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Subjective experiences matter. What do we know about consciousness?

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Summary

Consciousness is one of the most difficult and enigmatic problems in the science of the mind. For more than three decades, it has been the focus of research by scholars of different backgrounds, with major contributions from philosophy, psychology, computer science, and neuroscience. Such debate is taking place almost completely outside the mainstream of psychiatric discourse, although a greater understanding of the problem could help better understand the role of consciousness in the development of mental disorders. There is still no consensus on how to define consciousness, but scholars agree that the core and most problematic aspects concern simple subjective experiences such as the redness of red or the painfulness of pain. Concepts such as qualia, subjectivity and what-it-is-likeness of experience have helped better define these aspects. One of the most promising approaches for understanding how phenomenal experience is related to brain activity is the study of Neural Correlates of Consciousness (NCC). It has been shown that the brain areas most specifically associated with conscious mental activity are the cortical areas and that extensive neural networks are involved. It is still unclear which cortical areas are most involved and what the nature of this correlation is, especially in order to explain how and why such neural mechanisms would produce subjective experience. Several theories have attempted to formalize how the brain implements consciousness. This article briefly describes and discusses two of the most influential physical models, the Integrated Information Theory (IIT) and the Global Neuronal Workspace (GNW) theory, which differ mainly in their level of conceptual abstraction and anatomical specificity.

Key words: consciousness, experience, mind-brain problem, Neural Correlates of Consciousness (NCC), Global Neuronal Workspace (GNW), Integrated Information Theory (IIT)

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Taking consciousness seriously

Consciousness had engaged philosophers since at least the time of Aristotle, but only recently neuroscientists decided to set aside philosophical discussions on consciousness and instead search for its physical footprints [1]. For several decades, particularly since the late 1980s, consciousness has been the focus of multidisciplinary research by scholars of different backgrounds. These include neuroscientists (Pankstepp, Tononi, Koch, Llinàs, Libet, Damasio, Eccles, Dehaene, Changeux), philosophers and philosophers of mind (James, Nagel, Searle, Dennett, Chalmers, Block, Putnam, Churchland), experts in artificial intelligence and scholars involved in cognitive science (Fodor, Baars, Minskij, Marr, Noe, O'Regan), Nobel laureates (Edelman, Crick), as well as authors who take mystic and spiritual approaches.

Apart from a few exceptions, this interest has been counterbalanced by the lack of attention paid by "insiders" such as psychiatrists and psychologists who, like the experts above, should deal with consciousness and its relations with the non-conscious sphere. For a psychiatrist, the subjective consciousness of the other is, together with behaviour, the primary area of interest. When considering the importance of phenomenological inquiry, it is also the main instrument of investigation. Therefore, it is something that psychiatrists deal with directly every day in their clinical approach. Yet, despite the fact that consciousness is today at the very forefront of scientific and philosophical debate, such debate, strangely enough, is taking place almost completely outside the mainstream of psychiatric discourse [2].

Francis Crick wrote that, when he told people that he was working on the way we see objects, they were a bit embarrassed and wondered why there should be any difficulty about something as simple as seeing. "After all, we open our eyes and there the world is, large and clear, full of objects in vivid Technicolor, without our having to make any appreciable effort. It all seems so delightfully easy, so what can be the problem?" [3]. Although it may seem paradoxical, something similar has happened to me more than once when I have discussed the topic with psychologists and psychiatrists. Consciousness seems to be something that does not concern them and they are surprised to hear that a psychiatrist would focus on this kind of issue.

After all, until recently, the topic of consciousness did not even appear in textbooks on general psychology or on the physiology of the central nervous system. Throughout much of the twentieth century, psychologists rejected introspection to focus instead on observable behaviours and the stimuli that caused them. Even in the 1970s and 1980s, as cognitive science became established, consciousness remained a controversial topic among scientists, who openly questioned whether it was a valid area of scientific investigation. Eventually, prominent scientists did decide to tackle consciousness, which ushered in a shift in thinking that surged in the 1990s, fuelled by the increasing availability of brain-scanning technologies such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). At this point, scientists finally embarked on a major search for the mechanisms in the brain that are associated with the conscious processing of information [4].

In his famous article "Toward a philosophical structure for psychiatry", Kendler [5] seeks to sketch a coherent conceptual and philosophical framework for psychiatry that – at least with respect to consciousness – consists of four major propositions: 1) psychiatry is irrevocably grounded in mental, first-person experiences; 2) Cartesian substance dualism is false; 3) epiphenomenalism is false; 4) both brain-mind and mind-brain causality are real. Although the mind-brain problem (MBP) has marked implications for psychiatry, it has been poorly discussed in the psychiatric literature [6]. Twenty-three papers, published in the three general psychiatry journals with the highest impact factor from 1995 to 2015, revealed several misrepresentations of theoretical positions and lacked relevant contemporary literature. Without further discussion or evidence, they presented the mind-brain problem as solved, dualism as an old-fashioned or superstitious idea, and physicalism as the only rational and empirically confirmed option.

