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A review of the sufficient conditions for consciousness

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ABSTRACT

The neuroscience of consciousness has set out to find the sufficient conditions for subjective experience. Theoretical and empirical endeavours have placed a particular focus on the cortex and subcortex, whilst discounting the cerebellum. However, when looking at neuroimaging research, it becomes clear there is substantial evidence that cerebellar, cortical, and subcortical functions are correlated with consciousness. Neurostimulation evidence suggests that alterations in both the cortex and the cerebellum may provoke alterations in experience, however experimental stimulation of the subcortex may abolish, as well as induce, behavioural evidence of experience. Similarly, neuropsychological evidence shows that abnormalities in the cortex, subcortex and cerebellum may provoke changes in experience; but only damage to the oldest regions seems to completely obliterate experience. Finally, I review congenital and experimental decorticate cases and find that behavioural evidence of experience is compatible with the absence of the cortex. The evidence, taken together, indicates that the subcortex is sufficient for behaviours that suggest basic experiences. Based on the findings of this review, I emphasise both the importance of the individual's developmental trajectory and the interdependencies between different neural systems (e.g., cortex, subcortex and cerebellum) in neurologically typical individuals.

1. Paradigms underlying the current science of consciousness

Consciousness is often defined as qualitative subjective experience (Chalmers, 1995; Dennet, 1991; Tononi et al., 2016; Klein and Barron, 2016; Koch et al., 2016). The concept refers to "what it is like" to be a specific organism in a specific state (Nagel, 1974). This definition is based on a similitude, and is testament of the fact that the objective evaluation of qualitative subjectivity is problematic. Nonetheless, the evaluation of the presence of experience is an imperative in clinical settings, such as when assessing the depth of anaesthesia (Sanders et al., 2012), or diagnosing disorders of consciousness (DOC e.g., minimally conscious state and unresponsive wakefulness syndrome/vegetative state) (Edlow et al., 2021; World Health Organization, 2019). In clinical settings, consciousness is operationally evaluated via observable behaviours of varying degrees of complexity such as movement (automatic, purposeful, functional), verbalisation (intelligent or non; reporting), visual function (startle vs pursuit) (Edlow et al., 2021; World Health Organization, 2019; Giacino et al., 2004; Laureys et al., 2007), sometimes called the behavioural correlates of consciousness (Koch et al., 2016). Although such behaviours may imply the presence of experience, they may not do so infallibly (Russell, 2013) (e.g., blindsight, automatism in complex partial seizures). Similarity, absence of behaviour does not imply absence of consciousness (e.g., locked in syndrome/cognitive motor dissociation; catatonia; language deficits in understanding instructions during assessment etc.,) (Sanders et al., 2012; Laureys et al., 2007; Fu et al., 2021; Owen and Coleman, 2008; Posner et al., 2013). In fact, such difficulties are highlighted by the high rate of misdiagnosis of disorders of consciousness (Cortese et al., 2015; Wannez et al., 2017; Schnakers et al., 2009; Bodien et al., 2024) and intraoperative awareness (Odor et al., 2021) in anaesthesia.

Partly due to its subjective and private nature, just more than 35 years ago, it "was heresy to mention consciousness and neuroscience within the same breath" (Panksepp et al., 2007). Yet, now there are numerous yearly publications on the neuroscience of consciousness. Such investigations were inaugurated in 1990, when Francis Crick and Christof Koch proposed that at any one moment there will be some neuronal processes that will be associated with consciousness, whilst other processes will not be; "What are the differences between them?" (Crick and Koch, 1990). This led to the search for the neural correlates of consciousness (NCC) which are the "minimum neural mechanisms jointly sufficient for any one specific experience" (Koch et al., 2016; Crick and Koch, 2003; Chalmers, 2000). In 2016, Koch and colleagues

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further differentiate between the content-specific and full NCCs (Koch et al., 2016). The content-specific NCCs are the neuronal processes that determine a specific phenomenological distinction (e.g., a smiling face of a friend). The full NCC, on the other hand, refers to the union of all content-specific NCC for all possible contents of experience. This is much more complex, as would include many different contrasting brain states (e.g., dreaming vs awake) and even anatomical configurations (infant vs mature brains, before or after physical trauma). They propose that contrasting brain activity between conscious and non-conscious individuals (e.g., in unresponsive wakefulness syndrome) and perceptions (e.g., subliminal vs reportable) will yield an identification of the full and content-specific neural correlates of consciousness respectively.

In light of this paradigm, technological advancements have allowed a large number of sophisticated studies (Lenharo, 2023), and large collaborations have endeavoured to test theories that focus on higher-order cortical regions (Melloni et al., 2021). However, despite extensive work in the past 30 years, recently Christof Koch has recently conceded that the neural correlates of consciousness have not been elucidated (Lenharo, 2023). Thus, a renewed evaluation of which neuronal systems might be minimally sufficient for consciousness may provide important constraints for theoretical, clinical and experimental endeavours (Solms, 2021, 2013; Merker, 2007). This paper critically synthesises a substantial body of experimental and neurological evidence, including findings that have not yet been explored within this field.

The aim of this review is to explore the *minimum requirements for any experience. That is, the neural mechanisms that are sufficient for generating consciousness.* In this review, if an organism has behavioural evidence of any sort of experience, they are considered likely conscious (Koch et al., 2016; Birch et al., 2020; Tasserie et al., 2022). Consciousness may thus include complex experiences ("higher order" e.g., narrative self-representation in relation to the past and future) as well as relatively simple experiences (e.g., primary affects such as fear) (Edelman, 2001; Edelman et al., 2011; Panksepp and Watt, 2011). Thus, of concern is phenomenal consciousness ("what it is like to be"). Although the relationship between access consciousness and phenomenal consciousness is still debated (Overgaard, 2018), access consciousness is here considered relevant in as much as it is related to phenomenal experience (e.g., in reporting). In the present article, awareness relates to the contents of consciousness ("what" is experienced) (Laureys, 2005). The "level of consciousness (i.e., wakefulness or arousal)" is often represented as independent and dissociable from awareness (Hudetz, 2024). Its definition and precise operationalisation is also complex (Hudetz, 2024; Bayne et al., 2016). However, given that a high "level of consciousness" (wakefulness) can occur without subjective experience (e.g., vegetative state and absence seizures) (Laureys, 2005), this conception is not a focus of this article; but will be briefly discussed at the end of the article in light of the evidence presented.

For the purposes of this review, I ask **what are the neuroanatomical structures that are sufficient in generating subjective experience**. Even more simply, I ask whether the cortex, subcortex and/or cerebellum *are sufficient for generating consciousness (evaluated via behaviours that are indicative of experience)*. Of course, although rendering the question tractable, such a heuristic formulation may be fundamentally ill posed, something which will be discussed at the end of this review. Nonetheless, the conclusions of this review provide principled future directions towards a neuroscientific understanding of consciousness.

Many theorists and researchers believe that frontal and/or posterior midline regions of the cortex (Tononi et al., 2016; Koch et al., 2016; Boly et al., 2017; Lau and Rosenthal, 2011; Brown et al., 2019; Seth and Bayne, 2022) are important for consciousness. Specifically, modern discussions tend to focus on whether the NCCs are in the "front or the back of the brain" (Koch et al., 2016; Melloni et al., 2021; Boly et al., 2017; Lau and Rosenthal, 2011; Pennartz et al., 2019; Odegaard et al., 2017). Conversely, the cerebellum is often thought to contribute nothing directly to experience (Tononi et al., 2016; Koch et al., 2016; Crick and Koch, 1990; Baars, 2005; Alkire et al., 2008; Golkowski et al., 2019). Furthermore, other theories (Solms, 2013; Damasio, 1998; Parvizi and Damasio, 2001; Damasio and Damasio, 2022) propose that phylogenically older subcortical structures engender experience. In this review, I evaluate these statements with the available empirical evidence.

2. Functional neuroimaging evidence of the conditions for consciousness

In neuroimaging research, there are a considerable number of studies focusing exclusively on the cortex (Demertzi et al., 2019; Achard et al., 2012; Tagliazucchi et al., 2013; Dupont et al., 2018; Barttfeld et al., 2015; Naci et al., 2017; Deng et al., 2020; Cavanna et al., 2018; Bastos et al., 2021; Huang et al., 2020, 2018; Varley et al., 2021; Hutchison et al., 2014). These have been successful in showing differences in functional neuroimaging signals (e.g., electroencephalography, blood oxygenation level dependent (BOLD) signal) between unconscious and conscious individuals. Similarly to theory (Koch et al., 2016; Melloni et al., 2021; Boly et al., 2017; Pennartz et al., 2019; Odegaard et al., 2017), studies implicate both frontal and posterior regions (Naci et al., 2017; Huang et al., 2020; Guldenmund et al., 2012; Vatansever et al., 2017; Di Perri et al., 2016; Mashour et al., 2021; Luppi et al., 2019) (see Fig. 1), thus not leading to univocal conclusions as to whether the front or the back of the cortex is essential to consciousness. The cerebellum, conversely, is mostly discounted when it comes to the neuroscience of consciousness (Tononi et al., 2016; Koch et al., 2016; Crick and Koch, 1990; Baars, 2005; Alkire et al., 2008; Golkowski et al., 2019). However, when investigated, the cerebellum is repeatedly found across static and dynamic fMRI results (Golkowski et al., 2019; Di Perri et al., 2016; Luppi et al., 2019; Coppola et al., 2022a, 2022b; Demertzi et al., 2015; Vanhaudenhuyse et al., 2010; Guldenmund et al., 2013; Boveroux et al., 2010; Monti et al., 2013; Amico et al., 2014) (Fig. 1). In this research, the cerebellum is rarely discussed and often relegated to the supplementary materials. This evidence suggests that, just like the cortex, the cerebellum's functionality is related to consciousness as it paradigmatically (Koch et al., 2016) emerges from a contrast between consciousness and unconsciousness.

