen as part of a *core structure* into the brain-body structure.

Importantly, these nodes are the consequence of conscious operations as new coupling edge activities appear, but not the effective cause or generators of consciousness (see (Signorelli and Boils, 2021) for mathematical details and (Signorelli and Meling, 2021) for philosophical arguments). This is because the multilayer approach is a pragmatic meta-framework and it does not entail any ontological commitment. Therefore, we avoid reductive readings. We do not reduce conscious experience to regions of the brain or the body, but keep an holistic perspective where conscious experience is an entangled process of processes that can be mainly described/explained but not necessarily reduced to isolated mechanisms. Consequently, what we observe as nodes participating in consciousness processes may be the result of multiple processes interacting. For example, peaks of wave amplitude in the water correspond to the superposition of multiple waves. In cognitive neuroscience, however, we tend to forget that the activity of brain regions is the result of several processes in superposition. The contrast peaks observed between cognitive conditions in brain regions may be much more similar to the peaks of waves in a water recipient than the consequence of isolated local activity (Bolt et al., 2022; Gonzalez-Castillo, 2022) (also see final Section 6).

5. Multilayers and consciousness

The formal and mathematical introduction of rotation layers allow us to reason about brain and body configurations related to conscious experience. For instance, it is now possible to describe layer interactions by means of simple rotation diagrams, such as in Fig. 1B and Fig. 4B.

5.1. Biological layers and conscious experience

Evidence supporting the introduction of layers and multilayers in conscious research comes from the reinterpretation of empirical findings discussed in Section 3. A full multilayer framework, for example,

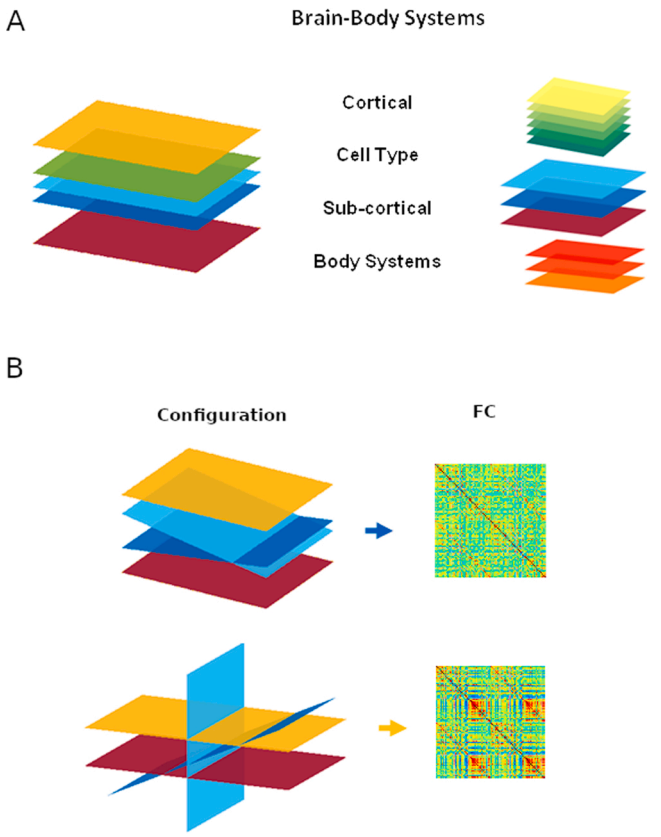


Fig. 4. Brain-body multilayers. (A) Layers may correspond to more general biological organizations, ranging from different neural layers, such cortical or subcortical networks, to different cells types layers, molecular layers, immune system, organs and body systems in general. (B) We hypothesize that a particular group of metabolic and anatomical layers (i.e., native layers) and their configurations trigger different functional observed patterns of connectivity (i.e., FCs). This global configurations may account for global states of consciousness while particular configurations may help to describe the phenomenal content of such states.

subsumes three types of empirical layers discussed above (Fig. 2 and Fig. 3). Namely, layers given by brain-body interactions, cell types and anatomy, and different types of interactions such as the functional, anatomical and molecular layer division. Some of these layers are brain networks while others are molecular systems connecting the otherwise anatomically disconnected regions.