According to Parnass et al. [2], symptoms and signs cannot be properly understood or identified apart from an appreciation of the nature of consciousness or subjectivity, which in turn cannot be treated as a collection of thing-like, mutually independent objects, accessible to context-free, "atheoretical" definitions or unproblematic forms of measurement (as is often assumed in structured interviewing). Abnormal mental phenomena, i.e., disorders of experience and expression, are "the object" of psychiatry as a science and as a pragmatic medical discipline [7]. A psychopathological description involves converting the patient's experiences (lived in the first-person perspective) into specific categories of symptoms and signs that are defined in third-person terms, thus providing "objective," sharable information for diagnosis, treatment, and research [8].

Anxiety and depression are pathological manifestations of emotions and feelings that are, at least in ordinary language, conscious. As abnormal forms of experience, the very symptoms of anxiety and depression occur on a conscious level. In almost all disciplines, disease is an important gateway to understanding normal functioning. But it cannot be so only for behaviour or its neural correlates. It should also be so with reference to manifestations whose functional or dysfunctional role occurs in the context of first-person, phenomenal experience. We never ask ourselves what their functional or dysfunctional role is as *conscious experiences* or as part of conscious experiences.

Studies on schizophrenia have mainly highlighted difficulties in patients' conscious experiencing and processing but rarely explored how unconscious and conscious mechanisms may interact in producing this experience. Giersh and Mishara [9] argue that focusing on unconscious, physiological and automatic processing of information in patients, while contrasting that processing with conscious processing, is a first required step before understanding how distortions or other impairments emerge at the conscious level. This justifies a focus on unconscious mechanisms and a distinction from those associated with consciousness.

Healthy individuals can be more or less aware of what they are thinking and perceiving in different situations. However, being too aware or dissociated from one's thoughts is linked to mental health disorders. People with depression, for example, often overthink and can feel like people are judging them. On the other hand, people who have experienced trauma can become out of touch with the self. Understanding more about how consciousness works could help us find treatments when things go wrong [10].

How have things changed over the last century?

At present, consciousness is the biggest mystery of the mind and one of the major unresolved questions in science [11]. But how have things changed over the last century?

At the beginning of the twentieth century, what was mysterious was not consciousness, which we mistakenly thought we understood. Freud and other scholars began to explore the unconscious part of our mind. After slightly more than a century, scholars realized that the real mystery lies not in unconscious processes, but in conscious ones. Over the last century it has become progressively clear that up to 95% of mental processes, even at a high level, are unconscious. Furthermore, our knowledge of mental processes relates *exclusively* to unconscious processes [12,13].

Another major change in perspective concerns the level at which we seek consciousness. Many fall into the trap of equating consciousness with self-consciusness – to be conscious it is only necessary to be aware of the external world [14]. For centuries, consciousness coincided with our spiritual and immortal soul, so we tend to identify it with something exclusively human, like verbal reasoning and self-awareness in its highest forms. Aristotle distinguished between the vegetative, sensitive and intellectual soul. For a long time, only the latter was investigated by philosophers and scientists.

However, scholars gradually realized that our conception of consciousness cannot ignore much simpler experiences, such as our feelings of red or pain. At the same time, the subjective nature of consciousness has become increasingly evident, so much so that Searle, in order to distinguish what is conscious from what is not, used the dichotomy between subjective, or first-person, ontology and objective, or third-person, ontology [15]. The questions relating to these aspects of consciousness have turned out to be so challenging as to deserve the definition "hard problem of consciousness". The term was coined in 1994 by Chalmers [16] who distinguished it from the 'easy problems of consciousness', such as explaining how the brain integrates information, categorizes and discriminates environmental stimuli, or focuses attention. As stated by Chalmers [16], the hard problem of consciousness is the problem of explaining how and why it is that some internal states are *felt* states, such as heat or pain, rather than unfelt states, as in a thermostat or a toaster. In other words, the term *sentience* may be used as shorthand for *phenomenal consciousness*, the capacity to have any subjective experience at all [17].

A related issue is the question of animal consciousness. The traditional – and perhaps still intuitive to many people – way of thinking about consciousness is as primarily an innate endowment of humans, which other animals may or may not share in virtue of being sufficiently like us [18]. In recent times, experts are increasingly accepting the idea that a number of animals also have some form of consciousness, albeit less evolved than ours. The idea that consciousness is something shared by a great number of species underlies a famous essay by the philosopher Thomas Nagel in which he asked "What is it like to be a bat?" [19].

The question of animal consciousness makes it even more pressing to address the problem of defining consciousness – also from a functional point of view – and of establishing to what extent it can be stratified into more or less complex and evolved forms. But the problem is above all a methodological one. In fact, it remains difficult to characterize convincing strategies of access to conscious experiences in other species, since we then have to rely on third-person access and mostly on behavioural data [20]. As we consider species that are progressively further removed from Homo sapiens in evolutionary and neuronal terms, the case for consciousness becomes more difficult to make. Two observations, one relating to complexity of behaviour and another one to complexity of the underlying nervous system, are critical. First, many animals are capable of sophisticated, learnt, non-stereotyped behaviours that we associate with consciousness if carried out by people. Second, the nervous systems of these species display a vast and still ill-understood complexity [21].