There are also several studies suggesting that subcortical structures display functions that are correlated to consciousness (Guldenmund et al., 2013, 2017; Gili et al., 2013; Tsurugizawa and Yoshimaru, 2021; Crone et al., 2014; Stamatakis et al., 2010; Arthuis et al., 2009; Mhuircheartaigh et al., 2010; Spindler et al., 2021). In particular the thalamus (Gili et al., 2013; Tsurugizawa and Yoshimaru, 2021; Crone et al., 2014; Guldenmund et al., 2017; Stamatakis et al., 2010; Arthuis et al., 2009) and the brainstem (Guldenmund et al., 2013; Gili et al., 2013; Spindler et al., 2021) are found to be different in consciousness versus unconsciousness. Thus, similarly to the cortex and cerebellum, there is evidence indicating subcortical regions are correlated to the emergence of consciousness.

Thus, neuroimaging evidence suggests that the cortex, subcortex and cerebellum all display activity that is correlated with consciousness. In view of this, it is possible (1) that the cortex, subcortex and cerebellum are jointly sufficient for the emergence of consciousness. Alternatively (2), some of these neuroimaging results may be explained as downstream effects of other disrupted processes. For example, posterior midline regions are amongst the most complex, interconnected and energy consuming regions of the brain (Smallwood et al., 2021). Hence, the posterior medial cortex may be reliably affected by any interruption of other processes on which it depends (e.g., metabolic, information processing, neuromodulation etc.,). In this case, it would be consistently found as a correlate of consciousness, although potentially being only tangentially related to consciousness itself. Further still (3), it is likely that many neural and cognitive processes are correlated with (or at least modulated by) consciousness. Therefore, the effects observed may be related to functional consequences of consciousness (e.g., decision

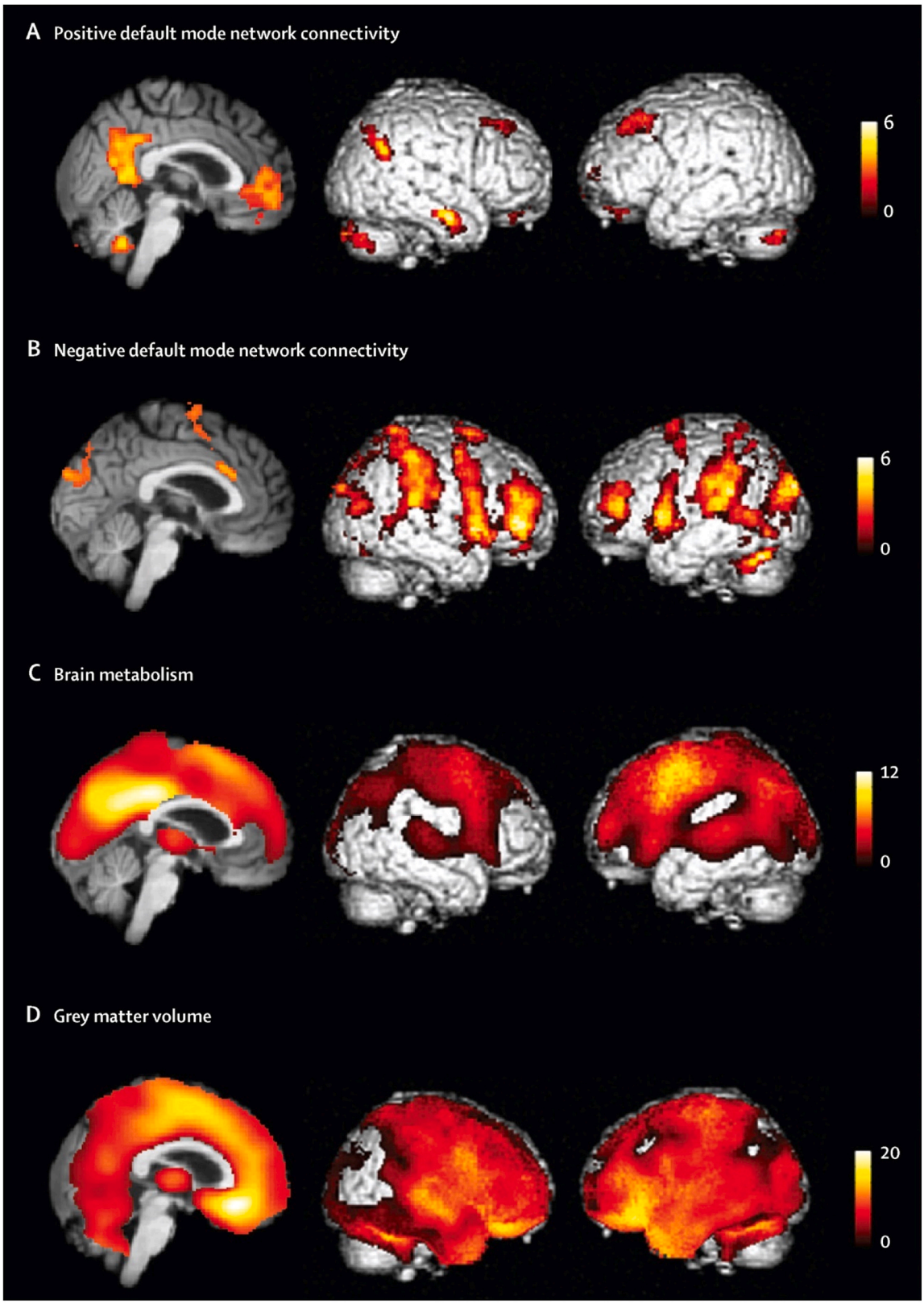

Fig. 1. In vivo brain measures that scale with levels of awareness. A) positive region of interest (prefrontal and posterior cingulate) functional connectivity. B) negative functional connectivity from the same regions. Note cerebellar involvement in A and B. C) Brain metabolism as measured by ^{18}F-fluorodeoxyglucose PET (note posterior midline region's intensity). D) Grey matter volume as measured by voxel-based morphometry (note frontal region's intensity). Colour bars indicate T-values as a function of scaling with presumed levels of awareness (controls> recovering/emergent minimally conscious state> minimally conscious state> unresponsive wakefulness syndrome). Note difference between C and D in posterior and frontal regions. Reproduced with permission from lancet neurology, Di Perri and colleagues (Di Perri et al., 2016).

making, report, prospective thought, mind wandering etc.,) rather than consciousness (i.e., experience) itself (Block, 2019). Many of such functional processes are related to the cortex; but are also found to be related to cerebellar function (Keren Happuch et al., 2014; Stoodley and Schmahmann, 2009; Gatti et al., 2021; Adamaszek et al., 2017; Baumann et al., 2015; Mariën et al., 2014).

Functional neuroimaging studies can show robust changes following causal manipulations of consciousness (e.g., anaesthesia). These analyses reveal that cortical, subcortical and cerebellar activity can be related to various aspects of consciousness (Birch et al., 2020; Bayne et al., 2016). However, conscious perception can also be associated with different attentional and cognitive processes (Block, 2019; Duman et al., 2022; Tsuchiya et al., 2015). Furthermore, changes in background (Koch et al., 2016) or prerequisite (Aru et al., 2012) conditions for consciousness (e.g., neuromodulatory Spindler et al., 2021; Sukhotinsky et al., 2016) may have various distal effects. Thus, it is challenging to disentangle to what extent neuroimaging effects may relate to the full NCCs (Koch et al., 2016), functional consequences of consciousness (Block, 2019; Aru et al., 2012), changes in "background conditions" for consciousness (Koch et al., 2016; Chalmers, 2000) or minimally sufficient conditions for consciousness. A review of neurostimulation and neurological evidence may offer further insights.

3. Neurostimulation studies

Experimental manipulations of neuronal activity in humans and animal models may provide insights into the mechanistic processes that generate subjective experience. There are many such reports over the last 80 years with variations in procedures and methodology (Selimbeyoglu and Parvizi, 2010).

In regards to the "back of the brain" (Boly et al., 2017), alterations of the function of posterior midline cortical regions via intracranial electrical stimulation could induce notable changes in the sense of self (e.g., perception of several entities within himself, in the patient's words "the system I know as 'myself' leaves my body") (Parvizi et al., 2021). Such experiences were reproduced in other patients (Lyu et al., 2023). The authors do not speak of alterations to consciousness, but rather of the sense of self. A complex and coherent sense of self is a prominent aspect of human consciousness in neurologically typical individuals, but nonetheless not necessarily equivalent to subjective experience per se'. In another study (Herbet et al., 2014), stimulating the white matter bundle connecting the thalami to the posterior cingulate cortex caused the surgical patient to stop responding. They consistently reported (upon reacquiring behavioural responsiveness) that they were "in a dream". Such a stimulation unequivocally produced an alteration in consciousness, described by the authors as a disruption of awareness of the external environment. However, subjective reports indicate that subjective experience was preserved (albeit, highly abnormal).

Conversely to the "back of the brain" (Boly et al., 2017), transcranial magnetic stimulation to the bilateral dorsolateral prefrontal cortex (Rounis et al., 2010) reduced the ability of participants to evaluate their performance on a forced choice task (although this was still above chance). However, TMS did not affect stimulus classification performance, suggesting these individuals could still perceive stimuli. Thus, it seemed that alteration to the dorsal lateral prefrontal cortex affected only a part of awareness ("meta-cognitive"). Nonetheless, stimulation of the dorsal lateral prefrontal cortex in disorders of consciousness reportedly produced some improvement in behavioural correlates of consciousness (Edlow et al., 2021; Xu et al., 2021a; Xia et al., 2018; Bourdillon et al., 2019), although such effects did not equivalate to a cure and tended to work in less severe forms of disorders of consciousness. A study (Pal et al., 2018) on anaesthetised rats showed that cholinergic and noradrenergic stimulation of the prefrontal and parietal cortexes produced electroencephalogram signals similar to those in wakefulness. However, only cholinergic stimulation of the prefrontal cortex could induce behavioural evidence of consciousness (Pal et al., 2018) as well as modulate sleep-wake cycles (Parkar et al., 2020). Optogenetic stimulation (Mao et al., 2024) in prefrontal and parietal regions in mice provoked awakening from sleep. Following GABAergic stimulation of a mesopontine tegmental brainstem area, unresponsiveness could be reversed via stimulation of such regions. However, this was not the case following systemically administered anaesthesia (Mao et al., 2024).

