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THEORETICAL ARTICLE

Do Religious Practices and Foraging Behavior Have a Common Motivational Basis?

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Abstract

The neuropsychological deciphering of religion suggests that the ability to believe in supernatural agents depends on cognitive mechanisms already present in our remote human ancestors. Current research has mainly focused on the cognitive accounts of religion, which do not satisfactorily explain religious *motivation*. Here, I defend the hypothesis that religious motivation recruits a motivational system that is not specifically human, and that underpins foraging activity under harsh environmental conditions. This motivational system, referred to as incentive hope, denotes motivational excitement for adversity avoidance (reward or relief) when difficulties (non-reward or punishment) are encountered. Incentive hope boosts foraging activity and therefore increases the probability of reward in a hostile environment, independent of any knowledge or awareness of what's going on. It is shown how religious practices, which largely consist of adversity-avoidance strategies when adversity in life is high, could rely on incentive hope—revealed and enriched through self-awareness and introspection as hope in humans. Some original predictions to test this hypothesis are discussed.

Keywords Faith · Worship · Religion · Motivation · Hope · Foraging

Introduction

Psychological and neuroscientific approaches to religion have revealed the cognitive abilities we need to possess—empathy, altruism, theory of mind, etc.—in order to believe in God (or in gods or spirits), as well as how the brain produces them (e.g., Atran 2002; Boyer 2001; Kapogiannis et al. 2009; Pinker 1997; Schjoedt et al. 2009; Torrey 2017). Such abilities, among others, may result from a collection of organized problem solving devices (or "modules"), shaped by natural selection to optimize the psychological adaptations to the ecological and social environments in which our human ancestors lived during the Pleistocene (Barkow et al. 1992; Barrett and Kurzban 2006; Carruthers 2006; Miller 2000; see also Barrett 2015).

Determining whether religion is a by-product of our adapted mind or created selective pressures capable of transforming some of our brain modules is off-topic here (e.g., see Pyysiäinen and Hauser 2009; Sosis 2009). Nevertheless, I defend the view that religion depends on some brain processes that, *at least initially*, had a non-religious origin. In particular, I am interested in the possibly non-religious motivational ground for religion. Religious motivation (faith or ancestor-spirit worship) is unlikely to be a mere consequence of our cognitive *ability* to believe in supernatural agents. For that, we should presuppose that our cognitive ability to believe explains the religious fervor that has existed for dozens of thousands of years throughout the human history. This idea is highly implausible because an ability is not, in itself, a motivation. I have the ability to cook eggs but will do this activity only if motivated to do it—e.g., because I *want* to eat eggs for lunch. Of course, motivation is unnecessary to activate some abilities such as the understanding of speech or the detection of perceptual illusions. But these are cognitive outputs, not behaviors. Cognitive outputs require motivational processes to be converted into action (Anselme 2016; Berridge 2012). Understanding the origins of religious motivation requires to question the motivation behind the religious beliefs and rituals. Specifically, we should be able to explain the practical implications of such beliefs, that is, the acceptance of paying an elevated price (in terms of personal investment) without any guarantee of gratification.

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Not all aspects of religious motivation (especially those related to group-belonging) are considered in this article. But the idea of effort-related costs without guaranteed counterpart (benefit or improvement) could play a central role in motivating religious behaviors. In other words, what appears to be a practical implication of having religious beliefs could actually be a natural propensity that facilitates such beliefs in humans. Deploying much effort without guaranteed counterpart is typically observed in organisms trying to avoid deprivation and starvation in unpredictable environments. Of course, I am not suggesting that human reward seeking involves invoking supernatural agents. But supernatural agents appear to be invoked for evolutionary reasons similar to those of individuals (humans or nonhumans) seeking rewards under harsh environmental conditions: *they are motivated to avoid adversity by adopting specific behaviors*.

In nature, this means that animals will intensify foraging, increase the duration of foraging bouts, and/or explore a vaster territory. In humans, because of their higher intelligence, actual or perceived adversity may lead to other forms of investment. In some traditions, people may deploy effort to pray to their God or to attend to various religious services for material or spiritual rewards. In other traditions, people do not pray and do not have specific requests, but practice ancestor-spirit worship in order to avoid the malicious influences of their ancestors. Indeed, unhappy ancestor-spirits are often believed to cause misfortune (sickness, accidents, repeated bad luck, etc.) in response to socially inappropriate behaviors, and sacrificing one or several animals through a specific ritual is necessary to satisfy and appease those ancestor-spirits (Boyer 2001). Here, people are not trying to obtain favors, but nevertheless *attempt to avoid an unfavorable situation by deploying some effort*—here, relief is viewed as a form of reward (see further). Thus, despite their differences, monotheistic and archaic religions seem to share common features with animal foraging in regard with their motivational origin.

There is no functional theory of the motivation underpinning religiosity and its mechanistic analysis is limited to few studies (Beauregard and Paquette 2006; Ferguson et al. 2018; McNamara et al. 2006a; Morgan et al. 2016; Schjoedt et al. 2008). However, these studies reveal an important fact: religiosity is controlled by the brain regions (striatum, prefrontal cortex) and the neurotransmitter (dopamine) chiefly involved in reward-related motivation in non-religious contexts—such as food, sex, money, game, and drugs. Religiosity both recruits the mesocorticolimbic pathway, which releases dopamine from the ventral tegmental area to the ventral striatum and the prefrontal cortex, and the nigrostriatal pathway, which releases dopamine from the substantia nigra to the dorsomedial striatum (caudate) and the dorsolateral striatum (putamen). These neuronal circuits originate in the midbrain and are present in all avian and mammalian species (Yamamoto and Vernier 2011). Dopamine is necessary to approach and flexibly seek rewards or stimuli that predict their occurrence (Berridge 2007; Yin and Knowlton 2006), and also to increase the willingness to deploy effort in the search of rewards or their predictive stimuli (Salamone and Correa 2002). Relief resulting from punishment avoidance can also be viewed as a form of reward because it is associated with dopamine release as well (Kohls et al. 2013; Oleson et al. 2012). Of course, our conscious experience gives us the feeling that punishment avoidance and reward are two different things which may have distinct behavioral effects—e.g., cheating is reduced when faced with a punishing rather than loving God (Shariff and Norenzayan 2011; see also Purzycki et al. 2016). However, the motivational effects of mesolimbic dopamine operate under the level of consciousness (Berridge 2007) and control behavioral components that may be similar in both cases. Mesolimbic dopamine is chiefly involved in seeking behavior, so whether the individual seeks punishment avoidance or reward may be relatively unimportant. This could explain why, in addition to punishment avoidance, reward seeking is also observed in some religions. In contrast, this influence is likely to be negligible in tasks consciously carried out and/or unrelated to seeking—such as cheating.

