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Review article

Brain mechanisms in religion and spirituality: An integrative predictive processing framework

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ABSTRACT

We present the theory of predictive processing as a unifying framework to account for the neurocognitive basis of religion and spirituality. Our model is substantiated by discussing four different brain mechanisms that play a key role in religion and spirituality: temporal brain areas are associated with religious visions and ecstatic experiences; multisensory brain areas and the default mode network are involved in self-transcendent experiences; the Theory of Mind-network is associated with prayer experiences and over attribution of intentionality; top-down mechanisms instantiated in the anterior cingulate cortex and the medial prefrontal cortex could be involved in acquiring and maintaining intuitive supernatural beliefs. We compare the predictive processing model with two-systems accounts of religion and spirituality, by highlighting the central role of prediction error monitoring. We conclude by presenting novel predictions for future research and by discussing the philosophical and theological implications of neuroscientific research on religion and spirituality.

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1. Introduction

The last decades have seen an increased interest in studying the biological and neurocognitive basis of spirituality and religion. Through the use of neuroimaging techniques, brain stimulation studies and studies with neuropsychological patients, our understanding of the brain areas and networks involved in religion has increased dramatically, thereby providing unique insight in the *proximate* mechanisms that support supernatural beliefs and experiences. However, many findings in the literature often appear to be contradictory, lack appropriate methods and analyses, and the results are inconclusive [e.g., Schjoedt, 2009]. Furthermore, there is currently no up-to-date review and integrative framework that accounts for the different findings that have been reported in the literature. The most recent systematic reviews of neuroimaging studies on religion and spirituality date from before 2010 (Schjoedt, 2009; Cahn and Polich, 2006; Fingelkurts and Fingelkurts, 2009) and since then many new studies have been conducted that are highly relevant for our understanding of the neurocognitive basis of religion and spirituality. Therefore the aim of this review article is to develop a theoretical framework to account for the neurocognitive basis of religious and spiritual beliefs and experiences and to show how this framework is substantiated by empirical findings. To this end we will discuss neuropsychological studies, experimental studies using brain stimulation techniques and psychopharmacological manipulations, and neuroimaging studies that have focused on the topic of religion and spirituality.

First, we present a novel integrative model regarding the neurocognitive basis of religion and spirituality. Building on concepts derived from predictive processing accounts (Apps and Tsakiris, 2014a; Clark, 2013; Seth, 2013), we propose a model in which religious beliefs and experiences are primarily related to a differential weighting of interoceptive and exteroceptive information. Next, to substantiate our model with empirical evidence, we distinguish four neurocognitive mechanisms underlying specific religious beliefs and experiences (see: Table 1). First, we describe the role of the temporal cortex and the limbic system in religious experiences and self-transcendent emotions. Second, we highlight how brain areas supporting multisensory integration and the default mode network (DMN) are involved in spiritual and self-transcendent experiences. Third, we focus on the so-called theory-of-mind (ToM) network that could play a role in personal experiences of God (Spreng et al., 2009). Fourth, the role of top-down processes (i.e., expectations, inhibition and prediction error-monitoring mechanisms) in religious beliefs and experiences is discussed.

Table 1
Overview of brain mechanisms and regions, their respective function and the supposed relation with religious and spiritual beliefs and experiences (R/S). STS = Superior Temporal Sulcus; MTL = Medial Temporal Lobes; FFA = Fusiform Face Area; TPJ = Temporo-Parietal Junction; SPL = Superior Parietal Lobe; IPL = Inferior Parietal Lobe; PCC = Posterior Cingulate Cortex; MPFC = Medial Prefrontal Cortex; ACC = Anterior Cingulate Cortex.

1. Temporal brain areas Brain Structures: Hippocampus; Amygdala; STS; MTL; FFA Function: Memory retrieval; Emotional coloring of experience; Biological motion perception; Face perception R/S: Visions; Hallucinations; Déjà-vu experiences
2A Multisensory Integration Brain structures: TPJ; SPL; IPL Function: Bodily self-consciousness; Multisensory integration R/S: Mystical experiences; self-transcendence; out-of body-experiences; feeling of a presence
2B Default Mode Network Brain structures: PCC; Precuneus; IPL; Lateral Temporal Cortex Function: Self-referential processing; Mind-wandering R/S: Mystical experiences; Ego-dissolution; Reflective religious beliefs
4. Theory-of-Mind Network Brain structures: MPFC; STS; TPJ Function: Social Cognition; Communication; Intentionality perception R/S: Prayer; Belief in personal God; Over-attribution of agency
5. Error-Monitoring Mechanisms Brain structures: ACC; MPFC; dopaminergic system Function: Prediction error-monitoring; Belief-maintenance and updating R/S: Openness to religious authority and rituals;

Our proposed model is unique as it provides a unifying account of the neurocognitive basis of religiosity and spirituality thereby integrating recent findings from different fields (e.g., contemporary cognitive psychology and neuroscience, the psychology and anthropology of religion). The model also provides a systematic overview of cognitive elicitors of religious and spiritual experiences and thereby allows generating novel and testable predictions to be addressed in future studies and we discuss the hypothesis-generating potential of our framework in Section 4. We also relate the predictive processing model to dual process accounts of religion and spirituality, such as the corrective model (Risen, 2016; Kahneman and Frederick, 2005) and cognitive-experiential self-theory (Kirkpatrick and Epstein, 1992; Epstein, 1994). In the final section we discuss the potential shortcomings and limitations of the different studies that we presented and we discuss the philosophical and theological implications of neuroscientific research on religion and spirituality.

2. Theoretical framework

2.1. Defining religion and spirituality

Religion and spirituality are broad phenomena that entail a wide range of different beliefs, practices and experiences and in the literature many different definitions have been proposed (Paloutzian and Park, 2013). In our review we start from a so-called building block approach to the study of religion and spirituality (Taves, 2011; Taves and Asprem, 2016), by focusing on the basic constituent neurocognitive mechanisms that enable the emergence of religious and spiritual phenomena. On this account, religion is not a sui generis category requiring a unique explanatory framework, but rather it should be investigated how beliefs and experiences are 'deemed religious' by specific persons in specific contexts. Accordingly, atheist beliefs or any other strong conviction for that matter (e.g., political worldviews) may have similar underlying mechanisms as religious beliefs. The predictive processing framework that we propose as a unifying neurocognitive model (see Section 2.2) fits well with this building-block approach, because a central tenet of this model is that prior beliefs shape our perception and experience (Clark, 2013; Taves and Asprem, 2015).

Nonetheless, when talking about religious and spiritual beliefs and experiences, of course we have specific phenomena in mind that are characterized by different key features. Religious beliefs typically refer to the more institutionalized aspects of belief in supernatural beings, such as within traditional religious communities. In contrast, spiritual beliefs refer to the individual and personalized beliefs regarding the transcendent or sacred, which are often based on personal experience rather than tradition. Examples of religious experiences may be found in personal prayer (e.g., a sense of communicating with God), religious perceptions (e.g., hearing the voice of God, seeing the virgin Mary) and experiences of ritualized religious actions (e.g., baptism, Eucharist). Spiritual experiences on the other hand involve the experience of a transcendent reality, and are often characterized by a sense of 'awe', feeling of oneness, loss of sense of space and time and the blurring of the boundaries between self and others (Hood and Chen, 2013).

Broadly speaking, different types of studies on the brain mechanisms in religion and spirituality can be distinguished that were all included in this literature review. First, some studies focus explicitly on contrasting neural activity in believers vs. non-believers, through the use of brain imaging techniques (e.g., focusing on prayer, receiving 'special messages etc.). Second, other studies rely on natural variability in religiosity or spirituality in neuropsychological patients associated with specific cortical damage or dysfunction (e.g., as observed in epilepsy or schizophrenia). A third group of neuroscientific studies focuses on aberrant phenomena and experiences more broadly, such as out-of-body-experiences, mystical experiences and psychedelic experiences. All these studies provide converging insight in the complex topic of religious and spiritual beliefs and experiences. We should note that in our review we did not include most research on meditation and mindfulness, which has been reviewed extensively elsewhere (Cahn and Polich, 2006; Fox et al., 2016; Tang et al., 2015). We only discuss meditation studies insofar as they directly relate to the topic of religion and spirituality, e.g., when discussing peak-experiences or mystical experiences.

2.2. Predictive processing

We propose that the predictive processing framework has the potential to provide a unifying theory to integrate different findings regarding the neurocognitive basis of religion and spirituality. In the last decade the theory of predictive processing has gained ground as a unifying computational framework in psychology and neuroscience to account for a wide range of different phenomena (Clark, 2013); for current debates on the explanatory scope and potential of predictive processing to account for more complex experiences, e.g., such as faith healing or the experience of miracles, see for instance: (Taves and Asprem, 2016; Schjoedt et al., 2013); on the relationship with alternative neurocognitive models, see for instance: (van der Helm, 2015).

The basic idea of the predictive processing framework is simple and straightforward: humans use prior cognitive models to predict and perceive the world, and these models are updated in case of conflicting predictions or sensory information. Similar ideas can be found already in the work of Piaget who referred to the process of updating one's mental schemas in the light of new information as 'accomodation' (Piaget, 1962). Also in the social-psychological literature similar notions of prior belief updating (or the lack thereof) in the light of novel information can be found, for instance in the meaning maintenance model (Proulx et al., 2012), cognitive dissonance theory (Harmon-Jones, 2000) and the corrective dual process model proposed by Kahneman and Frederick (2005) (Sloman, 2002). What primarily distinguishes the predictive processing model from these alternative accounts is that according to the predictive processing model, prior beliefs are hierarchically structured, in a recurrent hierarchical network. On top of the hierarchy complex representations yield predictions to lower-level systems, to anticipate the sensory input. The top-down predictive signals have a certain precision, based on one's prior experience. In case of a mismatch between the predicted and the observed sensory consequences, the prior model is updated according to the weight assigned to the prediction error signal.

Let's take an example to make the predictive processing model more concrete. Suppose you visit a church while being on holidays. In this case, based on your past experiences, your brain will generate strong predictions regarding the types of sensory events you will encounter while walking around in the church. You will expect to see paintings of Jesus for instance or statues of mother Mary. Now, suppose that none of these predictions comes true, as there turn out to be no paintings or statues at all. In that case, you can update your prior beliefs based on the sensory input (e.g., "Apparently this is not a Roman-Catholic but a Protestant church"). Or suppose that the church is quite dark and in a catacomb you see a dark statue. In this case, based on your prior expectations, you will be quite likely to infer that the statue represents mother Mary and your brain 'fills in' the dark shapes with the missing details (e.g., you may detect a veil around the head of the statue). In case you have very specific or detailed expectations about the type of church you visit (e.g., this is a Romanesque church from the early 13th century built in Italy) the precision of your predictions is quite high and this will yield even stronger top-down effect on perception (e.g., you expect to see a wooden statue seated on the 'Throne of Wisdom'). Importantly, top-down predictions are multisensory in nature and involve the different sensory modalities (e.g., when entering the church you expect to see specific images, hear organ music, smell incense etc.). Information from these different sensory modalities in turn can be used to update one's expectations and prior beliefs.

