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The Neural Basis of Religious Cognition

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Abstract

Religion's neural underpinnings have long been a topic of speculation and debate, but an emerging neuroscience of religion is beginning to clarify which regions of the brain integrate moral, ritual, and supernatural religious beliefs with functionally adaptive responses. Here, we review evidence indicating that religious cognition involves a complex interplay among the brain regions underpinning cognitive control, social reasoning, social motivations, and ideological beliefs.

Keywords

religious cognition, religious beliefs, cognitive neuroscience, neuroimaging, lesion mapping

An understanding of the brain basis of religion can help to clarify its role in cognitive, emotional, and social practices. By *religion*, we mean the cognitive and emotional representations that underlie beliefs in supernormal powers, often regarded as sacred or inviolable (Bulbulia & Sosis, 2011). Beliefs, which represent the relationship between an agent at a particular time and an object of belief, can have both qualitative and quantitative properties: a qualitative sense that the belief is more true than false and a quantitative sense that a belief is greater than a particular threshold (e.g., determined by computational evidence; see Huber, 2016, for a review of formal definitions of belief). Brain evolution and the corresponding development of higher cognitive and social functions are important to our understanding of religious belief—although these functions are heavily influenced by culture. Acquiring religious beliefs involves social and cognitive processes relevant to reasoning about other people's intentions, determining the value of internal and external states, developing emotional ties, enhancing social affiliation, and strengthening knowledge representations and retrieval (P. L. Harris & Koenig, 2006; Legare, Evans, Rosengren, & Harris, 2012). Acquiring religious beliefs is similar to the acquisition of other beliefs and suggests that an overlapping, if not common, set of brain regions and networks may modulate the various forms of belief, including religious belief (Bulbulia & Schjoedt, 2010; see Fig. 1).

In this review, we first describe studies in adults that primarily used functional neuroimaging or electroencephalography as tools to identify brain regions and networks concerned with religious belief. We then report on lesion-mapping studies. Although neuroimaging can be very useful for identifying brain regions and networks involved in a particular functional computation or behavior, the results tend to be correlative in nature. Lesion mapping attempts to demonstrate the effects of damage to one or more areas of the brain by focusing on a functional computation or behavior. Those effects are usually selective impairments due to a disrupted brain region or network, and they indicate the specific role of that brain region in performing the computation or executing a

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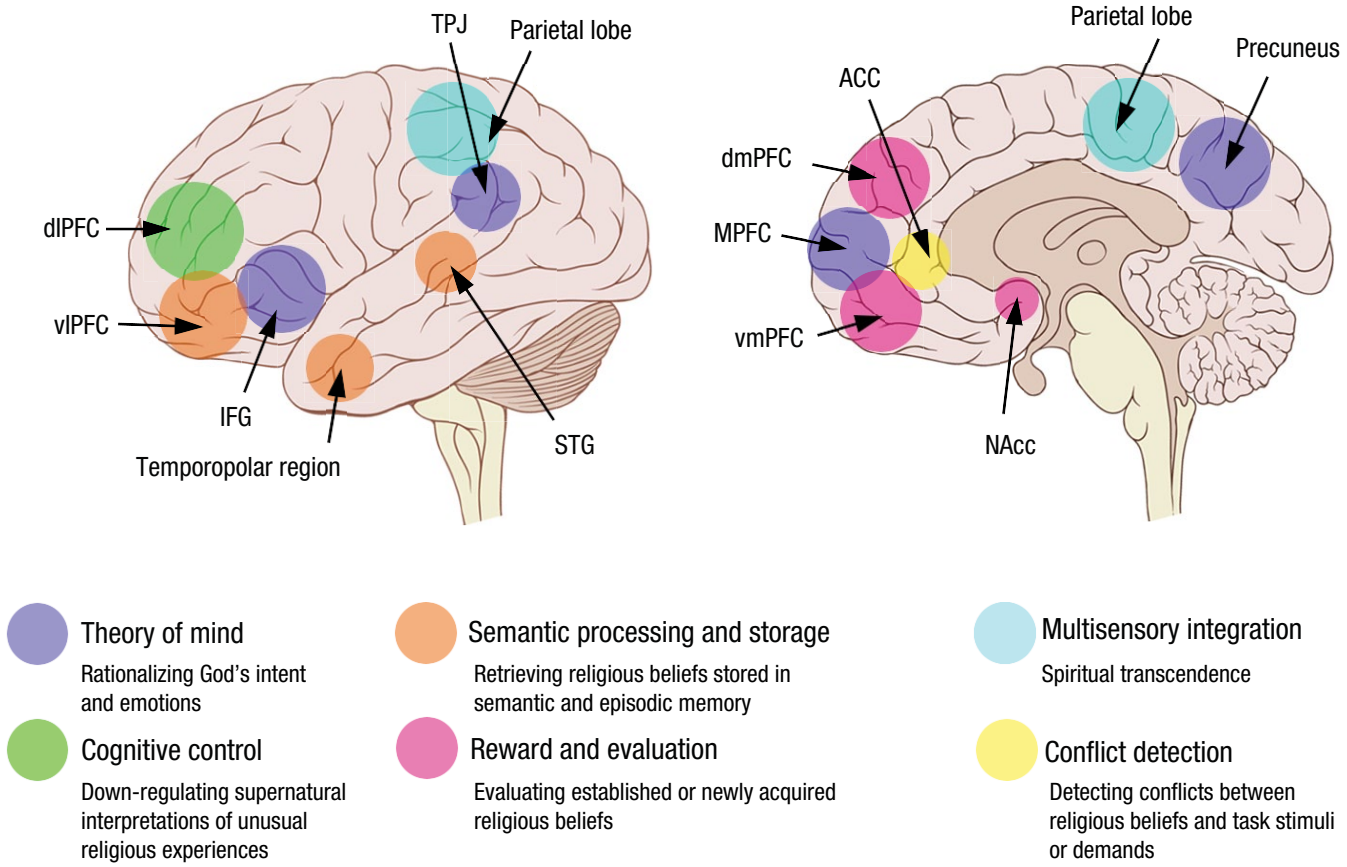