Interestingly, the release of mesolimbic dopamine is enhanced when predictive stimuli are unpredictably followed by reward or non-reward (Dreher et al. 2006; Fiorillo et al. 2003; Hart et al. 2015; Preuschoff et al. 2006), suggesting that environmental uncertainty and poverty may stimulate foraging motivation in both animals and humans. Elsewhere, I showed that this motivational boost under uncertainty cannot fully be explained in terms of incentive salience (or "wanting"), the modern interpretation of incentive motivation (Berridge 2007), and is referred to as *incentive hope*. In animals, incentive hope can compensate for the absence of cognitive control when finding food is uncertain (Anselme 2015, 2016; Anselme and Güntürkün in press) and can promote survival (Anselme et al. 2017, 2018). Incentive hope denotes motivational excitement for reward (or relief) when non-reward (or punishment) is likely, a process assumed to stimulate foraging activity and maintain organisms alive. Thus, incentive hope is a psychological mechanism with functional implications—two aspects discussed in this paper. I argue that any kind of religious motivation derives, at least in part, from an initially non-religious motivational system (incentive hope), shaped by natural selection to optimize foraging activity under harsh environmental conditions. In other words, foraging behavior and religious practices would have in common to offer protection against adversity through incentive hope—which is felt as a conscious mental state (hope) only in humans, nurturing religious ideas.

Avoiding Bad Things

Throughout the world, people want to be protected against bad things. Does this motivate them to believe in supernatural entities? According to terror management theory, the fear of death causes protectionist attitudes such as feelings of belonging to a community (Greenberg et al. 1986). Religions would offer a protection against the fear of death, because they all conceive death as a transition to something else instead of being an end in itself. This theory is appealing but overlooks the fact that there is no overall behavior protecting us against the fear of death, but distinct reactions to situations that imperil the transmission of our genes (Boyer 2001). For example, like other animals, the marsupial mice attempt to avoid harmful situations, but they do not seem to take into account the fact that they will die following a frenetic copulation period (Klarsfeld and Revah 2000).

Today, there is compelling evidence that the fear of punishment from supernatural agents can influence human behavior—in particular, it promotes cooperation (Johnson 2005) and reduces cheating (Shariff and Norenzayan 2011). People are also sensitive to punishment irrespective of its supernatural origin. Purzycki et al. (2012) showed that participants respond faster to an agent's socially strategic knowledge than non-strategic knowledge, but only if the agent is able to punish (e.g., God or governmental surveillance as opposed to omniscient, non-interfering aliens). Supernatural punishment might reinforce cooperation, but might not fully explain religious motivation—otherwise people would perceive their beliefs as a burden rather than a source of comfort. God and spirits punish but also protect. No doubt that religious beliefs are associated with positive feelings because supernatural agents offer some protection to believers; they have the power to cause but also to prevent misfortune. In a safe environment, protection may mean "keep things unchanged", while in an unsafe environment, protection is associated with reward or relief depending on the situation.

In this perspective, Norris and Inglehart (2011) proposed that religiosity originates in a lack of existential security. In poor nations, people's lives are insecure in many respects, because they are vulnerable to various risks related to limited access to the basic conditions of survival (hunger, contaminated water, absence of health care), and other threats they are not prepared to face with (deep-rooted ethnic conflicts, floods, earthquakes, etc.) due to governmental corruption and instability. This contrasts with the predictably greater security in richer nations (more abundant resources, better hospitals, better jobs, better infrastructures, effective governments, etc.). According to Norris and Inglehart (2011), people living under existential insecurity have a greater need to call on supernatural powers to help them. Although they analyze group-level patterns rather than individual-level phenomena, their conclusions are in line with the view proposed here. However, such a societal account cannot explain *how* adversity predicts religiosity.

The desire to avoid adversity is not specific to monotheistic religions and recalls the meaning of shamanism in traditional societies. Like people experiencing poverty, the members of those societies are constantly under the influence of societal and environmental factors they cannot properly manage. Shamans are widespread among hunter-gatherer societies (Peoples et al. 2016). They fall into trance to provide services, essentially asking spirits to defeat their enemies, to cure diseases, to have successful hunting, to influence the weather, and to reveal future events. Their intervention is typically requested in situations where the outcome is unpredictable and can affect existential security in case things are going bad. The role of shamans is to try to convince the group-members—as potential clients—that they are able to influence uncontrollable, important events (Singh 2018).

Adversity, Religiosity, and the Hope for an Upturn

There is some evidence that higher levels of religiosity correlate with higher levels of poverty and inequality (Baumard and Chevallier 2015; Crabtree 2009; Delamontagne 2010; Paul et al. 2005; Solt et al. 2011; but see Purzycki et al. 2018). Despite a minority of very religious affluent individuals in wealthy nations, religiosity is globally declining in those nations (Norris and Inglehart 2011; Putnam and Campbell 2012). A popular idea consists of explaining decline in terms of education. Although Bronner (2013) reports several studies showing that highly educated people (e.g., senior managers) are more inclined to believe in supernatural phenomena than people with low educational background (e.g., farmers), this might be not a general rule. Scientific training reduces the propensity to develop religious beliefs (Ecklund and Scheitle 2007), and there is a negative correlation between intelligence—measured by means of various tests, including the IQ test—and religiosity (e.g., Zuckerman et al. 2013). However, it must be noted that intelligence is a good predictor of academic and job performances (e.g., Schmidt and Hunter 1998; Strenze 2007), which offer more guarantee of a successful life. In other words, education and intelligence should be negatively associated with adversity; their role in religiosity might therefore be indirect compared with adversity itself.

All potential factors that may influence religiosity cannot be discussed here. However, actual or perceived adversity people would like to avoid is viewed as one major factor that contributes to religiosity. I argue that the origin of adversity (poverty, bad luck, angry spirits, etc.) does not actually matter; religious faith and worship have in common this principle:

deploying enough religious-related effort (*through religious rituals such as prayer and sacrifice*) *may protect against adversity*. This protection may, for example, consist of obtaining specific things (such as money and love) or some rewarding relief due to appeasement of an angry ancestor-spirit. People accept that effort is not always rewarded, and may attribute failures to themselves rather than calling this principle into question—e.g., "I did not pray strong enough" or "we did not sacrifice enough animals".

I defend that what *motivates* the belief in (one or several) supernatural agents is the *hope* that these agents will solve the problems encountered after providing some ritualized effort—even if those agents are sometimes thought to be at the origin of those problems. Hope means desiring something that is not guaranteed. Thus, hope offers a window of opportunity that can motivate people to seek reward or relief in an objectively unfavorable context. The Catholic religion, for example, places hope on a pedestal. In his John Paul 1994 book, Pope John Paul II defined a believer as a person who "crosses the threshold of hope". In a sense, religious beliefs are the slave of hope, because a believer can never totally be sure that the supernatural powers will act as desired—"belief" means that there is a part of uncertainty. In the USA, for example, although some believers are intimately convinced that their prayers are answered (25%), a majority of believers are not quite sure how and when (or if) their prayers are answered (72%; LifeWay Research 2014). To connect this with Norris and Inglehart's theory, I hypothesize that people in existential insecurity believe in supernatural agents because hoping that those agents can eliminate adversity appears to be a more effective strategy than doing nothing and is more realistic than strongly expecting significant, spontaneous improvements. With hope, successes are rewarding and failures relatively neutral (not non-rewarding) to motive future hopes, because people are prepared to accept a lack of success and naturally tend to overestimate low probabilities of success (e.g., Prelec 1998).