What is consciousness?

Medically speaking, consciousness is the state of the patient's awareness of self and environment and his responsiveness to external stimulation and inner need [22]. According to Zeman and Coeberg [23], consciousness has two key senses in colloquial English that are of relevance to clinical practice – wakefulness and awareness [24]. Consciousness, so defined, "begins when we wake in the morning from a dreamless sleep - and continues until we fall asleep again, die, go into a coma or otherwise become 'unconscious'. It includes all of the enormous variety of the awareness that we think of as characteristic of our waking life. It includes everything from feeling a pain, to perceiving objects visually, to states of anxiety and depression, to working out cross word puzzles, playing chess, trying to remember your aunt's phone number, arguing about politics, or to just wishing you were somewhere else. Dreams on this definition are a form of consciousness, though of course they are in many respects quite different from waking consciousness" [15].

One of the most frequently cited definitions of consciousness is the one by Stuart Sutherland [14]: Consciousness – the having of perceptions, thoughts, and feelings; awareness. The term is impossible to define except in terms that are unintelligible without a grasp of what consciousness means. Many fall into the trap of equating consciousness with self-consciousness – to be conscious it is only necessary to be aware of the external world. Consciousness is a fascinating but elusive phenomenon: it is impossible to specify what it is, what it

does, or why it has evolved. Nothing worth reading has been written on it.

Thomas Nagel's [19] famous "*what it is like*" criterion aims to capture the subjective notion of being a conscious organism. According to Nagel, a being is conscious just if there is "something that it is like" to be that creature, i.e., some subjective way the world seems or appears from the creature's mental or experiential point of view. In Nagel's example, bats are conscious because there is something that it is like for a bat to experience its world through its echo-locatory senses, even though we humans from our human point of view cannot emphatically understand what such a mode of consciousness is like from the bat's own point of view [25]. Nagel argued that the purely objective study of an entity, such as the one science provides, does not allow any inference about the subjective character of being such an entity.

The qualitative aspect of the subjective sensations that characterise experience is often associated with so-called qualia. Philosophers use the term 'qualia' (singular 'quale') to refer to the introspectively accessible, phenomenal aspects of our mental lives [26]. The qualia of our experiences are what give each of them its characteristic "feel" and also what distinguish them from one another [27].

This is how Chalmers summarises the issue of the definition of consciousness [16]: "the really hard problem of consciousness is the problem of *experience*… If any problem qualifies as *the* problem of consciousness, it is this one. In this central sense of 'consciousness', an organism is conscious if there is something it is like to be that organism, and a mental state is conscious if there is something it is like to be in that state. Sometimes terms such as 'phenomenal consciousness' and 'qualia' are also used here, but I find it more natural to speak of 'conscious experience' or simply 'experience'".

What do all these definitions have in common? The fact that they are in the first person. Consciousness can only be defined by our subjective knowledge of it. According to Sutherland [14], it is "impossible to define except in terms that are unintelligible without a grasp of what consciousness means". As suggested by Chalmers [28], consciousness coincides with what we know first-hand or have experienced. From this point of view, it is obvious and accessible. At the same time, it is unknowable and undefinable in the third person. From this point of view, it is mysterious and inaccessible. The problem of consciousness is radically unlike any other scientific problem. One reason is that consciousness is unobservable. You can't look inside someone's head and see their feelings and experiences [29].

Within such a broad notion as consciousness it is of course possible to make distinctions. Edelman [30] distinguishes between primary consciousness, which concerns sensations, images and perceptual experiences in general, and higher-order consciousness, which includes self-consciousness and language. However, the main problem is the description of primary consciousness, because higher-order consciousness emerges from processes that are already conscious. Damasio [31] distinguishes between core consciousness, which corresponds to the transient process that is incessantly generated relative to any object with which an organism interacts, and during which a transient core self and transient sense of knowing are automatically generated, and extended consciousness, which requires the gradual build-up of an autobiographical self, a set of memories of the individual's unique past and expected experiences.

A fundamental distinction is the one between 'Phenomenal' Consciousness and 'Access' Consciousness [32,33]. As proposed by Block in his seminal 1995 article, phenomenal consciousness is experience; the phenomenally conscious aspect of a state is what it is like to be in that state. The mark of access-consciousness, by contrast, is availability for use in reasoning, reporting and enabling rational control of action [34]. It also refers to phenomena that are closely related to consciousness in other aspects (e.g. attention or meta-cognition) [35]. Some theories of consciousness claim to be about exactly Phenomenal Consciousness and thus carry a distinct explanatory pretence [36]. It is worth noting that many conceptions of consciousness do not address this fundamental aspect. For example, Freudian consciousness is to all intents and purposes an access consciousness, since it can be defined as *the part of mental life or psychic content that is immediately available to the ego* [37].

Neural Correlates of Consciousness (NCC)

During the last three decades, the advent and development of new scientific procedures, such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), have allowed neuroscientists to study the activity of the living brain. These methods have been extensively used to identify with an acceptable degree of accuracy the neural correlates of any aspect of mental activity [38].