Fig. 1. Key brain regions involved in religious beliefs and the social, cognitive, and emotional processes mediated by these structures. Convergent evidence from functional neuroimaging, noninvasive brain stimulation, and lesion-mapping studies identified a set of brain networks important to religious cognition. The theory-of-mind network consists of the inferior frontal gyrus (IFG), medial prefrontal cortex (MPFC), temporoparietal junction (TPJ), and precuneus and is involved in rationalizing God's intent and emotions. The semantic-processing and storage network consists of the ventrolateral prefrontal cortex (vlPFC), superior temporal gyrus (STG), and temporopolar region and is involved in retrieving religious beliefs. The cognitive-control network encompasses the dorsolateral prefrontal cortex (dlPFC) and is involved in down-regulating supernatural interpretations of unusual religious experiences. The reward and evaluation network consists of the nucleus accumbens (NAcc), ventromedial prefrontal cortex (vmPFC), and dorsomedial prefrontal cortex (dmPFC) and is involved in evaluating established or newly acquired religious beliefs. Multisensory integration, processed in the parietal lobe, is crucial for experiencing spiritual transcendence. Finally, the conflict-detection and error-response network consists of the anterior cingulate cortex (ACC) and is involved in detecting conflicts between religious beliefs and task stimuli or demands.

behavior. Thus, lesion mapping goes beyond correlative findings by determining the causal effects of brain damage (and thus brain regions) on a specific aspect of the processing of religious beliefs. Both correlational and causal approaches are valuable in providing convergent evidence about the essential role of brain regions and networks for religious belief.

Brain Regions and Networks Involved in Religious Cognition

Certain aspects of religious and nonreligious beliefs share common neural underpinnings

Leshinskaya, Contreras, Caramazza, and Mitchell (2017) presented healthy volunteers with the names of a range of social groups with varying political orientations and spiritualism attributes and asked them to evaluate how similar pairs of social groups were during functional MRI (fMRI; Leshinskaya, Contreras, Caramazza, & Mitchell, 2017). Using multivoxel pattern analysis and representational similarity analysis, they found that only one brain area, the right precuneus, encoded properties of both political-orientation and spiritual-memory representations. Another study found that certainty in beliefs, regardless of whether they were empirically based or not, activated a set of brain regions including the medial prefrontal cortex (MPFC), caudate, posterior cingulate, and middle temporal gyrus (Howlett & Paulus, 2015), which suggests that a common evaluative brain network mediates the influence of different belief systems on behavior.

Religious beliefs recruit semantic-processing areas

An fMRI study found that sacred values associated with religious identities or moral norms affect behavior via

activation and retrieval of semantic rules but not through utilitarian valuation of costs and benefits (Berns et al., 2012). Participants performed a task in which they decided whether they would ignore their beliefs in exchange for money. *Sacred values* were beliefs that people refused to sell, and the processing of sacred values activated the left temporoparietal junction (TPJ) as well as the left ventrolateral prefrontal cortex (vlPFC). Both regions were previously implicated in semantic rule retrieval and processing.

Differences in the pattern of brain activation between religious and nonreligious beliefs

S. Harris et al. (2009) compared religious beliefs with nonreligious beliefs by asking participants to evaluate the truth of religious or nonreligious propositions. Results revealed that the ventromedial prefrontal cortex (vmPFC) was similarly engaged by beliefs from both categories of propositions, but religious statements distinctively activated the precuneus, anterior cingulate cortex (ACC), insula, and ventral striatum, whereas nonreligious statements distinctively activated the left parahippocampal, hippocampal, and temporal lobe regions. Religious-statement activations were distinguished by areas involved in emotion, motivation, and conflict, potentially awarding religious belief an enhanced and distinctive status in memory and behavior.