Why believe that a supernatural entity will help us? Singh (2018) suggests that a basis for shamanic and religious practices is superstition, because this psychological state can sustain beliefs in ineffective interventions. But the question remains: why do we superstitiously believe that good news could result from trance or prayer? Hope can be at the origin of superstition. For example, the flu pandemic of 1918–1919 killed about 100 million people (five times more than the First World War), including healthy adults. The situation overwhelmed the management capacity of governments, especially because there was no effective treatment against that disease (Crosby 2003). Distress was so high that a number of "miracle" cures were proposed. For example, *Le Petit Parisien* (26 October 1918), a French newspaper, suggested curing the flu with a mixture containing aspirin, quack grass, and cherry stems! This non-religious example illustrates the fact that existential insecurity naturally leads people to believe in ineffective interventions—whether the intervention is a cure or a prayer is, in a sense, anecdotal (e.g., praying to win the lottery is to ask God to change the laws of randomness to one's advantage). The reason for such a belief is always the same: people hope for a solution to their problem.

An alternative to hope would be to say that beliefs result from a need to explain misfortune. However, it is unclear whether religions really provide explanations of what happens (e.g., Boyer 2001; Sperber 1996) and how religious stories can motivate people to accept them. In contrast, people can accept religious stories more easily if they are naturally inclined to hope for supernatural intervention as an optimal strategy to avoid adversity in an unfavorable context. It could also be tempting to interpret religious motivation in terms of optimism rather than hope. Optimism results from the expectation of good things to happen, and optimistic cognitive biases have been identified in humans as well as in nonhuman animals (Brydges et al. 2011; Carver et al. 2010; Matheson et al. 2008). No need to hope for expected rewards (optimism) or for expected non-rewards (pessimism) because the two situations are fully predictable. People experiencing adversity are unlikely to be fully optimistic or fully pessimistic—why would they invoke supernatural powers if they already knew what is going to happen? The presence of uncertainty about reward or about relief is hardly compatible with these two concepts; people can only hope for good things.

Of course, not all people experiencing adversity become religious and not all people exposed to wealth become non-religious. Religiosity is a complex phenomenon that depends on how our evolved brains interpret the signals they receive, and multiple factors may play a role—including genetic factors (e.g., Inzlicht et al. 2009). But the fact that adversity/misfortune and religiosity tend to go hand-in-hand throughout the world (Boyer 2001) simply indicates that our human brains *tend* to accept religious beliefs as a result of this specific environmental stimulation.

Long before the invention of spirits and gods, hope was certainly useful in tasks such as food seeking. When food is scarce, the hope that some edible items will eventually be found can strengthen and lengthen foraging activity, increasing the chance of survival in comparison with hopeless people. In the next section, it is shown that something that resembles hope seems to exist in nonhuman animals too—at least in birds and mammals. This hope-like psychological state—called incentive hope (Anselme 2015)—can explain the invigoration of food-seeking behavior observed in animals exposed to harsh environmental conditions, and contributes to maintain them alive. Religious faith and worship are hypothesized to exploit this ancestral motivational system.

A Motivational Strategy Against Adversity: Function and Mechanism

The persons who believe in supernatural powers hope that they can influence the course of events through sacrifices or prayers, increasing their chance of obtaining an uncertain, desired outcome—i.e., deliverance from adversity. Sacrifice and prayer look like appetitive—rather than consummatory—behaviors, during which the individual is usually seeking rewards. Appetitive behaviors are flexible and apt to be shaped by learning (Tinbergen 1951; Domjan 2015), explaining the large variation in the act of praying or making a sacrifice throughout the world—just as there are many ways for humans to prepare foods or to engage in sexual foreplays. In the context of food seeking, uncertainty has the effect of boosting appetitive behavior in humans and nonhuman animals, as if the individuals were motivationally excited by rewards when non-rewards are likely—i.e., as if they hoped for rewards (Anselme 2015, 2016; Anselme and Güntürkün in press). I argue that hope-related motivation—called incentive hope—depends on mechanisms hardwired in the brain of human and nonhuman animals, promoting survival when access to food rewards is unguaranteed (Anselme et al. 2017, 2018; Anselme and Güntürkün in press). Sacrifice and prayer are unrelated to food seeking per se, but they are hypothesized to depend on its motivational system. If correct, this means that sacrifice and prayer depend on a motivational system that is not specifically human—although they occur only in humans because only humans have the cognitive abilities to believe in supernatural powers (Torrey 2017). To begin with, I would like to briefly present the evidence that justifies the concept of incentive hope, which is both described at the functional (adaptive) and the causal (mechanistic) level in "higher" vertebrates, including humans.

Uncertainty, Food-Seeking, and Survival in Humans and Nonhumans

Food abundance is infrequent in the wild. Especially for wintering and socially subordinate individuals, food accessibility is unpredictable because foraging can be unsuccessful on some days. On account of this, evolution designed animals in such a way that they tend to put on more fat reserves, avoiding starvation, under scarce food conditions (e.g., Cresswell 2003; Cuthill et al. 1997; Foster et al. 2006; Hake 1996; Lilliendahl 1998; MacLeod et al. 2007; Ratikainen and Wright 2013). Although fat reserves may increase independent of the amounts of food consumed (Cornelius et al. 2017), unpredictable access to food has been shown to increase food seeking and consumption (e.g., Bauer et al. 2011; Pravosudov and Grubb 1997; van Balen 1980). This phenomenon has also been observed in humans, and is referred to as the insecurity hypothesis (Nettle et al. 2017). Human participants merely exposed to words such as "shortfall" and "adversity" or to a scenario reporting bad socioeconomic conditions express a desire to eat, and actually consume, more food items of high-energy value than participants exposed to neutral words or to a more favorable scenario (Laran and Salerno 2013; Swaffield and Roberts 2015). Subjective feelings of lower socioeconomic status relative to other individuals is also sufficient to increase food intake and preference for high-calorie foods, even in the absence of objective differences in access to financial resources (Cheon and Hong 2017). Thus, human and nonhuman individuals exposed to food insecurity appear to be strongly motivated to seek food items, and may paradoxically consume and/or hoard more food items when food is scarce than when it is abundant. In fact, the absence of starvation risk under food abundance allows organisms to limit their consumption, hence remaining fast and agile to escape from predatory attacks and other forms of overweight-related risks (e.g., Cresswell 2003; Lima 1986; Gosler et al. 1995; Nettle et al. 2017; Witter and Cuthill 1993). Here, I am not interested in fat regulation, but in the evidence that unpredictable access to food seems to enhance reward-seeking motivation.