An important implication of the predictive processing view is that the way in which we perceive the world is strongly determined by our prior expectations and beliefs. At a basic level it has been shown for instance that manipulating participants' expectations regarding the type of stimuli that will be presented results in a top-down modulation of early sensory brain areas that become less responsive to predicted stimuli (e.g., seeing the virgin Mary in a church), whereas an unexpected stimulus results in a prediction error signal (e.g., seeing a statue of Lenin in a church; cf. (Kok et al., 2012). Thus, the predictive processing framework has been proposed as a unifying theory of brain function, according to which the

brain should be understood as an inference machine that continuously generates predictions about the surrounding world (Clark, 2013). Most research on predictive processing has focused on relatively low-level phenomena such as sensory perception and the framework also accounts for visual and auditory hallucinations, which may be related to imprecision in the coding of predictive signals (Fletcher and Frith, 2009; Horga et al., 2014; Vercammen and Aleman, 2010). Recently however, several theoretical proposals have been made to extend the predictive processing framework to more complex phenomena as well, such as emotion (Joffily and Coricelli, 2013), the feeling of 'presence' (Seth et al., 2012), self-recognition (Apps and Tsakiris, 2014a), bodily self-consciousness (Blanke et al., 2015) and theory of mind reasoning (Ondobaka et al., in press). In addition, the predictive processing framework has been applied to account for the effects of ritual on cognitive resource depletion (Schjoedt et al., 2013) and as a theoretical framework to understand the emergence of religious experiences (Taves and Asprem, 2016). These theoretical proposals provide an important extension of the predictive processing model to account for more high-level aspects of human cognition and experience.

2.3. Predictive processing: interoceptive and exteroceptive signals

Importantly, whereas the predictive processing model outlined above accounts for perceptual experiences of externally triggered events (e.g., seeing images in a church), an important aspect of human experience (and religious experience in particular) involves the body as well (Barsalou et al., 2005a). For instance, in many religious ceremonies believers adopt a specific body posture (e.g., kneeling, raising one's hands etc.), perform specific bodily actions (e.g., singing, chanting, moving in synchrony) or undergo specific bodily experiences (e.g., shaking, trembling, loss of awareness of the body). Accordingly, a unifying theory of religious experiences should account not only for the emergence of exteroceptive events (i.e., related to external stimuli from the environment), but also for interoceptive events (i.e., related body). Therefore, as a starting point for our theoretical framework, we take the predictive processing model as presented in Fig. 1 and as described in more detail elsewhere (Seth, 2013; Seth et al., 2012). Basically, prior beliefs are at the basis of a generative model that is used to generate both exteroceptive predictions about information in the surrounding world and interoceptive predictions about one's internal bodily states. In case of a mismatch between predicted and observed input, a prediction error signal is generated, which in turn leads to an updating of the generative model and one's prior beliefs.

According to the predictive framework presented in Fig. 1, higher-level multimodal brain areas aim to minimize 'prediction error' signals from lower-level sensory areas in a Bayes-optimal fashion, through the continuous updating of generative models of the 'self' (cf., (Seth, 2013). Hierarchically organized models are used to make predictions regarding both exteroceptive signals (i.e., bottom-up input from the environment; upper part of Fig. 1) and interoceptive signals (i.e., bottom-up input from the body, such as proprioceptive and visceral signals related to heart rate, blood pressure, temperature; lower part of Fig. 1) and feed-forward prediction-error signals are used to update these models. Top-down precision weighting determines the relative importance of prediction error signals for updating generative models (Friston, 2009) and the dopaminergic system plays an important role in this process (Friston, 2009). Thus, according to the predictive processing framework, prior experiences of the body and the environment are at the basis of a model that generates predictions about what the body and the world will be like in the future, thereby minimizing prediction error signals.

The predictive processing framework of the bodily self accounts for the fact that the bodily self is highly malleable and plastic, as observed in studies with neuropsychological patients and experimental studies in healthy subjects on body illusions (Apps and Tsakiris, 2014b). For instance, in the 'rubber hand' illusion exteroceptive signals regarding the visual presentation of a rubber hand are used to update the self-model, in order to explain away the prediction error signals generated by low-level visual and tactile brain areas. The model also offers a basic account of how the self is differentiated from the environment, which relies on the successful prediction of the sensory consequences of one's actions in the world. Imprecision in the coding of predictions about one's action effects may result in disturbances in self-other differentiation, as observed in schizophrenia for instance (Fletcher and Frith, 2009). Surprisingly, although the predictive processing framework has been applied in the context of bodily disorders that are characterized by an altered perception of the bodily self, such as in 'out-of-body' or 'heautoscopic experiences' (Blanke, 2012), religious and spiritual beliefs and experiences have remained beyond the scope of mainstream research in this area.

In the next section we will specify how the proposed predictive processing framework has the potential to account for the emergence of (1) religious visions and hallucinations, (2) mystical experiences, (3) personal experiences of God and (4) the acceptance and maintenance of religious beliefs. We will relate each of these mechanisms to neurocognitive research and highlight how the predictive processing framework can be used to integrate the different findings.

3. Overview of brain areas and mechanisms involved in religion and spirituality

3.1. Religious visions & hallucinations: temporal brain areas

3.1.1. Hallucinations and predictive signals

With respect to *religious hallucinations and visions* (e.g., seeing the virgin Mary; hearing the voice of God), on the predictive processing account these experiences are likely related to imprecise coding of predictive signals (Fletcher and Frith, 2009). Self-generated action, thought and mental imagery is typically accompanied by efferent signals that send predictive signals to lower-level sensory regions regarding the expected sensory consequences. Imprecision in the coding of these predictive signals may result in a failure to anticipate the sensory effects of one's own inner speech and as a consequence may result in the belief that the voice had an external source. A failure to update one's prior models based on prediction error signals in response to new incoming information may also result in an over-reliance on existing models. Such a mechanism may be at the basis of religious hallucinations (e.g., seeing angels or demons) and delusional beliefs, which are characterized by a persistent commitment to beliefs that do not correspond to reality (Coltheart et al., 2011) and which may occur specifically when sensory input is ambiguous or distorted (Arzy et al., 2005). Importantly, according to the predictive processing model the content of hallucinations is strongly determined by one's prior beliefs and generative models that are the basis of these predictions – in line with the proposed role of culture on shaping religious visions (Cassaniti and Luhrmann, 2014).

3.1.2. Religious visions and temporal lobe activity

Preliminary evidence for the role of altered predictive signals in the emergence of religious visions and hallucinations may be found in research on the relation between temporal lobe activity and religion and spirituality. Disturbed activity in the temporal lobes – as observed in patients with schizophrenia or epilepsy – may result in a disruption of the process whereby predictive signals are used to attenuate activity in sensory brain regions (Horga et al., 2014).

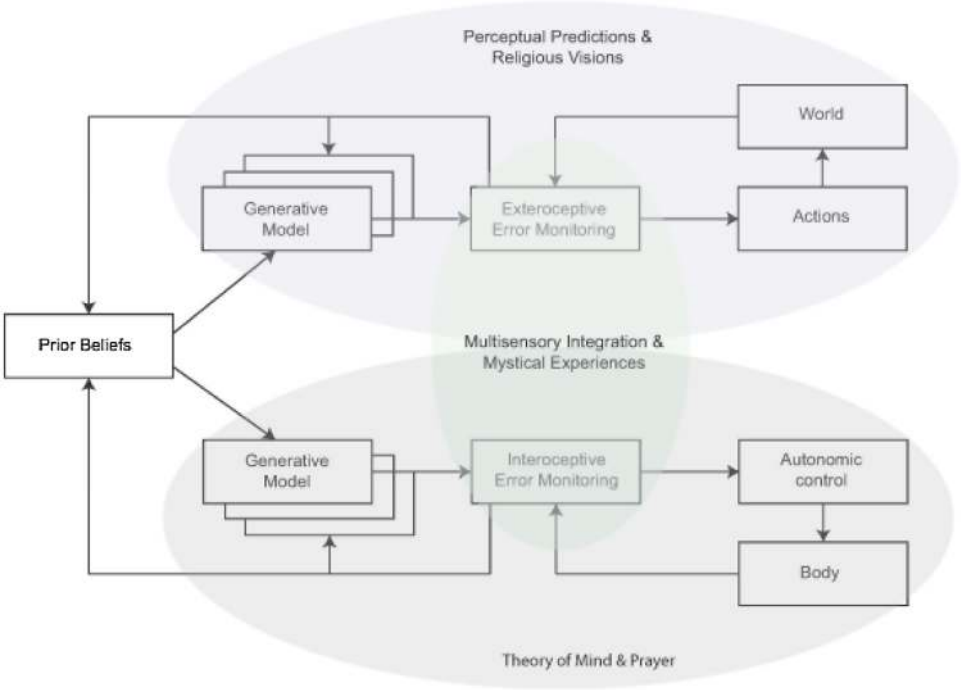

Fig. 1. A predictive coding model of religion and spirituality. An inferred model of the self and the world relies on generative models of both exteroceptive (upper part) and interoceptive signals (lower part), which are updated through a process of prediction error monitoring. Mystical and self-transcendent experiences may be related to a differential weighting of interoceptive and exteroceptive information for an inferred model of the self. Religious hallucinations and visions may occur due to changes in the exteroceptive prediction error monitoring process. Prayer and communication with supernatural entities may rely on an interoceptive inference process.

Indeed, traditionally religious experiences have been associated with altered functioning of the temporal lobes [for historical overview, see: (Devinsky and Lai, 2008). Patients with temporal lobe epilepsy may have profound religious experiences as a consequence of spontaneous discharges in temporal areas and the limbic system (Joseph, 2001; Saver and Rabin, 1997). However, we note that only a minority of all patients with temporal lobe epilepsy actually spontaneously report religious experiences and the experimental evidence for the supposed relation between temporal lobe epilepsy patients and hyper-religiosity is anecdotal at best (Ramachandran et al., 1998).[1]

Also, early attempts to obtain more causal evidence for the role of the temporal lobes in religious and spiritual experiences have suffered from methodological shortcomings (for critical review, see: (Schjoedt, 2009). Michael Persinger developed the highly publicized 'god helmet' that induced a weak complex magnetic field to directly stimulate the temporal lobes (Cook and Persinger, 1997; Hill and Persinger, 2003; Persinger and Healey, 2002; St Pierre and Persinger, 2006). Participants in his studies frequently reported spiritual and mystical experiences, such as seeing visions, hearing voices and feeling the presence of another being in the experimental room. However, independent replications showed that these effects could be accounted for by suggestibility (Granqvist et al., 2005; Granqvist and Larsson, 2006): even when the helmet was not turned on at all, participants still reported spiritual experiences and the strength of these experiences was fully predicted by their score on a proneness to suggestibility scale. Other studies that have systematically investigated the possibility to induce spiritual experience through the use of weak magnetic fields, also indicate that all subjective effects reported were related to individual differences in suggestibility rather than the presence or absence of magnetic stimulation (French et al., 2009). Indeed, researchers have capitalized on these findings by using placebo brain stimulation as a powerful tool to experimentally induce mystical experiences in the lab and to directly investigate the behavioral and neurocognitive effects of these self-induced experiences (Andersen et al., 2014a; van Elk, 2015a). These findings – in turn – have been framed in terms of a predictive processing account of religious experience (Andersen et al., 2014a): prior expectations and suggestibility result in specific predictions and shape subjective experiences. For instance, frequently reported spontaneous placebo-evoked somatic sensations (e.g., feeling heat, or body parts feeling heavy; cf., (Beissner et al., 2015) are interpreted in a spiritual fashion within the context of the placebo god-helmet (Andersen et al., 2014a; van Elk, 2015a).