Religious-belief processing involves a theory-of-mind brain network

Using ordinary theory-of-mind tasks, such as the "Reading the Mind in the Eyes" Test and false-belief tasks, neuroimaging studies with healthy volunteers have identified a network of brain regions consistently involved in nonreligious theory-of-mind processing; these regions include the MPFC, superior temporal sulcus, TPJ, precuneus, and inferior frontal gyrus (IFG; Carrington & Bailey, 2009; Goel, Grafman, Sadato, & Hallett, 1995; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). Would a similar brain network also reflect theory-of-mind processing about God? Among the first researchers to investigate theory of mind among other aspects of religious cognition were Kapogiannis et al. (2009). Multidimensional scaling analysis of religious-belief statements revealed three primary dimensions: (a) God's perceived level of involvement, (b) God's perceived emotion, and (c) doctrinal and experiential religious knowledge (for a replication of this latter dimension, see Modestino, O'Toole, & Reinhofer, 2016). Statements involving the perception of God's lack of involvement activated brain networks concerned with understanding an agent's actions, emotion processing, and self-relevance—all components required to understand the intentions of another agent. These same brain areas were activated during nonreligious theory-of-mind tasks. A follow-up study (Kapogiannis, Deshpande, Krueger, Thornburg, & Grafman, 2014) found that theory-of-mind regions played a key role in religious beliefs by modifying the brain activity of downstream non-theory-of-mind regions. A pathway from the right IFG, a key brain region concerned with theory of mind, modulated the dorsomedial prefrontal cortex (dmPFC) and precuneus while religious subjects verified statements concerning the involvement of God in their daily life; these brain regions have previously been found to be involved in self–other processing and episodic memory.

Other research with highly religious individuals while they prayed revealed that theory-of-mind regions are involved when one experiences a relationship with God during prayer. Schjoedt, Stødkilde-Jørgensen, Geertz, and Roepstorff (2009) reported that personal prayer recruited a network of brain regions involved in social cognition, including the temporopolar region, TPJ, precuneus, and MPFC, and suggested that praying to God is similar to nonreligious human interpersonal communication because in prayer, God may be viewed as an intentional agent with the ability to reciprocate.

Religious beliefs are associated with error- and conflict-monitoring brain networks

Theoretical frameworks such as predictive processing suggest that error monitoring is crucial to belief updating and maintenance (van Elk & Aleman, 2017). A stronger belief in God is associated with attenuated error-related-negativity signatures in the ACC in response to errors on a nonreligious cognitive task (the Stroop task), suggesting that religious conviction may buffer against anxiety in novel situations (Inzlicht, McGregor, Hirsh, & Nash, 2009). A conceptualization of God as punishing or forgiving also affected executive-control performance. A more recent study found that reflecting on God's love was associated with a dampened error-related-negativity response to errors and reduced monitoring for conflict between one's behavior and religious standards (Good, Inzlicht, & Larson, 2015).

Religious beliefs involve valuation and motivation systems

Religious beliefs, like other beliefs, acquire value and motivational properties via the prefrontal and dopaminergic circuits. Morgan et al. (2016) found that religiosity positively correlated with intertemporal discounting

rates. Higher discounting rates reflect a faster drop in perceived value over time. When performing delayed-discounting tasks, people who proclaim greater religious belief are more likely to forego instant gratification in exchange for larger future rewards, after analyses control for gender and personality traits (Carter, McCullough, Kim-Spoon, Corrales, & Blake, 2012). That study also found that the association between religious commitment and delayed gratification was partially mediated by future time orientation, which reflected "a preoccupation with the future and a sense that the future is approaching quickly" (Carter et al., 2012, p. 225; see also Gjesme, 1979). Religious practice routinely reinforces patience as a virtue and impulsivity as a bane. Another speculation was that the religious notions of afterlife and future divine punishments or rewards may have induced a more salient view of the future and influenced the believer's representation of time. Semantic priming with religious statements led to faster response times on this task in religious, healthy older adults. The acceleration in response time was associated with stronger resting-state fMRI functional-connectivity effects among the left ACC, right dorsolateral prefrontal cortex (dlPFC), and nucleus accumbens. This finding suggests that religious belief, particularly in the context of reaching the end of the life span, is associated with evaluative- and motivational-system activity that is relevant for accomplishing goals and obtaining rewards.

Social-processing differences between religious and nonreligious participants are reflected in neural responses

Studies have found that social processing differs between religious and nonreligious participants, both in religious and nonreligious settings. Peer influence exerted a greater effect on the late positive (event-related) potential in religious individuals compared with nonreligious counterparts during an attractiveness-evaluation task, suggesting that religious participants are more susceptible to social pressure (Thiruchselvam, Gopi, Kilekwang, Harper, & Gross, 2017) and that this susceptibility is reflected in activity in the late positive potential. The authors argued that social conformity and in-group membership is a key mechanism for the transmission and influence of religious beliefs.