In psychology, there is compelling evidence that animals in Skinner boxes approach and interact more vigorously with a conditioned stimulus (CS) that ambiguously predicts food or no food on each trial than animals exposed to a non-ambiguous CS that predicts food consistently (e.g., Anselme et al. 2013; Boakes 1977; Collins et al. 1983; Gottlieb 2004; Robinson et al. 2014; Torres et al. 2016). Autoshaping is a Pavlovian procedure in which an animal learns to associate the short presentation of a CS (e.g., a metal lever for rats or an illuminated key for pigeons) with the automatic delivery of food following termination of its presentation. The invigorating behavioral effects of reward uncertainty in autoshaping have been well documented in rats and pigeons, and this phenomenon is easily replicable. There is good reason to think that the brain control of incentive motivation is involved here, because dopamine levels in the ventral striatum are higher in animals trained under uncertainty—as opposed to certainty—autoshaping (Fiorillo et al. 2003; Hart et al. 2015), a neurophysiological effect reported in humans as well (Dreher et al. 2006; Preuschoff et al. 2006).

At first sight, CS-directed (sign-tracking) responses in certainty autoshaping appear irrational because this behavior occurs without necessity—the animal is rewarded on each trial, irrespective of its interaction with the CS (Tomie et al. 2016). The invigoration of the sign-tracking responses appears even more irrational under partial reinforcement, because reward rate is reduced compared to what it could be under continuous reinforcement. But from an evolutionary perspective, this behavior might be not irrational at all. We saw that, in wild animals, foraging effort increases when resources are scarce, and that this strategy contributes to reducing the risk of starvation.

To understand the functional dimension of sign-tracking behavior under partial reinforcement, we have to ask a simple question: why did Pavlov's dog salivate to the sound of a bell? The answer is: because salivation is useful to the digestion of the upcoming food. Animals learn to respond to a CS only if the conditioned response helps them cope with—is relevant to—the unconditioned stimulus or UCS (Domjan 2015). Therefore, some associations are easy to learn because they make sense in terms of evolution (e.g., location → food), while others are not due to their inappropriateness (e.g., light → malaise). The evolutionary established relationships between CSs and UCSs could similarly explain the higher response rates to an unreliable than to a reliable CS in Pavlovian autoshaping: animals would respond more to unreliability because, in nature, the distribution of food items is relatively random (even within a patch) and many CSs are imperfect predictors of food (a seed husk may be empty, a mulberry tree may have no fruits, etc.). Animals are simply prepared to work harder when part of their attempts to get food is non-rewarded. Here, "prepared" means that this response is hardwired in their (and our) brain; it does not require any knowledge or consciousness of the situation to be elicited. In other words, avidly responding to the CS presentations in uncertainty autoshaping is similar to avidly checking the available CSs in a poor-food environment; this schedule-induced behavior is the signature of a neurobehavioral adaptation that minimizes the risk of starvation in a natural setting. In conclusion, reward uncertainty boosts seeking behavior in humans and nonhuman animals, and this effect is likely to be a product of evolution. The mechanism responsible for this effect is called incentive hope (e.g., Anselme 2015; Anselme et al. 2017).

Underpinning Mechanism: Incentive Salience or Incentive Hope?

Before discussing incentive hope in relation to religious faith and worship, it is important to explain why incentive hope differs from incentive salience and to know a bit more about its hypothesized implementation in the brain. The incentive salience hypothesis is well established and posits that incentive motivation chiefly depends on the release of dopamine in the ventral striatum, causing enhanced attraction to rewards and their predictive CSs (Berridge 2007). This view does not tell us whether reward uncertainty should increase or decrease incentive motivation, because motivational strength is processed separately from the predictive value of a stimulus (Flagel et al. 2007; Robinson and Flagel 2009). But logically, if reward uncertainty was limited to increasing the attractiveness of CSs (as response rates and dopamine release seem to suggest), animals should prefer an ambiguous over a non-ambiguous CS in a free-choice task. Current evidence indicates that this is not the case: when individuals have to choose between an uncertain and a certain option, they often avoid uncertainty (Anselme in press; Kahneman and Tversky 1979; McDevitt et al. 2016). In fact, they select the uncertain option only if uncertainty is associated with survival-related advantages, such as a shorter delay or reliable CSs (Anselme and Güntürkün in press; e.g., see Smith and Zentall 2016; Chow et al. 2017). This finding is important; it clearly indicates that the stimulation of food-seeking behavior under unavoidable uncertainty—like in autoshaping or in the wild—cannot entirely depend on incentive salience. The stimulation of food-seeking behavior under unavoidable uncertainty of reward seems to reflect a survival requirement rather than preference (Anselme and Güntürkün in press).

The incentive hope hypothesis solves this paradox between the evidence that reward uncertainty increases response rates through mesolimbic dopamine release and the evidence that uncertainty is not preferred to certainty. Indeed, incentive hope can, as a motivational process, boost responding to a stimulus when reward uncertainty is unavoidable, but should favor reward certainty when accessible—there is no need to hope for uncertain rewards if the same rewards can be obtained for sure. Also, because reward uncertainty boosts seeking behavior despite similar food deprivation level (e.g., Anselme et al. 2013), incentive hope can contribute to stimulate seeking before the animal is close to starvation. This process has the effect of rendering animal foraging more effective than it would be under intense hunger. Here, hope is defined behaviorally. Like incentive salience (Berridge 2012), incentive hope denotes a motivational process which must be distinguished from cognition and consciousness; organisms exposed to reward uncertainty simply behave *as if* they explicitly hoped for a reward. Providing more details is unnecessary here. But it is important to distinguish incentive hope from human hopes and their associated subjective feelings. Incentive hope is viewed as an ancestral neurobehavioral mechanism that resembles human hopes but consists only of a "template" making human hopes possible within an appropriate brain structure.

How does incentive hope work? As shown, incentive hope is a motivational process partly related to incentive salience, but it should also closely be related to stress-induced corticotropin-releasing factor (CRF) and glucocorticoids. When an individual is exposed to stressful events, such as those associated with adversity in life, there is a release of corticosterone (or cortisol) via the activation of the hypothalamic-pituitary-adrenal (HPA) axis (Bauer et al. 2011; Marasco et al. 2015). CRF and corticosterone are known to boost the production of mesolimbic dopamine from the ventral tegmental area (Cabib and Pulgisi-Allegra 2012; Lemos et al. 2012; Piazza et al. 1996), and therefore provides the ground on which motivation can possibly be recruited by stressors (Sinha and Jastreboff 2013). This could explain Hellberg et al.'s (2018) findings that anxious rats sign-track more than non-anxious rats in

uncertainty autoshaping, and more than anxious rats in certainty autoshaping. Incentive hope is assumed to exploit the extra dopamine under uncertainty, a mild stressor, explaining why more dopamine does not necessarily mean more attraction (Anselme and Güntürkün in press). Moderate levels of glucocorticoids should facilitate incentive hope, while higher levels of glucocorticoids should favor stressful experience. At intermediate levels of glucocorticoids, incentive hope and stress could be expressed simultaneously, causing an exploration-exploitation tradeoff.