These descriptions can be extended to biological systems such as heart, lungs and gut, among others. Layer organization intends to represent the whole architecture of living systems, while intra and inter layer interactions represent the processing inside and between layers, respectively. One example is how different organs interact across global conditions and disruptions of the brain-body system, e.g., light sleep, deep sleep, anaesthesia, etc. (Bartsch et al., 2015). In general, biological systems and physiological signals can be modeled by different types of edges (e.g., different colour edges). Brain regions and bodily systems can be modelled either by nodes in a given network or by a full layer. For example, frontal brain regions may corresponds to nodes in a brain layer, while the heart could be either modelled as a node in a brain-heart layer or as a layer by its own. The choice will depend on the phenomenon to model.

In particular, one may like to define fixed/optimal layers and their interactions associated with conscious experience (e.g. our hypothetical native layers). In this case, we might specify biological layers through metabolic exchanges, in line with biological behaviour (Alexandrov and Pletnikov, 2022). In a biological multilayer structure, these layers may be defined by their intrinsic activity, specified by their self-sustained oscillatory activity, or metabolic self-sustained activity. One approach is to use eigendecomposition of metabolic activity from Positron emission tomographic (PET) imaging of the brain, incorporating visceral signals in the decomposition matrices. In the ideal case, operalizations of theoretical native layers may correspond to biological autonomous systems, meaning that they *self-produce* and *self-distinguish* their own elements and interactions (Paolo et al., 2021; Thompson, 2007; Signorelli and Meling, 2021). Furthermore, we can extend the current multiplex networks description to a general multilayer configuration where the number of nodes can also change among layers.

The multilayer framework also has the potential to integrate several signatures of consciousness (Signorelli, 2021) through the dynamic reconfiguration of brain and bodily layers (Fig. 4B). Each global configuration may trigger different observed brain states associated with awake and non-awake conditions. The main causal forces of functional patterns become the appearance of new couplings and compositions of multilayers. For example, during deep sleep heart and brain activity decouples, while heart influence increases during awake states. Modelling and simulations may show that this new configuration could explain the differences between observed functional brain patterns better than taking the brain as an isolated system.

Eventually, multiple brain-body configurations might account for global signatures of consciousness and specific conscious experiences (Bachmann and Hudetz, 2014; Storm et al., 2017). Under isolation, autonomous native layers may behave exactly how they behave under minimal consciousness interactions (e.g., deep sleep). Then, when layer interactions take place, the arising of new couplings can globally characterise states of consciousness such as dreaming, awake, etc, while fined-grained couplings may characterise the structure of experience. In our conceptual model, different distinctions such as pure awareness, phenomenal consciousness, access consciousness (Block, 1995; Block, 2005), among others (Dehaene et al., 2014; Dehaene et al., 2017; Signorelli, 2017; Signorelli, 2018a,b), corresponds to dynamical process configurations of layers interacting. For instance, phenomenal consciousness could be described by the types of layers continuously interacting, while access consciousness by the discrete process of beginning and ending specific layers interactions. In such a framework, no single area is necessary and sufficient for consciousness, but their complex interactions may be. For example, the brainstem, thalamus and other regions involving brain-body interactions provide the background for conscious experience; while others, such as cortical zones, become candidates for content specific conscious experience.

A multilayer framework allows us to hypothesize more general brain-body systems participating of conscious experience. Therefore, multiple layers will play a role in the structure of experience and have impact in our human cognition (Signorelli et al., 2020). We hypothesize that this variety of layers and couplings trigger complex configurations and global brain dynamics observed in awake condition. As such, they become the native networks driving resting state and task related networks mentioned at the beginning of this article.

5.2. *Simulations and testing*

Future empirical distinctions might bring light to the optimal native layer division regarding conscious experience. The empirical definition of these layers shall start under ideal conditions of minimal coupling. Some of these layers may correspond to molecular systems connecting the otherwise anatomically disconnected regions, immune system and different types of organs. The model can also be extended to other layers of description (e.g., social interactions between brain-body agents).

Moreover, different types of layers may couple and decouple from time to time and correlate with a reduction of awareness even under global awake conditions. For example, our framework predicts that this reduction is due to the recovery of intrinsic layer dynamics (i.e., decoupling of layers), together with a decrease on inter interactions that usually interfere with those intrinsic layer dynamics (i.e., decrease of

global coupling parameters). This reduction of awareness seems to appear during conscious resting-state and suggest partial moments of consciousness (Ward and Wegner, 2013; Naccache, 2018; Mortaheb et al., 2022). This reduction, however, presents two different signatures: mind blanking (Mortaheb et al., 2022) and unconsciousness brain signatures (Demertzi et al., 2019). The former is characterised by a highly integrated pattern of brain activity. The latest is described by functional patterns which are closer to structural connections (Mortaheb et al., 2022; Demertzi et al., 2019).

