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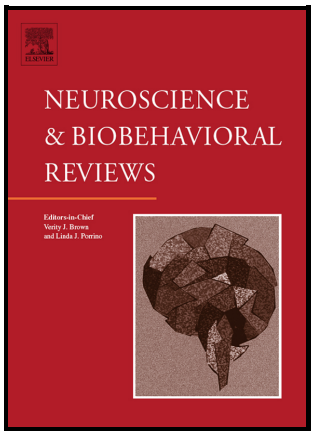

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Religious and spiritual experiences from a neuroscientific and complex systems perspective

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Abstract

The emergence of spiritual and religious practices can be seen as a major cognitive transition in the evolution of biological organisms. Spiritual and religious experiences are closely linked to evolved complex brain structures, as well as their dynamics and plasticity. In this review, we will focus on the neural mechanisms that make such experiences possible. We will also address the methodological, neurophilosophical and neurotheological questions concerning the extent to which religious and spiritual experiences can be neurobiologically explained. We will summarise the rapidly expanding knowledge about the neuroscience of meditation and prayer, near-death experiences, ecstatic epilepsy, psychedelic experiences, and changes in spirituality associated with brain lesions. Additionally, we will discuss the validity of suggestions, based on predictive processing theory, that ecstatic states may represent a pathology of the mind and brain in the form of impaired prediction. Finally, we will describe the beneficial and therapeutic effects of spiritual and religious routines and practices and put them in the context of evolutionary medicine. Overall, we will argue that 'neurospirituality' research can be fruitful if it avoids both excessive reductionism as well as dualism. Instead, it should be based on limited reductionism, balanced by more integrative, non-localisationist approaches, including dynamical systems, complex systems and network theory.

Highlights

- *We review current knowledge about the neural underpinnings of a wide range of spiritual experiences, including meditation, prayer, near-death experiences, ecstatic epilepsy, and psychedelics.*
- *We critically evaluate reductionist approaches to these experiences and emphasise the need for integrative, multiscale frameworks that incorporate predictive coding, complex systems theory and non-localisationist perspectives.*
- *We frame the beneficial effects of spiritual and religious practices in the context of evolutionary medicine.*
- *We discuss new perspectives on altered states of consciousness as complex dynamical phenomena, including insights into their potential adaptive significance.*

All living beings, including plants and animals, are able to process information from the environment and thus manifest cognitive properties in the form of more or less sophisticated sensory perception, decision making and learning (Baluška & Levin, 2016; Kováč, 2007; Reber, 2019; Sarto-Jackson, 2021). The extent such more or less complex cognitive processing abilities translate to conscious experience has been hotly debated (Draguhn et al., 2021; Jedlicka, 2020; Mallatt et al., 2023; Taiz et al., 2019). Nevertheless, there is substantial evidence that several species, including great apes, elephants, dolphins and some corvids, exhibit both a sense of primary self and the ability to process abstract information (Bayne et al., 2024; LeDoux et al., 2023) (although there is some debate about the methods used to measure them, such as the mirror test for self-awareness). In contrast, while there is some evidence for simple precursors of spirituality in other animals (Guthrie, 2002; McComb et al., 2006), religious thought and behaviour seem to have emerged quite specifically in humans (Bering, 2001). In this sense, spirituality may represent one of the few processing capacities that constitute a sudden, major transition (Harari, 2014; Szathmáry, 2015) and gap (Jedlicka, 2007; Suddendorf, 2013) in the evolution of cognitive abilities across species.

It is likely that the ability to imagine counterfactual world scenarios - and the associated cognitive processes - have been achieved only by humans ((Pearl & Mackenzie, 2018; Suddendorf, 2013). One of the oldest known works of art, the Lion Man from the Hohlenstein-Stadel in the Lone Valley, created approx. 40.000 years ago, is possibly an expression of this higher cognition (Pearl & Mackenzie, 2018), and may constitute one of humanity's first tentative steps towards art and religion (Harari, 2014). Given that religious and spiritual experiences seem to be a largely unique feature of human beings - and at the same time a universally human feature that extends across many cultures, humans seem to have undergone a cognitive "revolution" rather than evolution. Palaeontological evidence indicates that this human "revolution" of creating artifacts and complex cultures likely developed in a time frame of tens of thousands of years – perhaps a slow pace on the scale of human history, but extremely fast on the scale of evolution (Mcbrearty & Brooks, 2000; Scerri & Will, 2023).

This brings up an important question: If human spirituality evolved at such a high speed at which new spirituality-specific brain areas could not have emerged, this would indicate that existing brain structures must have shifted their function. In this article, we will focus on the following related questions: What do we know about the neural mechanisms that make spiritual and religious experiences possible, and their evolutionary roots? And to what extent can religious and spiritual experiences be explained in neurobiological terms?

In our article, first, we discuss the major methodological and conceptual challenges that the neuroscientific study of spirituality faces. Next, we review the empirical evidence for the neural correlates of different spiritual states, such as meditation, prayer, near-death experiences, psychedelic experiences and ecstatic epilepsy. After reviewing the therapeutic and adaptive effects of spiritual practice, we then examine theoretical models that aim to explain these experiences. Here, we focus particularly on predictive processing and complex systems theory, weigh localisationalist approaches against the concept of degeneracy, and explore the potential evolutionary roots and trade-offs of spiritual experiences. The final sections outline prospects for future research and reflect on the philosophical implications of reductionist and dualist approaches to understanding spiritual experiences.

1. Four approaches to "neurospirituality" research and their methodological limitations

Andrew Newberg names four neuroscientific approaches to researching spirituality (Newberg, 2014): 1) Examination of the brain in connection with spiritual practices such as prayer, meditation, or religious rituals. In this context, for example, electrical activity, blood flow, metabolism and neurotransmitter activity of the brain can be measured (mainly by EEG, PET, SPECT, or MRI; Newberg, 2014). We will discuss this approach in sections 2, 3 and 4. (2) Investigation of the brain in the context of drug-induced spiritual experiences. We describe this approach in section 4 (3) Examination of the brain in the context of spiritual experiences associated with neuropathological and psychopathological processes. We address this approach in section 5. (4) Study of the brain in relation to therapeutic effects of spiritual experiences and practices or interventions. This approach is briefly described in section 6. Based on the insights these approaches have yielded so far, we then discuss frameworks that might be used to synthesize current neuroscientific perspectives on spiritual experiences: Localized versus non-localized neuronal coding (section 7), predictive coding and complex system theory (section 8) and evolutionary trade-offs (section 9).

Neuroscientific research of religious and spiritual experiences is still in its early stages (McNamara et al., 2024) and faces a number of challenges. Many of the empirical findings described below have not yet been replicated. While publication bias - the tendency to prioritize significant or positive results, often difficult to replicate - is a general issue across biological and medical research, it also affects neurotheology research. However, a greater challenge lies in the technological limitations of human brain imaging and EEG/MEG studies. For instance, functional MRI (fMRI) offers limited temporal resolution, capturing changes over seconds rather than milliseconds, while EEG and MEG suffer from poor spatial resolution. These and other constraints (see below) undermine claims in popular media, such as 'the site of God perception has been found in the brain,' oversimplifying complex phenomena and obscuring the need for replication and methodological rigor.