Notwithstanding, the notion that the temporal lobes and its deeper structures such as the amygdala and the hippocampus (see Fig. 2) are related to religiosity is compatible with research on neuropsychological patients, deep-brain stimulation studies and neuroimaging experiments. In a comprehensive study the neuropsychological profile of a group of patients characterized by right-sided temporal lobe atrophy was assessed and compared with a group of patients with semantic dementia and mostly left-sided temporal lobe atrophy (Chan et al., 2009). The patients with right-temporal lobe atrophy showed strong impairments in episodic memory, spatial orientation and behavioral disinhibition. Interestingly, the authors also report that symptoms specifically associated with temporal lobe atrophy in a sub-group of patients included hyper-religiosity, visual hallucinations of animate objects and multi-modal sensory experiences. In another large-scale prospective study in older adults, a relationship was observed between hippocampal size and life-changing spiritual experiences (Owen et al., 2011): participants who reported having had an impactful religious experience were characterized by a stronger reduction of the size of the hippocampus (while controlling for demo-

[1] For instance, an often cited experimental study reporting a stronger autonomic skin-conductance response to religious stimuli in temporal lobe epilepsy compared to control participants that is described in the book 'Phantoms in the Brain' (1998) has never been published in the peer-reviewed literature.

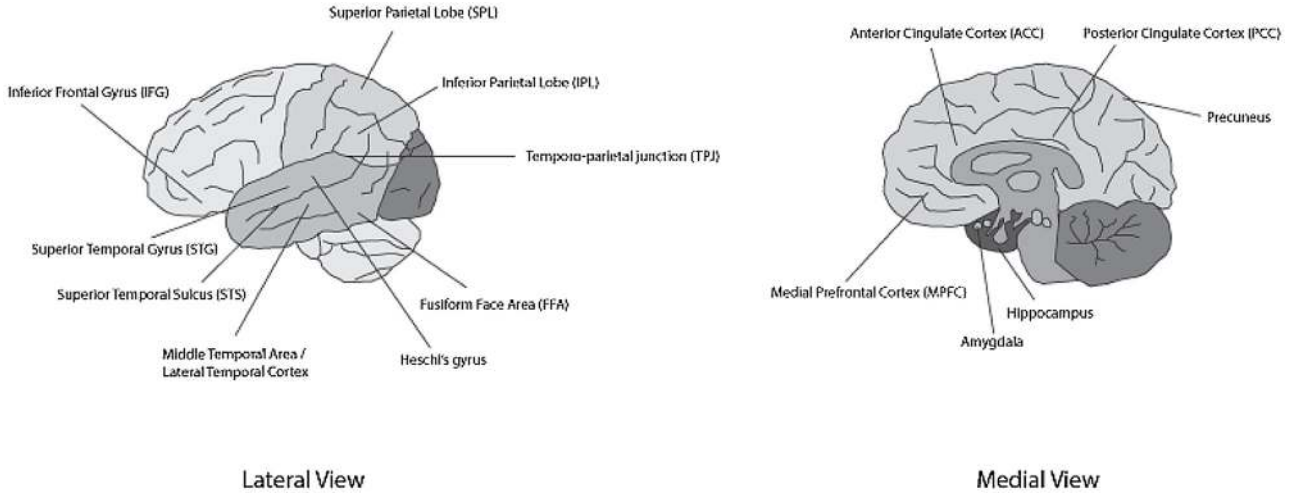

Fig. 2. Overview of different brain regions that have been related to religious and spiritual beliefs and experiences. Left side: lateral view of the brain. Right side: medial view of the brain.

Table 2
Open questions regarding the involvement of limbic system, multisensory processing and the default mode network, the Theory of Mind network and prediction error monitoring mechanisms in religious beliefs and experiences. TPJ = Temporo-Parietal Junction; SPL = Superior Parietal Lobe; DMN = Default Mode Network; rTPJ = right Temporo-Parietal Junction.

Temporal brain areas
• What are the longitudinal effects of religiosity on temporal lobe structure? Are structural differences in temporal lobe structure between believers and skeptics the cause or the consequence of religious experience?
• How does one's religious upbringing determine the type and content of religious experiences? Do Catholics for instance more often report visual religious experiences whereas Protestants predominantly report auditory religious experiences?
Multisensory Integration & the Default Mode Network
• What is the precise relation between the function and structure of multisensory brain regions, such as the TPJ and SPL and mystical experiences? Are these experiences characterized by an activation or de-activation of multisensory brain regions? Does damage to the TPJ and SPL impair multisensory integration and facilitate self-transcendent experiences?
• Do mystical and self-transcendent experiences rely on a differential weighting of exteroceptive compared to interoceptive information for an inferred model of the bodily self?
• Are people who frequently report having had self-transcendent experiences characterized by an increased decoupling between brain networks involved in exteroceptive compared to interoceptive processing?
• Are there differences between believers and non-believers in performance on tasks that have been associated with DMN activation, such as mind-wandering, self-referential processing or interoceptive awareness?
ToM network
• Are religious believers characterized by larger ToM-related areas, such as the rTPJ, as identified through voxel-based morphometry (VBM)?
• Are religious believers characterized by a hyperactive ToM-network and a stronger functional connectivity within the ToM-network?
• Does vividness of prayer experiences correlate with functional connectivity within the ToM-network and what is the relation with practice (e.g. h of experience practicing prayer)?
Prediction error-monitoring mechanisms
• Are believers compared to skeptics characterized by structural brain differences in prediction error-monitoring mechanisms, such as the anterior cingulate cortex and in differential tonic levels of dopamine?

graphic variables) and greater hippocampal volume reduction was associated with religious affiliation and identification as born-again Christian. More specifically, Protestants not identifying as born-again had the least grey matter loss: significantly greater hippocampal atrophy was observed from baseline to final assessment among born-again Protestants, Catholics, and those with no religious affiliation. In contrast however, in a different study, an increased volume of the right middle temporal lobe in religious believers was associated with experiencing an intimate relationship with God (Kapogiannis et al., 2009a). Thus, the evidence pertaining to the relationship between religiosity and hippocampal volume is mixed and more research is needed before strong conclusions are warranted (see Table 2).

Interestingly, in a recent study researchers had the unique opportunity to study religious conversion in a patient suffering from temporal lobe epilepsy (Arzy and Schurr, 2016). In the postictal period following the epileptic seizures, the patient had a messianic revelation experience, during which he experienced

receiving special messages from God. Analysis of the EEG signal and source-analysis of the gamma-frequency band comparing the post-ictal to the pre-ictal period showed increased activity of the left medial prefrontal cortex in association with this religious experience, potentially reflecting the involvement of the theory-of-mind network in receiving supernatural messages (see also: Section 3.4). Thereby this study provides strong evidence for the causal relation of disturbed activity in the temporal lobe for religious and conversion experiences.

Studies using stimulation through implanted electrodes in patients provide more direct insight in the phenomenological characteristics of altered temporal lobe functioning. For instance, electrical stimulation of the hippocampus and the amygdala has been shown to result in déjà-vu like experiences, visual hallucinations of well-known scenes and feelings of 'strangeness' (Vignal et al., 2007). This finding is corroborated by other studies, showing for instance that stimulation of the parahippocampal place area results in the perception of indoor and outdoor familiar places (Megevand et al., 2014). Stimulation of more lateral parts of the temporal lobe, such as the fusiform face area (see Fig. 2) resulted in the perception of illusory faces (i.e., pareidolia) and strong distortions in face perception and recognition (Parvizi et al., 2012). Similarly, in a study using transcranial magnetic stimulation (TMS) it was found that inhibition of the left lateral temporal area resulted in a reduced tendency to perceive meaningful information in visual noise (Bell et al., 2007).

Together these studies are in line with the notion that temporal brain areas contain complex visual representations of objects, humans and scenes (Grill-Spector and Malach, 2004) and disturbed activity of these regions may result in the perception of stored visual representations. A potential mechanism whereby these brain regions may become activated is described by the predictive processing framework – similar to the neurocognitive account that has been proposed to explain hallucinations in schizophrenia (see also: Section 2.2). More specifically, imprecision in the coding of efferent predictive signals (e.g., in association with self-generated visual imagery or speech) may result in the experience of 'unpredicted' sensory events. Indeed, many patients suffering from temporal lobe epilepsy frequently experience psychosis-like experiences, especially during post-ictal phases (DuBois et al., 2011; Devinsky et al., 1995). Similarly, patients with schizophrenia frequently report auditory hallucinations, which have also been related to a deficit in coding prediction error signals in temporal brain regions (Horga et al., 2014).

3.1.3. Effects of context and culture

As indicated above, an important implication of the predictive processing framework is that the specific perceptions that people report, will strongly depend on their prior perceptual experiences. With respect to religion an interesting suggestion that has been made in the literature, for instance, is that religious experiences in Catholics may primarily be characterized by visual reports (e.g., of seeing the virgin Mary) given the predominance of visual images in catholic worship, whereas Protestants may more often report auditory religious experiences, given the emphasis on the Word in Protestantism (Cassaniti and Luhrmann, 2014). To our knowledge this suggestion has never been directly confirmed (for suggestions for future studies, see Table 2), but indirect evidence for the role of culture on perceptual experiences can be found in cross-cultural studies, reporting for instance that the type of auditory hallucinations differ strongly between cultures (Luhrmann et al., 2015). Whereas patients with psychosis in the USA often reported hearing auditory commands, in Ghana and India people more often reported engaging in a rich relationship with the perceived voice [for discussion and overview of research in this field, see: (Laroi et al., 2014)]. In addition, we note that the conversion experience that was recently reported in a patient suffering from temporal lobe epilepsy was also strongly shaped by the cultural and religious context (Arzy and Schurr, 2016): during the experience, the patient engaged in Jewish ritualistic action, responded by shouting the Jewish word for God ('Adonai') and received specific instructions regarding the people of Israel. In a recent line of experimental studies we systematically investigated the role of prior expectations on self-induced mystical experiences (Andersen et al., 2014b; van Elk, 2015b). By using a placebo God-helmet participants were induced to believe that electromagnetic stimulation of their temporal lobes would elicit feeling-of-a-presence experiences. Especially highly suggestible participants and people with a strong background of paranormal experiences were more likely to report extraordinary experiences during sham-stimulation with the helmet. These studies show the strong role of cultural context and prior expectations in shaping religious experience – in line with the building-block approach to religion (Taves, 2011) and the predictive processing framework as outlined in Section 2.

3.2. Mystical experiences & multisensory integration

In the second section we will focus on the topic of spiritual and mystical experiences, that are often characterized by a reduced awareness of one's body, the loss of sense of space and time and strong feelings of connectedness to the surrounding world (Hood and Chen, 2013). A key mechanism that could be involved in these experiences is the process of multisensory integration – as will be discussed in Section 3.2.2–and changes in self-referential processing and default mode network (DMN) activity – as discussed in Section 3.2.3.

3.2.1. Predictive processing, interoception & exteroception

Multisensory integration refers to the process whereby information from different sensory modalities (e.g., vision, touch, sound, smell, proprioception, vestibular information) is integrated to form a coherent percept of our body and the environment (Blanke et al., 2015). According to a predictive processing framework our brain forms a coherent perception of our body based on both exteroceptive input from the environment and interoceptive input related to bodily signals (see Fig. 1; (Apps and Tsakiris, 2014a; Blanke et al., 2015)). In addition, information is shared between sensory modalities to 'predict' or 'explain away' sensory signals in other sensory modalities (e.g., based on proprioceptive signals our brain makes visual predictions about the expected location of our arm). Changes in this process of multisensory integration may result in an altered perception of our body, as observed for instance in out-of-body experiences (Blanke, 2012) and psychiatric disorders such as depersonalization and derealization (Seth et al., 2012). In these cases a different weighting of sensory signals results in a discrepancy between the felt and the observed location of one's body, as in an out-of-body-experience for instance.