Huang and Han (2014) measured event-related potentials (ERPs) from Christian and atheist participants while they viewed painful or neutral faces of Christians and atheists. They found that an early frontal ERP response to painful expressions was stronger when subjects viewed faces of people with similar religious beliefs, and there was an additional enhanced late central/parietal empathic signal in Christian participants. The results showed that using stimuli containing representations of people with a similar religious affiliation is associated with stronger in-group preferences and empathy for others' suffering that is reflected in frontal and parietal ERPs. Finally, a Danish study examined how assumptions about speakers' abilities changed neural responses in secular and Christian participants who received intercessory prayer (Schjoedt, Stødkilde-Jørgensen, Geertz, Lund, & Roepstorff, 2011). The recipients' assumptions about senders' charismatic abilities led to modulation of the executive-function network only in Christian participants, who showed *diminished* frontal brain activity (in MPFC and dlPFC) in response to charismatic speakers. These results suggest that charismatic influence potentially devalues critical thinking in believers compared with nonbelievers by dampening prefrontal cortex (PFC) activity. Trust in authorities, including religious authorities, may form expectations for outcomes that manufacture reinforcing experiences in further support of this trust.

Prayer down-regulates pain

Religious beliefs can affect social and personal behavior and experiences by modulating sensory perception (Good et al., 2015). For example, it has been shown that religious prayers help people cope during physical pain (Elmholdt et al., 2017). Devout Protestants performed religious prayer and a secular contrast prayer during painful electrical stimulation while undergoing fMRI. Findings showed that ratings of both pain intensity and unpleasantness were reduced during religious prayer compared with secular prayer and were accompanied by a reduction in neural activity in a large frontal and parietal network. The diminished frontoparietal activity suggested that prayer attenuated pain via reduced processing of pain-stimulus saliency and enhanced executive (prefrontal) control.

Repetitive prayer activates reward systems

Religious prayers can activate the reward system (Schjødt, Stødkilde-Jørgensen, Geertz, & Roepstorff, 2008), and that effect may be partially responsible for their role in top-down control. For example, Schjødt and colleagues found increased activity in the striatum while Danish Christians were performing repetitive religious prayer. The authors suggest that recurring prayer activates the dopaminergic reward system (including the dorsal striatum), implying that reinforcement from practicing repetitive prayers contributes to elaborating

motivations to persist with this practice. A recent study by Ferguson and colleagues (2018) reported that in devout Mormons, religious experience elicited by ecological religious stimuli and practices activated reward, salience, and attentional networks, including the nucleus accumbens, vmPFC, ACC, and frontal attentional regions. As abstract religious concepts became more salient, they also became increasingly associated with intrinsic reward in religious individuals and further reinforced the maintenance of religious beliefs and behavior.

Localized Brain Lesions May Modulate Religious Cognition

Some of the earliest studies on the brain basis of religious belief began with observations of religious episodes in patients with right temporal lobe epilepsy (Devinsky & Lai, 2008). Our group has attempted to understand the neural underpinning of religious beliefs by analyzing the associations among religious beliefs, cognitive processing, and the location of brain damage in male Vietnam combat veterans with penetrating traumatic brain injuries (Cristofori et al., 2016; Zhong, Cristofori, Bulbulia, Krueger, & Grafman, 2017). Cristofori et al. and Zhong et al. both found that reported mystical experiences appear to be regulated by the dlPFC and middle/superior temporal cortex. Executive functions controlled by the dlPFC causally contributed to the down-regulation of mystical experiences. Individuals with damage to the dlPFC, who thus have diminished executive functioning, reported more mystical experiences than individuals with damage elsewhere in the brain. These findings reinforced the idea that some aspects of religious experience are modulated by the relaxation of inhibitory networks. In this context, religious experience can be conceived of as the opening of a cognitive doorway (Huxley, 1954/2009). This doorway activates default intuitive thinking that ordinarily is inhibited by hierarchical evolved brain regions, such as the PFC, which are concerned with rational analytic thinking.

Another study by our group (Zhong et al., 2017) found that individuals with dlPFC and vmPFC lesions have increased fundamentalist beliefs (see also Asp, Ramchandran, & Tranel, 2012). The dlPFC lesions in particular led to an increase in fundamentalism that was mediated by decreased cognitive flexibility and openness. Magical ideation was also investigated by our group and found to be positively correlated with religious experience in patients with brain injuries but not in matched control subjects. PFC lesions were significantly associated with increased magical-ideation scores. This relationship was mediated by religious experience, suggesting that suppressing the PFC allows people to experience certain religious events as supernatural in origin, which in turn increases reported magical ideation (Bulbulia, Osborne, & Sibley, 2013; Zhong, Krueger, Wilson, Bulbulia, & Grafman, 2018).