There are also statistical issues, such as small sample sizes or the dominance of cross-sectional studies over controlled longitudinal studies and the lack of control groups (Rim et al., 2019; Y. Y. Tang et al., 2015). These and other methodological problems make it difficult to draw conclusions about the causal links between neuronal phenomena and subjective spiritual experiences. Specifically, determining such causal relationships would require longitudinal studies, which compare data from the same subjects across multiple time points and ideally include a control condition, and/or intervention studies with randomized assignment to experimental conditions (cf. (Bergmann & Hartwigsen, 2021; Siddiqi et al., 2022; Weichwald & Peters, 2021)). For example, in studies of brain activity in meditators, differences in brain activity or structure may be related to differences in the subjects' interest in meditation, personality or temperament (Y. Y. Tang et al., 2015). Correlational studies suggest that more meditation practice is associated with greater changes in brain structure or function. However, such correlations cannot prove that meditation caused the changes, as it is possible, for example, that individuals with a certain brain structure or function are attracted to consistent long-term meditation practice (Y. Y. Tang et al., 2015). Controlled longitudinal studies are more informative and show, for example, that meditation enhances

mindful awareness as well as electric microstates of the brain (Zanesco et al., 2021) and increases the grey matter density in specific brain regions including the hippocampus, the posterior cingulate cortex, the temporo-parietal junction, and the cerebellum (Hölzel et al., 2011) see also (Cotier et al., 2017; Sevinc et al., 2020; R. Tang et al., 2020; Yoshida et al., 2020).

Another methodological problem is that spiritual and religious experiences are very complex (Yaden et al., 2017). To study them and their neural mechanisms rigorously and quantitatively, their diverse aspects would need to be defined and described more precisely (Timmermann et al., 2023; Yaden et al., 2017). Different measures of religiosity in different studies make comparisons and generalisations difficult (Rim et al., 2019). However, initial attempts have been made to introduce psychometrically validated measures of spirituality and religiosity with standardised validation ((Koenig & Al Zaben, 2021), see also (Kapogiannis et al., 2009)). Moreover, the 30-item Mystical Experience Questionnaire (MEQ30) has been developed as a widely used measure of individual mystical experiences (F. S. Barrett et al., 2015). The MEQ30 has been validated for experiences with psilocybin, which can lead to long-lasting changes in well-being, behaviour and attitudes (F. S. Barrett et al., 2015). As we mention below the research on near-death experiences (NDEs) and awe-related experiences, it is also worth noting the 16-item Grayson NDE scale questionnaire (Greyson, 1983; Martial, Simon, et al., 2020) as well as the multifactorial Awe Experience Scale (AWE-S) (Yaden et al., 2019).

Because conscious religiosity or spirituality is unlikely to occur in animals, it is very difficult to study the underlying cognitive and neural mechanisms in detail in animal models (see e.g. (Bayne et al., 2024)), as is the case with learning and memory, for example. Nevertheless, it is at least possible to conduct pharmacological studies in animals to investigate the toxicological, behavioural, and neural aspects of the effects of hallucinogens that are known to induce spiritual experiences (Daldegan-Bueno et al., 2023). It is also possible to study the neurophysiological basis of bodily expressions of simple precursors of spiritual experience in animals. For example, tears, shivering and vocal bursts ("whoas") are among the awe-related emotional bodily expressions that have evolved in many social mammals (Keltner, 2023).

When discussing the neural correlates of religious and spiritual experiences, we should be aware of the complexity of terms such as "religion", "spirituality", "rituals", etc. For example, in antiquity there was no separation between religious and secular spheres of life. The concept of a private religious or spiritual domain of life, separated from the public (economic, political) domain of life, is a recent European view of religion (Nongbri, 2013). In addition, nowadays, the community aspect of religion may or may not be part of spirituality. Moreover, as Boyer and Baumard argue, humans do not seem to have special cognitive functions for religious representations, but rather use common cognitive capacities in religious and non-religious domains (Boyer & Baumard, 2016). Similarly, the scientific study of ritual is complicated by the fact that rituals represent diverse behaviours that are supported by a variety of different cognitive mechanisms (Boyer & Liénard, 2020).

Despite these conceptual and methodological challenges, the neuroscience of religion is an exciting and much needed field of research into a uniquely and universally human cognitive capacity, whose rigorous establishment has recently been called for (McNamara et al., 2024). The following is an overview of the current state of knowledge on the neural correlates of religious and spiritual experiences and states of consciousness. Rather than providing a comprehensive review, we will focus on four selected phenomena: a) meditation or prayer, b) near-death experiences c) psychedelic states, and d) spiritual experiences arising from neuronal pathologies. While these phenomena may seem highly diverse in some ways, a new classification of states of consciousness has recently been proposed that locates these conscious states and more along three axes - wakefulness, connectedness to the environment and inner conscious awareness (Martial, Cassol, et al., 2020). Figure 1 depicts examples of the relation between different conscious states, including the four discussed in this review, within this classification system.

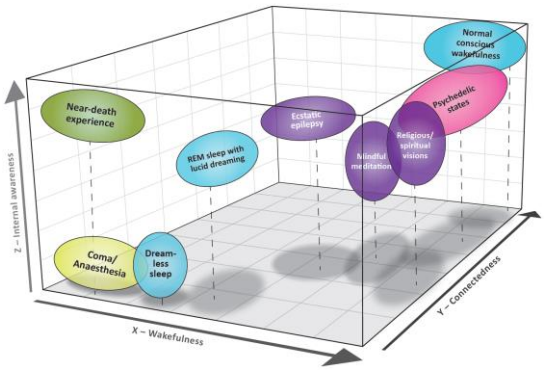

Figure 1: Altered states of consciousness associated with religion and spirituality, tentatively placed in a 3D space. For example, mindful meditation is typically associated with moderate to high X (wakefulness), moderate to low Z (inner awareness - associated e.g. mind-wandering with DMN activation) and moderate to high Y (connectedness). In contrast, in religious/spiritual visions or ecstatic epilepsy, X would typically be high or moderate to high, while Y would be low to moderate. Modified and supplemented on the basis of (Martial, Cassol, et al., 2020).

Once we have explored the neuronal signatures of meditation and prayer, near-death experiences, psychedelic states and ecstatic epilepsy, we will discuss to what extent three broad theoretical frameworks – localized versus non-localized coding, predictive coding and complex systems, and evolutionary medicine can shed light on unifying principles of these neuronal dynamics and provide insights into adaptive and maladaptive forms of spirituality.

2. The neuroscience of meditation and prayer

The neural mechanisms of mindfulness meditation have been investigated in a multitude of studies (for a review see (Y. Y. Tang et al., 2015), see also e.g.(Singer et al., 2008)). In this section, we emphasize predominantly, although not exclusively, longitudinal and acute (during practice) as opposed to post-acute (immediately following) effects of meditation/prayer.

Overall, mindfulness meditation was primarily associated with brain structures that influence self-perception, attention control and emotion regulation. For self-perception, these were the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC) and the precuneus; for attention control, the anterior cingulate cortex (ACC) and the striatum; and for emotion regulation, prefrontal regions, limbic regions, and the striatum. Interestingly, meditators were found to have reduced activity in the so-called default mode network (DMN), which can be interpreted as reduced self-referential processing (Ganesan et al., 2023; Y. Y. Tang et al., 2015; Van Buuren et al., 2010).