In conclusion, we have seen that, in nature, incentive hope is functionally able to boost foraging activity, reducing the risk of starvation when food is scarce. This connects to the evidence that, in humans exposed to feelings of deprivation, hope can enhance the effort deployed to reach a desired future (Bloch 1996). This view is in apparent contrast with the fact that when people cannot act to change an unfavorable situation (incurable disease, political oppression, etc.), hope allows them to passively endure and simply maintain initial activity level despite an objectively low chance of success (Oettingen and Chromik 2018). But passive waiting occurs relative to the commitment in concrete actions, which have failed to be rewarding. It is not, for example, about religion-related actions, such as prayer, which are perceived as more effective in causing specific outcomes—reward or relief: as shown earlier, religiosity is more frequent when people experience a low chance of success in their life. If religious motivation depends on incentive hope, it is unsurprising that faith and worship share essential properties with incentive hope, such as being mainly expressed when adversity is high (e.g., poor countries/scarce food) and leading to unusual deployment of effort to get rewarded (praying, attending to religious services, remaining chaste, building monuments, promoting wars/increasing food seeking and food handling, remembering the caches of thousands of food items). In other words, incentive hope is assumed to be the core psychological process of human hopes, and its function is to motivate and facilitate adversity avoidance through enhanced ritualized behaviors. Now that the evolutionary and mechanistic dimensions of incentive hope have been considered, I would like to show how incentive hope could work in a religious context—with special reference to religious faith.

Religious Motivation Could Require Incentive Hope

Faith and Striatal Dopamine

Assuredly, religious faith is a phenomenon much more sophisticated than the approach of a CS predictive of food by a hungry animal. However, both have in common to recruit mesolimbic dopamine. According to McNamara (2002), dopamine release might explain the addictive, maladaptive effects of religiosity. Increased dopamine release is indeed more often reported in people with strong religious convictions (e.g., Schjoedt et al. 2008). But it is also likely that dopamine is crucial for the development of religious motivation itself. Human patients with disorders of excessive dopaminergic functioning, such as schizophrenia and obsessive compulsive disorders, often show an increase in religiosity (e.g., Brewerton 1994; Tek and Ulug 2001). In contrast, patients with Parkinson's disease, which is associated with reduced dopamine production in the substantia nigra and the nucleus accumbens, often show a decrease in religiosity (e.g., Harris and McNamara 2009; McNamara et al. 2006b).

Dopamine projections from the ventral tegmental area to the ventral striatum (nucleus accumbens) is strongly correlated with incentive motivational processes (Berridge 2007). In a neuroimaging study, Ferguson et al. (2018) demonstrated that Mormons devouts exposed to an audiovisual stimulus with a religiously evocative content, and requested to press a button when experiencing peak spiritual feelings, show bilateral activation in their nucleus accumbens 1–3 s prior to button press. Dopamine can also project to the dorsal striatum, from the substantia nigra, and has motivational effects as well (Balleine et al. 2007; Volkow et al. 2002). The density of dopamine receptors in the dorsal striatum is high, and we suggested elsewhere that its dorsomedial part (called caudate nucleus in humans) could be involved in incentive hope (Anselme and Güntürkün in press). Indeed, the dorsomedial striatum is necessary for the invigoration of the sign-tracking responses observed under reward uncertainty in Pavlovian autoshaping. Torres et al. (2016) showed that massive lesions of the dorsomedial striatum specifically eliminate uncertainty-induced behavioral invigoration in rats; lesioned rats trained under reward uncertainty come to press the lever at the same rate as non-lesioned rats under reward certainty. In other words, lesions of the dorsomedial striatum do not suppress incentive salience (the rats from both groups approached and pressed the lever CS), but the specific effects of reward uncertainty are abolished. Interestingly, religious faith appears to activate this brain region (Beauregard and Paquette 2006). Schjoedt et al. (2008) found that prayer activates the right caudate nucleus in strong Danish Christian believers. The authors let open the question whether the involvement of dopamine neurons in the caudate is due to the rehearsal of religious rituals (habit formation) or due to the strong religious conviction of the participants. However, current evidence suggests that habit formation is mainly processed by the putamen (dorsolateral striatum) rather than the caudate (Everitt and Robbins 2005; Yin and Knowlton 2006). The caudate plays a crucial role in goal-directed behavior, when behavior is not yet a habit and can be adjusted to contextual changes, like an appetitive act is. Of course, caudate activation is, in itself, insufficient to justify the incentive hope hypothesis. But this hypothesis is the only one to predict that

strong religious conviction associated with the uncertainty of how and when the prayers will be answered contributes to the activation of the caudate nucleus.

Faith and Anxiety

Dawkins (2006) defined faith as "a belief without evidence". This definition connects faith and belief, but presenting faith as a special kind of belief fails to explain the motivational power of faith. It does not explain why many people have such inappropriate beliefs, and why having those beliefs may lead some people to devote significant parts of their lifetime to cultivate them. According to Atran (2002), religious rituals arouse "existential anxieties that motivate religious beliefs and quests for deliverance" (p. 165). Here, faith is not viewed as a belief but as a consequence of some behavioral processes (rituals, rehearsals) aimed to incite adversity-related feelings (starvation, injustice, oppression, loneliness, etc.), and to motivate people to believe in supernatural powers capable of delivering them from these threats. This interpretation is compatible with the incentive hope hypothesis, for which faith is basically a motivation against adversity rather than a belief. More specifically, the hypothesis predicts that if adversity-related feelings were not at the very origin of faith, the belief in God would not have had powerful effects on human lives and, a fortiori, on human civilizations. Some people may believe in the existence of unicorns and dragons, but as long as they do not believe that these entities can save them from adversity, religious practices and devotion are unlikely to develop. Similarly, most everyday rituals (brushing one's teeth, tying one's shoes, etc.) differ from religious rituals in that they are ineffective in offering protection against adverse events the individual cannot control. As a result, they are performed without much enthusiasm. Indeed, escaping from adverse situations is what people typically request when they pray. A 2014 survey from LifeWay Research, conducted on 1137 Americans about the content and frequency of their prayers, indicates that they massively pray for family and friends (82%) or themselves (74%) when faced with difficulties, and less for good things that have recently occurred (54%).

Even sudden changes in existential anxieties/insecurity have the effect of transiently altering the desire to believe in God. Shrimali and Broota (1987) studied how pre- and post-surgical stress influences superstition and the belief in God. Preoperatively, major-surgery patients were more superstitious and showed stronger belief in God than minor-surgery patients and control participants. However, those effects decreased postoperatively in major-surgery patients and remained unchanged in the other two groups. Similarly, Norenzayan and Hansen (2006) created scenarios in which people were primed with thoughts about their own death as a form of existential anxiety, and they found that the awareness of mortality reliably increased the propensity to believe in supernatural powers and in the efficacy of supernatural interventions. In fact, concrete reference to existential anxieties (e.g., death) is not necessary to encourage such beliefs. Kay et al. (2010) demonstrated that participants primed with randomness-related words ("chance," "random," etc.) showed enhanced beliefs in spiritual control than participants primed with negative-valence words ("poorly," "slimy," etc.). So, the simple evocation of randomness, independent of any actual traumatic events, may magnify spiritual beliefs. Here, the incentive hope hypothesis establishes a parallel (discussed earlier) with food-directed behavior in humans: adversity-related words increase the desire to consume high-calorie items (Laran and Salerno 2013), even in the absence of group differences in access to financial resources (Cheon and Hong 2017). In both cases, incentive hope favors behaviors assumed to increase the chance of reward under conditions perceived as suboptimal. According to the incentive hope hypothesis, anxiety is not the direct cause of faith. But the neurobiological underpinnings of anxiety or stress (CRF and glucocorticoids) contribute to release neurochemicals (especially dopamine) that may facilitate faith in the human brain. Importantly, I am not trying to establish a causal relationship between adversity-induced dopamine release and faith but simply suggest that adversity-induced dopamine release increases the brain's receptiveness to religious ideas and behaviors.