Importantly, a review of subjective reports during intracranial stimulation of the cortex (Raccah et al., 2021) ($n = 1537$ stimulations in 67 patients) suggests that subjective changes due to stimulation of the prefrontal cortex and the posterior medial cortex are rare. Conversely, it is relatively easy to evoke subjective reports of altered experience in unimodal sensory systems. This is rather surprising, given the integratory nature of higher-order regions and the theoretical proposals that integration is fundamental to consciousness (Tononi et al., 2016; Baars, 2005). However, subjective effects from transmodal cortical stimulation, when present, tended to be more complex.

Of interest is that modification of the cerebellum activity via TMS seemed to have a bearing on content-specific awareness, such as short-term memory of visual sequences (Ferrari et al., 2018), motion discrimination (Cattaneo et al., 2014), emotional perception (Ferrari et al., 2019). A meta-analysis of 44 studies suggests medium effect size on perception accuracy (Gatti et al., 2021). This may suggest that the cerebellum does have a causal role in reportable perception (~content-specific experience) in neurologically typical individuals. Furthermore, similarly to prefrontal stimulation, transcranial direct stimulation of the cerebellum produced improvements in behavioural and neural markers in minimally conscious patients (Naro et al., 2016).

Compared to cortical and cerebellar stimulation, modulation of subcortical activity produces rather extreme behavioural and experiential changes (Panksepp, 2011). Examples may include the induction of major depression by stimulation of the left substantia nigra in an adult human (Bejjani et al., 1999), intense desire arising out of direct stimulation of the nucleus accumbens (Linden, 2011; Berridge and Kringelbach, 2015) and complex negative emotions through stimulation of the hypothalamus (Parvizi et al., 2022). Modern reports suggests that stimulation of the amygdala only gave rare (although extreme) emotional responses (Inman et al., 2020, 2018), whilst a review of older studies suggest substantial emotional responses do arise (Selimbeyoglu and Parvizi, 2010). In treatment of disorders of consciousness, stimulation of the thalamus is associated with improved outcomes for DOC patients (Schiff et al., 2007; Monti et al., 2016; Cain et al., 2022, 2021). Three independent studies (Tasserie et al., 2022; Bastos et al., 2021; Redinbaugh et al., 2020) found that direct stimulation of the thalamus in anaesthetised unconscious non-human primates induced behavioural signs of wakefulness (e.g., movement, eye-pursuit). Conversely, abnormally low or high frequency stimulation of the thalamus produced absence epilepsy-like signs in primates (Redinbaugh et al., 2022). Whilst stimulation of the thalamus could cause rats to awaken from sleep, particularly low frequency stimulation would induce a similar seizure-like state of unresponsiveness (Liu et al., 2015). Such a phenomenon has also been reported in humans when reticular and thalamic structures were simultaneously stimulated (Velasco et al., 1996).

In a classic study, stimulation of the "reticular activating system" (pontine and tegmental areas), produced wakeful-like widespread cortical activation in anesthetised cats (Moruzzi and Magoun, 1949). Simultaneous stimulation of the thalamic central lateral nucleus and the pontine nucleus oralis induced both cortical and behavioural markers of wakefulness during experimentally induced epileptic seizures, during anaesthesia and natural sleep (Kundishora et al., 2017). Furthermore, modern studies in rodents show that stimulation of different brainstem regions can markedly affect consciousness. Activation of the medial parabrachial nucleus could provoke continuous wakefulness in rats, whilst inhibition of this region would decrease wakefulness (Xu et al., 2021b). Similarly, optogenetic activation of the dorsal raphe nucleus could induce wakefulness and decease the time spent in sleep (Wang

et al., 2024). Stimulation of dorsal raphe 5-HT neurons could also facilitate recovery from general anaesthesia (Li et al., 2021) and induce behavioural activation from sleep (Moriya et al., 2021). Activation and lesioning of different types of neurons in the ventral tegmental area could produce a profound sedation-like state, continuous wakefulness (Yu et al., 2019) and modulate induction and emergence time from anaesthesia (Yin et al., 2019). Ultrasound stimulation of this regions could also precipitate emergence from anaesthesia and recovery from traumatic brain injury symptoms (Bian et al., 2021). Devor and colleagues' (Sukhotinsky et al., 2016) identified a mesopontine tegmental region in which minute quantities of bilaterally injected GABAergic anaesthetics induce a state resembling general anaesthesia or coma. Damage to this region does not produce unresponsiveness, but substantially reduces the animal's susceptibility to systemically administered anaesthetics. These rather strong effects of brainstem stimulation are perhaps not surprising, as the brainstem has long been considered "a background condition" for consciousness; that is, *necessary, but not sufficient (*Koch et al., 2016; Crick and Koch, 1990).

The claustrum has also been a point of interest in the neuroscience of consciousness (Koch et al., 2016). High intensity stimulation of a small fibre bundle between the anterior insula and the claustrum provoked amnesia and disruption of volitional behaviour in one human patient with resected amygdala (although some motor response was still present) (Koubeissi et al., 2014). Analogously, following extended stimulation of the claustrum, there seemed to be behavioural inactivation and reduced awareness of the external environment in five out of eight cats (Gabor and Peele, 1964). However, there are also reports of a patient with this region completely destroyed who displays strong signs of subjective experience (Damasio et al., 2013). Furthermore, a study in a military veteran cohort shows that claustrum injuries are associated with duration (but not frequency) of loss of consciousness (Chau et al., 2015). A possible explanation of this inconsistency is considered at the end of this review in conjunction with the other evidence reviewed below.

Of interest here is that evidence suggests that various cortical markers associated with consciousness can occur without behavioural evidence of consciousness (Pal et al., 2018; Mao et al., 2024; Boly et al., 2008) and vice versa, that behaviours suggesting experience can occur without such cortical features (Whyte et al., 2024; Qiu et al., 2015; Frohlich et al., 2021). Either way, these neurostimulation studies suggest that changes in function in different parts of the brain (cortex, subcortex and cerebellum) can be causally related to changes in subjective experience. One among several issues with such data (e.g., frequency, type and duration of stimulation), is that any subjective effect elicited may be ascribed to changes to other components of a larger network (Selimbeyoglu and Parvizi, 2010; Fox et al., 2020). However, modulation of activity in different parts of the brain seem to change experience in different ways and to different extents (or in some cases even induce it). This evidence may suggest a primary role for older subcortical structures of the brain, given the relatively powerful and consistent effects stimulations in such regions can have. To further explore which regions may be important for experience to arise, I investigate cases of acquired and congenital brain abnormalities.

4. Neurological studies

4.1. Neurological studies of the cortex

Evaluations of changes in consciousness after acquired brain damage may provide strong evidence as to what is required for consciousness. Similarly, although of complex interpretation, the presence of experience given congenital abnormalities may provide clues as to what structures are mechanistically fundamental to experience.

There is a report (Kumral et al., 2021) of 11 patients with unilateral ischemic damage to the precuneus exclusively. Of interest here, alterations to "normal" consciousness were reported, including confusion, inability to recognise themselves, loss of sense of agency, impairment in autobiographical memory, body awareness disorders (e.g., alien hand, fading limb) and hemispatial neglect. Thus, damage to this highly connected and complex region may produce severe alterations in consciousness. There are also reports of bilateral damage to the parietal lobe. In the resulting syndrome, patients can be aware of one specific aspect or parts of a scene, but struggle to have a global visual awareness and display mnemonic deficits (Berryhill et al., 2007). Damage to these regions did not seem to abolish experience, but alter it.

There are, conversely, several studies on frontal lobe damage. A study (Del Cul et al., 2009), utilising patients with frontal lobe damage ($n = 15$) and a masking paradigm (disrupting stimulus presentation), found that these individuals had higher thresholds than controls in being able to detect the target stimuli. The patients could still detect stimuli suggesting content specific conditions of consciousness were not eliminated. Of recent interest has been an old report of a human that had his bilateral frontal lobes removed (Brickner, 1952). Despite this, the patient could still display emotionally laden complex behaviours that were recognisable to people who knew him. Again, even with reports of severe cognitive impairment after "the complete obliteration" of the frontal lobes, consciousness seemed to be preserved. However, although cited by some neuroscientists of consciousness as evidence that the frontal lobe is not necessary to consciousness (Koch et al., 2016; Boly et al., 2017), others (Boly et al., 2017; Odegaard et al., 2017) suggest that the prefrontal cortex was not completely removed in this case. Another more modern patient report with accompanying video (https://www.jneurosci.org/content/37/40/9593/tab-figures-data) shows a clinician investigating the autonomic reflexes of a patient with bilateral dorsal prefrontal damage (Odegaard et al., 2017). There is a noticeable impairment in normal cognition and perhaps extreme disconnectedness from the external environment. The authors state that this patient shows impaired meaningful and wilful behaviour taking this as evidence of impaired subjective experience. However, of importance is that in this short video the patient did follow more than one command, which, would conservatively indicate a minimally conscious state diagnosis rather than a diagnosis indicating complete unawareness (The Multi-Society Task Force, 1994). In fact, such bilateral frontal damage is clinically associated with abulia ("lack of will") (Posner et al., 2013) which may be a better description of this individual's subjective experience. The syndrome of this patient may be reminiscent of frontal lobotomy treatments (Koch et al., 2016; Solms, 2000), which despite altering patients substantially, seemingly did not affect the capacity to "have" experiences. Nonetheless, there is a report of a case with bilateral extensive frontal lobe agenesis in an 8-year-old child. Despite near complete absence of frontal lobes and impairment in abstraction and attention, the child showed relatively normal emotional processing, language and memory (Fig. 2, links to video footage in caption). Similarly, Solms (2021) reports a 13-year-old patient in which a burst aneurysm, chronic brain infection and multiple surgical operations led to the "total destruction of the prefrontal lobes on both sides". This patient could verbally report regarding their experience and would show signs of humour. This evidence suggests that the frontal cortex is not necessary for there to be any type of experience (analogously to cerebellar agenesis below). Similarly to the frontal, parietal cortex and anterior cingulate cortex (Solms, 2021), destruction of large portions of the temporal lobe (claustrum and insula (Damasio and Carvalho, 2013), and hippocampus (Wilson and Wearing, 1995)) did not seem to abolish experience. However, damage to the parieto-temporo-occipital junction or the white matter surrounding the frontal horns can cause cessation or near cessation of reportable dreaming (Solms, 2000).