Mystical and self-transcendent experiences can be understood in relation to changes in multisensory integration resulting in an altered self-referential processing. According to the predictive processing framework the induction of a mystical experience relies on a change in the relative weighting of exteroceptive compared to interoceptive signals for constructing a generative model of the self (see Fig. 1). A reduced weighting of interoceptive signals for the bodily self-model, may result in a reduced awareness of the spatiotemporal limits of one's body. On the other hand, increasing the reliance on exteroceptive signals may result in strong feelings of connectedness with the surrounding world. Thus, according to the model, mystical experiences may emerge because of (1) a differential weighting of interoceptive compared to exteroceptive signals, (2) changes the interoceptive or exteroceptive error monitoring

process and (3) individual differences in practice, brain structure and function and development in relation to interoception.

For instance, in the rubber hand illusion visual information is weighted more strongly than proprioceptive information in a generative model of the bodily self, which in turn results in top-down effects on the processing of bodily signals (e.g., the position of one's hand; (Apps and Tsakiris, 2014a)). Similarly, in the full body illusion a visual representation of the self results in an updating of the bodily self model and a subsequent mislocalization of the position of one's body (Blanke et al., 2015). Mystical experiences could be understood as an extreme case in which the weighting of interoceptive signals for the bodily self-model is strongly reduced, while the reliance on exteroceptive signals increases, resulting in a reduced awareness of one's physical body and the feeling of a strong connection with the surrounding world.

Importantly, the predictive processing framework also offers a powerful theoretical tool to understand the consequences of mystical and spiritual experiences at both a behavioral, brain and developmental level of investigation. Think for instance about how a mountaineer undergoes a process of spiritual transformation upon having a mystical experience at a mountain (Arzy et al., 2005). Initially, the mountaineer has a clearly defined representation of his/her bodily self (e.g., the body is constrained in space and time, the body constitutes our centre of conscious experience etc.). Through the mystical experience, which is characterized by changes in bodily self-perception and feelings of a strong connection between the self and the environment, the bodily self-model may be updated. On the predictive processing model, different responses are possible to a transcendent experience. First, the original bodily self-model could be revised with an updated prediction (typically implemented by some form of gradient descent; cf., (Friston, 2002), for example by changing one's self-model (e.g., 'the "self" is seen as unconstrained and can be extended to the surrounding world). Alternatively, the parameters of the generative model that generated the predictions about the bodily self could be revised (Friston, 2003) such that exteroceptive signals receive more importance compared to interoceptive signals. An alternative response could be to obtain additional information, i.e., by sampling the world (Friston et al., 2012a), as in this case by asking other mountaineers about their experience. Finally, the state of the world could be changed, i.e., by active inference (Brown et al., 2011): the mountaineer may engage in behavior to bring the self model and the environment closer together (e.g., developing a preference for visiting specific places). Which strategy is employed depends on various aspects, for example the amount of reducible versus irreducible uncertainty in the environment (Yu and Dayan, 2005). On a longer time scale, prediction errors (or the relative absence thereof) shape the generative self models, to improve future predictions (Montague et al., 2012) and the effects of mystical experiences on personality and behavior can be framed in terms of such high-level generative models (e.g., the mountaineer may become more susceptible to having a mystical experience, through changes in the self-model).

3.2.2. Neurocognitive mechanisms in mystical experiences: multisensory integration

Below we will outline how studies on bodily disorders, neuroimaging studies on meditation and studies with neuropsychological patients are broadly congruent with these theoretical notions derived from the predictive processing framework. It has been found for instance that focal electrical stimulation of the right temporo-parietal junction (rTPJ; see Fig. 2) – a multisensory brain region that integrates inputs from different sensory modalities – can result in the experimental induction of an out-of-body-experience, whereby the patient perceives him/herself from a different spatial perspective (Blanke et al., 2002). In a different patient, stimulation of the left TPJ resulted in the induction of an illusory shadow person, who was perceived to be looming slightly behind the participant's body (Arzy et al., 2006). Similar observations were made in a group of patients characterized by damage of the left TPJ, who frequently reported the feeling of a presence in daily life (Blanke et al., 2003; Blanke et al., 2014). Notably, such experiences can also be induced experimentally by manipulating the congruence between felt and observed touches, as in the 'full body illusion' (Ehrsson, 2007; Lenggenhager et al., 2011) and more recently in a setup involving a robotic device manipulating the congruence between performed and felt touches resulting in the 'feeling of a presence' (Blanke et al., 2014). Together these findings suggest that top-down influences on multisensory integration result in a differential weighting of sensory information, which may underlie the dissociation between the observed and the felt perspective in out-of-body-experiences or the experiences of a felt presence. Of course, these experiences – though strange and bizarre – are not intrinsically religious or spiritual. Rather, it is often through a process of cultural learning that these experiences are framed within a religious or spiritual framework, e.g., as presenting evidence for an afterlife (e.g., as in near-death experiences) or the existence of invisible supernatural agents. Thus, extraordinary experiences may be 'deemed' religious based on one's specific cultural and religious background – in line with the predictive processing model according to which one's prior expectations shape perception and experience.

Interestingly, although multisensory integration has been primarily related to clinical disorders, hardly any attention has been paid to the involvement of this process in so-called self-transcendent and mystical experiences that are characterized by a loss of sense of space and time, the blurring of self-other boundaries and a strong feeling of unity and connectedness with the world as a whole [for discussion, see: van Elk, 2015a]. Some initial evidence for the involvement of multisensory integration in religion and spirituality can be found in early studies on the neural correlates of mystical experiences (Beauregard and Paquette, 2008, 2006a; Newberg and Iversen, 2003). Andrew Newberg notoriously studied neural activity in monks reporting a peak-experience, labeled 'absolutely unitary being' [actually close related to the so-called 'relaxation response'; cf., Lazar et al., 2000]. He showed that this experience was associated with a decreased activation of the superior parietal lobes (SPL) and the temporo-parietal junction (TPJ; see Fig. 2), which was interpreted as being in line with phenomenological reports of a reduced awareness of space (Newberg et al., 2001a) – in which these areas play a key role (e.g., as evidenced by neglect patients who are often characterized by damage to the right SPL; cf. Mesulam, 1981). Similarly, it was found that prayer experiences were associated with an increased activation of prefrontal areas, which in turn were correlated to a decreased activation of the SPL (Newberg et al., 2003). In contrast, another study reported increased activation of the parietal cortex when Carmelite nuns were required to remember and reflect on a mystical experience, which was interpreted as reflecting changes in the body schema (Beauregard and Paquette, 2006). In studies involving long-term meditators similar changes in the activation of bilateral parietal regions have been observed (Brefczynski-Lewis et al., 2007), but rather than reflecting changes in space- or self-perception, these effects could also be related to differences in directing attention, which is a key component of focused attention meditation. More recently, in a completely different research field, it was found that the experience of flow during online video gaming was also associated with a decreased activation of the bilateral IPL (Klasen et al., 2012). Together, these studies corroborate the notion that a changed activation in areas involved in spatial and bodily processing may be at the basis of mystical and flow-like experiences.

Another line of evidence for the involvement of multisensory integration in religion and spirituality can be found in studies with neuropsychological patients, indicating dramatic changes in spirituality traits following brain damage to the right inferior parietal lobe [IPL; see Fig. 2; Johnstone et al., 2012; Urgesi et al., 2010]. For instance, a study on patients with traumatic brain injury showed that spirituality measures were negatively associated with right parietal lobe function, as measured using a judgment of line orientation task (Johnstone and Glass, 2008). Similar findings were obtained in follow-up studies in which also a negative correlation was observed between performance on the judgment of line orientation task and spirituality – and specifically forgiveness (Johnstone et al., 2012; Johnstone et al., 2014). The authors interpret these findings as being related to a process of selflessness (see also: Beauregard and Paquette, 2006): a reduced awareness of the self and the spatial and temporal limits of one's body may make it easier to experience feelings of self-transcendence. A similar suggestion was made in a study involving patients who had undergone neurosurgery, while the personality trait of 'self-transcendence' was measured several days prior and following the brain surgery (Urgesi et al., 2010). Selective lesions to the bilateral TPJ – but not to other brain regions – were associated with an increase in self-transcendence and the authors suggest that a reduced process of multisensory integration could facilitate transcending the boundaries of one's self, thus explaining the increase in self-transcendence observed. In a brain stimulation study, a TMS-induced reduced activation of the TPJ enhanced one's implicit attitude toward spirituality, as measured using an implicit association task, again indicating a critical role of this region for spirituality (Crescentini et al., 2014). Specifically, it was found that TMS pulses delivered over the TPJ resulted in an increased congruency-effect for religious and spiritual items, as measured with an implicit association task, indicating that participants more readily associated themselves with spirituality when activity in the TPJ was reduced. In a follow-up study using a similar experimental design but with excitatory (intermittent theta-burst) TMS, it was found that increased activation of the TPJ resulted in a reduced tendency to associate oneself with spiritual or religious items (Crescentini et al., 2015). Together these findings suggest that a reduced activity in the TPJ may predispose people for becoming more open to spirituality. In contrast, however, in a voxel-based morphometry (VBM) study with healthy human volunteers, a positive relation was observed between the volume of the inferior parietal lobe and the personality trait of self-transcendence (Van Schuerbeek et al., 2011). Thus, though the precise relation between multisensory brain regions is still a matter of ongoing debate (see Table 2 for key questions), overall the findings converge in suggesting that an altered activity in the TPJ and the SPL – related to the integration of interoceptive and exteroceptive signals – may be associated with an altered experience of the self, as in mystical and transcendent experiences.

3.2.3. Neurocognitive mechanisms in mystical experiences: the default mode network

According to the predictive processing model, mystical experiences arise because of a differential weighting of interoceptive compared to exteroceptive signals. Although interoceptive signals are primarily related to the body, an inferred model of the self (as represented in Fig. 1) also involves reflective beliefs about the self. During mystical experiences these reflective aspects of the self are likely also suppressed – resulting in an experience that has been referred to as ego-dissolution. The neurocognitive mechanisms underlying these experiences can be found in an altered activity of the default mode network (DMN) – an interrelated network of brain regions that is involved in self-referential processing.

The *DMN* consists of the medial prefrontal cortex (MPFC), the posterior cingulate cortex (PCC)/precuneus, the inferior parietal lobe (IPL), the lateral temporal cortex (LTC), and the hippocampal formation (Spreng et al., 2010; Vincent et al., 2008; Raichle, 2015). The DMN was first described by identifying brain areas that were found consistently activated during 'rest' compared to 'task' blocks (Raichle and Snyder, 2007; Raichle et al., 2001), reflecting the involvement of this network in participants' spontaneous engagement in self-referential processing and ruminative thought. Indeed, several studies have suggested that the DMN is anti-correlated with task-related networks, such that activity in the DMN decreases when participants are working on an attention-demanding task (Raichle and Snyder, 2007). Complementary methods that have been used to identify the DMN are provided by functional and structural connectivity analyses (Greicius et al., 2009), showing that the DMN consists of a network of highly interconnected brain regions that correlate with each other even in the absence of external stimuli. A homologue of the DMN has been identified in primates (e.g., macaque monkeys) and the size of this network was found to be associated with the animal's position within the social hierarchy of the group [for review, see: (Mars et al., 2012)]. This indicates that the DMN may represent a phylogenetically old mechanism that may have evolved to support social cognition, interaction and coordination.