The DMN comprises several interconnected brain regions that become active when a person focuses not on external stimuli but on internal stimuli or thought processes in the context of self-reflection or daydreaming (Menon, 2023; Raichle et al., 2001). The cortical regions of the DMN include the above-mentioned PCC/precuneus, the PFC (including its ventromedial part/vmPFC, which is involved in emotional decisions, see (Sapolsky, 2017), but also the retrosplenial cortex (RSC), the anterior temporal cortex (ATC); middle temporal gyrus (MTG) in the lateral temporal cortex; medial temporal lobe (MTL) and angular gyrus (AG) in the lateral parietal cortex as well as some subcortical structures (cf. (Menon, 2023)). Meditators often focus strongly on their body or on external stimuli (e.g. sounds, music) and try to let go of self-referential thoughts about themselves or others, or about the past and future. Therefore, it is not surprising that, during meditation, their DMN is less active and more functionally connected to brain regions implicated in self-control (Brewer et al., 2011; Jao et al., 2016). In addition, greater DMN deactivation in experienced than in unexperienced meditators indirectly supports the idea that long-term experience enhances this effect.

Another important brain structure that is influenced by meditative states is the insula (Fox et al., 2014; Tang et al., 2015). It shows greater activation during mindfulness training, which could be interpreted as an enhanced conscious experience of the present moment (Tang et al., 2015). The insula appears to support improved awareness of bodily states (interoception). Experienced meditators show greater cortical thickness in the area of the insula (again indicating a long-term effect). In addition, a decoupling of the right insula and the mPFC and increased connectivity with the dorsolateral PFC (dlPFC) was observed in connection with meditation ((Brewer et al., 2011; Ganesan et al., 2022; Jao et al., 2016)). In simplified localisationist terms, the mPFC can be attributed to the processing of emotional information and the dlPFC to the processing of cognitive (rational) information and cognitive executive self-control (Hare et al., 2009; Sapolsky, 2017). A stronger functional connectivity of the insula with the dlPFC in contrast to the weaker connection with the mPFC can be seen as a shift in self-referential processing

towards a less emotional and more detached and objective analysis of interoceptive and exteroceptive sensory events (Tang et al., 2015). (In addition, there are also connections between the insula and the PAG - see part 9 below.) The insula supports the prediction of physical states (Livneh & Andermann, 2021). This makes it a good candidate for a brain structure that is involved in the neural correlates of meditative states and experiences through its activity and plasticity.

Meta-analyses (Fox et al., 2014, 2016; Tomasino et al., 2013) identified other brain areas that change in meditators in addition to the insula and the DMN structures mentioned above, including the hippocampus (important for long-term memory) and intra- and interhemispheric connections (fasciculus longitudinalis superior and corpus callosum). Interestingly, meta-analyses have also shown that different styles of meditation (e.g. Hindu vs. Buddhist or focused attention vs. mantra recitation) may be characterised by different patterns of brain activation (Fox et al., 2016; Tomasino et al., 2014).

There are numerous other studies that have investigated neural structures in connection with mystical and religious experiences. For example, one study used functional imaging to show that religious recitation leads to activation of the frontal-parietal areas of the cerebral cortex, namely the dlPFC, the dorsomedial frontal cortex, and the medial parietal cortex (Azari et al., 2001). Functional magnetic resonance imaging has also shown that religious thinking is associated with greater activation of brain regions responsible for processing emotions or self-representation such as the ventromedial prefrontal cortex ((Harris et al., 2009), see also (Brooks et al., 2022; Bulbulia & Schjoedt, 2012; Inzlicht et al., 2009; L. Miller et al., 2019; Schjødt et al., 2009)). This suggests, not surprisingly, that religious thinking (when considered in a narrow, rationalistic sense, involving mainly propositional knowledge, see (Vervaeke & Ferraro, 2013)) tends to activate rather than suppress the DMN and other areas whose activity is related to self-presentation and emotions. Other studies have shown changes in brain activity in cortical areas of nuns during a mystical experience measured by fMRI and EEG ((Beauregard & Paquette, 2006, 2008), see also (Chung et al., 2022)). An earlier fMRI study has revealed that different dimensions of religious belief are associated with corresponding brain regions known to be involved in evolutionarily adaptive cognitive processes such as abstract semantic processing, imagery, theory of mind and emotional-cognitive integration (Kapogiannis et al., 2009). Several review articles and books have been written on these topics (Afonso et al., 2020; Barnby et al., 2015; Brandmeyer et al., 2019; Fenwick, 2010; Fox et al., 2014; Ganesan et al., 2022; Magalhaes et al., 2018; Maselko, 2012; McNamara, 2009; McNamara & Grafman, 2024; Newberg, 2018; Raffone et al., 2019; Rim et al., 2019; Sim et al., 2024; van Elk & Aleman, 2017).

Using the three time scales for neural changes in meditation and prayer, we can emphasise, that (1) acute effects involve reduced DMN (Brewer et al., 2011; Garrison et al., 2015; Tomasino et al., 2013) and increased insula activation (Fox et al., 2016), (2) post-acute effects involve post-meditation changes in functional connectivity, particularly in prefrontal and limbic areas, or more generally in the DMN, salience network (SN) and central executive network (CEN) (Bremer et al., 2022), although the evidence is limited to minutes (Berkovich-Ohana et al., 2016; Bremer et al., 2022; Garrison et al., 2013; Jao et al., 2016; Kral et al., 2019), (3) long-term effects lasting weeks, months or years involve not only changes in functional connectivity (Kilpatrick et al., 2011) but also in gray matter density and to some extent cortical thickness and white matter connectivity (Fox et al., 2014) in the hippocampal formation (memory/emotion) (Hölzel et al., 2011; Luders et al., 2009, 2013; Sevinc et al., 2019)), insula (interoception/self-awareness) (Hölzel et al., 2008), posterior cingulate cortex (self-refential processing), temporo-parietal junction (social cognition), and cerebellum (motor and cognitive functions) (Cotier et al., 2017; Hölzel et al., 2011; R. Tang et al., 2020).

One could summarise that meditation is associated with decreased activity of DMN and with enhanced recruitment of neural structures involved in cognitive control (Afonso et al., 2020; Ganesan et al., 2022; Sim et al., 2024; Tang et al., 2015). Consistent with this, a recent synthesis (McNamara & Grafman, 2024) has put novel findings into the context of the triple network theory (Menon, 2011) emphasising that religious and spiritual experiences are in addition to the DMN and the cognitive control network (i.e. CEN, which is synonymous with the frontoparietal network, FPN) linked to one other key network, namely the SN. This makes neurobiologically sense since the SN is involved in switching between internal (self-referential) and external cognitive states, which are in turn supported by the DMN and the CEN/FPN, respectively, and in identifying the salient profound and meaningful experiences. The authors extend the triple network model (or the tripartite model, TPM) to a TPM cycling model (McNamara &

Grafman, 2024). Overall, the TPM framework, with its emphasis on the interactions among the three networks (instead of isolated individual networks) and their cyclic and integrative nature is well in line with the integrative and anti-localisationist viewpoint of our article. Moreover, the TPM can also be used as an explanatory neurobiological framework also for seizure-associated ecstasy and psychedelically altered states of consciousness (McNamara & Grafman, 2024), which we discuss below.

3. The neuroscience of near-death experiences (NDEs)

Near-death experiences, i.e. the occurrence of vivid perceptual experiences as vital body functions are shutting down, are a rare but well-documented phenomenon (Martial, Cassol, et al., 2020). Within the classification system introduced in Figure 1, classical NDEs can be regarded as decoupled from the environment (low connectedness), but with strong inner awareness (Figure 1).