Importantly, authoritative consciousness scientists (Koch et al., 2016; Edlow et al., 2021) write that the complete destruction of the cortex may induce unconsciousness. They cite from a fundamental clinical text for the clinical practice related with disorders of consciousness (Posner et al., 2013). This states that the "diffuse, bilateral destruction" of the cortex is a cause of coma. In support of this, they

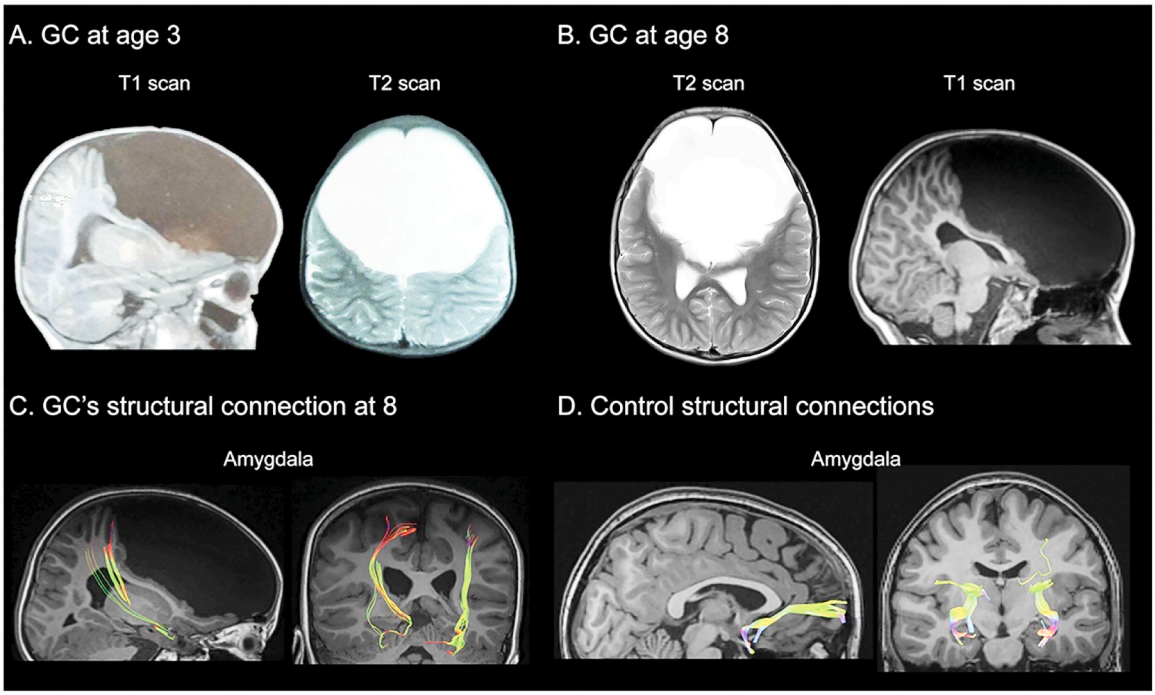

Fig. 2. Frontal agenesis case. T1 and T2 images (1.3.1) of a child (named GC) with very little frontal cortex (A at age 3; B at age 8). DTI structural connections of the amygdala in GC (C) and in an age and sex matched control (D). Despite very little frontal lobe remaining, this patient showed behavioural vivacity strongly suggestive of subjective experience (see supplementary videos in https://www.sciencedirect.com/science/article/pii/S2213158218300603#ec0005). Image taken lawfully from Ibanez and colleagues, Neuropsychologia (Ibáñez et al., 2018).

report a clinical case in which demyelination of the whole brain produced a coma.

However, upon more detailed investigation, the aetiology of reported cases of complete destruction of the cortex seems to be fundamentally metabolic or neurotoxic (Posner et al., 2013). Hence, with such fundamental biological requirements no being met, impairment of diencephalic regions may not be excluded. Such reflections are corroborated by another authoritative clinical text on disorders of consciousness (Young et al., 1998), which reports, the "surprising" lack of evidence that destruction of the cortex (exclusively) may provoke a disorder of consciousness given the necessary implication of other regions in metabolic pathologies. Furthermore, cited (Posner et al., 2013) cases with cortical trauma causing unconsciousness, all have subcortical damage (Adams et al., 2000). There are important considerations to be made on the interdependency between the cortex to the subcortex which are detailed below. Nevertheless, although "diffuse bilateral destruction of the cortex" is classically thought of as a cause of coma (therefore implying that the cortex is necessary to consciousness in a normally developed individual), a careful investigation reveals that the relevant aetiologies are likely affecting regions beyond the cortex.

4.2. *Neurological studies of the cerebellum*

Although the cerebellum may be found as a correlate of consciousness in neuroimaging studies (Golkowski et al., 2019; Di Perri et al., 2016; Luppi et al., 2019; Demertzi et al., 2015; Vanhaudenhuyse et al., 2010; Guldenmund et al., 2013; Boveroux et al., 2010; Monti et al., 2013; Amico et al., 2014), this system is rarely considered in the neuroscience of consciousness. When it is discussed, it is to discredit any role in consciousness it may have (Tononi et al., 2016; Koch et al., 2016; Crick and Koch, 1990; Boly et al., 2017; Baars, 2005; Golkowski et al., 2019). Nonetheless, there is sufficient neuroimaging evidence (Golkowski et al., 2019; Di Perri et al., 2016; Luppi et al., 2019; Coppola et al., 2022a, 2022b; Demertzi et al., 2015; Vanhaudenhuyse et al., 2010; Guldenmund et al., 2013; Boveroux et al., 2010; Monti et al., 2013; Amico et al., 2014) (reviewed above) that, just like the cortex, the cerebellum's functionality is correlated with consciousness.

When consciousness researchers and theorists posit that the cerebellum is not relevant to consciousness (Tononi et al., 2016; Koch et al., 2016; Boly et al., 2017) they cite cases of cerebellar agenesis (specifically Yu et al., 2015; Boyd, 2010). These are individuals who do not have a cerebellum due to complete congenital failure to develop. Of note is that the effects that cerebellar agenesis has on cognition and normal functioning can be variable and sometimes pronounced (see table 1 in Yu et al., 2015); also see other cases of cerebellar damage in consensus papers regarding the cerebellum (Adamaszek et al., 2017; Baumann et al., 2015; Mariën et al., 2014). Nonetheless, as far as assessable, these individuals seem to be experiencing, analogously to the frontal lobe agenesis above. Thus, this suggests that the cerebellum is not, strictly speaking, necessary for consciousness.

However, in cases of acquired rather than congenital cerebellar defects, effects on subjective experience can be substantial. A study of 8 patients with circumscribed cerebellar lesions revealed impaired emotional face recognition processing, and changes in electrophysiological function (Adamaszek et al., 2015). Furthermore, A 38-year-old patient suffered a tumour to the posterior fossa and had rather marked cognitive and affective changes, among other symptoms. After the tumour resection in the cerebellum, there were reports of extreme behavioural changes (diagnosed as posterior fossa syndrome), including hallucinations and uncontrollable bursts of emotional and disinhibited behaviour (Mariën et al., 2013; Hoche et al., 2018). The importance of the cerebellum in typical experience is also exemplified by the cerebellar cognitive affective syndrome (Posner et al., 2013; Mariën et al., 2014; Hoche et al., 2018). These patients, often displaying isolated focal cerebellar injuries (Hoche et al., 2018), show a wide variety of symptoms, ranging from executive function, working memory, psychosis-like symptoms, and affective changes. Furthermore, in several large consensus papers, integrating findings across many neuroscientific disciplines, there are reports that alterations to the typically developed cerebellum may provoke changes in social cognition (Adamaszek et al.,

2017), verbal working memory (Mariën et al., 2014) and various forms of perception (Baumann et al., 2015).

Thus, despite some cases of cerebellar agenesis with relatively negligible effects (analogously to frontal lobe agenesis (Ibáñez et al., 2018), Fig. 2), interruptions of the cerebellum's role in the wider neural system (Naro et al., 2016; Mariën et al., 2013; Buckner, 2013) (Fig. 3) may potentially provoke substantial changes to behaviour and experience (e.g., affective, perceptual), and therefore may be considered as a part of the full neural correlates of consciousness. Yet, despite a role in specific contents of awareness, analogously to the cortex (e.g., frontal lobe agenesis ~ cerebellar agenesis), experience was not completely abolished by disruptions of cerebellar functions.

4.3. Neurological studies of the subcortex

Subcortical structures are evolutionarily more ancient than the cortex and are involved in fundamental physiological functions (Panksepp and Watt, 2011; Damasio and Carvalho, 2013). Of particular interest here are subcortical regions such as thalamus, the hypothalamus and the brainstem (composed by the midbrain, pons and medulla).

The destruction of such regions are recognised causes for coma (Posner et al., 2013; Young et al., 1998). In fact, in diffusion imaging studies, subcortical white matter integrity is able to impressively distinguish between healthy participants and different severities of disorders of consciousness (minimally conscious state and unresponsive wakefulness syndrome) (Fernández-Espejo et al., 2011) and be predictive of outcome measures (Lutkenhoff et al., 2020a, 2020b).