Interestingly, an altered activity of the DMN has been associated with the use of psychedelic drugs, such as psilocybin and ayahuasca. Traditionally these drugs have been used as part of indigenous religious ceremonies to achieve self-transcendent states. At a phenomenological level the use of psilocybin has been associated with the experience of 'ego-dissolution': the awareness of the self is reduced and people often report mystical experiences characterized by a loss of sense of space, time and body-awareness (Griffiths et al., 2006). The use of psilocybin has been associated with a decreased activation of the DMN using a design in which subjects were scanned before and after intravenous infusions of psilocybin and placebo with a task-free protocol (Carhart-Harris et al., 2012). A decreased activity was observed in the anterior cingulate cortex (ACC), the PCC and the MPFC (see Fig. 2) and the strength of the decrease was related to the intensity of the subjective effects. In addition, a decreased functional connectivity was observed between the PCC and the MPFC, indicating that the communication within the DMN is reduced during a drug-induced mystical state. A follow-up magneto-encephalography (MEG) study indicated that the use of psilocybin is associated with an overall decrease in oscillatory power that was localized primarily to the DMN (Muthukumaraswamy et al., 2013). In another study the use of psilocybin and the accompanying experience of 'ego dissolution' was associated with a decreased coupling between the medial temporal lobe and higher-level cortical regions and a disintegration of the fronto-parietal salience network (Lebedev et al., 2015). Similarly, the use of ayahuasca has been shown to result in a strong deactivation of the DMN and a decreased functional connectivity between the PCC and the MPFC (Palhano-Fontes et al., 2015). Together these studies indicate that the experience of ego-dissolution is associated with a decreased activity of the DMN, which could reflect reduced self-referential processing.

Recently, a number of studies have also elucidated the neural correlates of the experience of ego dissolution in association with the use of Lysergic acid diethylamide [LSD; Carhart-Harris et al., 2016; Tagliazucchi et al., 2016; Speth et al., 2016]. These studies provide further evidence for the notion that the experience of ego-dissolution is associated with a decreased activation of the DMN. In addition, LSD induced a strong disintegration of the intrinsic connectivity *within* specific brain networks, while enhancing the connectivity *between* different networks, thereby potentially highlighting a key neurocognitive mechanism under-

lying the psychedelic experience, of which synesthesia (i.e., the involuntary perception of events in a different sensory modality) is a key feature (Carhart-Harris et al., 2014). This intriguing finding also indicates that a key feature of mystical-type experiences is a change in multisensory integration – whereby information from different sensory modalities becomes excessively coupled – as discussed in Section 3.2.

Additional evidence for the involvement of the DMN in experiences characterized by a loss of self-awareness can be found in research on 'flow': it was found for instance that experimentally induced flow (by dynamically adjusting task difficulty as a function of the participant's competence) was associated with a decreased activation of the MPFC, which was also interpreted as reflecting a process of reduced self-referential processing (Ulrich et al., 2014). In contrast, in a recent study it was found that shamanic practitioners who engaged in a trance-like state showed an increased centrality and a stronger coupling between the posterior cingulate cortex (PCC; again a key region of the DMN) with the attentional control network, involving the dorsal anterior cingulate cortex (ACC), the insula and the IPL (Hove et al., 2016). This finding was interpreted as reflecting the increased relevance of self-generated thought and self-referential processing – associated with the experience of 'insight' during an absorptive state of mind.

Although these studies are broadly congruent with the notion that an altered processing in brain areas involved in multisensory integration may underlie mystical and self-transcendent experiences, so far we do not have unequivocal evidence for the theoretical notion that mystical experiences indeed rely on a stronger weighting of exteroceptive compared to interoceptive signals (as suggested in Fig. 1). Recent studies showing a bidirectional relation between interoceptive and exteroceptive processing provide preliminary support for our theoretical proposal (Ainley et al., 2013; Suzuki et al., 2013; Ronchi et al., 2015; Sel et al., 2016). Behavioral studies are needed to establish whether people actually show a reduced awareness of bodily signals during mystical states and whether mystics are characterized by long-term changes in body awareness (e.g., as measured by the rubber hand illusion for instance; see Table 2 for research suggestions).

3.3. Prayer experiences & the theory-of-mind network

3.3.1. Theory-of-mind reasoning & interoceptive inference

A central feature of most mono- and polytheistic religions is the belief in a supernatural agent that is powerful, omniscient and benevolent (Atran and Norenzayan, 2004). An important prerequisite for belief in supernatural agents is the ability to attribute mental states to other agents and to make mental state inferences– a capacity that is often referred to as theory of mind (ToM) reasoning or mentalizing (Leslie, 1994). The ToM-network may be considered a key neurocognitive mechanism involved in belief in supernatural agents, reflective aspects of religious beliefs and personal experiences of God.

On the predictive processing account outlined above, a process of interoceptive predictive inference could underlie the attribution of emotions and mental states to others (Ondobaka et al., in press; Barrett and Simmons, 2015). Based on observed social cues we make an inference to the most likely model allowing us to explain and predict the other's mental states. Similarly, we can engage in a process of imagined predictive inference, by simulating offline inferences about mental state attributions to others. Extending this framework to the context of religion, a potential implication is that believers tend to engage in interoceptive predictive inference to infer mental states of God, e.g., during prayer experiences or when making inferences about God's mind. Indeed it has been argued that a process of mentalizing and theory-of-mind reasoning is a prerequisite for the endorsement of supernatural beliefs. A parallel may be drawn with theories suggesting that believers may be characterized by a hyperactive theory-of-mind (ToM) or agency-detection module, while at the same time skeptics and atheists may be characterized by a hypo-active theory-of-mind mechanism (Norenzayan et al., 2012). Believers may tend to attribute intentionality even in cases where this is not applicable [e.g., attributing intentions to physical objects, to nature etc.; Bering, 2002], whereas deficits in ToM reasoning makes it difficult for people to conceive God (Norenzayan et al., 2012). According to the predictive coding account, believers compared to skeptics may display stronger interoceptive inference, and a stronger engagement in interoceptive inference may be associated with more vivid and more frequent experiences of God (Luhrmann et al., 2010). This leads to novel and testable hypotheses regarding the relation between supernatural beliefs and experiences and interoceptive awareness [Seth et al., 2012; van Elk et al., 2014; see Table 2].

Neural evidence that is broadly compatible with this view can be found in neuroimaging studies on prayer and reflective thinking about God, indicating that the Theory-of-Mind (ToM) network plays a crucial role in these activities. The ToM network consists of several regions that are activated depending on the specific task and experimental paradigm (Carrington and Bailey, 2009). The ToM-network shows some overlap with the DMN and core regions include the medial prefrontal cortex (MPFC)/orbitofrontal cortex, the superior temporal sulcus and posterior temporal areas around the temporo-parietal junction (TPJ; see Fig. 2). The ToM network is typically found active in association with the processing of social information (Schilbach et al., 2008), involving for instance the observation of animated movies, interactive paradigms, story comprehension and the processing of mental state terms (Carrington and Bailey, 2009). Specifically, the MPFC has been associated with mental state attribution and the TPJ in differentiating between self and others (Eichele et al., 2008). Below we will outline how the ToM network is involved in mentalizing, reflective aspects of religious beliefs and prayer experiences.

3.3.2. Neurocognitive mechanisms in mentalizing, reflective beliefs & prayer

Evolutionary psychologists have proposed that the universal propensity for anthropomorphism and mentalizing may be at the basis of belief in supernatural beings (Barrett, 2000). Interestingly, it has been found that individual differences in anthropomorphism, i.e., the tendency to attribute mental properties to physical objects, was associated with structural differences in the size of the right TPJ (Cullen et al., 2014), thereby indicating a crucial role of the ToM network (of which TPJ is a key region) in anthropomorphism. In addition, it has been proposed that hyperactivity of the ToM-network may underlie communication with supernatural entities, for instance during prayer or facilitated communication (Dein and Littlewood, 2011), akin to the hyperactive ToM-network activity observed in schizophrenia (Walter et al., 2009). Given the strong relation between schizophrenia and psychic beliefs (Thalbourne, 1994), this hypothesis could apply specifically to paranormal believers who often engage in personal communication with supernatural entities (e.g., channeling) and frequently report spontaneously receiving 'special' messages (Lindeman and Svedholm, 2012). Related to this, it has been found that disfunctioning of the DMN (which shows some overlap with the ToM-network) is related to psychopathology (Whitfield-Gabrieli and Ford, 2012). For instance in schizophrenia and depression the DMN was found to be hyperactive and hyperconnected compared to healthy control participants, whereas autism has been associated with a decreased functional connectivity within the DMN (Assaf et al., 2010).

Other studies have investigated the relation between DMN activity and self-referential processing in believers and non-believers (Wu et al., 2010; Han et al., 2008). Whereas non-religious

participants showed a stronger activity for self- compared to other-related processing in the ventral MPFC, religious participants primarily showed activity for self-related processing in the dorsal MPFC (Han et al., 2008). The strength of the dorsal MPFC activity was related to the subjective importance of Jesus' judgments in evaluations of another person, suggesting that religiosity has an effect on the processing of self-referential information. In a related study two different ethnic groups of Chinese Han and Tibetan participants were compared (Wu et al., 2010). It was found that whereas the Han participants showed the classical pattern for self-referential processing, the difference between self- and other-related processing was less pronounced for Tibetan Buddhists, suggesting that one's belief system directly affects the neurocognitive mechanisms underlying self-referential processing (Wu et al., 2010). Finally, in another study it was found that Christian compared to non-religious participants showed an altered functional connectivity between the VMPFC and the posterior parietal cortex (PPC) for trait judgments about religious compared to political leaders (Ge et al., 2009). Specifically, Christian participants showed a similar functional connectivity pattern between the VMPC and the PPC for making self-judgments and judgments about Jesus, but not when making judgments about a political leader. In contrast, non-religious participants showed an increased functional connectivity between the VMPC and the PPC both for the retrieval of knowledge about religious and political leaders (e.g., Jesus and Sakyamuni) compared to when making self-referential judgments. These findings suggest a strong overlap for Christians in the neural representation of the self and religiously important others.

Several studies have focused on the neural correlates of the retrieval of religious knowledge. For instance, the retrieval of semantic knowledge about God (e.g., indicating whether God is powerful, all-knowing etc.) by believers was associated with an increased activation of the MPFC (Kapogiannis et al., 2009b). By using granger-causality analysis the relation between different brain networks associated with particular dimensions of religious beliefs was characterized (Kapogiannis et al., 2014): it was found that the ToM-network was driving activity in the other networks – consistent with a role for ToM and mentalizing in supporting supernatural beliefs. In another study it was found that the evaluation of religious (and ordinary) statements was associated with activation of the ventral MPFC (Harris et al., 2009) – however the specific contrast between evaluating religious and non-religious statements revealed activity in many different areas as well, including the precuneus, and the anterior and posterior cingulate, thus obscuring the precise role of the DMN in religious beliefs.