Noninvasive Neurostimulation

A variety of noninvasive brain-stimulation techniques including transcranial magnetic stimulation, transcranial electrical-current stimulation, and even vagal-nerve stimulation have been used either to create a temporary disruption over a cortical region (e.g., parietal lobes) or, conversely, to stimulate a cortical region (e.g., dlPFC) to suppress or enhance spirituality (Crescentini, Aglioti, Fabbro, & Urgesi, 2014; Finisguerra, Borgatti, & Urgesi, 2019; Finisguerra, Crescentini, & Urgesi, 2019; Johnstone, Bodling, Cohen, Christ, & Wegrzyn, 2012; Johnstone, McCormack, Yoon, & Smith, 2012).

A Note on Spiritual Transcendence

Besides adhering to and processing didactic religious beliefs, people may have moments of spiritual transcendence that they interpret as a sacred experience that enables them to transcend their difficulties and ordinary experiences. Although not completely distinct from artificially induced transcendence, as can occur with some psychoactive drugs or certain kinds of environmental provocation (e.g., the death of a loved one or, conversely, a loved baseball team winning the world series after a century of frustration), this state has been associated with parietal lobe functioning and the frontoparietal attention network (Lifshitz, van Elk, & Luhrmann, 2019).

Summary of Findings: Common Human Social and Cognitive Systems Support Religious Beliefs

Regardless of the religious-belief task used, convergent evidence measuring ERPs, neuroimaging results, and lesion-mapping studies (Cristofori et al., 2016; Urgesi, Aglioti, Skrap, & Fabbro, 2010) indicates that the frontal and anterior temporal lobes play prominent and disproportionate roles in storing key aspects of religious belief and behavior while exerting a modifying influence on perceptual and other sensory processes that may be biased toward reflexive, intuitive, and supernatural interpretations of sensory experience. Social-cognition brain networks, including theory-of-mind regions in the MPFC, IFG, TPJ, and precuneus, and

emotional regulation and reappraisal regions in the dmPFC and vlPFC, are critically involved in rationalizing God's intent and emotions. Retrieving religious beliefs stored in semantic and episodic memory may also induce the emotional branding of belief or disbelief reflected in the activation of the anterior insula, amygdala, and related structures concerned with the emotionally relevant content of stimuli (S. Harris et al., 2009; S. Harris, Sheth, & Cohen, 2008). The processing of religious beliefs also may recruit the ACC, particularly when conflicts or discrepancies in prediction arise between beliefs and task stimuli or demands (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Brain regions involved in reward and evaluation, including the vmPFC, striatum, and nucleus accumbens, are also implicated in religious beliefs and ensure the enhanced valuation and reinforcement of established or newly acquired religious beliefs. Furthermore, the dlPFC plays an important role in down-regulating supernatural or magical interpretations of unusual religious or other experiences (Andersen, Pfeiffer, Müller, & Schjoedt, 2019) through the mechanisms of context-dependent cognitive control and executive functions. The dmPFC is also involved in evaluating religious beliefs (Azari et al., 2001; Han et al., 2008; Howlett & Paulus, 2015; Kapogiannis et al., 2009). Almost all of these brain regions, by virtue of their complex morphology and connectivity, distinguish humans from other species and do not mature until adulthood. Thus, religion, like other beliefs (Krueger & Grafman, 2013), depends on a variety of cognitive and emotional functions mediated by distinct brain networks (Seitz, Paloutzian, & Angel, 2018), and the relative involvement of each region or network depends on the experimental design or stimuli used in a study on religion.

Religious beliefs can provide an individual with comfort and contentment when facing a medical disorder, but they may also be diminished, particularly in patients with neurodegenerative disorders. For example, patients with Parkinson's disease (Butler, McNamara, & Durso, 2010) may show decreased access to religious concepts that may be connected with reduced dopamine availability. Patients with frontotemporal degeneration may have impaired moral judgment, although direct tests of religious cognition (Moll et al., 2011; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005) have rarely been administered to patients with other forms of neurodegenerative disorders such as Alzheimer's disease. Regardless of the effects of brain injury or damage on religious belief, the majority of studies on the effects of religious belief on coping with disease is positive (e.g., Parisi, Roberts, Szanton, Hodgson, & Gitlin, 2017).

Limitations

There are a number of limitations in reviewing the literature on the brain basis of religious belief. Most of the articles reviewed were based on research studies conducted in countries in Europe or North America with participants who were steeped in the Judeo-Christian tradition. Most of these studies contained small sample sizes, were not preregistered, and had a questionable lack of appropriate control subjects (for a comprehensive review of these issues, see van Elk & Aleman, 2017, and van Elk & Snoek, 2019). In addition, in certain studies, believers and nonbelievers may have similar profiles of brain activation when judging the relevance or validity of religious beliefs (e.g., Kapogiannis et al., 2009), suggesting that differences between believers and nonbelievers are more likely to occur when researchers study other features of religious belief, such as emotional commitment, disagreement or conflict with statements threatening religious belief, or the attainment of an altered state of spiritual consciousness associated with the religious belief.