Brainstem death and brain death are nearly identical when it comes to observable diagnostic criteria (Posner et al., 2013) and the brainstem is routinely implicated in disorders of consciousness (Edlow et al., 2021; Posner et al., 2013; Parvizi and Damasio, 2001, 2003; Spindler et al., 2021; Brickner, 1952; Cairns, 1952). In a study of lesions detectable in MRI, the brainstem (pontine tegmentum, and midbrain peduncles), as well as the caudate, predicted not only unconsciousness, but also recovery from unconsciousness (Rohaut et al., 2019). Parvizi and Damasio (Parvizi and Damasio, 2003) showed that, in absence of any other detectable lesions beyond the brainstem, bilateral lesions to the pons or upper pons and midbrain was related with loss of consciousness (whilst damage outside the tegmentum, or small and unilateral damage to the tegmentum, was not associated with coma). Although the lesion mapping overlap between these studies is not perfect, a more modern study (Fischer et al., 2016) replicates these findings. In another study, patients who presented in coma all had microbleeds in the midbrain (in particular mesopontine tegmentum and ventral midbrain) (Bianciardi et al., 2021). Snider and colleagues (Snider et al., 2020), in a veteran cohort with computerised tomography scans approximately 30 years from the time of injury, showed that detectable subcortical lesions (n = 20/171, none overlapping the dorsal brainstem) were not more likely associated with unconsciousness than cortical lesions (n = 151/171). However, they show that cortical lesions predicted loss of consciousness in as much as they had connectivity with dorsal brainstem regions. In a large sample (n = 143), DOC patients had significantly higher brain atrophy in all the subcortical regions investigated compared to controls (Lutkenhoff et al., 2015). Furthermore, experimentally induced damage to brainstem regions in animal models is known to consistently provoke sleepiness or coma (Posner et al., 2013; Merker, 2007; Young et al., 1998; Cairns, 1952; Magoun, 1948), and markedly change cortical activity (resembling sleep or sedation) (Lindsley et al., 1949). Cairins reviewed several human neurological cases in which damage to the brainstem or thalamus were likely to precipitate a disorder or consciousness (Lutkenhoff et al., 2020b).

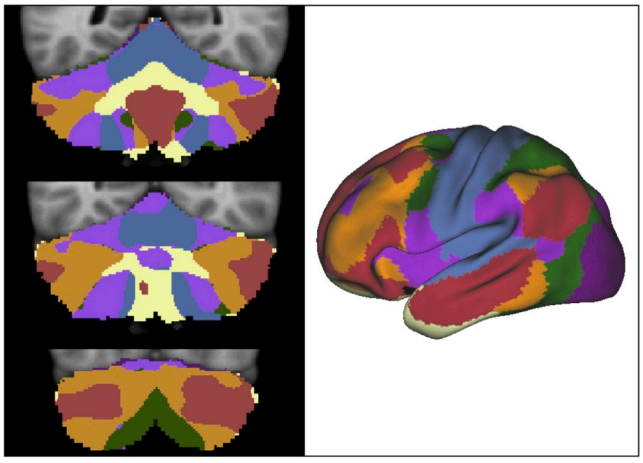

Fig. 3. Functional relationships between cortex and cerebellum. Functional relationships between cerebellar regions (left) and canonical cortical networks (right) as assessed by functional magnetic resonance imaging (n = 1000). Most of the cerebellum shows functional coupling to higher order cortical regions (default mode network in red, executive control network in orange). Blue regions indicate somatomotor regions. This may be taken as evidence that the cerebellum has a role in several complex functions. Reproduced with permission from Buckner, 2011 (Buckner et al., 2011).

In fact, the thalamus is a primary point of focus in the neuroscience of consciousness (Koch et al., 2016; Whyte et al., 2024). There are reports of transient unresponsiveness and hyper somnolence following bilateral thalamic infarcts, although this is not the case in all patients (Gentilini et al., 1987; Guberman and Stuss, 1983; Bogen, 1995; Hawkes et al., 2015; Lahnine et al., 2024; Caballero, 2010). Of interest is that the occlusion of blood supply to the bilateral thalami can affect the midbrain (Gentilini et al., 1987; Hawkes et al., 2015; Lahnine et al., 2024; Arauz et al., 2014). A recent study (Hindman et al., 2018) found that ischemic-induced, brainstem and thalamic lesions were associated with a severe alteration of consciousness, whist thalamic lesions alone did not have effects of comparable severity. However, MRI evidence for midbrain damage has not been found for all bilateral thalamic infarct cases that presented with unconsciousness (Hawkes et al., 2015) (although these patients displayed oculomotor signs that may suggest midbrain involvement (Bogousslavsky et al., 1994)). In experimental ablations performed on rats, extensive thalamic lesions surprisingly did not produce unconsciousness, but complete bilateral destruction of the basal forebrain, parabrachial and precoreleus brainstem regions was sufficient to produce a comatose state (Fuller et al., 2011).

In humans, hypothalamic damage can provoke sleep and behavioural disorders (e.g., impaired social and emotional functioning) (Müller et al., 2022; Sanchez Jimenez and De Jesus, 2023). Bilateral destruction of the hypothalamus in macaques noticeably reduced or abolished emotional behavioural and induced persistent somnolence and drowsiness (Ranson, 1939) (similarly to a modern study on mice (Gerashchenko et al., 2001)). Conversely, cats with the cortex removed but the hypothalamus intact can display the complete constellation of behaviours that suggest "anger" (Bard, 1934a; Bard and Macht, 1958).

Penfield and Jasper (1954), were in an exceptionally privileged position in that they diligently probed subjective reports after in-vivo stimulation and resection of hundreds of human brains. They state that "vertical" fibres (i.e., between subcortex and cortex, in humans) are more important to consciousness than horizontal transcortical association fibres. In their clinically driven "centrencephalic" hypothesis, the brainstem is viewed as the super-ordinate system where all information is "re-represented" and ultimately integrated (e.g., to output one motor response despite multifarious information processing in the whole brain). They believed that such loci were "indispensable" to consciousness (Merker, 2007; Penfield and Jasper, 1954), as their disruption would have marked effects on consciousness. Similarly to the modern studies reviewed above, they were struck by the fact that extensive stimulation and ablation of the cortex "interfered little with consciousness".

4.4. Decortication studies

4.4.1. Human decorticate cases and consciousness

The evidence reviewed above suggests that, whilst stimulation of the cortex and cerebellum provoke changes in experience, rather notable effects are obtained by stimulating the subcortex. Neuropsychological studies seem to show markedly stronger effects when subcortical areas are damaged. This may be taken to suggest that subcortical structures play an important role in consciousness. However, such a relevance to consciousness may be explainable by the fact (1) that perturbations on the subcortex have an effect on the cortex (Bastos et al., 2021; Inman et al., 2018; Moruzzi and Magoun, 1949; Penfield and Jasper, 1954; Kennard, 1943) which is required for experience. An alternative explanation (2) is that subcortical structures may be sufficient for the emergence of simple forms of experience (Solms, 2013; Panksepp and Watt, 2011). Thus, I review "decorticate" cases (with particular attention as to whether such cases display behavioural evidence of having experiences) to attempt to resolve these divergent hypotheses.

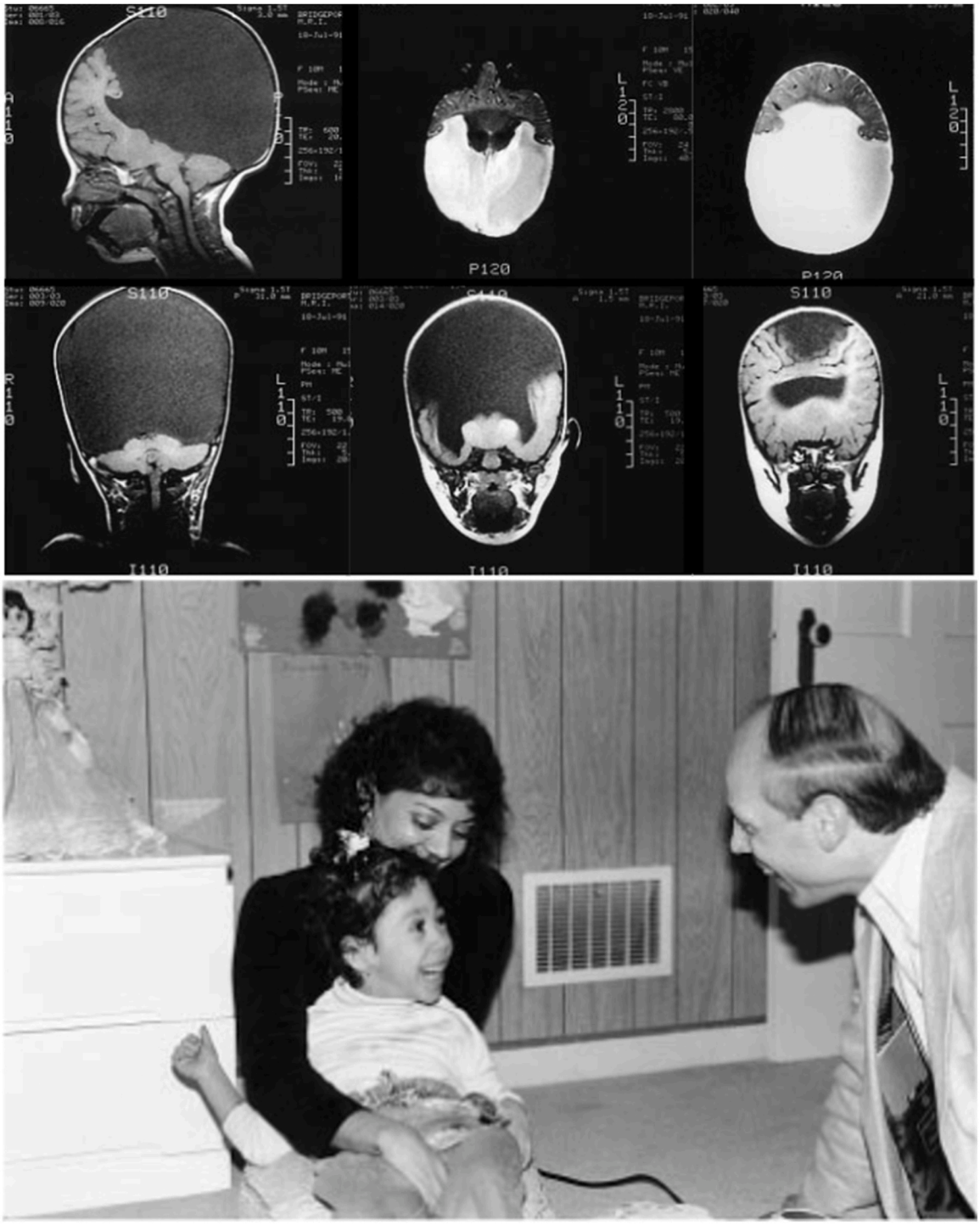

Fig. 4. Subject 3 from Shewmon et al. (1999)**.** In the upper panel, from left to right, top to bottom, midline sagittal (t1 images), lower and higher axial (t2 images), and coronal planes from anterior to posterior (t1). In the lower panel subject three interacting with an author of the article (Shewmon et al., 1999). Images obtained with permission.