Those results impose difficulties to current models of consciousness (Mortaheb et al., 2022). Nevertheless, our conceptual model explains the first case of "reduction of awareness" by bodily layer interactions that usually do not dominate resting-state activity, as the role of global signal indirectly suggests (see (Mortaheb et al., 2022) for details). While the second case is explained by the biological need to go back to the intrinsic dynamics of decoupled layers, which is more in line with unconscious patterns.

In future research, the multilayer framework can be implemented via causal simulations that incorporate more general biological systems. Under our conceptual framework, we have several ways to study layer configurations. First, we can define and modify the internal dynamic of the system-layer, e.g., defining different layer systems and their dynamical evolution via differential equations (Deco et al., 2018b; Kringelbach et al., 2020). Second, we can modulate the inter-connectivity via coupling functions, e.g., exploring the coupling parameter (inter-edges) to fit the empirical data (Fig. 3B, non-modulation and cut dynamic). Third, we can study the effects of intra-connectivity in the whole system, e.g. changing the anatomical connectivity map or the neuromodulatory map (Fig. 3B, with different receptors maps). Until now, however, multilayers have been implemented as monoplex (single layer) and multiplex (more than one layer, all sharing same nodes). In multiplex networks all regions are present in the layers and each layer is different due to their type of interaction (e.g., anatomical, functional, etc). The multilayer framework can be certainly extended to more complex scenarios where layers invoke other types of interactions and regions are not present in all layers (e.g., brain-gut interactions).

5.3. Other models of consciousness

The multilayer framework also has the advantage to synthesise and integrate several current models of consciousness. This can be done through different instantiations of a multilayer structure (Fig. 5). Some examples are the recent mathematization of some aspects of the enactive and radical embodiment approach given in (Signorelli and Boils, 2021; Signorelli and Meling, 2021), and an ongoing project doing the same with global workspace model (GNW). In terms of multilayers, the GNW seems equivalent to a fix multilayer architecture (Fig. 5A); while the integration information model (IIT) may correspond to a monoplex time-evolving layer (Fig. 5B). These two models of conscious experience (GNW and IIT) define their nodes as idealized neurons. More recently, models such as Temporo-spatial theory of consciousness (TTC) have tried to integrate different models of consciousness in a complex structure of levels (Northoff and Huang, 2017; Northoff and Lamme, 2020). This structure could be understood as a multilayer time-evolving architecture; and therefore, together with an embodied structure, becomes a more general model than GNW and IIT. Hypothetically, other models can be subsumed in a multilayer structure, despite being based on different metaphysical assumptions. One example includes conscious agent networks (CAN), which start from an idealist position (Hoffman and Prakash, 2014). Considering certain mathematical restrictions and definitions, CAN suits a mathematical multilayer description where layers become agents (Fig. 5C).

Finally, a mathematical multilayer structure and hypergraph structure can give a more integrative picture of how different models relate to each other. This can be done in light of their philosophical, axiomatic and mathematical priors. Formal mathematics allow such an attempt thanks to its rigor and transparency (Signorelli et al., 2021c; Northoff et al., 2019; Prentner, 2019; Signorelli et al., 2021d; Tull et al., 2020). We believe that some aspects of GNW, IIT, TTC, and embodiment models of conscious experience, among others, respond to certain commonalities that we can study through mathematical structures. Independent of the metaphysical commitment, we thing such theoretical integration is a pragmatic endeavour with several important consequences in the clinics.

6. Conclusions

In this article we reviewed empirical evidence and introduced a formal mathematical definition for multilayers in the context of brain-body functioning and their links with awake states and conscious experience. Here, a multilayer network framework consists of two main generalization aspects. On the one hand, it incorporates a new semantic to describe biological systems (Kivela et al., 2014; Boccaletti et al., 2014), neural, physiological, metabolic, among other types of interactions. On the other hand, it has the potential to integrate different signatures and models of consciousness by different instantiations and types of layers structure. These aspects are important in order to account for all the relevant elements of a sound theoretical and empirical framework.