Tracking the correlations between brain processes and states of phenomenal consciousness, such as feelings of pain, seeings of blue, hearings of trumpet sounds, is the basic method of scientific consciousness research [39]. Chalmers [40] has provided the most informative and influential definition of NCC, according to which neural correlates are minimally *sufficient* for consciousness [41]. The Neural Correlates of Consciousness (NCC) can be defined as the minimal set of neural events jointly sufficient for a specific conscious experience – given the appropriate enabling conditions [42]. In other words, if we would stimulate or generate these neural events, a particular conscious experience would happen [43].

Fink [44] identified two constraints in the definition of NCC, the mere-sufficiency-constraint and the minimality-constraint. There are good reasons to reject a "necessity-constraint". For otherwise, neither artificial experiencers, i.e., non-biotic conscious machines, nor silicon brain

prostheses, nor redundancy (we rule out *a priori* that the activation of *different* populations of neurons in a brain could bring about the *same* experience) or plasticity are possible. On the other hand, under the assumption that the brain is sufficient to give rise to any given conscious experience, we cannot count the whole activation of a brain as a neural correlate of an experience.

Methodological issues

To unravel NCC, a common scientific strategy is to compare perceptual conditions in which consciousness of a content is present with those in which it is absent, and to determine differences in measures of brain activity [43].
The neural mechanisms that are jointly sufficient for being conscious in a broad sense, irrespective of the particular contents of experience, are usually identified through state-based approaches. These involve contrasting brain activity when consciousness is present, typically in awake healthy participants performing no task, with brain activity when consciousness is severely diminished – for example, during dreamless sleep, general anaesthesia or disorders of consciousness such as coma and vegetative states. Their correlates are also called full NCC, as opposed to content-specific NCC [45].
The full NCC are the neural substrates supporting conscious experiences in their entirety, irrespective of their specific contents [41,45]. The content-specific NCC are the neuronal mechanisms, the activity of which determines a particular phenomenal distinction within an experience. For example, the NCC for experiencing the specific content of a face are the neurons that fire whenever a person observes, imagines or dreams a face, and are silent in other circumstances [36]. Paradigms looking for contents of consciousness survey conscious experiences through contrasting perceptual analysis (perceived vs. unperceived) and multiple psychophysical reporting paradigms. Examples include masked stimuli, high-contrast figures, binocular rivalry, flash suppression, motion-induced blindness and attentional paradigms, among others [46].
It is also important, both conceptually and empirically, to distinguish between the NCC and the background conditions for being conscious. These are the distal or proximal enabling factors that must be present for any conscious experience to occur, without contributing directly to its content – the heart must beat and supply the brain with oxygenated blood, various nuclei in the midbrain reticular formation and brainstem must be active, cholinergic release needs to occur within the cortico-thalamic complex and so on [45].
Furthermore, it is necessary to distinguish between the prerequisites for and the consequences of conscious perception [43]. When brain events are found to covary with conscious experience, these brain events can be the neural substrates of the experience, as is often suggested, but they can also be neural prerequisites or neural consequences of the experience [47]. At least part of the neural activity that co-varies with the perception of a particular conscious content reflects processes that precede or follow the experience – such as selective attention, expectation, self-monitoring, unconscious stimulus processing, task planning and reporting – rather than the experience itself [45].
For example, for binocular rivalry it was proposed more than a century ago and shown recently [48] that adaptation leading to weakening of reciprocal inhibition determines the alternations between competing stimuli. More precisely, neurons coding for the dominant stimulus adapt over time, which in turn weakens the inhibition of the suppressed stimulus, increasing its neuronal responses and thus bringing that stimulus into consciousness. Importantly, (reciprocal) inhibition could be seen as NCC-prerequisite, as it contributes to which target will be consciously perceived and is different between the two contrastive conditions. However, it is not part of the neural processes sufficient for generating or maintaining conscious experience of that target.
The existence of processes that are the consequences of conscious perception [47,49] is a logical consequence of assigning any function to conscious perception – if conscious perception enables certain processes that unconscious perception does not, these processes would inevitably appear in the contrast between trials with and without conscious perception, even if they are solely the consequences and not the direct correlates of consciousness. For example, it is known that neurons in the medial temporal lobe (MTL) respond in all-or-none fashion, closely following the subjective report of the patient [50]. However, damage to the MTL-system does not affect moment-to-moment conscious perception [51], but only the formation of a memory trace. That is, subjects will continue to have subjective experience but will have no memory of it.
Although experiences are private, we can usually infer that people are conscious if they are awake and act purposefully, in particular if they can report what they experience and if that report accords with what is experienced by others. In a clinical setting, simple behavioural criteria are often used to infer consciousness, such as the ability to respond to a command. In an experimental setting, the content of consciousness is typically evaluated by verbal report or by button-press by the participant in response to a yes or no question (such as “did you see a face?”).