More direct evidence for the involvement of the ToM-network in religious beliefs and experiences can be found in neuroimaging studies contrasting brain activation during religious activities in believers versus non-believers. In one study, religious (N = 6) and non-religious participants (N = 6) were required to recite a religious verse (i.e. Psalm 23), a nursery rhyme or to read a passage from a phone book (Azari et al., 2001). By using Positron-Emission Tomography (PET) scanning, it was found that religious recital compared to the control conditions specifically recruited the dorsomedial prefrontal cortex and the medial parietal cortex – which are areas that show an overlap with the ToM network (in addition the dorsolateral prefrontal cortex was also found to be activated, but this area is not considered part of the ToM network).

Interestingly, several studies provide converging evidence for the notion that activation of the ToM network in believers may be specifically involved in mentalizing and relating the self to God. In an fMRI study, religious participants were required to perform an improvised prayer or a ritualized prayer in the MRI scanner and as a control condition they were required to make a wishing list for Santa Claus or to say a nursery rhyme (Schjoedt et al., 2009). It was found that improvised prayer compared to the other conditions resulted in an increased activation of areas in the ToM-network, involving the MPFC, precuneus and the temporo-parietal junction – suggesting that spontaneous prayer recruits brain areas involved in social cognition. Similar findings were obtained in a follow-up study, in which a strong overlap was found between the areas involved in improvised personal prayer and thinking about a loved one (Neubauer, 2014). These studies provide direct support for the notion that praying in the presence of an inferred supernatural being recruits similar neurocognitive resources, as involved in social cognition and interaction. These findings can be framed in the predictive processing account – outlined above – according to which mentalizing involves the predictive inference of interoceptive states of others.

So far most studies that we discussed in this review have focused on neurocognitive mechanisms in religious believers. In addition, a lot of research has focused on the cognitive biases and neural mechanisms associated with paranormal beliefs (Irwin, 2009). Belief in paranormal phenomena entails an eclectic range of different beliefs and practices, ranging from belief in precognition, astrology and witchcraft, to telekinesis and channeling (Lindeman and Svedholm, 2012). The precise relation between religious and paranormal beliefs is fuzzy: on the one hand paranormal beliefs are often explicitly rejected by mainstream religions, while on the other hand religious and paranormal beliefs may also be highly correlated depending on the specific group that was tested (Lindeman and Svedholm, 2012). Still, studies on paranormal believers can provide fascinating insight in the neurocognitive mechanisms underlying supernatural beliefs – which are shared by most psychics (e.g., belief in ghosts, spirits, demons, angels etc.).

With respect to the involvement of the ToM-network in supernatural beliefs, in an fMRI study a group of paranormal believers were presented with movements representing random, mechanical or intentional movements (Riekki et al., 2014). It was found that psychics compared to skeptics tended to attribute more intentions to random movements and showed a stronger activation of the MPFC in association with the observation of random movements; furthermore strength of activity of the MPFC was correlated to the intentionality ratings. The authors interpreted this finding as reflecting that a stronger engagement of ToM processing may underlie paranormal beliefs, which are often characterized by an over-attribution of intentionality.

Thus, the ToM network may be primarily involved in supporting mentalizing about supernatural agents and over-attributing intentionality to natural objects and phenomena. In addition, activity in parts of the ToM-network has been associated with the retrieval of religious knowledge and religious self-referential processing (i.e., relating oneself to one's religion). A number of open questions with respect to the involvement of the ToM-network remain: e.g., to what extent structural and functional differences in the ToM-network are related to vividness of prayer experiences, the amount of practice with prayer and interoceptive awareness (see Table 2). Recent research has shown for instance that through extensive practice, religious believers can have very intense and vivid experiences of God's presence – a process that has been referred to as 'inner sense cultivation' (Luhrmann et al., 2010). Through specific practices involving prayer and meditation, mental imagery and spontaneous thoughts are attributed to God and the ToM-network likely plays a key role in this process.

3.4. Top-down processing: expectations, inhibition and prediction error monitoring

3.4.1. Prediction error monitoring

An intriguing question is why so many people across the world maintain their religious beliefs, in spite of being confronted with evidence that is potentially in conflict with their worldview. Within

the predictive processing framework it has been suggested that religious believers are characterized by a reduced process of prediction error monitoring (Schjoedt et al., 2013). As a consequence religious believers increase the reliance on prior beliefs and charismatic religious authorities, while they decrease the impact of error signals triggered by potentially conflicting sensory information. In addition, according to the naturalness of religion account (Barrett, 2000; McCauley and Cohen, 2010), because of a reduced process of prediction error monitoring or cognitive inhibition, believers more easily give in to the natural tendency for endorsing supernatural beliefs and having supernatural experiences. We will discuss the empirical evidence for the notion of altered error monitoring in religious believers in more detail in Section 3.4.2.

Also religious and spiritual experiences may be related to a process of cognitive resource depletion or prediction error monitoring (Schjoedt et al., 2013). More specifically, religious experiences could be induced by (1) boosting prior expectations or beliefs, (2) reducing prediction error signals by removing sensory input (i.e., sensory isolation or deprivation) and (3) reducing the prediction error monitoring process itself; or a combination of these three factors [e.g., Andersen et al., 2014a]. This framework also receives support from different lines of research focusing on the role of the frontal lobes in religion and spirituality.

Indeed several authors have suggested that the frontal lobes and specifically, mechanisms involved in cognitive inhibition and error-monitoring, play an important role in religious beliefs. On the predictive processing account outlined in Section 2 the maintenance of religious beliefs has been related to a reduced processing of error-monitoring, resulting in a strong reliance on prior models that are not updated in the face of conflicting evidence. Furthermore, according to the 'naturalness of religion' hypothesis, humans are characterized by universal cognitive biases that predispose them to believe in the supernatural (McCauley and Cohen, 2010). Such biases involve for instance a tendency to engage in dualistic reasoning, a bias toward detecting agency and anthropomorphic reasoning biases. On the naturalness-of-religion account, atheists are thus prone to similar cognitive biases as believers, but through a process of education and socialization they have learned to suppress their natural tendencies to respond according to these biases. An implication of this view is that skeptics compared to believers may show a stronger process of inhibition, while believers compared to skeptics may be characterized by a reduced process of cognitive inhibition. We note that reduced cognitive inhibition could actually be reflected in a stronger reliance on one's prior (intuitive) knowledge (i.e., stronger top-down processing) as well as an increased proneness to suggestibility and a tendency to agree with suggestions made by others (e.g., charismatic religious leaders) and in the studies discussed below we will find evidence for both processes.

3.4.2. Neural evidence for altered top-down processing in religious beliefs

A first line of evidence supporting the hypothesis of differences in top-down influences can be found in research on paranormal believers who are characterized by a wide range of different beliefs, such as precognition, telekinesis, mind-reading and spiritism (Lindeman and Svedholm, 2012). It has been found that paranormal believers compared to non-believers showed a reduced N400-effect in response to statements reflecting ontological violations (Lindeman et al., 2008), which may reflect a reduced tendency to detect potentially conflicting information. At a behavioral level it has been found that paranormal believers compared to skeptics have a strong tendency to report seeing illusory meaningful patterns in random noise (Blackmore and Moore, 1994) and display a bias toward detecting illusory faces and agency (Riekki et al., 2014; van Elk, 2013), which may also be related to reduced inhibitory processing (or a stronger reliance on top-down prior knowledge) in believers. Finally, in an fMRI study it was found that seeing more 'meaning' in random pictures in paranormal believers was associated with a reduced activation of the right inferior frontal gyrus (IFG; see Fig. 2). The authors argue that this effect could also be related to a process of reduced inhibition of automatic associations (Lindeman et al., 2013). These studies provide tentative evidence for the notion that psychic believers may be characterized by reduced inhibitory processing.

A different line of evidence regarding the involvement of top-down mechanisms in religious beliefs can be found in a study directly manipulating prior expectations regarding the source credibility of a religious message in believers (Schjoedt et al., 2011). In this study religious believers and a control group of participants listened to excerpts of intercessory prayer and they were instructed that the prayer was pronounced either by a Christian, a Christian who was known for his healing powers or a non-Christian. Interestingly, a decrease in neural activation of the frontal executive network (i.e., the anterior cingulate cortex) and the social cognitive brain networks (i.e., the temporo-parietal junction) was observed in believers in response to listening to a Christian who was known for his healing powers. This study demonstrates the dramatic effects of prior expectations: even though the message was the same across conditions, participants' expectations regarding the source of the message affected their interpretation and the error monitoring process during listening to the message. Religious beliefs can also exert a top-down effect on other processes: in an fMRI study it was found that Catholics compared to agnostics and atheists showed a stronger analgesic effect of religious stimuli vs. non-religious stimuli and this effect was associated with an increased up-regulation of the right ventrolateral prefrontal cortex (Wiech et al., 2008). Thus, these studies show that religious beliefs and expectations can exert a strong top-down effect on error-monitoring and pain perception, thereby providing an interesting neurocognitive model for the effects of religious authority and faith healers on believers [i.e., akin to research on hypnosis suggestibility and the placebo effect; cf., Schjoedt et al., 2013].

In another series of studies the error-monitoring mechanism in believers and skeptics was directly probed, by focusing on the error-related negativity (ERN), which represents a neural marker in the EEG signal in response to errors and which has been localized to the ACC (Inzlicht et al., 2009; Inzlicht and Tullett, 2010). It was found that religious believers compared to non-believers showed a reduced ERN in a color-word Stroop task and the authors interpret this finding in relation to the role of religion in providing anxiety-relief (Inzlicht et al., 2009). Furthermore, when presented with religious primes religious participants showed a reduced ERN whereas non-believers showed an enhanced ERN (Inzlicht and Tullett, 2010), and the authors argue that this finding indicates that for believers reminders of religion can reduce anxiety and uncertainty, whereas for non-believers it increases feelings of anxiety. The notion that believers may be characterized by a reduced ERN fits well with the suggestions that a key process underlying religious beliefs is a reduced error-monitoring mechanism, thereby making believers more likely to accept suggestions made by religious authorities or to update their behavior in the light of erroneous responses (Schjoedt et al., 2013).

The involvement of prefrontal areas such as the MPFC and the ACC in religious beliefs is further corroborated by studies with neuropsychological patients. It has been found for instance, that patients with fronto-temporal dementia are characterized by profound changes of the self, including changes in one's religious conviction and even conversion (Miller et al., 2001). In a longitudinal study including a large group of participants the relation between religiosity, church attendance and atrophy of the left and right orbitofrontal cortex (OFC) was investigated (Hayward et al.,

2011). It was found that participants who reported a life-changing religious or spiritual experience or who identified themselves as born-again Protestants were characterized by reduced atrophy of the OFC. The authors interpret this finding as reflecting the positive consequence of religious experiences on mental health and draw a parallel with a study showing that volumetric changes in the OFC were related to negative perceptions of God (Kapogiannis et al., 2009a).

More recently, it was found that lesions to the dorsolateral prefrontal cortex (DLPFC) in patients suffering from traumatic brain injury were also associated with increased mystical experiences (Cristofori et al., 2016). The authors also interpreted this finding in relation to the central role of the DLPFC in executive functioning: a reduced error-monitoring process may predispose people to having a mystical experience. More specifically, mystical experiences may be facilitated by increasing the reliance on prior beliefs, which can be achieved by boosting the participants' expectations, using sensory deprivation and reducing the error monitoring process (Schjoedt et al., 2013). Thus, reduced top-down processing and changes in prefrontal cortex functioning may be associated with an increased tendency to accept supernatural beliefs and an openness to religious and mystical experiences.