Conclusions

We can conclude by affirming that the learning, representation, and expression of religious cognition and belief depend on brain networks committed to related forms of cognitive- and social-knowledge acquisition and expression. Even though religious beliefs have played a critical role in influencing our personal and social worlds, their neural basis remains only partially understood. In the decades ahead, we expect that the neural basis of religious belief and practice will become an increasingly prominent research focus for social and political scientists who wish to uncover the mysterious operations of the human mind. This importance mandates that we continue to provide a more thorough understanding of religious belief by investigating its neural foundations.

Recommended Reading

Atran, S., & Norenzayan, A. (2004). Religion's evolutionary landscape: Counterintuition, commitment, compassion, communion [Target article and commentaries]. *Behavioral & Brain Sciences, 27*, 713–770. A review that comprehensively addresses issues concerned with the psychological contributions to the evolution of religion.

Krueger, F., & Grafman, J. (Eds.). (2013). (See References). One of the first books to encompass the neural basis of different belief systems, including religion.

van Elk, M., & Aleman, A. (2017). (See References). A comprehensive review of the brain basis of religious belief and supernatural experiences.

Transparency

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References

Andersen, M., Pfeiffer, T., Müller, S., & Schjoedt, U. (2019). Agency detection in predictive minds: A virtual reality study. *Religion, Brain & Behavior*, 9, 52–64. doi:10.1080/2153599X.2017.1378709

Asp, E., Ramchandran, K., & Tranel, D. (2012). Authoritarianism, religious fundamentalism, and the human prefrontal cortex. *Neuropsychology*, *26*, 414–421. doi:10.1037/a0028526

Azari, N. P., Nickel, J., Wunderlich, G., Niedeggen, M., Hefter, H., Tellmann, L., . . . Seitz, R. J. (2001). Neural correlates of religious experience. *European Journal of Neuroscience*, *13*, 1649–1652. doi:10.1046/j.0953-816x.2001.01527.x

Berns, G. S., Bell, E., Capra, C. M., Prietula, M. J., Moore, S., Anderson, B., . . . Atran, S. (2012). The price of your soul: Neural evidence for the non-utilitarian representation of sacred values. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 754–762. doi:10.1098/rstb.2011.0262

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*, 624–652.

Bulbulia, J., Osborne, D., & Sibley, C. G. (2013). Moral foundations predict religious orientations in New Zealand. *PLOS ONE*, *8*(12), Article e80224. doi:10.1371/journal.pone.0080224

Bulbulia, J., & Schjoedt, U. (2010). Charismatic culture and prediction under risk: Perspectives from social neuroscience. In I. Pyysiainen (Ed.), *Religion, economy, and cooperation* (pp. 35–59). New York, NY: De Gruyter.

Bulbulia, J., & Sosis, R. (2011). Signalling theory and the evolution of religious cooperation. *Religion*, *41*, 363–388. doi:10.1080/0048721X.2011.604508

Butler, P. M., McNamara, P., & Durso, R. (2010). Deficits in the automatic activation of religious concepts in patients with Parkinson's disease. *Journal of the International Neuropsychological Society*, *16*, 252–261. doi:10.1017/S1355617709991202

Carrington, S. J., & Bailey, A. J. (2009). Are there theory of mind regions in the brain? A review of the neuroimaging literature. *Human Brain Mapping*, *30*, 2313–2335. doi:10.1002/hbm.20671

Carter, E. C., McCullough, M. E., Kim-Spoon, J., Corrales, C., & Blake, A. (2012). Religious people discount the future less. *Evolution & Human Behavior*, *33*, 224–231. doi:10.1016/j.evolhumbehav.2011.09.006

Crescentini, C., Aglioti, S. M., Fabbro, F., & Urgesi, C. (2014). Virtual lesions of the inferior parietal cortex induce fast changes of implicit religiousness/spirituality. *Cortex*, *54*, 1–15. doi:10.1016/j.cortex.2014.01.023

Cristofori, I., Bulbulia, J., Shaver, J. H., Wilson, M., Krueger, F., & Grafman, J. (2016). Neural correlates of mystical experience. *Neuropsychologia*, *80*, 212–220. doi:10.1016/j.neuropsychologia.2015.11.021

Devinsky, O., & Lai, G. (2008). Spirituality and religion in epilepsy. *Epilepsy & Behavior*, *12*, 636–643. doi:10.1016/j.yebeh.2007.11.011

Elmholdt, E. M., Skewes, J., Dietz, M., Moller, A., Jensen, M. S., Roepstorff, A., . . . Jensen, T. S. (2017). Reduced pain sensation and reduced BOLD signal in parieto-frontal networks during religious prayer. *Frontiers in Human Neuroscience*, *11*, Article 337. doi:10.3389/fnhum.2017.00337

Ferguson, M. A., Nielsen, J. A., King, J. B., Dai, L., Giangrasso, D. M., Holman, R., . . . Anderson, J. S. (2018). Reward, salience, and attentional networks are activated by religious experience in devout Mormons. *Social Neuroscience*, *13*, 104–116. doi:10.1080/17470919.2016.1257437