Empirical evidence

Early evidence on the neural correlates of consciousness was summarised by Chalmers [40] (Tab. I), but only some of this evidence has been later confirmed. The literature on NCC, especially in terms of reviews, is not very extensive. In this area, the main contributions come from the work of Koch et al. [45]. With regard to subcortical structures, the cerebellum has four times more neurons than the

Table I. Early evidence on the neural correlates of consciousness [40].

• 40-Hz oscillations in the cerebral cortex [52]
• Intralaminar nuclei in the thalamus [53]
• Re-entrant loops in the thalamocortical systems [54]
• 40-Hz rhythmic activity in thalamocortical systems [55]
• Extended reticular-thalamic activation system [56]
• Neural assemblies bound by NMDA [57]
• Certain neurons in inferior temporal cortex [58]
• Visual processing in the ventral stream [59]
• Neurons in extrastriate visual cortex projecting to prefrontal areas [60]

cortex, is densely connected to the rest of the brain, receives mapped inputs from several modalities and is heavily involved in input and output control. Lesions of the cerebellum have little effect on consciousness and its contents, however [61].

By contrast, brainstem lesions typically cause immediate coma by damaging the reticular activating system and its associated neuromodulatory systems. However, neurological patients with a severely damaged cortex, but with relatively spared brainstem function, typically remain in a vegetative state. This suggests that brainstem activity is insufficient to sustain consciousness in a clinical sense. Rather, it is likely that the activity of heterogeneous neuronal populations within the brainstem, hypothalamus, and basal forebrain, which project diffusely to thalamic and cortical neurons and promote their depolarization, provides an important background condition for enabling consciousness by facilitating effective interactions among cortical areas [62]. Unilateral or bilateral lesions of the basal ganglia can produce akinetic mutism, an abulic, emotionless state associated with preserved tracking of visual stimuli that is difficult to evaluate with respect to experiential content [63].

The role of the thalamus in consciousness remains controversial. Small bilateral lesions in the intralaminar nuclei of the thalamus can lead to coma, and chronic thalamic electrical stimulation may promote recovery in some patients with disorders of consciousness. Although the so-called core neurons in primary thalamic nuclei have focused connectivity, several higher-order thalamic nuclei are rich in widely projecting matrix cells, which may facilitate interactions among distant cortical areas. Thus, some thalamic cells may represent critical enabling factors for consciousness [45,64,65].

Whether the primary visual cortex (V1) contributes to visual consciousness directly or whether it has only an indirect role is the subject of ongoing debate [60,66]. Several visual stimuli that are known to affect the activity of V1 neurons do not elicit a corresponding visual experience. Single-neuron recordings in monkeys, carried out during paradigms such as binocular rivalry, suggest that activity in most V1 neurons is linked to the identity of the physical stimulus rather than the percept. This contrasts with the activity of neurons higher up in the visual hierarchy, which correlates with the percept rather than the stimulus [67]. In a series of elegant experiments, Logothetis [68] recorded from a variety of visual cortical areas in the awake macaque monkey while the animal performed a binocular rivalry task. In primary visual cortex (V1), only a small fraction of cells weakly modulate their response as a function of the percept of the monkey. The majority of cells responded to one or the other retinal stimulus with little regard to what the animal perceived at the time. Conversely, in a high-level cortical area such as the inferior temporal (IT) cortex, almost all neurons responded only to the perceptually dominant stimulus, implying that the NCC involves activity in neurons in the inferior temporal cortex.

Lesions of V1 lead to the striking phenomenon of unconscious vision or blindsight, whereby the affected participants report not seeing an item but still perform above chance on forced-choice tasks. Their subjective blindness could be a result of the insufficient feedforward activation of higher visual areas, or to lack of feedback to V1, in which case V1 would be necessary for conscious vision [69]. Cortical neural responses to visual stimuli, such as natural scenes and faces, can occur quickly (within 120-140 ms) and presumably are mediated by a feedforward volley through the V1 into the extrastriate cortex and inferior temporal cortex. It has been suggested that a stimulus-evoked feedforward sweep only gives rise to a conscious percept when it is joined by a re-entrant sweep from the higher-level cortex coming back to the visual cortex [70].

Goodale and Milner [71] argue that humans possess two distinct visual systems. The ventral stream (also known as the “what pathway”) leads to the temporal lobe, which is involved with conscious, stable visual object identification and scene formation. The dorsal stream (or “where pathway”) leads to the parietal lobe, which is involved with the unconscious, moment-to-moment visual control of skilled actions [72]. However, it is still unclear whether the former is predominantly related to conscious and the latter to nonconscious visual perception as argued in the literature [73].