Of primary interest are cases of hydranencephaly. This is a congenital malformation disorder in which most of the cortex is missing (in most cases there are remnants of occipital or frontal lobes) (Pavone et al., 2014; Takada et al., 1989). The typical prognosis is irreversible vegetative state (given diffuse bilateral destruction of the cortex, Section 4.1) and survival rates can exceed expectations (Merker, 2007; Shewmon et al., 1999; Aleman and Merker, 2014). In fact, a 32-year-old hydranencephalic woman with little frontal cortex preserved (Counter, 2007) was diagnosed with persistent vegetative state and displayed groaning vocalisation, demonstrations of facial expressions of joy at the presentation of music and preserved brainstem auditory function. Despite comparing the patient (by presentation analogy) to a minimally conscious state patient, the author states that "in absence of cerebral hemispheres there can be no consciousness" (Counter, 2007). Shewmon and colleagues in 1999 (Shewmon et al., 1999) sustain that such prognoses will engender a self-fulfilling prophecy, as hydranencephalic children's severely affected development would be further stunted by the absence of an adequate environment. Shewmon and colleagues present four hydranencephalic cases (all having variably preserved small remnants of cortex, see Fig. 4) which were given a relatively normal developmental context by caregivers who had bonded with these children. The authors report behaviours such as the distinguishing of and playing with toys, the enjoyment of and preference for different types of music, distinguishable social responses, anxiety to unfamiliar people, visual discrimination, a sense of object permanence, and affective responses as well as a basic form of empathy. Despite the presence of minimal cortical matter, in all of these cases, the attending neurologists prognosed with absolute certainty permanent vegetative state, in accordance with guidelines (Edlow et al., 2021; Posner et al., 2013; The Multi-Society Task Force, 1994; Young et al., 1998). Similar reports are given elsewhere (Solms, 2021; Merker, 2007), including reports of different types of learning. In fact, a survey of over 100 caregivers of hydranencephalic children gave consistent evidence of certain types of awareness (e.g., recognizing family members 91 % positive), but, importantly, not others (e.g., behavioural localisation to bodily pain 91 % negative) (Aleman and Merker, 2014).

Interestingly, caregivers can recognise the onset and ending of *absence* epilepsy in hydranencephalic individuals, which implies the presence of experience (Merker, 2007; Shewmon et al., 1999). As Shewmon and colleagues point out (Shewmon et al., 1999), any "ethnologist" would not have difficulty to ascribe basic consciousness (e.g., experience of pain) to the behaviour of such organisms. The rarity of such cases may be partially due to the fact that the caregivers usually do not disregard prognoses (i.e., permanent unresponsive wakefulness syndrome/vegetative state) (Posner et al., 2013; The Multi-Society Task Force, 1994), thus further affecting development. Nonetheless, in most cases, such individuals tend to have remnants of cerebral cortex. The argument could be made that experience is mechanistically mediated by what is left of cortical structures. However, preserved cortical tissue is highly abnormal (Takada et al., 1989) and potentially non-functional[28197].

To my knowledge, there is one modern hydranencephaly case that is reportedly absolutely decorticate (Pavone et al., 2014) (as per neuroradiological assessment, see Fig. 5). This three-year-old female presented with "severe neurodevelopmental delay", flattened and slow EEG, an observable difference between wakefulness and sleep and was unable to walk without support. Clinicians who observed the child state she was not in a vegetative state and "definitely felt emotions" (personal communication). As of 2019 she was still alive, could recognise her mother's voice, could fixate, vocalised, seemed to experience pain but did not localise the source. The clinicians thought the child could distinguish between environments, could cry and laugh, and play with her mother with a degree of intentionality (rather than displaying purely reactive and automatic behaviours).

There is also another older hydranencephalic case, with reportedly no neo-cortex preserved (as per neuroanatomical investigation following death). In this case, who was in a vegetative state of decorticate rigidity, sensory reinforcement learning was recorded as well as vocalisations and head turning in apparent response to "discomfort" (Deiker and Bruno, 1976). A modern anencephalic case, who survived much longer than is typical, showed evidence of independent feeding, making cooking noises and smiling spontaneously (Dickman et al., 2016). The first author recalls "her getting upset and being comforted by her mother" (personal communication, similar cases have been reported in the news).

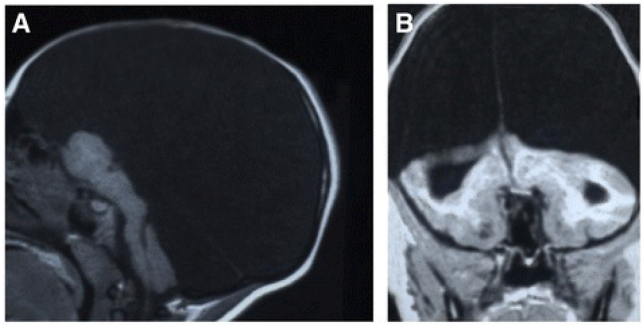

Fig. 5. Brain of hydranencephalic individual with no cortex. Case of a hydranencephalic child (Pavone et al., 2014) with no cerebral cortex remaining according to clinical neuroradiological assessment. Sagittal (left) and coronal (right) T1 MRI images. Senior author (R.F.) confirmed that the patient did not have any cerebral cortex remaining in personal communication. A clinician who saw the child affirmed that the patient was not in a vegetative state in personal communication. Another affirmed that she "definitely felt emotions". Image reused under CC-BY.

Of note, the behaviours of decorticate individuals may be displays of automatic reactions devoid of experience. It should be said, more generally, that the presence of consciousness is non falsifiable (i.e., presence or absence cannot be conclusively proved, see philosophical zombies thought experiment, locked in syndrome, Descartes' evil genius, etc. (Chalmers, 1995; Dennet, 1991; Owen and Coleman, 2008). However, the evidence regarding hydranencephaly, taken together with the implications arising from neurostimulation and neuropsychological/neurological evidence, suggests that, whilst the cortex may be important for the subjective experience of a neurologically typical human, it is not necessary to experience in the strictest sense (i.e., sine qua non). Rather, in mammals, the subcortex seems to be the only brain system required for the emergence of basic subjective experience.

However, the hydranencephalic children reported above are congenital cases. The rather surprising functionality of these human cases may be ascribed to plasticity and a reorganisation of function. The question arises whether the removal of the cortex further along development provokes irreversible unconsciousness (perhaps via diaschisis and development of an essential interdependency between systems). The human decorticate cases indicate that the cortex's anatomical structure is not necessary to experience. However, the subcortex, in absence of a cortex, may have acquired "cortical functions" (such as those enabling the emergence of experience) during such atypical development. Hence, the following section is dedicated to studies which performed an experimental removal of the cortex in animals. Such reports may provide further clues as to what structures may be important for consciousness.

4.4.2. *Experimental decortication in animals*

Similarly to a number of observations in different animals reported by William James over a century ago (James, 1890), experimentally decorticated rats are surprisingly comparable to control rats. In rats with no cortex, there are reports (reviewing decades of research (Whishaw et al., 1991; Whishaw, 1990) of successful mating and associated rituals (variably across individuals), sufficiently preserved maternal behaviour,

grooming behaviours, preserved simple association learning (although failing in more complex types of learning) and normal postures. Furthermore, completely decorticate rats showed essentially the same playing behaviour as control rats (with minor differences) (Panksepp et al., 1994). On the other hand, deficits are reported in skilled behaviours (e.g., grooming, although these can improve with learning), and hoarding (Whishaw, 1990).

Decorticate cats displayed a comparable range of complex behaviours (Bjursten et al., 1976) and are indistinguishable to other cats in the first month of life. Play, sexual (Sue Carter et al., 1982; Whishaw and Kolb, 1983), grooming, emotional and maternal behaviours were observed (Bjursten et al., 1976). The decorticate cats made use of haptic, auditory and visual senses (although the latter was impaired; especially so in adult preparations (Bard, 1934b)). Similarly to other observations in cats and dogs (Bard, 1934a) they display full, if not heightened, aggressive responses. Some behavioural differences (mostly to do with social behaviour) were observed and these became more prominent as time went by. Partially preserved learning capabilities in these animals are also documented (Merker, 2007; Bjursten et al., 1976). In hypothalamus preparations (removing all rostral matter), there are reports of a full behavioural expression of anger, in contrast to decerebrate cats (i.e., brainstem truncations). Similarly, grooming, arousal from sleep, localisation of sound (but no sight or olfaction), righting posture, running and "vocalisation suggestive of pain" are reported in "mesencephalic rats" (where hypothalamus was preserved but its connectivity to the brainstem severed (Woods, 1964) or with "decerebration at the supracollicular level" (Grill and Norgren, 1978)). This evidence does not prove unequivocally that these experimentally decorticated animals retained subjective experience (an epistemic problem that persists with humans), however, they displayed complex behaviours which, parsimoniously, are likely associated with certain experiences (Bard, 1934a).