3.4.3. Dopamine, precision and maintenance of religious beliefs

It has been suggested that the dopaminergic system plays a central role in the prediction error monitoring process, by coding the precision whereby errors impact subsequent cognitive processing and by serving as a prediction error signal on reward (Friston, 2009; Friston et al., 2012b). A neurobiological account of the role of dopamine in the development and maintenance of delusional beliefs and superstitious behavior has also been developed within the context of the predictive processing framework (Corlett et al., 2010). As dopamine determines the signal-to-noise ratio of prediction error signals, low levels of dopamine result in imprecise priors and small prediction errors. Interestingly, in line with the proposed role of dopamine in coding prediction error signals, and the notion that changes in predictive signaling may be associated with the acceptance and maintenance of religious beliefs, several researchers have pointed out a relation between the dopaminergic system and religious and paranormal beliefs (Butler et al., 2010, 2011a,b; Krummenacher et al., 2010; Schjoedt et al., 2008; Sasaki et al., 2013). For instance, when directly comparing a large group of Parkinson patients with age-matched healthy controls it was found that Parkinson patients (who are characterized by reduced levels of dopamine) scored lower on overall measures of religiosity, in line with the proposed role of dopamine in shaping and maintaining prior beliefs (Butler et al., 2011b). It has also been found that Parkinson patients were less influenced by religious primes compared to control participants (Butler et al., 2010), providing further evidence for the inverse association between dopamine and religiosity. Another study showed that religious priming was only effective among people who had a gene coding for the dopamine 4-receptor (Sasaki et al., 2013). Dopamine also serves to signal reward prediction errors and specific aspects of religious experiences may be reinforced based on their intrinsically rewarding properties (Schjoedt et al., 2008). Increased levels of dopamine in turn may render coincidental events as highly salient, resulting in the development of delusional beliefs (Kapur, 2003). In addition, increased dopamine levels may result in exaggerated precision of prediction error signaling, resulting in a malfunctioning learning process and potentially producing delusional beliefs (Adams et al., 2013). People with schizotypal personality features and unfounded delusional beliefs are for instance characterized by a higher level of dopaminergic activity (Schmack et al., 2015). It was found for instance that the administration of Levodopa to a group of skeptic participants rendered their performance on a perceptual decision making task similar to that of a group of paranormal believers. (Krummenacher et al., 2010). However, there is a lack of studies investigating dopamine transmission in relationship to religiosity in healthy people. Such research is needed before stronger conclusions on the role of dopamine in religious beliefs can be reached.

Thus, the notion that error monitoring mechanisms play a central role in adopting and sustaining religious and paranormal beliefs and the supposed involvement of the dopaminergic system in this process opens interesting avenues for future research (see Table 2). In addition, as will be outlined in more detail in Section 4.2, 'prediction error monitoring' may be considered a central and unifying mechanism that could account for the acceptance and maintenance of religious and spiritual beliefs, as exemplified by the predictive processing framework and dual systems account of religion and spirituality.

It is important to note that the notion of a reduced process of prediction error monitoring does not entail that believers in general are less critical, more impulsive and/or lacking cognitive control. On the contrary: several studies have shown that religion helps people to exert stronger cognitive control in a variety of settings (McCullough and Willoughby, 2009). For example, prayer has been shown to foster self-control (Fincham et al., 2010), to reduce aggression (Bremner et al., 2011) and to counteract self-control depletion (Friese et al., 2014). Notably, Miller et al. (2014) reported a positive association between importance of religiosity and spirituality, but not of church attendance, with cortical thickness of parietal, frontal and occipital regions. These areas overlap with the cognitive control network and the DMN, thereby providing a potential neurocognitive mechanism underlying the observed relation between religion and self-control.

4. Implications of the predictive processing framework

In this section we will shortly discuss the hypothesis-generating potential of the predictive processing framework. We will highlight how the proposed framework leads to novel and testable predictions and what type of studies would be needed to confirm the framework. In the second part we will discuss the relation between the predictive processing framework and other psychological accounts of religious and spiritual beliefs and experiences (i.e., most notably dual process theories). We will highlight that a central and converging theme of the different theoretical proposals is the relative importance of error monitoring for the acquisition of religious beliefs.

4.1. Hypothesis-Generating potential of the predictive processing framework

Throughout this review based on the existing empirical findings, we highlight hypotheses and theoretical predictions to be addressed in future research, as summarized in Table 2. An important question is which specific predictions and hypotheses can be derived from the theoretical framework that we propose – which could not be predicted by existing accounts in the literature.

First, we argue that a central feature of the predictive processing framework is the importance of prediction error signals *within different levels* of a recurrently organized hierarchical network. That is, prediction errors may occur at relatively low levels in the hierarchy (e.g., at a visual level, as when one is expecting a specific visual event) or prediction errors may signal adaptation of high-level predictions (e.g., when updating one's beliefs regarding the existence of UFOs). Low-level changes in prediction error signaling may result in illusory percepts (e.g., visual or auditory hallucinations), while specifically changes in high-level prediction error signaling may be associated with the acceptance and maintenance of complex

belief systems (e.g., conspiracy beliefs; meaningful worldviews). Although most research within the predictive processing framework has focused so far on low-level prediction error signals, the updating of complex belief systems (or the failure thereof) may be central to the acceptance and maintenance of religious beliefs. This could potentially be studied by incorporating methods from social psychology for instance, such as meaning-threat violations (Heine et al., 2006), terror-management manipulations (Greenberg et al., 1997) or manipulating participants' feelings of control (Landau et al., 2015) to investigate how participants respond at a behavioral and neurocognitive level to 'high-level' prediction errors.

Second, prediction error signals are characterized by a certain *precision* determining the effects of prediction error signaling on belief updating and as indicated in Section 3.4.3 dopamine plays an important role in determining the precision of prediction error signaling (Friston, 2010). Imprecise predictions may result in a failure to properly update one's prior models, while hyper-precise prediction error signals may result in a malfunctioning learning process potentially leading up to delusional beliefs (Adams et al., 2013). An interesting parallel may be drawn with research on aging, also indicating that during adolescence, changes in dopaminergic projections are associated with profound changes in the development of one's beliefs and preferences (Wahlstrom et al., 2010). The precision of prediction error signals is also inversely related to the ambiguity of the sensory information: more ambiguous information results in more imprecise predictions and reduced error monitoring (Schjoedt et al., 2013). Thus, our theoretical framework makes testable predictions about when we may expect the development and maintenance of fixed belief systems.

Third, our theoretical model also proposes that prediction error signals may be related to *exteroceptive signals* from the environment or to *interoceptive signals* related to one's body. As outlined in our theoretical model, exteroceptive prediction errors may be related to religious visions and hallucinations, interoceptive prediction errors may play a role in pretend-play and interactions in the presence of a supposed other, and the integration between interoceptive and exteroceptive signals may underlie spiritual and mystical experiences. Theoretical proposals regarding the role of interoceptive and exteroceptive predictive signals have been proposed to account for the 'feeling of presence' and disorders related to depersonalization and derealization (Sethi et al., 2012). Similarly, an interoceptive predictive processing framework has been developed in association with a constructivist view of emotion, which could explain neurocognitive findings with depressive patients and eating disorders (Barrett and Simmons, 2015). Our framework is the first to propose the role of both exteroceptive and interoceptive signals to account for religious beliefs and experiences. Thereby our framework takes into account the importance of the human body in religious practice and experiences (Barsalou et al., 2005b).

As outlined in more detail in Section 3.2.1, the distinction between interoceptive and exteroceptive predictive signals yields testable predictions regarding the role of individual differences in religious and spiritual beliefs and the effects of spirituality on one's body. For instance, spiritual experiences appear to have a strong effect on both physical and mental well-being (Cloninger, 2004). The experience of self-transcendence may help one to cope with difficulties and to experience higher feelings of purpose and meaning (Nygren et al., 2005). In addition, spiritual experiences may be associated with strong changes in autonomous nervous system activity (e.g. the 'relaxation response'), which in turn may directly benefit physical well being (Benson, 1983). Spiritual experiences have also been associated with long-term effects on personality and feelings of meaning and significance (Griffiths et al., 2006; MacLean et al., 2011). Several studies have shown that spiritual and religious experiences can foster environmental awareness and prosocial behavior, possibly through a process of enhanced identification with the surrounding world and a strong feeling of interconnectedness (Kamitsis and Francis, 2013; Piff et al., 2015; Schnall et al., 2010; Zhang et al., 2014). As these examples illustrate, on the predictive processing account, changes in the weighting of interoceptive and exteroceptive signals may have both short-term and long-term consequences.

4.2. Relation with dual process accounts of religion & spirituality

An interesting parallel may be drawn between the predictive processing model outlined above and dual process accounts of religion and spirituality that have been proposed in the social-psychological literature. Dual process accounts come in many different forms, such as the popularized account of System 1 vs. System 2 thinking by Kahneman (2011), Epstein's cognitive-experiential self theory according to which humans process information through a parallel experiential and rational system (Kirkpatrick and Epstein, 1992; Epstein, 1994), and Sloman's two-system model according to which an associative and a rule-based system underlie human reasoning (Sloman, 2002). Basically, these dual process models share the notion that two separate systems or mechanisms underlie all human behavior and cognition: an intuitive, associative, emotional and fast system (usually labeled System 1), and a deliberative, rational and slow system (usually labeled System 2).

Dual process models have been applied to account for superstitious and magical beliefs (Risen, 2016), paranormal beliefs (Lindeman and Aarnio, 2007) and religious beliefs (Gervais and Norenzayan, 2012; Pennycook et al., 2012). Typically, supernatural beliefs have been associated with the intuitive, emotional and associative system 1, while disbelief and atheism are associated with corrective responses from the rational and analytical system 2. Evidence that is broadly congruent with this notion can be found for instance in studies showing that believers compared to non-believers score higher on intuitive compared to analytical thinking (Pennycook et al., 2012; Jack et al., 2016; Shenhav et al., 2012). In addition, many magical intuitions and superstitious biases can be considered as the product of system 1 thinking, resulting for instance in heuristic processing, causal intuitions and the confirmation bias (Risen, 2016). Several studies have also shown that when skeptics are required to reason under time-pressure, they tend to show similar teleological and intuitive reasoning biases as typically observed in supernatural believers (Kelemen and Rosset, 2009; Svedholm and Lindeman, 2013; Kelemen et al., 2013).

Thus, according to dual-process accounts, religious and spiritual beliefs are primarily related to a stronger reliance on the output of system 1 compared to system 2. Importantly, according to the corrective dual process model proposed by Kahneman and Frederick (2005) (Sloman, 2002), by default the intuitive system dominates our beliefs about the world, by generating fast and intuitive responses, which may or may not be corrected by system 2 (see Fig. 3A). When the intuition is overruled, this results in a rejection of supernatural beliefs. However, in some cases the intuition may be sustained – even despite the fact that system 2 detects an error – a process that is referred to as superstitious or religious *acquiescence* (Risen, 2016). Factors determining whether a corrective process is applied or not are individual differences in the ability to engage in analytical thinking, motivational processes and contextual cues. Indeed, individual differences in reliance on respectively analytical (rational) and intuitive (experiential) thinking could contribute to proneness to supernatural beliefs (Epstein, 1994). However, at the same time situational and contextual factors can also determine the relative reliance on system 1 vs. system 2 thinking (Risen, 2016). For instance, during times of stress and uncertainty people are typically more willing to engage in superstitious and magical thinking (Friedland and Keinan, 1991; Keinan, 1994). In addition,

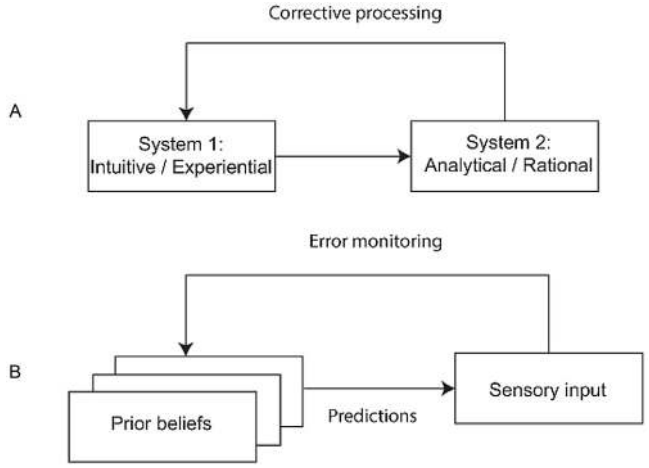

Fig. 3. Comparison between dual process accounts (A) and the predictive processing framework (B) and the central role of corrective processing and prediction error monitoring in updating one's beliefs on both theoretical accounts.

when the stakes of a decision are high people also show a motivated tendency to engage in superstitious behavior and to maintain their beliefs – even though they consider them irrational (Subbotsky, 2001).