The neurophysiological mechanisms underlying the development of NDEs and near-death-like experiences (NDE-like) have not yet been researched in detail, but there are some interesting initial observations. NDE experiences have been associated with altered activity in the mediamanl temporal lobe and in the temporoparietal junction (TPJ) (Martial, Cassol, et al., 2020). The TPJ is a brain region that belongs to the DMN and supports the sense of unity of self and body as well as the distinction between self and others (theory of mind, (Saxe & Kanwisher, 2003)). Changes in activity in the TPJ are involved in out-of-body experiences (OBE, (Blanke & Arzy, 2005)). As the TPJ integrates several different sensory streams related to self-localisation (Ionta et al., 2011), it makes neurobiological sense that altered multisensory integration could lead to OBE (Blanke et al., 2002; Ionta et al., 2011).

The insula also seems to play an important role in NDE, especially its anterior part (Martial, Cassol, et al., 2020). NDE-like experiences have been reported with direct cortical stimulation, lesions, or epileptic seizures in these brain structures (i.e., temporal lobe, TPJ, and insula) (Martial, Cassol, et al., 2020). A case study using EEG recordings during the near-death phase has reported that a dying human brain displays altered oscillations including an increase in gamma power and a decrease in theta power (Vicente et al., 2022). Based on data from human and animal recordings (for a review see (Shlobin et al., 2023) and the references therein), three distinct electrophysiological phases of the dying brain can be distinguished: 1) a rise in oscillatory activity, 2) an isoelectric “wave of death” and 3) a potential recovery phase with a “wave of resuscitation”. However, technical and methodological limitations make it difficult to relate NDEs to these different phases of electrical activity (Shlobin et al., 2023).

It is an open question whether states of consciousness during NDE can be quantified with an empirical measurement method (Shlobin et al., 2023). It would be interesting to test whether the Perturbational Complexity Index (PCI), which can be measured using transcranial magnetic stimulation (TMS) of the brain combined with EEG (Casali et al., 2013), makes it possible to determine the intensity of consciousness during NDE. PCI makes it possible to distinguish different levels of consciousness in states such as sleep, anaesthesia, wakefulness or awakening from a coma. States of consciousness can be seen as different points on a complexity landscape. If coma has a very low complexity, then spiritual experiences would presumably be more complex than sleep or ordinary wakefulness.

4. The neuroscience of psychedelic experiences

Psychedelics such as psilocybin, DMT and LSD have been used, often for centuries to millennia (George et al., 2022; M. J. Miller et al., 2019), to induce intense spiritual or mystical experiences with lasting personal meaning (e.g. (Griffiths et al., 2006)). In this section, we explore their neural correlates, mainly focusing on acute effects (Carhart-Harris et al., 2012) and some post-acute plasticity (Siegel et al., 2024), although we also mention longitudinal effects (Knudsen, 2023).

Imaging studies using functional magnetic resonance have shown reduced activity in the ACC and mPFC during psychedelic states after psilocybin (Carhart-Harris et al., 2012). Both structures have already been mentioned above as structures relevant to meditation. The medial part of the PFC (mPFC) is involved in the processing of emotional states and is part of the DMN (see above).

Research into the neural correlates of psychedelic-induced states and psychedelic-induced neuroplasticity is currently very intensive and is providing more and more information (for recent reviews and meta-analyses see (Aleksandrova & Phillips, 2021; Atasoy et al., 2018; Calder & Hasler, 2023; Calvey & Howells, 2018; de Vos et al., 2021; Halberstadt et al., 2017; Johnson et al., 2019; Knudsen, 2023; McCulloch et al., 2022; Olson, 2022; Shafiee et al., 2024; Stoliker et al., 2022)). Interestingly, increased signs of so-called criticality (Beggs & Plenz, 2003; O'Byrne & Jerbi, 2022) have been observed when investigating the spatiotemporal dynamics of the brain under the influence of psychedelics (Atasoy et al., 2018; Gervais et al., 2023; Huels et al., 2021). This suggests that concepts from dynamical systems theory and complexity theory can be used to better understand the brain dynamics related to states induced or affected by psychedelics (Girn et al., 2023) or, more generally, to any spiritual or religious state. In this 'dynamic' context, it is exciting to see that psychedelics are very likely to increase the functional integration of large interconnected brain structures and support the flexibility and criticality of brain activity ((Gervais et al., 2023; Girn et al., 2023), see also (Huels et al., 2021; Schartner et al., 2017)). Predictive coding theory has also been used to explain the neuromodulatory serotonergic effects of psychedelics (via 5-HT2A receptors) on large-scale brain networks in the context of imaging data (Stoliker et al., 2022).

The neural correlates of psychedelic and meditative states are closely linked. Recently, a neural model of mystical experience has been proposed in which changes in the above-mentioned DMN observed during meditation or after the administration of classical hallucinogens play a central role (F. S. Barrett & Griffiths, 2018). Within the framework of integrative and network-based (antilocalisationist) approaches to understanding the brain (S. Noble et al., 2024; Pessoa, 2023), it makes sense that not only the DMN, but also limbic networks are discussed as neural mechanisms of psychedelics and their antidepressant effects (Kuburi et al., 2022). Interestingly, the research on awe also often emphasises the 'diminution of self', which is consistent with the reduced DMN reported for psychedelics and meditation. This also suggests that for the neural correlates of awe, predictive coding may be an appropriate unifying framework that could potentially link these different, but to some extent similar, spiritual experiences and phenomena (Monroy & Keltner, 2023).

Paradoxically, although Picard and Friston (Picard & Friston, 2014) used predictive coding arguments to interpret ecstatic epilepsy-related states as a failed prediction (see below section 5 and 8), a more recent proposal by Carhart-Harris and Friston allows for a more positive interpretation of psychedelic-induced ecstatic states, although still based on predictive coding (free energy principle) - and its combination with the criticality-enhancing „entropic" or „anarchic" brain states. This newer conceptual model of psychedelic action is called REBUS: „relaxed beliefs under psychedelics" (Carhart-Harris & Friston, 2019).

It is surprising that psychedelics can induce long-lasting effects after a single dose, such as an improvement in depressive symptoms (Fang et al., 2024) or a greater openness of personality (Knudsen, 2023) (but sometimes also serious adverse events, see (Hinkle et al., 2024)). This observation means that psychedelics alter the brain persistently and induce long-term plasticity (Cameron et al., 2021; Raval et al., 2021; Shao et al., 2021). The existing electrophysiological, biochemical, imaging, and behavioural data demonstrating such brain plasticity have recently been summarised in review articles (de Vos et al., 2021; Knudsen, 2023; Shafiee et al., 2024). New evidence from functional magnetic resonance imaging of the human brain has confirmed that a single dose of psilocybin can dramatically reduce the synchronisation of brain areas, in particular persistently reducing functional connectivity between the anterior hippocampus and the DMN for weeks (Siegel et al., 2024)

There is currently a debate between reductionist and non-reductionist interpretations of the effects of psychedelics (Barksdale et al., 2024; Gründer et al., 2024; Yaden & Griffiths, 2021). However, old-school reductionism, which regards pharmacotherapy as superior to merely supportive psychotherapy (Gründer et al., 2024), is unlikely to provide a satisfactory account of psychedelic-mediated effects.

5. The neuroscience of pathology-based spiritual experiences

One of the most prominent examples of spiritual experiences being caused observably by a brain pathology is the phenomenon of ecstatic epilepsy. It has long been known that focal epileptic seizures can be accompanied by ecstatic auras with feelings of happiness (e.g. (Bear, 1979; Ogata & Miyakawa, 1998; Trimble & Freeman, 2006)). Dostoyevsky famously reported ecstatic or mystical feelings during his epilepsy. Such symptoms are therefore sometimes called Dostoyevsky's epilepsy and belong to what is

known as Geschwind or Gastaut-Geschwind syndrome (Devinsky & Lai, 2008; Trimble & Freeman, 2006). Common causes are epileptic discharges in the temporal lobe. Recently, direct stimulation of the dorsal anterior insula was reported to produce ecstatic experiences in three patients with drug-resistant focal epilepsy who had brain electrodes implanted for this reason (Bartolomei et al., 2019).