However, of primary importance is whether surgical decortication performed later in development would induce irreversible unconsciousness (given the differences between the congenital and acquired cases reviewed, and possible reorganisation of function (Chalmers, 2000)). Reports suggest that behavioural deficits are surprisingly comparable between rats and cats that received complete decortication neonatally and in adulthood (Whishaw, 1990; Kolb and Whishaw, 1981; Villablance et al., 1986). Neonatal lesioning leads to improved performance in a variety of behaviours (e.g., maternal behaviour) compared to adult decortication. As expected, decortication provokes secondary changes to subcortical structures (e.g., necrosis; diaschisis (Karplus and Kreidl, 1914), as evaluated in post-mortem) which differ between adult or neonatally decorticated rats (Whishaw, 1990; Kolb and Whishaw, 1981; Villablance et al., 1986). Nonetheless, animals that had their cortex removed in adulthood seemed to display behaviours that may suggest the presence of experience (e.g., fear, anger, restlessness, eating, sexual behaviour; certain forms of learning, excessive curiosity; however expressions of joy and preoperative personality are mostly reported to be abolished) (Solms, 2021; Bard, 1934a, 1934b; Whishaw, 1990; Whishaw and Kolb, 1983, 1984; Kolb and Whishaw, 1981; Zeliony, 1929; Bromiley, 1947; Denton et al., 2009). This evidence suggests that abnormal compensatory development cannot wholly explain the behaviours that decorticate animals display.

The impossibility of probing verbal report in such organisms reduces the certainty that such decorticate animals and humans did experience (anything at all). It must be said, these might effectively be "zombie" rats and cats (Chalmers, 1995; Dennet, 1991), displaying mechanical behaviours without any experience. Nonetheless, if behaviours can be taken to suggest experience, as is the gold standard in the clinic (Giacino et al., 2004), the evidence reviewed above suggests that the subcortex is sufficient for the emergence of a basic form of experience.

4.4.2.1. Primate decortication. Nonetheless, rats and cats may not be comparable to primates. Although behavioural evidence of experience does exist when rats, cats and dogs have their cortex removed; primates, which have phylogenically and ontogenically highly developed cortexes may perhaps have a different mechanism for the generation of consciousness (as suggested by Penfield and Jaspers (Penfield and Jasper, 1954)). There are in fact very few obtainable studies to my knowledge that look at experimentally decorticated primates. This is partly due to the difficulty of performing such surgery with the primate surviving and recovering sufficiently (Woolsey, 1943; Travis and Woolsey, 1956), but also the ethical dubiousness of such experiments (which may suggest the possibility of experiences of suffering). In these studies, descriptions tend to focus on motor function and do not give much behavioural detail.

With a surgical procedure involving two sequential hemispherectomies, Kennard describes two decorticated Macaques showing strong startle responses to auditory stimuli. Two other infant-decorticated monkeys showed appropriate vocalisations to pain as well as other startle responses somewhat suggestive of "emotional expression" (Kennard, 1944). However, in these cases, the decorticate monkeys did not survive long after surgery. Karplus and Kreidl in 1914 (Karplus and Kreidl, 1914), report 7 cases that survived more than 24 h (up to 26 days) after two sequential hemispherectomies (where reported, animals were approximately 1 year of age). Out of these seven, only one was observed to substantially recover its functions, whilst the others displayed the highest functionality the day after the second hemispherectomy. Importantly, the authors sometimes report finding small remnants of cortex during the autopsy (e.g., gyrus uneinnatus, orbital gyrus, gyrus fornicates). They write of clear transitions between sleep-like and wakeful states. In the former state, animals did not perform spontaneous movements, did not react to stimuli or vocalise, and had their eyes shut. They describe one decorticated individual who used its limbs on the cage bars to right itself into a seated position. They report occasional behavioural responses to auditory, tactile and visual stimuli (eye opening and movements, limb movements), "cries of pain" (but often no facial expression), as well as other vocalisations. In another case the totally decorticated monkey removed a cotton bandage, emitted vocal sounds and cries, pulls itself up with the bars of the cage, and swallowed food and drinks. After the second hemispherectomy, they report "there are no clear signs of change of the state of consciousness". Although their lack of specification of their conception of consciousness is problematic, fewer behavioural signs have been interpreted as indicative of consciousness in recent, high impact, animal-model literature (Redinbaugh et al., 2020; Kundishora et al., 2017). Another macaque (shown in Fig. 6) showed vigorous movement, alternating periods of sleep and wakefulness in which it positions the body via use of limbs (e.g. seated, righting reflex, often used as an indication of consciousness in animal

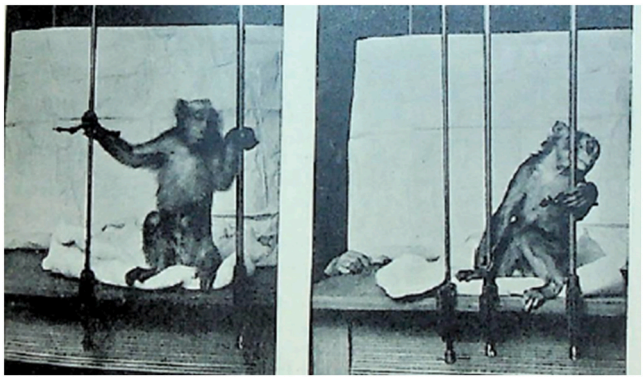

Fig. 6. Pictures of decorticated monkey in Karplus and Kreidl (1914)**.** Left panel would show the monkey in a more "awake" state; right panel in a more "sleepy" state. Note, reportedly, a portion of basal ganglia was also removed, although minimal remnants of cortical gyrus uneinnatus and substatia perforate remained, as assessed in post mortem; Copyright expired.

studies (Bian et al., 2021)). It moved around the whole cage, and emitted vocalisations comparable to a healthy monkey although with a striking lack of facial expressions. It showed behavioural responses to tactile and auditory stimuli although could not feed itself independently.

Another case (surviving 26 days) shows evidence of feeding, startle reaction to acoustic (e.g., call from another monkey) and tactile stimuli, righting response and vocalisations. It walked and hopped and spontaneously scratched itself. It started recovering strength and had lively responses when manipulated until it succumbed to dysentery. The author explicitly comment that they cannot draw conclusions as to the full functional potential of a decorticated monkey, due to a lack of maximum recovery in these animals.

A decade later, Travis and Woolsey (Travis and Woolsey, 1956) succeeded in fully decorticating (neocortex) two *adult* macaques via serial surgery. Whilst one required help, one of the monkeys was able to right itself independently (traditionally, a sign of consciousness in animal research (Fuller et al., 2011)). This monkey could also walk on its own (showing a degree of "caution", being blind). Similarly to above, the authors also suggest that the monkeys in question were not permitted to recover to their full potential (Travis and Woolsey, 1956).

The lack of research and relevant detail on the available cases requires a degree of caution. Although there seems to be a difference between phylogenic and ontogenic development on the effect of decortication, there is still a remarkable capability of function retained across decorticated animals. Importantly, however, these behavioural descriptions are sufficient cause for doubt that the near complete destruction of the cortex in adult primates is unequivocally associated with unconsciousness.

5. Discussion

5.1. Subcortical functions for consciousness

To draw the evidence together, I reviewed how all major structures of the brain display correlations with consciousness in neuroimaging studies. In neurostimulation and neuropsychological studies, changes to cortical and cerebellar regions were related to quite substantial changes in experience. However, the subcortex showed the strongest and most consistent effects, which may abolish or even induce behavioural evidence of consciousness. Taking into account various epistemic problems, a review of animal and human decorticated cases shows that the cortex, strictly speaking, is not necessary for experience. Conversely, the embodied subcortex is sufficient for behaviours that indicate consciousness.

Subcortical structures, which tend to be evolutionarily conserved across species, have the function of representing the state of the animal's basic physiological functions (Panksepp, 2011; Mashour and Aikire, 2013). These provide the animal crucial information regarding its survival (e.g., hunger vs satiety). Such fundamental physiological responses to value-laden stimuli can be described as affective, interoceptive and homeostatic (Damasio and Damasio, 2022; Panksepp, 2011; Craig, 2002) and are related to "unconditioned responses" in behavioural psychology. Such affective information underlies actions and behaviours motivated by sexual lust, feelings of cold, pain, hunger, the need to breath, play, attachment, and many others. Thus, they are essentially a representation of the state of the system to the system itself (Damasio and Damasio, 2022; Damasio and Carvalho, 2013). Plausibly, this information provides the foundations of conscious experiences (Denton et al., 2009). Importantly, such fundamental subcortical responses mediate reinforcement learning in the environment (Linden, 2011; Deiker and Bruno, 1976; Bjursten et al., 1976) and can therefore lead to relatively complex behaviours (e.g., in decorticate cases (Bjursten et al., 1976)). Whilst accounts of consciousness that tend to focus on the cortex emphasise higher forms of awareness (e.g., regarding the self, access consciousness; working memory), the most basic forms of qualitative experiences, such as primary affects, may not be necessarily reliant on the cortex. Different authors have thought that such basic feelings were the first experiences to be engendered in the history of our world (Merker, 2007; Damasio, 1998; Panksepp, 2011; Denton et al., 2009), and perhaps the "lowest level of consciousness" (Damasio and Damasio, 2022; Damasio and Carvalho, 2013). We can understand such primary affects in the context of the free energy principle (Friston, 2010). Such feelings cause a discomfort that have the overall function of reducing free energy ("surprising" states that are not conducive to bodily function over the long term). On this view, subjective experience has an origin that is very much pertaining to survival. Hence, whilst the cortex and the cerebellum enable essential parts of the experience of a typical human being, the sufficient neural conditions of fundamental experiences likely lie in the embodied subcortex.