Conscious perception is believed to require more sustained, reverberatory neural activity, most likely via global feedback from frontal regions of neocortex back to sensory cortical areas [66] that builds up over time until it exceeds a critical threshold. At this point, the sustained neural activity rapidly propagates to parietal, prefrontal and anterior cingulate cortical regions, thalamus, claustrum and related structures that support short-term memory, multi-modality integration, planning, speech, and other processes intimately related to consciousness. This is the core hypothesis of the global workspace model of consciousness [74,75]. In brief, while rapid but transient neural activity in the thalamo-cortical system can mediate complex behaviour without conscious sensation, it is

surmised that consciousness requires sustained but well-organized neural activity dependent on long-range cortico-cortical feedback [76].
However, no-report paradigms suggest that frontal activation is more important for task preparation and execution than for conscious perception per se. More than a century of reports describing electrical brain stimulation carried out during neurosurgery suggest that it is difficult to directly elicit experiences from the stimulation of frontal sites, whereas it is easier to trigger specific experiences by stimulating the posterior cortex, such as the perception of faces or the feeling of wanting to move a limb. Most importantly, the commonly held view that the content of consciousness is linked to fronto-parietal activation ignores the ample evidence obtained from lesion studies that consciousness does not require an intact prefrontal cortex. For example, complete bilateral frontal lobectomy and large bilateral prefrontal resections do not impair consciousness [45].
Evidence across lesion, stimulation, and recording studies consistently point to regions in the "back" of the cortex, including temporal, parietal, and occipital areas, as a "posterior hot zone" that seems to play a direct role in specifying the contents of consciousness [77].
Regarding the neurophysiological markers of consciousness, hopes that gamma activity or synchrony, or the ERP P3b, could be signatures of consciousness have proved illusory. An activated EEG, one of the oldest electrophysiological indices of consciousness, is a better marker of consciousness than these measures, as long as it is taken into account that it is the local rather than global EEG activation that is important [45].

Consciousness theories

Several sophisticated models and theories have attempted to formalize how the brain implements consciousness using insights from philosophy, psychology, computer science, and neuroscience (Tab. II). These include two major and perhaps competing theories, the Integrated Information Theory (IIT) and the Global Neuronal Workspace (GNW) theory, which differ mainly in their level of conceptual abstraction and anatomical specificity [79].

The Global Neuronal Workspace model

Capitalizing on the earlier concept of a *blackboard system* in artificial intelligence (a common data structure shared and updated by many specialized modules), Baars [74] proposed a psychological model where the current conscious content is represented within a distinct mental space called *Global Workspace*, with the capacity to *broadcast* this information to a set of other processors. Baars [80] emphasized the stark contrast between the few contents available in consciousness at any given moment and the large number of unconscious processes. Metaphorically, focal consciousness acts as a bright spot directed by attention at different actors on the stage. This bright spot is surrounded by a fringe of events that are only vaguely conscious. The audience sitting in the dark receives the information transmitted by the bright spot. Behind the scenes, several systems contextualize the event.
The Global Neuronal Workspace (GNW) model [81] is a part of Bernard Baars's Global Workspace model [80]. It is a model according to which conscious access occurs when incoming information is made globally available to multiple brain systems through a network of neurons with long-range axons densely distributed in prefrontal, parieto-temporal, and cingulate cortices. Consciousness relates to the activity of a GNW that evolved to select and broadcast, in a brain-wide manner, a relevant piece of information, allowing it to be reported. The GNW hypothesis proposes that, in the conscious state, a non-linear network ignition associated with recurrent processing amplifies and sustains a neural representation, allowing the corresponding information to be globally accessed by local processors [82].
The GNW theory [83] was empirically derived from EEG and imaging studies in humans and primates. These studies have shown that when a stimulus is presented but not consciously perceived, activation can be seen mainly in the associated primary sensory cortices. When the stimulus is consciously perceived, however, activation in primary cortical areas is followed by a delayed 'neural ignition' in which a sustained wave of activity propagates across prefrontal and parietal association cortices [84]. Conscious access corresponds to the "ignition" of workspace neurons, distributed in prefrontal and other associative cortices, and which send top-down signals back to all processors [79].
According to the GNW theory, a subset of cortical pyramidal cells with long-range excitatory axons, particularly dense in prefrontal, cingulate, and parietal regions, together with the relevant thalamocortical loops, form a horizontal "neuronal workspace" inter-connecting the multiple specialized, automatic, and nonconscious processors. A conscious content is assumed to be encoded by the sustained activity of a fraction of GNW neurons, the rest being inhibited. Nonconscious stimuli can be quickly and efficiently processed along automatized or preinstructed processing routes before quickly decaying within a few seconds. By contrast, conscious stimuli would be distinguished by their lack of "encapsulation"in specialized processes and their flexible circulation to various processes of verbal report, evaluation, memory, planning, and intentional action, many seconds after their disappearance. This global availability of information is what we subjectively experience as a conscious state [85].