This perspective offers a way of understanding how money dampens religious beliefs. Money is a very potent CS that has been associated with power and abundance throughout human history, increasing the feeling of security in rich people. The money-induced reduction in existential insecurity—and hence, in existential anxieties—tends to attenuate incentive hope, and therefore the need for faith and prayer. Indeed, when money is in sufficient amounts, there is no need to hope for rewards because they are (almost) guaranteed; a high expectation of rewards leads people to consider that the rewards are already obtained (Oettingen and Chromik 2018). If the need for supernatural protection is reduced, people are less inclined to deploy effort for their God, are less inclined to believe that God plays a role in what happens, and therefore care less about possible divine punishment. People living in high-income countries are less inclined to be faithful perhaps for the same reason as rats under certainty autoshaping or birds in summer: they are less motivated to seek rewards—and protection in general—due to the absence of incentive hope.

Additional Predictions

Prediction 1 We saw that rats press a lever for food more avidly when the presentation of the lever is occasionally rather than consistently followed by food delivery. The incentive hope hypothesis suggests that the motivation behind

behavioral invigoration under food uncertainty is the same as that of a person praying in front of a cross for more gratifications in the near future. Here, I am not trying to reduce the behavior of a human believer to that of a hungry rat, but there is an interesting prediction to draw. If correct, it is predicted enhanced praying activity in people experiencing adversity in their life and considering that not all their requests are positively answered, compared to people in similar situations who consider that all their requests are positively answered.

Prediction 2 We saw that existential anxieties increase the propensity to believe in God, but it is unknown whether these anxieties are directly or indirectly related to religious motivation. The dopamine released under mild stress could be a determining factor here. Indeed, studies with healthy participants and patients with dopaminergic deregulations indicate that dopamine is involved in religiosity. The incentive hope hypothesis predicts that anxiety-induced dopamine rather than anxiety itself boosts religious faith.

Prediction 3 The incentive hope hypothesis predicts that people praying to ask God for some help to overcome a difficulty should release more dopamine in the ventral and the dorsomedial striatum than people praying to thank God for having helped them overcome a difficulty. Indeed, in the former situation, they hope for reward, while no hope is involved in the latter situation.

The view presented in this article would be refuted if some people strongly believed in supernatural entities exclusively (or mainly) for reasons unrelated to adversity avoidance—e.g., people who would thank God for what they received instead of asking for any kind of reward or relief, whether directed to themselves or to other people.

Conclusion

The concept of incentive hope is, like many psychological constructs, a hypothesis. But it has proved to be useful to explain many aspects of food-seeking behavior under reward uncertainty, both in animals and humans (Anselme and Güntürkün in press). If we consider faith and worship as measures to avoid adversity (obtaining rewards, conserving wealth, appeasing spirits), incentive hope could be appropriate to account for their very origin. Of course, faith and worship are conscious acts that require conscious hopes as mental states. Incentive hope is not a mental state; it is only assumed to be a process hardwired in the brain of animals by means of natural selection because this process increases their chance of survival. But it is assumed that conscious hopes are simply revealed to ourselves and enriched from incentive hope on the basis of our human cognitive and metacognitive tools, including self-awareness and introspection. Conscious hopes are supposed to originate in incentive hope (just as conscious desires are likely to stem from incentive "wanting"), and this is why testing empirical predictions of the incentive hope hypothesis may contribute to account for the psychology of religiosity.

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Compliance with Ethical Standards

Conflict of Interest The author declares that he has no conflict of interest.

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References

Anselme, P. (2015). Incentive salience attribution under reward uncertainty: a Pavlovian model. *Behavioural Processes, 111*, 6–18.

Anselme, P. (2016). Motivational control of sign-tracking behaviour: a theoretical framework. *Neuroscience and Biobehavioral Reviews, 65*, 1–20.

Anselme, P. (in press). Uncertainty processing in bees exposed to free choices: lessons from vertebrates. *Psychonomic Bulletin and Review*. https://doi.org/10.3758/s13423-018-1441-x.

Anselme, P., & Güntürkün, O. (in press). How foraging works: uncertainty magnifies food-seeking motivation. *Behavioral and Brain Sciences*. https://doi.org/10.1017/S0140525X18000948.

Anselme, P., Robinson, M. J. F., & Berridge, K. C. (2013). Reward uncertainty enhances incentive salience attribution as sign-tracking. *Behavioural Brain Research, 238*, 53–61.

Anselme, P., Otto, T., & Güntürkün, O. (2017). How unpredictable access to food increases the body fat of small passerines: a mechanistic approach. *Behavioural Processes, 144*, 33–45.

Anselme, P., Otto, T., & Güntürkün, O. (2018). Foraging motivation favors the occurrence of Lévy walks. *Behavioural Processes, 147*, 48–60.

Atran, S. (2002). *In gods we trust. The evolutionary landscape of religion*. Oxford: Oxford University Press.

Balleine, B. W., Delgado, M. R., & Hikosaka, O. (2007). The role of the dorsal striatum in reward and decision-making. *Journal of Neuroscience, 27*, 8161–8165.

Barkow, J. H., Cosmides, L., & Tooby, J. (1992). *The adapted mind: evolutionary psychology and the generation of culture*. New York: Oxford University Press.

Barrett, H. C. (2015). *The shape of thought. How mental adaptations evolve*. Oxford: Oxford University Press.

Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychological Review, 113*, 628–647.

Bauer, C. M., Glassman, L. W., Cyr, N. E., & Romero, L. M. (2011). Effects of predictable and unpredictable food restriction on the stress response in molting and non-molting European starlings (*Sturnus vulgaris*). *Comparative Biochemistry and Physiology A, 160*, 390–399.

Baumard, N., & Chevallier, C. (2015). The nature and dynamics of world religions: a life-history approach. *Proceedings of the Royal Society B, 282*, 20151593.

Beauregard, M., & Paquette, V. (2006). Neural correlates of a mystical experience in Carmelite nuns. *Neuroscience Letters, 405*, 186–190.

Berridge, K. C. (2007). The debate over dopamine's role in reward: the case for incentive salience. *Psychopharmacology, 191*, 391–431.

Berridge, K. C. (2012). From prediction error to incentive salience: mesolimbic computation of reward motivation. *European Journal of Neuroscience, 35*, 1124–1143.

Bloch, E. (1996). *The principle of hope (Vol. 1)*. Cambridge, MA: MIT Press.

Boakes, R. A. (1977). Performance on learning to associate a stimulus with positive reinforcement. In H. Davis & H. M. B. Hurvitz (Eds.), *Operant Pavlovian interactions* (pp. 67–97). Hillsdale, NJ: Erlbaum Associates.