Finisguerra, A., Borgatti, R., & Urgesi, C. (2019). Non-invasive brain stimulation for the rehabilitation of children and adolescents with neurodevelopmental disorders: A systematic review. *Frontiers in Psychology*, *10*, Article 135. doi:10.3389/fpsyg.2019.00135

Finisguerra, A., Crescentini, C., & Urgesi, C. (2019). Transcutaneous vagus nerve stimulation affects implicit spiritual self-representations. *Neuroscience*, *412*, 144–159. doi:10.1016/j.neuroscience.2019.05.059

Gjesme, T. (1979). Future time orientation as a function of achievement motives, ability, delay of gratification, and sex. *The Journal of Psychology: Interdisciplinary and Applied*, *101*, 173–188. doi:10.1080/00223980.1979.9915069

Goel, V., Grafman, J., Sadato, N., & Hallett, M. (1995). Modeling other minds. *NeuroReport*, *6*, 1741–1746.

Good, M., Inzlicht, M., & Larson, M. J. (2015). God will forgive: Reflecting on God's love decreases neurophysiological responses to errors. *Social Cognitive and Affective Neuroscience*, *10*, 357–363. doi:10.1093/scan/nsu096

Han, S., Mao, L., Gu, X., Zhu, Y., Ge, J., & Ma, Y. (2008). Neural consequences of religious belief on self-referential processing. *Social Neuroscience*, *3*, 1–15. doi:10.1080/17470910701469681

Harris, P. L., & Koenig, M. A. (2006). Trust in testimony: How children learn about science and religion. *Child Development*, *77*, 505–524. doi:10.1111/j.1467-8624.2006.00886.x

Harris, S., Kaplan, J. T., Curiel, A., Bookheimer, S. Y., Iacoboni, M., & Cohen, M. S. (2009). The neural correlates of religious and nonreligious belief. *PLOS ONE*, *4*(10), Article e0007272. doi:10.1371/journal.pone.0007272

Harris, S., Sheth, S. A., & Cohen, M. S. (2008). Functional neuroimaging of belief, disbelief, and uncertainty. *Annals of Neurology*, *63*, 141–147. doi:10.1002/ana.21301

Howlett, J. R., & Paulus, M. P. (2015). The neural basis of testable and non-testable beliefs. *PLOS ONE*, *10*(5), Article e0124596. doi:10.1371/journal.pone.0124596

Huang, S., & Han, S. (2014). Shared beliefs enhance shared feelings: Religious/irreligious identifications modulate

empathic neural responses. *Social Neuroscience*, *9*, 639–649. doi:10.1080/17470919.2014.934396

Huber, F. (2016). Formal representations of belief. In E. N. Zalta (Ed.), *Stanford encyclopedia of philosophy*. Retrieved from https://plato.stanford.edu/archives/spr2016/entries/formal-belief/

Huxley, A. (2009). *The doors of perception & heaven and hell*. New York, NY: HarperCollins. (Original work published 1954)

Inzlicht, M., McGregor, I., Hirsh, J. B., & Nash, K. (2009). Neural markers of religious conviction. *Psychological Science*, *20*, 385–392. doi:10.1111/j.1467-9280.2009.02305.x

Johnstone, B., Bodling, A., Cohen, D., Christ, S. E., & Wegrzyn, A. (2012). Right parietal lobe-related "selflessness" as the neuropsychological basis of spiritual transcendence. *International Journal for the Psychology of Religion*, *22*, 267–284. doi:10.1080/10508619.2012.657524

Johnstone, B., McCormack, G., Yoon, D. P., & Smith, M. L. (2012). Convergent/divergent validity of the brief multidimensional measure of religiousness/spirituality: Empirical support for emotional connectedness as a "spiritual" construct. *Journal of Religion and Health*, *51*, 529–541. doi:10.1007/s10943-011-9538-9

Kapogiannis, D., Barbey, A. K., Su, M., Zamboni, G., Krueger, F., & Grafman, J. (2009). Cognitive and neural foundations of religious belief. *Proceedings of the National Academy of Sciences, USA*, *106*, 4876–4881. doi:10.1073/pnas.0811717106

Kapogiannis, D., Deshpande, G., Krueger, F., Thornburg, M. P., & Grafman, J. H. (2014). Brain networks shaping religious belief. *Brain Connectivity*, *4*, 70–79. doi:10.1089/brain.2013.0172

Krueger, F., & Grafman, J. (Eds.) (2013). *The neural basis of human belief systems*. Hove, England: Psychology Press.