Integrated Information Theory

An origin of the Integrated Information Theory (IIT), first proposed by Tononi [86], can be traced back to the association between consciousness and complexity. Why should the simple distinction between light and dark performed by the human be associated with conscious experience, while the distinction performed by the photodiode is not? To the

photodiode, the distinction between darkness and light is the only one available, and is therefore only minimally informative. To a human, by contrast, an experience of complete darkness and an experience of complete light are selected out of an enormous repertoire. What makes a conscious state informative is the fact that its presence discriminates among billions of different situations, each of which could generate different behaviours [87]. High values of complexity correspond to an optimal combination of a high degree of functional specialization and functional integration. IIT does not address the hard problem from the brain and ask how it could give rise to experience; instead, it starts from the essential phenomenal properties of experience, or axioms, and infers postulates about the characteristics that are required of its physical substrate. The theory identifies five essential properties that are immediate, indubitable, and true of every conceivable experience, namely intrinsicality, composition, information, integration, and exclusion [88]:

- intrinsicality (existing for the subject of experience, from its own intrinsic perspective, independent of external observers);
- composition (being structured by phenomenal distinctions and their relations, e.g. blue/book);
- information (being the specific way it is, differing from other possible experiences);
- integration (every experience is unitary, meaning that it is composed of a set of phenomenal distinctions, bound together in various ways, that is irreducible to non-interdependent subsets, e.g. left and right side);
- exclusion (being definite – it contains what it contains, neither less nor more, e.g. less or more content) [21,89].

The physical substrate is intended as a system of connected units in a state, such as a set of active and inactive neurons in our brain. If every experience has the essential properties of being intrinsic, structured, specific, unified, and definite, its physical substrate must satisfy these properties in terms of cause-effect power. For something to exist in a physical sense, it must have cause-effect power – that is, it must be possible to make a difference to it (that is, change its state) and it must be able to make a difference to something.

- intrinsicality: a candidate substrate of consciousness must have cause-effect power upon itself, rather than just with respect to sensory inputs and motor outputs;
- composition: one must consider the structure of intrinsic cause-effect power – how various combinations of neurons can have causes and effects within the system (causal distinctions) and how these distinctions overlap causally (causal relations);
- information: the causes and effects specified by various combinations of neurons are specific states of specific subsets of neurons, yielding a specific cause-effect structure;
- integration: causal distinctions and relations, as well as the overall cause-effect structure they compose, only exist if they are irreducible – if they cannot be reduced to independent causes and effects;
- exclusion: causal distinctions and relations, as well as the cause-effect structure they compose, must be definite, containing what they contain – neither less nor more. What defines the set of neurons that constitute the physical substrate of consciousness – as opposed to any of its subsets or supersets – is being maximally irreducible, as measured by integrated information (Φ) [21,89].

Table II. Specific theories of consciousness [25].

• **Higher-order theories**. A mental state is conscious as long as it is related to a simultaneous and non-inferential higher-order state whose content is the one actually in the mental state
• **Reflexive theories**. Like higher-order theories, they imply a strong link between consciousness and self-awareness. They differ in that they locate the aspect of self-awareness directly within the conscious state itself rather than in a distinct meta-state directed at it
• **Representationalist theories**. Conscious mental states have no mental properties other than their representational properties
• **Narrative interpretative theories**. Consciousness is the result not of determinate facts, but of a larger context of interpretative judgments, finally emerging as a narrative process devoid of intrinsic reality (Dennett's Multiple Drafts Model)
• **Cognitive theories**. Consciousness is associated with a distinct cognitive architecture or with a special pattern of cognitive activities. GNWT Theory describes consciousness as a competition among processors for a limited capacity resource that broadcasts information, which is conscious as long as it is available to the global workspace [80,81,83]
• **Information Integration Theory (IIT)**. Consciousness is essentially defined by the integration of information; this integration is necessary and sufficient for consciousness, regardless of the substrate in which it is realized [86,89]
• **Neural theories**. Neural theories of consciousness come in many forms, though most in some way concern the so called "neural correlates of consciousness" or NCCs. Unless one is a dualist or other non-physicalist, more than mere correlation is required; at least some NCCs must be the essential substrates of consciousness [52,54,55]
• **Quantum theories**. The natural locus of consciousness is placed beyond the neural, at the micro-physical level of quantum phenomena [78]
• **Non-physical theories**. Consciousness is described as a non-physical aspect of reality, i.e. something that cannot be reduced to the natural/physical world (e.g. panpsychism) [16]

On this basis, the Integrated Information Theory proposes an identity between a particular experience and the particular cause-effect structure specified by a physical substrate in its current state. The proposed correspondence is with the cause-effect structure unfolded from a neural substrate, not with the substrate as such. The goal is to account in physical terms for experience as such – the causal distinctions and relations that compose it – rather than merely for how the brain represents and performs functions. The fundamental identity of IIT states that the quality or content of consciousness is identical to the form of the cause-effect structure, and the quantity or level of consciousness corresponds to its irreducibility. A crucial advantage of the IIT is that it provides a mathematical metric of irreducibility (or integration), Φ, that can be related to the level of consciousness [88].

An index of the level of consciousness is the Perturbational Complexity Index (PCI). PCI measures the complexity of electroencephalographic (EEG) responses to transcranial magnetic stimulation. It is calculated by perturbing the cortex with transcranial magnetic stimulation (TMS) to engage distributed interactions in the brain (integration) and compressing the spatiotemporal pattern of these electrocortical responses to measure their algorithmic complexity (information) [90]. The perturbational complexity index showed a remarkable sensitivity in detecting minimal signs of consciousness in severely brain-injured patients [91].