Ecstatic states in epilepsy raise an interesting neurotheological and neurophilosophical question. Is ecstasy, with its intense feelings of happiness and harmony, a fundamentally pathological mental state? Some neuroscientists have proposed such an interpretation, for example Picard and Friston in the context of predictive coding theory (Picard & Friston, 2014). We have mentioned their hypothesis in section 4 and will discuss it in more detail in section 8.

Another example of neuropathological triggers for spiritual experiences is brain damage. For example, lesions in the parietal lobe have been observed to correlate with increased feelings of self-transcendence (Urgesi et al., 2010). In a more recent study, the same data set of patients before and after brain tumour surgery was used together with additional data from Vietnam War veterans to provide evidence that increased spirituality and religiosity related to brain trauma are often associated with lesions to brain circuits connected to the so-called periaqueductal grey (PAG) (Ferguson et al., 2022). The PAG is an evolutionarily old brainstem structure with connections to the limbic system and the prefrontal cortex, and is involved, for example, in the processing of fear and pain and, more generally, in instinctive behaviours such as escape from threatening stimuli (Stempel, 2024). As such, one might argue that spirituality in such cases would spring from a lesion-related decrease in threat perception.

6. Benefits of spiritual and religious experiences

As mentioned above, Andrew Newberg has described the investigation of the positive therapeutic effects of spiritual experiences and practices and their mechanisms as the fourth approach to the neuroscientific study of spirituality ((Newberg, 2014), see also(Lee & Newberg, 2005; Yaden et al., 2017)). Several studies and meta-analyses support the observation that certain spiritual and religious practices can contribute to the improvement of cognitive as well as non-cognitive health problems (e.g. (Balboni et al., 2022; Brinsley et al., 2021; Chida et al., 2009; Farhang et al., 2019; Hoge et al., 2023; L. Miller et al., 2012; Van Cappellen et al., 2021; Vancampfort et al., 2021; Verzili et al., 2023), but see also (Sabe et al., 2019)).

Numerous studies and observations convincingly show that some religious and spiritual practices and rituals can lead to improvements in mental and physical well-being and increase psychological resilience. For example, an earlier systematic review of original research has found that religion/spirituality is often associated with better mental health outcomes, including lower rates of depression and anxiety (Koenig, 2012). A more recent systematic and integrative review (Balboni et al., 2022) has confirmed that spirituality plays an important role in patients' quality of life and physical and mental health outcomes. For example, there is evidence that frequent attendance at spiritual/religious services reduces the risk of substance abuse and dependence, depressive symptoms, suicidal behaviour and overall mortality (Balboni et al., 2022; Chida et al., 2009; Garssen et al., 2021; VanderWeele, 2021), for the latter in a dose-dependent manner. The effects were consistently significant, although the effect sizes ranged from small to moderate (Balboni et al., 2022; Garssen et al., 2021). This may be related to the fact that not all forms of religiosity or spirituality are beneficial. For example, negative and positive psychological adaptations to stress have been associated with negative and positive forms of religious coping (Ano & Vasconcelles, 2005; Koenig, 2012). Negative meditation or prayer experiences and bad trips have also been reported (Carbonaro et al., 2016; Haijen et al., 2018; Hinkle et al., 2024; Lindahl et al., 2017; Schlosser et al., 2019). It would be exciting if future research could help to distinguish between positive and negative forms of spiritual and religious habits, attitudes and experiences, and their respective neurobiological signatures.

Interestingly, there are many similarities between the effects of meditation, prayer and psychedelics and the underlying neural mechanisms, including, for example, similar changes in the DMN mentioned above (see also (Barnby et al., 2015)). Experiences of awe have also been associated with many positive effects on mental health and social behaviour (Bai et al., 2021; Chirico & Gaggioli, 2021; Monroy & Keltner, 2023; Sturm et al., 2022; Yin et al., 2024). This has led to the proposal that awe may be a

common cognitive process that is triggered by a variety of positive spiritual experiences (including meditation, prayer, nature experiences, psychedelics) (Monroy & Keltner, 2023),involving five distinct processes: neurophysiological changes, decreased self-focus, increaseded social integration and relationality, and enhanced meaning (Monroy & Keltner, 2023). However, awe is rarely elicited without other positive emotions, such as gratitude (Portocarrero et al., 2020; Wood et al., 2010), and other positive emotions sometimes occur without awe, so it is unlikely that awe is a sole or dominant mediator of all positive spiritual experiences and their beneficial effects on mental and physical health.

A more recent systematic review analysed eighteen studies focused on neural correlates of spirituality and religion in the context of mental health problems (Rosmarin et al., 2022). It emphasized potentially protective effects of religiosity with respect to depression and positive effects of prayer on alcohol cravings and control of attention and emotion (Galanter et al., 2017; Rosmarin et al., 2022). However, the authors concluded that further research is necessary to elucidate the relationship between the lowered risk for depression, its neural mechanisms and symptomatology (Rosmarin et al., 2022). Similarly, further research is required for clarifying the links between anxiety or psychosis and brain mechanisms of spirituality/religion.

Indeed, there are still many unanswered questions about the precise effects and mechanisms of the increased resilience observed in people who meditate regularly and long-term, or who incorporate other spiritual or religious practices into their rituals. For example, it has been suggested that greater cortical thickness is associated with a high importance of spirituality or religion and may promote resilience to the development of a depressive disorder in individuals with a high familial risk of major depression (Liu et al., 2017; L. Miller et al., 2014, 2021). However, how such cortical changes can reduce the risk of depression is still poorly understood. Furthermore, if we look at this question again through the lens of holistic, integrative and nonlocalisationist approaches, such as complex systems and network theory, it is unlikely that these morphological changes can be the sole explanation for the increase in resilience.

7. Spiritual experiences as localized neural phenomena – or not?

As discussed in Part 5, ecstatic epilepsy has at times been framed as a breakdown of predictive coding in the neuronal network. In line with this, intense spiritual or religious experiences can sometimes (but not exclusively) occur in the context of neuropathological and psychopathological processes. Another example of such a correlation is brain damage. For example, lesions in the parietal lobe correlated with increased feelings of self-transcendence (Urgesi et al., 2010). The authors speculated that the parietal parts of the brain may play an important role in modulating self-transcendence as a feature of spirituality and religiosity. In a more recent study, the same data set of patients before and after brain tumour surgery was used together with additional data from Vietnam War veterans to provide evidence that spirituality and religiosity are associated with brain circuits connected to the so-called periaqueductal grey (PAG) (Ferguson et al., 2022). The PAG is an evolutionarily old brainstem structure with connections to the limbic system and the prefrontal cortex, and is involved, for example, in the processing of fear and pain and, more generally, in instinctive behaviours such as escape from threatening stimuli (Stempel, 2024).