Boyer, P. (2001). *Religion explained: the evolutionary origins of religious thought*. New York: Basic Books.

Brewerton, T. (1994). Hyperreligiosity in psychotic disorders. *Journal of Nervous and Mental Disease, 182*, 302–304.

Bronner, G. (2013). *La démocratie des crédules*. Paris: Presses Universitaires de France.

Brydges, N. M., Leach, M., Nicol, K., Wright, R., & Bateson, M. (2011). Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour, 81*, 169–175.

Cabib, S., & Pulgisi-Allegra, S. (2012). The mesoaccumbens dopamine in coping with stress. *Neuroscience and Biobehavioral Reviews, 36*, 79–89.

Carruthers, P. (2006). *The architecture of the mind*. Oxford: Oxford University Press.

Carver, C. S., Scheier, M. F., & Segerstrom, S. C. (2010). Optimism. *Clinical Psychology Review, 30*, 879–889.

Cheon, B. K., & Hong, Y.-Y. (2017). Mere experience of low subjective socioeconomic status stimulates appetite and food intake. *Proceedings of the National Academy of Science, 114*, 72–77.

Chow, J. J., Smith, A. P., Wilson, A. G., Zentall, T. R., & Beckmann, J. S. (2017). Suboptimal choice in rats: Incentive salience attribution promotes maladative decision-making. *Behavioural Brain Research, 320*, 244–254.

Collins, L., Young, D. B., Davies, K., & Pearce, J. M. (1983). The influence of partial reinforcement on serial autoshaping with pigeons. *Quarterly Journal of Experimental Psychology, 35B*, 275–290.

Cornelius, E. A., Vezina, F., Regimbald, L., Hallot, F., Petit, M., Love, O. P., & Karasov, W. H. (2017). Chickadees faced with unpredictable food increase fat reserves but certain components of their immune function decline. *Physiological and Biochemical Zoology, 90*, 190–200.

Crabtree, S. (2009). Religiosity highest in world's poorest nations. http://news.gallup.com/poll/142727/religiosity-highest-world-poorest-nations.aspx.

Cresswell, W. (2003). Testing the mass-dependent predation hypothesis: in European blackbirds poor foragers have higher overwinter body reserves. *Animal Behaviour, 65*, 1035–1044.

Crosby, A. W. (2003). *America's forgotten pandemic: The influenza of* (p. 1918). Cambridge: Cambridge University Press.

Cuthill, I. C., Hunt, S., Cleary, C., & Clark, C. (1997). Colour bands, dominance, and body mass regulation in male zebra finches (*Taeniopygia guttata*). *Proceeding of the Royal Society of London B, 264*, 1093–1099.

Dawkins, R. (2006). *The God delusion*. Oxford: Bantam Books.

Delamontagne, R. G. (2010). High religiosity and societal dysfunction in the United States during the first decade of the twenty-first century. *Evolutionary Psychology, 8*, 617–657.

Domjan, M. (2015). *The principles of learning and behavior*. Connecticut: Cengage Learning.

Dreher, J.-C., Kohn, P., & Berman, K. F. (2006). Neural coding of distinct statistical properties of reward information in humans. *Cerebral Cortex, 16*, 561–573.

Ecklund, E. H., & Scheitle, C. P. (2007). Religion among academic scientists: distinctions, disciplines, and demographics. *Social Problems, 54*, 289–307.

Everitt, B. J., & Robbins, T. W. (2005). Neural systems of reinforcement for drug addiction: from actions to habits to compulsion. *Nature Neuroscience Review, 8*, 1481–1489.

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

Fiorillo, C. D., Tobler, P. N., & Schultz, W. (2003). Discrete coding of reward probability and uncertainty by dopamine neurons. *Science, 299*, 1898–1902.

Flagel, S. B., Watson, S. J., Robinson, T. E., & Akil, H. (2007). Individual differences in the propensity to approach signals vs goals promote different adaptations in the dopamine system of rats. *Psychopharmacology, 191*, 599–607.

Foster, M. T., Solomon, M. B., Huhman, K. L., & Bartness, T. J. (2006). Social defeat increases food intake, body mass, and adiposity in Syrian hamsters. *American Journal of Physiology, 290*, R1284–R1293.

Gosler, A. G., Greenwood, J. J. D., & Perrins, C. (1995). Predation risk and the cost of being fat. *Nature, 377*, 621–623.

Gottlieb, D. A. (2004). Acquisition with partial and continuous reinforcement in pigeon autoshaping. *Learning and Behavior, 32*, 321–334.

Greenberg, J., Pyszczynski, T., & Solomon, S. (1986). The causes and consequences of a need for self-esteem: a terror management theory. In R. F. Baumeister (Ed.), *Public Self and Private Self* (pp. 189–212). New York: Springer-Verlag.

Hake, M. (1996). Fattening strategies in dominance-structured greenfinch (*Carduelis chloris*) flocks in winter. *Behavioral Ecology and Sociobiology, 39*, 71–76.

Harris, E., & McNamara, P. (2009). Neurologic constraints on evolutionary theories of religion. In E. Voland & W. Schiefenhövel (Eds.), *The biological evolution of religious mind and behavior* (pp. 205–215). Berlin: Springer-Verlag.

Hart, A. S., Clark, J. J., & Phillips, P. E. M. (2015). Dynamic shaping of dopamine signals during probabilistic Pavlovian conditioning. *Neurobiology of Learning and Memory, 117*, 84–92.

Hellberg, S. N., Levit, J. D., & Robinson, M. J. F. (2018). Under the influence: effects of adolescent ethanol exposure and anxiety on motivation for uncertain gambling-like cues in male and female rats. *Behavioural and Brain Research, 337*, 17–33.

Inzlicht, M., McGregor, I., Hirsh, J. B., & Nash, K. (2009). Neural markers of religious conviction. *Psychological Science, 20*, 385–392.

John Paul, I. I. (1994). *Crossing the threshold of hope*. New York: Knopf, Inc.

Johnson, D. D. P. (2005). God's punishment and public goods: a test of the supernatural punishment hypothesis in 186 world cultures. *Human Nature, 16*, 410–446.

Kahneman, D., & Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica, 47*, 263–292.

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 Science, 106*, 4876–4881.

Kay, A. C., Moscovitch, D. A., & Laurin, K. (2010). Randomness, attribution of arousal, and belief in God. *Psychological Science, 21*, 216–218.

Klarsfeld, A., & Revah, F. (2000). *Biologie de la mort*. Paris: Odile Jacob.

Kohls, G., Perino, M. T., Taylor, J. M., Madva, E. N., Cayless, S. J., Troiani, V., Price, E., Faja, S., Herrington, J. D., & Schultz, R. T. (2013). The nucleus accumbens is involved in both the pursuit of social reward and the avoidance of social punishment. *Neuropsychologia, 51*, 2062–2069.

Laran, J., & Salerno, A. (2013). Life-history strategy, food choice, and caloric consumption. *Psychological Science, 24*, 167–173.