Discussion and conclusions

When correlations are found between neural events and conscious experiences, we must consider all the following possibilities [92]:

- neural events cause conscious experiences;
- conscious experiences cause neural events;
- something else causes both of them;
- neural events are conscious experiences;
- we have so misconstrued one or the other that none of these is true.

With respect to these possibilities, positions may differ. The most straightforward approach is to try to explain the correlations in causal terms: NCC are the causes of the states of consciousness. To "go from correlation to causation" is a move typical of the sciences and it might seem intuitively appealing to treat brain states as the causal sources of states of consciousness. Still, this explanatory strategy is deeply problematic. A neurophysiological process *causes* a phenomenal state of consciousness; therefore, it is *different* from that state, because causes and effects are always distinct. However, materialist principles dictate that every conscious state must be implemented materially. Since the conscious state is different from the neurophysiological processes that are causing it, it must, on pain of dualism, be implemented by a material process distinct from its neural cause. Thus we end up with *two* material processes involved in the production of the conscious mental state, not one [39]. Francis Crick, one of the initiators of the search for the neural correlates of consciousness, emphasized that he used the word "correlate" as an ontologically *neutral* term [52]. Gallotto et al. [93] affirm that the neural substrates of experience "are directly *causing*, or are *identical with*, the phenomenal conscious experience".

The GNW model is a dynamical global network approaches and therefore non-localist in principle [85]. The network is relevant; the nodes alone are not. GNW is often misunderstood as a fixed architecture encompassing the fronto-parietal cortices. In actuality, it comprises dynamic neural contributions that define this hypothetical global network. The only anatomical constraint is that relevant regions should be connected by long axons of pyramidal neurons [36]. However, perhaps the most significant problem is that these studies primarily aim to identify which particular neural circuits are involved in consciousness, but not how and why exactly such neural mechanisms would produce subjective experience [24].

With regard to the two theories discussed in this review, it is unclear whether the GNW theory actually addresses the hard problem of consciousness. Even if the authors underscore that the global availability of information is what we subjectively experience as a conscious state [85], the GNW theory is essentially an Access Consciousness theory. As such, it would not account for phenomenal consciousness. However, Naccache [34] tries to show how a strict Access Consciousness theory can account for our conscious experience. In the global workspace, subjective reports are not conceived as the mere passive broadcasting of information, but as resulting from a dynamic and active chain of internal processes that include interpretative and belief attribution stages.

An attempt to explain the quality of experience is exemplified by IIT. IIT tries to identify the mechanisms behind the phenomenal character of experience, i.e. the quality of its content. In that vein, it poses that the quality of consciousness is in one-to-one correspondence with the geometry, concepts and relations encapsulated by the Maximally Irreducible Conceptual Structures [88]. IIT predicts that the contents of consciousness are entirely specified by the internal workings of elementary mechanisms of the main complex. Notably though, IIT's agenda to target quality is still in its nascent stages and has not gone beyond trying to explain the spatiality of experience yet [36].

The problem lies not only in the identity between the form of a cause-effect structure and the quality of the experience [94,95]. Indeed, we must consider whether the properties identified by IIT can account for the quality of experience. Can we say that intrinsicality, composition, information, integration, and exclusion provide a comprehensive description of phenomenal experience as an explanandum? Although Haun and Tononi [88] state that these five essential properties are immediate, indubitable, and true of every conceivable experience, whether the

current set of five axioms are truly valid, complete and independent remains open [21].

In conclusion, one may say that the major difficulty in understanding consciousness consists in what Levine [96] called the *explanatory gap*, i.e., the metaphysical gap between physical phenomena and phenomenal experience. The explanatory gap consists in the fact that, no matter how deeply we explore the structures of neurons and the chemical transactions that take place when they fire, there will always be something we cannot explain, in particular how and why these physical and objective changes – of whatever nature they may be – generate these subjective sensations, or any kind of subjective sensation. Whereas a basic robot can unconsciously detect conditions such as colour, temperature or sound, consciousness describes the qualitative feeling that is associated with those perceptions, together with the deeper processes of reflection, communication and thought [4]. One thing is to provide neurological distinctions between qualia – to say that one group of neurons is activated by blue, another by salt, another by pain – but quite another to explain how blueness *as you or I experience it* comes out of what our brains are doing [97]. Bridging this gap is known as the hard problem of consciousness [98].

To date, consciousness remains the biggest mystery of the mind and one of the major unresolved questions in science. "After decades of concerted effort on the part of neuroscientists, psychologists, and philosophers, only one proposition about how the brain makes us conscious – how it gives rise to sensation, feeling, subjectivity – has emerged unchallenged: we don't have a clue. Even enthusiasts for the new neuroscience of consciousness admit that at present no one has any plausible explanation as to how experience arises from the action of the brain. Despite all the technology and the animal experimentation, we are no closer now to grasping the neural basis of experience than we were a hundred years ago" [99].

However, our knowledge is advancing. The interest in consciousness, which started at the end of the 1980s, has progressively increased, while the number of publications on the subject has been multiplying in recent years [100]. Consequently, we can be optimistic that the mystery around consciousness may at least partially dissipate in the coming decades.

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