While the neuropathological phenomena discussed in section 5, both in terms of epileptic ecstacy and brain lesions, would suggest that the PAG circuit as well as parts of the parietal and temporal lobe are tightly linked to religious experience, an anti-localisationist intuition (Noble et al., 2024) suggests that it would be an exaggeration to claim that e.g. the PAG represents a "spirituality centre" of the brain. Such strong localisationist conclusions would need to be replicated by other studies. Moreover, other lesion studies indeed indicate that religious cognition cannot be linked to a single specific brain region but to a complex network of brain regions ((Cohen-Zimerman et al., 2020; Cristofori et al., 2022; Grafman et al., 2020), see also (Ferguson et al., 2018)). Furthermore, we know that complex mental states, experiences, and actions are associated with high inter-individual variability.

In addition, it is known that different mechanisms - e.g. disparate temporal and spatial patterns of brain activity - can lead to similar cognitive states, a phenomenon known as "degeneracy" (see also below) (Albantakis et al., 2024; Edelman & Gally, 2001; Westlin et al., 2023). This means that several different brain states can lead to similar cognitive or affective processes or produce similar behaviour, so there is not a strict one-to-one relationship between specific brain areas, their activation and associated functions (Cropper et al., 2016; Nakuci et al., 2025; Pessoa, 2014; Seifert et al., 2016; Westlin et al., 2023). For

example, a recent fMRI study has reported that very different patterns of large-scale brain activations can be observed during an identical perceptual decision task (Nakuci et al., 2025). This is in line with our arguments that a particular region is not solely responsible for a particular spiritual or religious experience or behaviour. Instead, these experiences appear to emerge from flexible, overlapping activity of disparate neural networks. Moreover, surprisingly, the distinct patterns of brain activation during the perceptual decision-making tasks sometimes involved strong DMN activation (Nakuci et al., 2025). This shows that the dichotomy of the DMN being active 'off-task' (mind-wandering) and inactive 'on-task' is too simplistic.

Neuroscientific studies have not yet explicitly examined religious and spiritual experiences in the context of degeneracy. However, several studies have highlighted the involvement of distributed and overlapping neural networks and the dynamic interplay of multiple brain regions in spiritual and religious experiences (McNamara & Grafman, 2024; L. Miller et al., 2019; Rim et al., 2019), which is consistent with the notion of degeneracy in neural activity and cognition. In this context, it would be interesting to determine the inter-individual heterogeneity of different circuits and their activations within the above-mentioned triple network framework (TPM, (McNamara & Grafman, 2024)) that contribute to similar outcomes in the form of similar spiritual states.

These methodological and conceptual aspects and limitations of reductionist localisationism should not be ignored when studying spirituality in the context of brain pathologies. Furthermore, caution should be exercised not to reduce spirituality to pathological processes (Newberg & Lee, 2005), not least because it appears to have evolved as an adaptation for prosociality and cooperation ((Norenzayan & Gervais, 2013; Purzycki et al., 2016; Pyysiäinen & Hauser, 2010). Keeping these limitations of reductionism in mind, the neuroscientific study of spirituality in relation to brain pathology is a very fruitful and valuable approach.

8. Spiritual experiences as predictive coding errors

One of the currently most popular theories in neuroscience and cognitive science is the theory of predictive coding (Aitchison & Lengyel, 2017; Clark, 2013; Friston, 2018; Wiese & Metzinger, 2017). According to this theory, our brain is not a static system that passively perceives and processes sensory information, but a highly dynamic system that actively creates internal neural models of the outside world as well as the body (Luhmann, 2020; Seth, 2015). The brain makes predictions about the future, in particular about the presence or absence of surprising (potentially dangerous), unexpected events (i.e. identifying chaos versus predictable order) and compares them to the current state (Luhmann, 2020). The brain works in a proactive and energy-efficient manner to keep its own state stable. Bottom-up information from the sensory organs is constantly compared with the internal model and deviations are registered (Luhmann, 2020). The internal models are constantly updated by the plasticity of the brain (related to learning and memory) (Luhmann, 2020). Our perceptions, insights, actions, and memories are the brain's means of minimising surprises as energy-efficiently as possible in order to increase our chances of survival (see also the related concept of "free energy", (Friston, 2010): "Reduce surprise - live longer"). Predictive coding is thought to operate at all cortical levels, with 'top-down' information from higher cortical regions predicting 'bottom-up' information from lower cortical regions, as well as from sensory organs and receptors (Friston, 2018).

In this context, Picard and Friston view for instance the ecstasy experienced before or during an epileptic seizure as resulting from a malfunction in the predictive machinery (but see (Jaeger et al., 2024)). Epileptic discharges in the insula (Picard et al., 2021) or temporal lobe result in the 'comparator' between the brain's predictions and the inputs no longer functioning properly, meaning that prediction errors are no longer generated (Picard & Friston, 2014). This leads to feelings of happiness, confidence, well-being, and inner peace. In other words, the absence of prediction errors, i.e. discrepancies between the actual multisensory and interoception inputs and their predictions, leads to the emergence of Mumford's (Mumford, 1992) "ultimate stable state", in which top-down signals perfectly predict lower cortical representations. This is "the state the brain is trying to achieve: a perfect prediction of the world, like the Oriental nirvana" (Picard & Friston, 2014). In the case of ecstatic epilepsy, this state would be achieved due to pathological discharges spreading from the epileptogenic zone.

Although this hypothesis is very attractive and is partly supported by experiments, it should be critically reflected upon. Firstly, the theory of predictive coding is relatively new and has not yet been sufficiently researched and experimentally corroborated (Cobb, 2020; Litwin & Miłkowski, 2020; Nave, 2024). There are proposals on how to implement predictive coding at the level of individual neurons and their dendrites (Aru et al., 2020; Mikulasch et al., 2023), but these proposals need to be tested more thoroughly. Second, even if neuroscience substantiates the theory of predictive coding, this does not mean that emotions evoked by pathologically altered brain activity represent pathological cognition in the form of incorrect predictions. Ecstatic or mystical feelings do not only occur exclusively as a side effect of epileptic discharges or artificial stimulation of the temporal lobe or the insula. They are also reported in the context of meditation or prayer. It is therefore quite possible that such extraordinary experiences are not just symptoms of a neurological disorder, as they can also occur in the healthy brain. Evolutionary thinking also suggests that ecstatic and mystical states may have evolved as cognitive phenomena with evolutionary benefits for human organisms. Moreover, the recently proposed cyclic TPM ((McNamara & Grafman, 2024); see above) offers a more integrative neurobiological view of ecstatic epilepsy as a consequence of aberrant activations and interactions within the three networks: DMN, CEN, and SN. As the authors emphasise, predictive processing may be part of the explanation, but not a sufficient one (McNamara & Grafman, 2024). Finally, a reductionist view of cognition as an expression of computational machinery is at odds with proposals that cognition is fundamentally non-computational (Jaeger et al., 2024).

9. Spiritual experiences as evolutionary trade-offs

Evolutionary medicine (Medzhitov & Stearns, 2015; Stearns, 2012; Stearns et al., 2010) is a useful conceptual framework for understanding both adaptive and maladaptive forms of spirituality and religion. This framework considers cognitive function and dysfunction within the context of evolutionary trade-offs (Del Giudice & Crespi, 2018).

The evolutionary and cultural roots of religion and spirituality have been the subject of many articles and books (Atran, 2011; Banerjee & Bloom, 2013; J. L. Barrett & Zahl, 2012; Baumard & Boyer, 2013; Bloom, 2012; Boyer, 2001, 2004; Boyer & Baumard, 2016; Boyer & Bergstrom, 2008; Dunbar, 2022; Geertz, 2012; Rossano, 2006; Seitz & Angel, 2020; White, 2021; Wilson & Green, 2012). However, the evolutionary trade-off between the benefits and costs of spirituality and religion, as well as the corresponding costs of their cognitive and neural mechanisms (see e.g. (André et al., 2020; Bulbulia, 2012; Potz, 2022)), with respect to mental and neural disorders (e.g. epilepsy and anxiety), require further research.