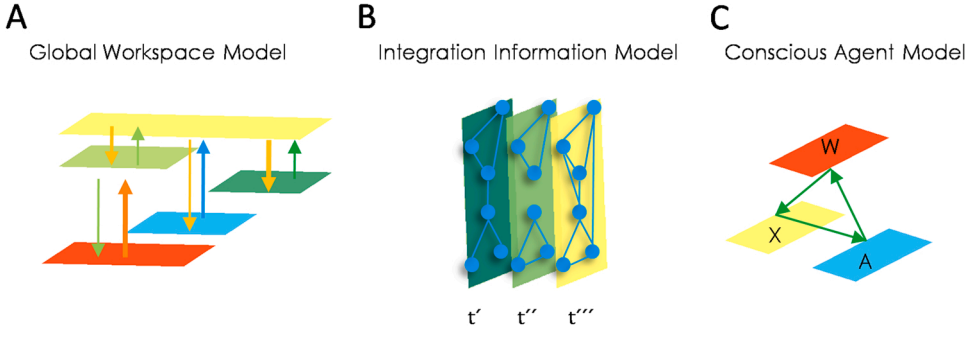


Fig. 5. Generalizing models according to multilayer structure. (A) Global workspace model. This model postulates a group of pyramidal neurons as fixed structure on top of a hierarchy of processes. In the picture, one layer and their regions (yellow) form a workspace with the ability to receive and broadcast signals from the other primary layers. According to that model, layers are defined only by neural systems and conscious experience correspond to the broadcast activity from the workspace layer. (B) Integration information model. This model is one dynamic layer network which reorganizes according to neural activity. As before, layers are defined only in terms of neural systems, although it is not always specified. Conscious experience corresponds to the maximal subgroup of neurons/nodes that maximized the integration and segregation of neural activity across time. (C) Conscious agent model. Differently than computational neural models, this model states that conscious experience and subjectivity are fundamental. Therefore, layers are defined as purely abstract mathematical constructions to describe agents (A), the world (W), and actions (X), all them interacting between them. Among all these models, the structural consequences and interpretations are different, but the same semantic of multilayers may account for all of them and further generalisations.

Empirical and modelling evidence suggests that brain organization conveys richer dynamic repertoires under conscious experience. This dynamic scenario is commonly characterised by bifurcations points (e.g. criticality) in dynamic system theory. These points, however, can not be explained by neural activity in the form of action potentials only (e.g., organized as functional networks). We require coupling and decouplings of several bodily systems and intricate forms of interaction to account for the complexity of brain activity during conscious experience. Bodily interactions, we follow, may be key components of the driving forces of these observed dynamical patterns. Different evidence, for example, is showing how visceral inputs are indeed influencing brain activity. Then, the semantic of the multilayer framework becomes a natural extension to describe and model all these new systems and interactions. This approach has several advantages and it is currently implemented in social science, physics and neuroscience, among other fields. In particular, we introduced a simple reasoning example where layers in a multilayer structure merge to account for conscious experience.

In particular, our dynamical layer approach fits well with the non-reductive stand of the enactive and radical embodiment model (Varela et al., 2001, 2016; Thompson and Varela, 2001; Paolo et al., 2017), but also extends it. In such a model, conscious experience co-arises with entangled mechanisms of brain-body interactions. These mechanisms compound a new irreducible whole-system, given by inter-interactions that become intra-interactions under conscious conditions. This new whole-system is not reduced to the relationships between these mechanisms but co-defined by the whole process of interconnected layers (Signorelli and Meling, 2021). These properties are in line with the particular case of multilayers introduced in Section 4, its composition of layers and their allowed interactions.

Finally, this multilayer framework presents several advantages: (i) it may integrate different dimensions of interactions accounting for the embodiment of conscious experience (Thompson and Varela, 2001), (ii) it is a dynamic approach, accounting for the rich spatiotemporal structure of consciousness (Deco et al., 2015; Deco et al., 2017; Ipiña et al., 2020), (iii) it is pragmatic framework already applied to relevant data, giving us new insight on the complex intertwined within brain systems and their relationship with consciousness (Deco et al., 2018b; Kringelbach et al., 2020), (iv) it offers simple concepts to reason about dynamical couplings and relevant systems (Signorelli and Meling, 2021; Signorelli and Boils, 2021), (v) it inspires computational model extensions to brain and body interactions and motivates multimodal experimental paradigms, since new data sets are required to test the major hypotheses, (vi) it comes with a concrete mathematics from which further perspectives may exploit their current implementations in other fields (Kivela et al., 2014; Boccaletti et al., 2014), and eventually, vii) the semantic of multilayer networks interacting has the potential to integrate other models of consciousness which are based on, implicitly or explicitly, graph and network theory.

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