An important distinction in the literature is that between content and level of consciousness (Laureys, 2005). In this conceptualisation, which has heuristic utility in the clinic, consciousness is represented as having two dissociable dimensions (Laureys, 2005). The level of consciousness ("arousal/wakefulness") is associated with the brainstem, the content of consciousness ("awareness") is associated with the cortex. As can be found in previous literature (Hudetz, 2024; Bayne et al., 2016), the concept of a one dimensional "level of consciousness (i.e., wakefulness or arousal)" (Laureys, 2005) is far from clear and univocal (e.g., noradrenaline vs dopamine mediated arousal vs behavioural arousal; eye opening in vegetative state patients, but no normal sleep-wake cycles as measured by EEG etc.,). Nonetheless, this review suggests that these dimensions ("awareness" and "level of consciousness") may not be as independent as implied (Hudetz, 2024) and suggests the hypothesis that some systems associated with basic "arousal", such as the brainstem, may hold the potential to support contents of experience (i.e., "awareness") (Wallace et al., 1989). In fact, this region is complex (Parvizi and Damasio, 2001), enables neuromodulation for the whole brain (Hansen et al., 2024) and processes sensory, interoceptive, emotional, reward, motor and proprioceptive information (Damasio and Damasio, 2022; Venkatraman et al., 2017).

In summary, it thus seems likely that fundamental forms of consciousness may be as simple as a feeling of pain or basic interoception (Panksepp et al., 2007; Merker, 2007; Edelman et al., 2011; Damasio, 1998; Damasio and Carvalho, 2013). Such basic experiences can emerge from dynamic interactions between subcortical structures, the body and the environment (Klein and Barron, 2016; Merker, 2007; Damasio, 1998; Parvizi and Damasio, 2001; Varela et al., 2001). Biologically, phylogenically and ontogenically, it is evident that the cortical and cerebellar functions depend on the subcortex. Thus, cortical remapping of basic, subcortically instantiated information may provide higher-order, more finely discriminative experiences (Whyte et al., 2024) (integrating, for example, bodily alloceptive and proprioceptive coordinates, cognitive expectation and self-appraisal to a simple emotion in relation to a social environment etc.) (Damasio and Carvalho, 2013). Primary or fundamental forms of consciousness (Panksepp et al., 2007; Merker, 2007; Edelman et al., 2011; Damasio, 1998; Damasio and Carvalho, 2013) can be hypothesised to provide a fundamental precursor to more complex cortex-mediated experience (Crick and Koch, 1990; Edelman et al., 2011) (e.g., social identity, moral considerations).

5.2. Intrinsic and extrinsic context as a solution to empirical paradoxes

There is still a fundamental problem arising out of the evidence reviewed above. When reviewing the evidence, there seems to be a causal role of the subcortex in consciousness. Yet, the evidence of rather extreme (reported) changes to subjective experience with the alteration of frontal and posterior midline cortices (Odegaard et al., 2017; Parvizi et al., 2021) cannot be ignored. Similarly, whilst cases of cerebellar agenesis (Yu et al., 2015) show that the cerebellum may not be necessary for consciousness in the absolute sense, in cases of posterior fossa syndrome or cerebellar cognitive affective syndrome, quite severe changes

to experience can be reported (Adamaszek et al., 2017; Mariën et al., 2013; Hoche et al., 2018). There is, in fact, a clear difference between cases of hydranencephaly (Shewmon et al., 1999) compared to posterior midline stimulation (Parvizi et al., 2021); of cerebellar agenesis (Yu et al., 2015) versus cerebellar damage (Adamaszek et al., 2017; Mariën et al., 2013; Hoche et al., 2018); of frontal lobe agenesis (Ibáñez et al., 2018) contrasted with frontal infarct in an adult (Odegaard et al., 2017). In one case the abnormality is congenital, in another it is acquired (respectively). This highlights the importance of the context (both internal and external) of the individual for experience. A viable system would adapt and develop within its own context. The destruction of brain regions, once the individual is fully developed (and systemic functionality is calibrated across many dimensions) may provoke great functional obliteration and a considerable impairment to consciousness. The rest of the system will be missing something through which it has always functioned (Kennard, 1943). Conversely, a system without significant parts that would "typically" be there (i.e., abnormal), would adapt and develop intrinsically, within that context, regardless of extrinsic expectations. Thus, although the evidence in this review seems to suggest a "hierarchy" in the importance of structures for consciousness, the evidence reviewed here, when taken together, also shows that these systems cannot understood in isolation: the interaction of subcortical, cortical and cerebellar systems likely determine different ranges of possible experiences.

Perhaps the Sprague effect, as suggested by Merker (2007) (who's work is foundational to this article), illustrates the mutual dependence between the cortex and the subcortex in normal function. After occipital cortical damage there is a loss of visual function (see also Ffytche and Zeki, 2011; Silvanto and Rees, 2011). However, astonishingly, some visual function is restored by *additional* damage to the superior colliculi in the brainstem. This is interpreted as the absence of cortical input provoking a secondary brainstem effect preventing its normal visual processing function (e.g., via excessive inhibition, diaschisis). Thus, analogously to what is shown by Snider and colleagues (Snider et al., 2020), normal brainstem function may be impaired by the absence of a cortical input through which its function was calibrated, and restored to an extent once the need for this input is destroyed.

In the language complex systems, via the destruction of parts, the systemic functioning of the whole is severely impaired. On the other hand, in congenital cases, the brain body and environment interactions (Varela et al., 2001) can develop within their own "atypical" context, thus permitting the representation of basic forms of interoceptive and homeostatic self and perhaps the development of more complex types of experience over time (e.g., via operant conditioning in hydranencephalic individuals). The importance of the temporal and physical context in the emergence of consciousness is perhaps evidenced by the fact that hydranencephalic individuals who were given species-typical environmental interactions, displayed behavioural signs that would not conform to a vegetative state presentation (in opposition to those who were not (Shewmon et al., 1999)). Beyond the fundamental physiological context of the **body** and its various structures, this furthermore highlights the temporal context, not only in terms of biology (e.g., development, tonic modulation) but also from a phenomenological point of view: in the stream of consciousness, the present must have its own past, which will lead to a more or less expected future (Damasio and Damasio, 2022; Coppola et al., 2022a; Friston, 2018).

5.3. Limitations and future directions

The conclusions of this review warrant further analysis of the clinical and ethical implications by the wider academic and clinical community. If the embodied subcortex is truly sufficient for experience to emerge, then investigations may be undertaken to narrow down what specific subcortical functions engender experience. An ad hoc critical review of hypothalamic and mesencephalic preparations may yield further insights as to minimal neural circuitry required for an experience.

Given the interdependencies between different systems (e.g., cortex, thalamus and brainstem), it is plausible that empirical investigations that focus solely on cortico-cortical interactions may be incomplete. Empirically, this review suggests that investigating multidimensional "vertical" (Penfield and Jasper, 1954) connectivity patterns in vivo between ancient and more recent structures (Bayne et al., 2016; Spindler et al., 2021) might yield statistically powerful and reproducible distinctions between different states of consciousness (e.g., vegetative state, sedation, psychedelic states).

Theories of consciousness often focus on the cortex (Melloni et al., 2021; Seth and Bayne, 2022). This review challenges the notion that the cortex is necessary for subjective experience. However, if specific anatomical predictions are excluded, the evidence reviewed here does not seem to provide conclusive evidence in favour of any of the major theories of consciousness. For example, the brainstem, with its varied and complex representations (bodily, sensory etc.,) and high degree of bi-directional connectivity with the whole brain and body (Hansen et al., 2024; Venkatraman et al., 2017), could be plausibly thought to integrate information (as per Information Integration Theory (Tononi et al., 2016)), broadcast information (as per the Global Neuronal Workspace Theory (Seth and Bayne, 2022)) and re-represent information (e.g., of interoceptive states, as per Higher-Order Theories (Seth and Bayne, 2022)). More work is needed to elaborate on theories given the present review. Further work may also integrate the present evidence with accounts that highlight thalamic contributions (Whyte et al., 2024; Storm et al., 2024; Suzuki and Larkum, 2020).

Notions of a primary, minimal phenomenological type of consciousness are found in the work of both consciousness scientists and philosophers (Edelman et al., 2011; Pennartz et al., 2019; Parvizi and Damasio, 2001). There are many subtle distinctions and different possible formulations of such "pre-reflective" primary forms of awareness. Of importance to consciousness science, the various empirical and theoretical difficulties seen above (Koch et al., 2016) are exacerbated by the lack of a clear definition and operationalisation of consciousness, as well as a lack of reporting of relevant behavioural detail. Future work may have to identify the differences in conceptual formulations of consciousness and try to match them with empirical data. For example, a further exploration of what the evidence presented here might mean for concepts such as levels of consciousness and access consciousness might be interesting, if not fruitful.

Furthermore, the present article investigates consciousness via observable behaviours. This, however, may include widely differing types of data (e.g., complex verbal reports vs perceptual performance in a task vs observation of behaviours of play). This variation may therefore lead to potential systematic differences in interpretation of the data, in particular in relation to the preliminary distinction between primary and higher order forms of consciousness. Thus, this distinction should be viewed with caution and further explored, potentially with ah-hoc experimental designs and additional conceptual analyses. Furthermore, the variation in the quality and detail of the evidence presented poses a further issue in relation to the extent subjective experience may be inferred. This issue is somewhat mitigated in this article via conservative interpretations and convergence of evidence. Nonetheless, it is advisable that future studies report exhaustive behavioural and methodological details.

Of note is that important studies may not have been published (e.g., clinical and experimental). Although I endeavoured to capture the relevant literature comprehensively, the vast scope of available studies means that some pertinent works may have been inadvertently excluded.

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Conflict of interest

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Data availability

No data was used for the research described in the article.

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