According to evolutionary medicine, mental disorders are potential by-products of exaggerated defence mechanisms (Stearns & Medzhitov, 2016). Such costly defence mechanisms, including fear and related behaviours such as fast or slow escape (Blumstein et al., 2016; Qi et al., 2018)), evolved to protect organisms from dangerous conditions such as predators or infections. However, their deregulation can lead to pathological anxiety, phobias, or obsessive-compulsive disorders (Stearns & Medzhitov, 2016). Similarly, drug addiction can be viewed as the consequence of hijacked reward systems that originally evolved to reinforce adaptive behaviours or to alleviate pain (Stearns & Medzhitov, 2016). An exciting open question is which (and how) spiritual and religious experiences and rituals contribute to shifting the deregulated defence mechanisms towards normal homeostatic setpoints, thereby transforming them from maladaptive to adaptive cognition (Pargament, 1997). Exploring how different forms of religion and spirituality affect the trade-off between cognitive flexibility and stability (Zmigrod et al., 2019) in relation to the classical trade-off between neural network plasticity and stability (Abraham & Robins, 2005; Jedlicka et al., 2023) could also be interesting.

Religious cognition may have evolutionary roots in pre-existing cognitive processes (Azari et al., 2001; Kapogiannis et al., 2009). According to evolutionary frameworks, religion evolved from "ordinary" forms of mental or cognitive abilities, such as agency detection (J. L. Barrett, 2000). The main cognitive and motivational mechanisms that promote religious beliefs and behaviours have been summarised in previous work (Norenzayan & Gervais, 2013). These 'ordinary', non-religious cognitive abilities may subsequently have been shaped by natural selection into adaptive mechanisms that promote cooperation and prosociality (Kapogiannis et al., 2009; Norenzayan & Gervais, 2013; Purzycki et al., 2016; Pyysiäinen & Hauser, 2010). In agreement with this, the Costly Signaling Theory (CST) views the prosociality of religion as the benefit that outweighs the costs of religious behaviours. Religious rituals such as fasting, prayer and pilgrimage are costly in terms of time and resources, but they signal the commitment to shared goals and thereby enhance social group cohesion (Bulbulia, 2012; Potz, 2022).

The brain regions and functions that support the “ordinary” cognitive abilities, such as agency detection, can provide insight into which brain regions and functions may have evolved to facilitate spiritual and religious experiences or thought. For example, agency detection is supported by certain parts of the three key networks (DMN, CEN/FPN and SN) that comprise the above-mentioned TPM (McNamara & Grafman, 2024). These include the TPJ and mPFC, which are both implicated in theory of mind (Saxe & Kanwisher, 2003). Similarly, brain regions supporting social interaction and theory of mind have been shown to be active during prayer (Schjødt et al., 2009) and the psychological processing of religious statements (Kapogiannis et al., 2009). Again, however, it is important to bear in mind that the structures that belong to these key networks do not operate in isolation. They are constantly interacting, increasing or decreasing their activation depending, for instance, on the introspective or extrospective nature of ongoing cognitive processes.

The framework of evolutionary trade-offs could partially explain the spread of religious concepts. There is a trade-off between counterintuitiveness, which enhances memorability (Atran & Norenzayan, 2004), and the cognitive resources required to understand and represent counterintuitive concepts (J. L. Barrett, 2000). Religious concepts may belong to the category of 'minimally counterintuitive concepts', which are close to a 'conceptual optimum' (J. L. Barrett, 2000; Sommer et al., 2023). That is to say, they are salient and interesting yet can still be grasped without extensive cognitive resources. This balanced trade-off, although not the only factor, supports their spread. Future work could address whether this cognitive balance, combined with other factors such as the mentioned prosociality of certain religious frameworks (e.g. Abrahamic religions), might account for their global spread. ((Interestingly, evolutionary medicine also has the potential to contribute to theological thinking, for example regarding theodicy (Horvat, 2023).)

The above-discussed hypothesis that the ecstasy associated with seizures is an expression of impaired predictive coding in the brain (Picard & Friston, 2014), can also be revisited in the context of evolutionary medicine. Another possibility is that ecstatic states evolved as a psychological defence against existential threats. Seizures during epilepsy may coincidentally activate a subcircuit of protective neural networks. Additonally, the brain’s high sensitivity to seizures could be a significant evolutionary cost incurred for the highly evolved cognitive abilities that maximise information processing per unit of energy expenditure (Stöber et al., 2023). These cognitive capabilities include those that support religious and spiritual experiences ((Boyer & Baumard, 2016; Boyer & Liénard, 2020); see also (Kapogiannis et al., 2009)), which might explain the partial overlap between seizure- and ecstasy-related spatiotemporal brain activity. However, all of these possibilities remain speculative hypotheses require empirical studies.

10. Prospects for further research

Several possible avenues for future research have already been mentioned. As neuroscientific research into spirituality and religiosity is still in its infancy, many questions remain unanswered, particularly with regard to cellular and subcellular changes. Empirical tests of initial proposals are needed to understand the effects of psychedelics on individual cells and their neuronal processes - dendrites (Savalia et al., 2021). Also relevant in this context is the new cellular theory of conscious perception mentioned above, which links conscious sensations to the integration of ascending and descending signals in the dendrites of the cortical pyramidal cells in the fifth layer of the cerebral cortex and to their role in predictive coding (Aru et al., 2020). This "Dendritic Integration Theory" (DIT,(Aru et al., 2020; Storm et al., 2024)) is partly linked to the popular "Integrated Information Theory" (IIT, (Tononi et al., 2016)), which has recently been highly controversially criticised (Arnold et al., 2025; Fleming et al., 2023). The criticism of IIT as "pseudoscience" has been exaggerated, but the controversies show that we cannot yet mathematically and neurobiologically capture states of consciousness satisfactorily.

In addition to IIT/DIT, there are other, and not necessarily mutually exclusive theories of consciousness, such as global neuronal workspace theory (GWNT), recurrent processing theory (RPT), higher-order theories (HOT), predictive processing (PP) but also less mainstream theories such as conscious electromagnetic information (cemi) field theory, orchestrated objective reduction (Orch-Or) or cellular

basis of consciousness (CBC) theory and many others (for recent reviews see (Bayne et al., 2024; Kuhn, 2024; Mudrik et al., 2025; Storm et al., 2024). The plethora of different theories of consciousness (Kuhn, 2024) shows that consciousness is still an unsolved problem of neuroscience and cognitive science. And this is all the more true for altered states of consciousness during spiritual and religious experiences. It may be that conscious states, or cognitive processes in general, are not fully reducible to computation (Jaeger et al., 2024; Jedlicka, 2005; Tononi et al., 2025). However, this does not mean that we should stop developing computational models of cognitive and neural states, including those related to religious and spiritual experiences, as even incomplete models provide insights and reveal gaps in our understanding.

In addition, little is known about whether new non-invasive methods of brain stimulation (e.g. TMS) can be used to influence spiritual or religious experiences and/or their neural effects. It is possible that TMS can induce or enhance meditation-like effects with antidepressant-like structural changes in the brain. In the future it may be possible to identify optimised interventions that combine meditation and TMS. Multi-scale modelling of TMS-induced plasticity (Shirinpour et al., 2021) may be a complementary method in the search for optimised TMS protocols.