The predictive processing model and (corrective) dual process accounts of religion and spirituality converge on the central importance of an error monitoring and correction mechanism in sustaining or rejecting supernatural and superstitious beliefs (see Fig. 3). We note that the main difference between both accounts is that in predictive processing error monitoring is primarily related to the potential conflict between prior beliefs and interoceptive/exteroceptive input, while the corrective dual processing account proposes that error monitoring occurs between the intuitive and analytical system. In addition, on the predictive processing account error monitoring is used for the updating of a hierarchically organized system, while dual systems accounts do not presuppose the existence of generative recurrent belief structures. Finally, an important difference is that the predictive processing framework proposes that prediction error signals are characterized by a certain precision, which in turns determines the updating of one's prior beliefs. Thus, the predictive processing framework leads to more specific predictions regarding the role of prediction error signaling in different aspects of religious beliefs and experiences.

Still, we propose the notion that error detection and correction may be a central and defining feature of adhering to or for updating existing beliefs. This view provides a compelling unifying theoretical perspective – that fits well with the existing literature on the role of error monitoring in religious and spiritual beliefs, as discussed in Section 3.4. Reduced error monitoring and error correction is associated with acceptance of religious and superstitious beliefs; heightened error monitoring is associated with the rejection of religious and superstitious beliefs (Risen, 2016; Schjoedt et al., 2013).

We note that this mechanism may not be exclusive or specific to the acceptance of religious and superstitious beliefs; a similar mechanism of reduced error monitoring could play a role in sustaining any ideological belief system or worldview (e.g. in politics, atheism etc.). Accordingly, a reduced process of prediction error monitoring may be a domain-general mechanism that also plays a role in sustaining religious beliefs, but that is not exclusive to the domain of religion. Therefore, a more complete account of religious beliefs and experiences needs to take into account other neurocognitive mechanisms that play a role in religion, as discussed in our review (i.e., pertaining to religious experiences; see Table 1).

5. Limitations and philosophical and theological implications

5.1. Critical remarks and limitations

Throughout this review we have discussed and presented relevant research findings as if taken at face value, without paying close attention to the potential methodological and statistical shortcomings of the different studies. Although the studies that we discussed provide a fascinating perspective on the potential neurocognitive mechanisms underlying religious and spiritual beliefs and experiences, we note that at present they provide anecdotal evidence at best. That is, many studies suffer from methodological problems such as extremely small sample sizes, the lack of an appropriate control condition, fuzzy measures of religiosity and spirituality and indirect measures of neuropsychological functioning that strongly limit the conclusions that can be drawn based on these studies [for detailed discussion of methodological problems of several of the studies that we discussed, see: Schjoedt, 2009]. In addition, it often remains unclear to what extent the effects reported in different studies were predicted a priori, whether alternative dependent measures were included that have not been reported and to what extent the field suffers from publication bias, with many non-significant findings having ended up in the file-drawer (as in many other research fields as well). Especially in the light of recent advances aimed at fostering more rigorous research methods in psychological and neurocognitive research (Pashler and Wagenmakers, 2012), most studies of religion and spirituality do not meet up to the current standards of research practice. Important steps to be taken in future research would involve conducting replication studies of previously published findings, pre-registration of hypotheses and research methods and using larger sample sizes resulting in sufficiently powered studies (van Elk et al., 2015). In addition the field could benefit from introducing more standardized measures of religious and spiritual beliefs and experiences, thereby allowing a more direct comparison between different studies.

Nonetheless, we think that the existing literature leads up to interesting hypotheses regarding the neurocognitive processes that play a role in different aspects of religion and spirituality. In our review we have shown that many of the different studies that have been conducted can be related to four brain areas and mechanisms, namely: temporal brain areas, multisensory integration and brain networks involved in understanding self and other (DMN and ToM network) and reduced inhibition of intuitive belief mechanisms, hence necessitating less prediction error monitoring (see Table 1). As indicated, the predictive processing framework allows a theoretical integration of the different findings and mechanisms that we discussed.

5.2. Reductionism

What are the theoretical and theological implications of our review of the existing literature, indicating that religious beliefs and experiences may be supported by different neurocognitive mechanisms?

It could be argued that the finding that religion is 'hardwired' in our brain reflects a natural tendency to endorse religious beliefs – which is compatible with the 'naturalness of religion' hypothesis (McCauley and Cohen, 2010). Evolutionary theorists would argue that this tendency has evolved over the course of millions of years through a process of natural selection shaping our cognitive systems in response to adaptive challenges (Norenzayan et al., 2014; Pyysiäinen, 2009). Eventually this view could be compatible with a theistic view, according to which a supernatural agent (e.g., God) guided or at least used these processes to ultimately

allow the emergence of human beings with the ability to endorse supernatural beliefs and to engage in experiences of the supernatural (Plantinga, 2011). Some researchers make even stronger claims and suggest that the fact that humans have the apparently unique ability to get in contact with the supernatural, is actually supportive of the existence of a spiritual realm beyond our visible world (Beauregard and O'Leary, 2007; Newberg et al., 2001b). At the same time, research on the neurocognitive basis of religion and spirituality could also be interpreted in a strongly reductionistic way, according to which religious beliefs and experiences are merely a consequence of patterns of neural activity (Saver and Rabin, 1997; Dawkins, 2008; Swaab, 2014).

We would like to express our support for a more nuanced view on the relationship between brain, experience and behavior – especially when it comes to religion and spirituality. Many religious and spiritual beliefs and experiences are unique and idiosyncratic phenomena and it remains questionable to what extent universal neurocognitive mechanisms can be evoked to account for such a diverse array of beliefs and experiences (Wildman and McNamara, 2008). Different types of beliefs and experiences may require a different explanations in terms of the brain mechanisms that could underlie these phenomena (Schjoedt, 2009), although some mechanisms may be more general than other (e.g., we propose reduced inhibition of intuitive belief mechanisms, which represent enhanced influence of priors, and the corresponding reduction in prediction error monitoring as a central theoretical principle). Therefore we suggest that a multilevel approach to the study of religion is necessary, integrating insights from religious studies, anthropology, evolutionary psychology, cognitive science and neuroscience in order to get a fuller understanding of religious phenomena (Geertz, 2010; Slingerland, 2008).

5.3. Epistemic warrant

A related question is whether the dual systems account of religion and the notion that specific neurocognitive mechanisms underlie religious and spiritual beliefs, provide a defeater for religious beliefs. From the studies that we discussed above a picture emerges according to which religious believers are less analytical, critical and rational in certain contexts than non-believers (Risen, 2016; Lindeman and Aarnio, 2007). Moreover, the notion of reduced error monitoring in religious compared to non-religious believers – at least under certain conditions (Schjoedt et al., 2013; Schjoedt et al., 2011) – could be taken to imply that believers compared to skeptics endorse more inaccurate beliefs. Based on these findings one could argue that supernatural beliefs are epistemically unwarranted, because they are the product of cognitive faculties that are not aimed at producing true beliefs (i.e., failing to update one's beliefs based on incoming sensory evidence). This criticism echoes classical 'de jure' objections to religious belief, as can be found for instance in the Freudian and Marxist critiques of religion, suggesting that religious beliefs are an adaptive illusion or serve as wish fulfillment. These critiques have been objected by for instance Alvin Plantinga, who notes that these de jure objections do not impede the possibility for religious beliefs to have warrant, i.e., be produced by cognitive faculties functioning properly in the proper environment and being aimed at truth (Plantinga, 1999). In addition, it should be considered that intuitive mechanisms could effectively guide adaptive goal-directed behavior (Kahneman, 2011; Damasio, 1994). Finally, it should be noted that other convictions and beliefs (be they atheistic, agnostic or for example political) also emerge from the same cognitive faculties that some consider not to be aimed at producing true beliefs but to merely subserve adaptation to the environment.

However, one could argue that dual systems accounts and the notion of reduced error monitoring provide an even stronger defeater for the truth of religious beliefs, as these theories imply that religious beliefs are false because they are produced by *unreliable* cognitive faculties (Dawes and Jong, 2012). A potential response from the religious believer to this objection could be to acknowledge the possibility that some religious beliefs indeed emerge from a fast and intuitive cognitive system. But again, this would not impede religious beliefs from having warrant: it could be that under the right circumstances justified beliefs are indeed unreflectively produced by intuitive cognitive systems. Plantinga argues for instance that religious beliefs are properly basic and accordingly it could well be that these beliefs are produced by an intuitive system that also produces other (often unwarranted but also frequently justified) beliefs. Related to this, the Bayesian framework of prediction error monitoring discussed above (Clark, 2013), primarily applies to updating one's beliefs based on incoming sensory evidence. However, many supernatural beliefs are not based on sensory evidence at all, but on personal revelation, persuasiveness in addressing ultimate questions regarding human existence or the experience of purpose and meaning for instance. Religious believers in turn may be considered to be fully in their epistemic rights when referring to these experiences as the primary basis of their beliefs (Barrett and Church, 2013).

Thus, we would like to highlight that the theories and the neuroscientific findings that we discussed in no way provide a defeater for religious beliefs; but neither should they be used as an argument for the existence of a supernatural realm. Neuroscientific findings can be integrated in both a theistic as well as an atheistic worldview but these views are not entailed by the empirical evidence itself (Plantinga, 2011).

6. Conclusions

As becomes apparent from our literature review there is no specialized module supporting supernatural beliefs and experiences. We have shown that different aspects of religious beliefs and experiences are subserved by different neurocognitive mechanisms. The predictive processing framework provides a unifying account of these different findings, by describing how a differential weighting of interoceptive and exteroceptive information and a process of reduced prediction error monitoring may be at the basis of religious beliefs and experiences. Both the predictive processing framework and dual process accounts of religion and spirituality highlight the central role of top-down influences for religion and spirituality. On the proposed account individual differences in brain structure and function and environmental influences (e.g., sensory deprivation or overstimulation; use of drugs) may influence the probability that individuals have supernatural and mystical experiences. William James already alluded to the possibility that these experiences may have been at the basis of all major religious and spiritual movements (James, 2002). Cognitive neuroscience and specifically the computational model of predictive processing now offer powerful tools to directly investigate the neurocognitive basis of these experiences. This is likely to yield novel insights into the relatively understudied topic of neurocognitive mechanisms underlying religion and spirituality.

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