Legare, C. H., Evans, E. M., Rosengren, K. S., & Harris, P. L. (2012). The coexistence of natural and supernatural explanations across cultures and development. *Child Development*, *83*, 779–793. doi:10.1111/j.1467-8624.2012.01743.x

Leshinskaya, A., Contreras, J. M., Caramazza, A., & Mitchell, J. P. (2017). Neural representations of belief concepts: A representational similarity approach to social semantics. *Cerebral Cortex*, *27*, 344–357. doi:10.1093/cercor/bhw401

Lifshitz, M., van Elk, M., & Luhrmann, T. M. (2019). Absorption and spiritual experience: A review of evidence and potential mechanisms. *Consciousness and Cognition*, *73*, Article 102760. doi:10.1016/j.concog.2019.05.008

Modestino, E. J., O'Toole, P., & Reinhofer, A. (2016). Experiential and doctrinal religious knowledge categorization in Parkinson's disease: Behavioral and brain correlates. *Frontiers in Human Neuroscience*, *10*, Article 113. doi:10.3389/fnhum.2016.00113

Moll, J., Zahn, R., de Oliveira-Souza, R., Bramati, I. E., Krueger, F., Tura, B., . . . Grafman, J. (2011). Impairment of prosocial sentiments is associated with frontopolar and septal damage in frontotemporal dementia. *NeuroImage*, *54*, 1735–1742. doi:10.1016/j.neuroimage.2010.08.026

Moll, J., Zahn, R., de Oliveira-Souza, R., Krueger, F., & Grafman, J. (2005). Opinion: The neural basis of human moral cognition. *Nature Reviews Neuroscience*, *6*, 799–809. doi:10.1038/nrn1768

Morgan, J., Clark, D., Tripodis, Y., Halloran, C. S., Minsky, A., Wildman, W. J., . . . McNamara, P. (2016). Impacts of religious semantic priming on an intertemporal discounting task: Response time effects and neural correlates. *Neuropsychologia*, *89*, 403–413. doi:10.1016/j.neuropsychologia.2016.07.020

Parisi, J. M., Roberts, L., Szanton, S. L., Hodgson, N. A., & Gitlin, L. N. (2017). Valued activities among individuals with and without cognitive impairments: Findings from the National Health and Aging Trends Study. *Gerontologist*, *57*, 309–318. doi:10.1093/geront/gnv144

Schjødt, U., Stødkilde-Jørgensen, H., Geertz, A. W., & Roepstorff, A. (2008). Rewarding prayers. *Neuroscience Letters*, *443*, 165–168. doi:10.1016/j.neulet.2008.07.068

Schjoedt, U., Stødkilde-Jørgensen, H., Geertz, A. W., & Roepstorff, A. (2009). Highly religious participants recruit areas of social cognition in personal prayer. *Social Cognitive and Affective Neuroscience*, *4*, 199–207.

Schjoedt, U., Stødkilde-Jørgensen, H., Geertz, A. W., Lund, T. E., & Roepstorff, A. (2011). The power of charisma—Perceived charisma inhibits the frontal executive network of believers in intercessory prayer. *Social Cognitive and Affective Neuroscience*, *6*, 119–127. doi:10.1093/scan/nsq023

Schurz, M., Radua, J., Aichhorn, M., Richlan, F., & Perner, J. (2014). Fractionating theory of mind: A meta-analysis of functional brain imaging studies. *Neuroscience & Biobehavioral Reviews*, *42*, 9–34. doi:10.1016/j.neubiorev.2014.01.009

Seitz, R. J., Paloutzian, R. F., & Angel, H. F. (2018). From believing to belief: A general theoretical model. *Journal of Cognitive Neuroscience*, *30*, 1254–1264. doi:10.1162/jocn_a_01292

Thiruchselvam, R., Gopi, Y., Kilekwang, L., Harper, J., & Gross, J. J. (2017). In God we trust? Neural measures reveal lower social conformity among non-religious individuals. *Social Cognitive and Affective Neuroscience*, *12*, 956–964. doi:10.1093/scan/nsx023

Urgesi, C., Aglioti, S. M., Skrap, M., & Fabbro, F. (2010). The spiritual brain: Selective cortical lesions modulate human self-transcendence. *Neuron*, *65*, 309–319. doi:10.1016/j.neuron.2010.01.026

van Elk, M., & Aleman, A. (2017). Brain mechanisms in religion and spirituality: An integrative predictive processing framework. *Neuroscience & Biobehavioral Reviews*, *73*, 359–378. doi:10.1016/j.neubiorev.2016.12.031

van Elk, M., & Snoek, L. (2019). The relationship between individual differences in gray matter volume and religiosity and mystical experiences: A pre-registered voxel-based morphometry study. Retrieved from https://osf.io/qzkmh/

Zhong, W., Cristofori, I., Bulbulia, J., Krueger, F., & Grafman, J. (2017). Biological and cognitive underpinnings of religious fundamentalism. *Neuropsychologia*, *100*, 18–25. doi:10.1016/j.neuropsychologia.2017.04.009

Zhong, W., Krueger, F., Wilson, M., Bulbulia, J., & Grafman, J. (2018). Prefrontal brain lesions reveal magical ideation arises from enhanced religious experiences. *Peace and Conflict*, *24*, 245–249. doi:10.1037/pac0000336