Furthermore, it is an exciting and unresolved question as to how cognitive phenomena such as wonder and awe (Fuller, 2009; Keltner, 2023), flow (Kotler et al., 2022), insight (Aru et al., 2023), gratitude (Henning et al., 2017), laughter (Palagi et al., 2022) or trance (Hove et al., 2016; Hove & Stelzer, 2018; Huels et al., 2021; Mainieri et al., 2017; Schoeller, 2023) are associated with or different from other spiritual or spirituality-related phenomena (such as mind-wandering, see (Wahbeh et al., 2023)) and their mechanisms. It would be interesting to investigate whether distinct types of spirituality or spiritual-like states are characterized by common neural mechanisms. In this context, it can be mentioned that there are various altered states of consciousness (ASC) that are induced through meditation, prayer, or psychedelics, but also through techniques that have no direct connection to spirituality (e.g. hyperventilation, (Havenith et al., 2024; Uthaug et al., 2022)). From a phenomenological and neurobiological perspective, it would be intriguing to closely examine the similarities and differences between the various ASCs. Future research could therefore help to discover common neural and cognitive principles of the different ASCs. General frameworks have begun to be formulated, for example, as mentioned above, based on predictive coding or complex systems theory (e.g. (F. S. Barrett & Griffiths, 2018; Berkovich-Ohana et al., 2020; Gervais et al., 2023; Girn et al., 2023; Stoliker et al., 2022; van Elk & Aleman, 2017)). However, these conceptual frameworks, including predictive processing, may need to be refined and extended, or even revised (Nave, 2024).

11. Philosophical implications: Hard and easy problems and the danger of exaggerated reductionism and dualism

David Chalmers famously distinguished between the hard and easy problems of consciousness (Chalmers, 1995). The hard problems are related to the difficulty of explaining how objective, physical mechanisms can give rise to subjective, abstract, first-person conscious experiences (“qualia”) that may be irreducible to physical mechanisms. In contrast, the easy problems are related to the search for the neural correlates of conscious processes. Following David Chalmers' categorisation (Chalmers, 1995), we can distinguish between hard and easy problems regarding the neurobiological basis of religious and spiritual experience. The hard problems relate to answering the question how and why can the observed brain processes give rise to subjective religious or spiritual experiences, often associated with altered states of consciousness. In our review, we have focused on the (philosophically but not scientifically) easier problems, related to answering the question that can be investigated empirically: What neural processes What neural processes or what spatial and temporal patterns of brain activity accompany religious and spiritual experiences? In prior sections, we detailed brain regions and networks (e.g., DMN, SN, CEN/FPN) linked to meditation, prayer, and psychedelics.

The study of neural mechanisms of spiritual and religious experiences is important not only in and of itself but also in understanding dynamics of largely self-generated cognitive processes and their evolutionary development. As such, it can contribute to the progress of neuroscience, neurophilosophy and neurotheology (Newberg, 2018; Schjoedt, 2009). However, in order to fulfil this potential, we believe

it is important to take a critical look at two popular perspectives that in our view may end up standing in the way of scientific progress in this field:

(1) Excessive reductionism downplays the hard problems of consciousness mentioned above and assumes that complex mental phenomena such as higher consciousness and related spiritual and religious experiences can be fully explained neurobiologically. Neurobiological reductionism regards mental events as "nothing else but" neural events. Such "nothing else but" reductionism ("nothingelsebuttery") is a philosophical or ontological reductionism and not a legitimate scientific or methodological reductionism (Jedlicka, 2005). Methodological reductionism in the natural sciences legitimately attempts to explain complex phenomena by simpler phenomena. Such scientific reductionism is often successful. However, when complex phenomena such as conscious experience, cannot be linearly attributed to lower-level mechanisms, reductionism should be seen as a possible philosophical or metaphysical view, but not as the only view clearly supported by empirical neuroscience. Furthermore, there are valid anti-reductionist approaches within the natural sciences that view mental events as emergent phenomena, which are not fully or linearly reducible to lower (e.g. neuronal or molecular) mechanisms or levels (e.g., (Bunge, 1977; Clayton, 2004; Ellis, 2012; Turkheimer et al., 2019)). There is now an increasing number of authors whose conceptions of emergence and causation include irreducible causal links at the macroscale (Grasso et al., 2021; Hoel et al., 2013) or even top-down (downward) causation from mental phenomena to neuronal ones (Ellis, 2005, 2012; Juarrero, 2009; Mitchell & Potter, 2024; D. Noble, 2012). Moreover, the so-called multiple realisability ((Bickle, 1998; Figdor, 2010) or related degeneracy (i.e. the ability of several structurally different low-level mechanisms to underlie similar high-level phenomena, (Cropper et al., 2016; Edelman & Gally, 2001; Goaillard & Marder, 2021; Seifert et al., 2016; Stöber et al., 2023; Westlin et al., 2023)), suggest the impossibility of a fully mechanistic and monocausal top-down reduction of high-level phenomena. A single molecule or neuron or neural circuit will likely not be able to account for complex cognitive states because there is no evidence of linear one-to-one mapping between lower and higher levels (Albantakis et al., 2024; Stöber et al., 2023; Westlin et al., 2023). For example, a recent thought experiment suggests that neuronal spiking may not be sufficient to account for conscious perception (Gidon et al., 2022). The failure of such simplistic, bottom-up models of neurophenomenological causation (Grasso et al., 2021; Mitchell & Potter, 2024) is the reason why we see a shift towards non-reductionist, multi-causal, anti-localisationist, network-oriented and multiscale approaches in neuroscience and cognitive science (Deacon, 2018; Dickinson et al., 2022; Gründer et al., 2024; C. T. Miller et al., 2022; Mitchell, 2018; S. Noble et al., 2024; Parker, 2022; Pessoa, 2017, 2023). Anti-localisationist views are often a critical response to radical localisationism, which holds that cognitive functions correspond to very specific parts of the brain.

(2) On the other end of the philosophical spectrum, we find strongly dualistic theories (Mudrik & Maoz, 2015), which draw a strong line between physical and mental processes, and as a consequence claim that neural mechanisms do not contribute at all to the emergence of spiritual experiences and are insignificant for their explanation. The successes of reductionist neuroscientific approaches in highlighting neuronal structures and dynamics that are closely associated with (discussed above) show the limitations of such dualistic theories.

By critically examining these two extreme positions we can take a more integrative approach towards the complex, reciprocal and likely highly nonlinear interactions between neuronal and subjective dynamics of spiritual experiences. In this way, we can open up a constructive dialogue between natural science, philosophy and theology within the framework of the "neuro" subfields of these three disciplines; neuroscience, neurophilosophy and neurotheology (see Phillips et al., 2020). This avoids the reductionist conclusion that neuroscience has proven spirituality and religion to be mere ‘brain constructs’ just as much as the dualistic idea that spirituality can exist purely ‘outside the brain’.

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Highlights

- *We review current knowledge about the neural underpinnings of a wide range of spiritual experiences, including meditation, prayer, near-death experiences, ecstatic epilepsy, and psychedelics.*
- *We critically evaluate reductionist approaches to these experiences and emphasise the need for integrative, multiscale frameworks that incorporate predictive coding, complex systems theory and non-localisationist perspectives.*
- *We frame the beneficial effects of spiritual and religious practices in the context of evolutionary medicine.*
- *We discuss new perspectives on altered states of consciousness as complex dynamical phenomena, including insights into their potential adaptive significance.*