Lemos, J. C., Wanat, M. J., Smith, J. S., Reyes, B. A. S., Hollon, N. G., Van Bockstaele, E. J., Chavkin, C., & Phillips, P. E. M. (2012). Severe stress switches CRF action in the nucleus accumbens from appetitive to aversive. *Nature, 490*, 402–406.

LifeWay Research. (2014). American prayer practices. http://lifewayresearch.com/wp-content/uploads/2014/09/American-Prayer-Practices.pdf.

Lilliendahl, K. (1998). Yellowhammers get fatter in the presence of a predator. *Animal Behaviour, 55*, 1335–1340.

Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology, 67*, 377–385.

MacLeod, R., Lind, J., Clark, J., & Cresswell, W. (2007). Mass regulation in response to predation risk can indicate population declines. *Ecology Letters, 10*, 945–955.

Marasco, V., Boner, W., Heidinger, B., Griffiths, K., & Monaghan, P. (2015). Repeated exposure to stressful conditions can have beneficial effects on survival. *Experimental Gerontology, 69*, 170–175.

Matheson, S. M., Asher, L., & Bateson, M. (2008). Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Applied Animal Behaviour Science, 109*, 374–383.

McDevitt, M. A., Dunn, R. M., Spetch, M. L., & Ludvig, E. A. (2016). When good news leads to bad choices. *Journal of the Experimental Analysis of Behavior, 105*, 23–40.

McNamara, P. (2002). The motivational origins of religious practices. *Zygon, 37*, 143–160.

McNamara, P., Durso, R., & Brown, A. (2006a). Religiosity in patients with Parkinson's disease. *Neuropsychiatric Disease and Treatment, 2*, 341–348.

McNamara, P., Durso, R., Brown, A., & Harris, E. (2006b). The chemistry of religiosity: evidence from patients with Parkinson's disease. In: P. McNamara (Ed.), *Where God and science meet*. Vol. 2: The neurology of religious experience (chap. 1, pp. 1–14). London: Praeger Perspectives.

Miller, G. (2000). *The mating mind. How sexual choice shaped the evolution of human nature*. London: Vintage.

Morgan, J., Clark, D., Tripodis, Y., Halloran, C. S., Minsky, A., Wildman, W. J., Durso, R., & McNamara, P. (2016). Impacts of religious semantic priming on an intertemporal discounting task: response time effects and neural correlates. *Neuropsychologia, 89*, 403–413.

Nettle, D., Andrews, C., & Bateson, M. (2017). Food insecurity as a driver of obesity in humans: the insurance hypothesis. *Behavioral and Brain Sciences, 40*, 1–53.

Norenzayan, A., & Hansen, I. G. (2006). Belief in supernatural agents in the face of death. *Personality and Social Psychology Bulletin, 32*, 174–187.

Norris, P., & Inglehart, R. (2011). *Sacred and secular: religion and politics worldwide*. Cambridge: Cambridge University Press.

Oettingen, G. & Chromik, M.P. (2018). How hope influences goal-directed behavior. In: S.J. Lopez &.M.W. Gallagher (Eds.) The Oxford handbook of hope (pp. 69–79). New York City, NY: Oxford University Press.

Oleson, E. B., Gentry, R. N., Chioma, V. C., & Cheer, J. F. (2012). Subsecond dopamine release in the nucleus accumbens predicts conditioned punishment and its successful avoidance. *Journal of Neuroscience, 32*, 14,804–14,808.

Paul, R., Shriberg, L., McSweeny, J., Cicchetti, D., Klin, A., & Volkmar, F. (2005). Brief Report: relations between prosodic performance and communication and socialization ratings in high functioning speakers with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 35*, 861–869.

Peoples, H. C., Duda, P., & Marlowe, F. W. (2016). Hunter-gatherers and the origins of religion. *Human Nature, 27*, 261–282.

Piazza, P. V., Rouge-Pont, F., Deroche, V., Maccari, S., Simon, H., & Le Moal, M. (1996). Glucocorticoids have state-dependent effects on the mesencephalic dopamine transmission. *Proceedings of the National Academy of Science, 93*, 8716–8720.

Pinker, S. (1997). *How the mind works*. W. W. Norton & Company.

Pravosudov, V. V., & Grubb, T. C. (1997). Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology, 8*, 332–339.

Prelec, D. (1998). The probability weighting function. *Econometrica, 47*, 313–327.

Preuschoff, K., Bossaerts, P., & Quartz, S. R. (2006). Neural differentiation of expected reward and risk in human subcortical structures. *Neuron, 51*, 381–390.

Purzycki, B. G., Finkel, D. N., Shaver, J., Wales, N., Cohen, A. B., & Sosis, R. (2012). What does God know? Supernatural agents' access to socially strategic and non-strategic information. *Cognitive Science, 36*, 846–869.

Purzycki, B. G., Apicella, C., Atkinson, Q. D., Cohen, E., McNamara, R. A., Willard, A. K., Xygalatas, D., Norenzayan, A., & Henrich, J. (2016). Moralistic gods, supernatural punishment and the expansion of human sociality. *Nature, 530*, 327–530.

Purzycki, B. G., Ross, C. T., Apicella, C., Atkinson, Q. D., Cohen, E., McNamara, R. A., Willard, A. K., Xygalatas, D., Norenzayan, A., & Henrich, J. (2018). Material security, life history, and moralistic religions: a cross-cultural examination. *PLoS One, 13*, e0193856.

Putnam, R. D., & Campbell, D. E. (2012). *American grace: how religion divides and unites us*. New York, NY: Simon & Schuster.

Pyysiäinen, I., & Hauser, M. (2009). The origins of religion: evolved adaptation or by-product? *Trends in Cognitive Sciences, 14*, 104–109.

Ratikainen, I. I., & Wright, J. (2013). Adaptive management of body mass by Siberian Jays. *Animal Behaviour, 85*, 427–434.

Robinson, T. E., & Flagel, S. B. (2009). Dissociating the predictive and incentive motivational properties of reward-related cues through the study of individual differences. *Biological Psychiatry, 65*, 869–873.

Robinson, M. J. F., Anselme, P., Fischer, A. M., & Berridge, K. C. (2014). Initial uncertainty in Pavlovian reward prediction persistently elevates incentive salience and extends sign-tracking to normally unattractive cues. *Behavioral Brain Research, 266*, 119–130.

Salamone, J. D., & Correa, M. (2002). Motivational views of reinforcement: implications for understanding the behavioral functions of nucleus accumbens dopamine. *Behavioral Brain Research, 137*, 3–25.

Schjoedt, U., Stødkilde-Jøergensen, H., Geertz, A. W., & Roepstorff, A. (2008). Rewarding prayers. *Neuroscience Letters, 443*, 165–168.

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.

Schmidt, F. L., & Hunter, J. E. (1998). The validity and utility of selection methods in personnel psychology: practical and theoretical findings of 85 years of research findings. *Psychological Bulletin, 124*, 262–274.

Shariff, A. F., & Norenzayan, A. (2011). Mean gods make good people: different views of God predict cheating behavior. *The International Journal for the Psychology of Religion, 21*, 85–96.

Shrimali, S., & Broota, K. D. (1987). Effect of surgical stress on belief in God and superstition: an in situ investigation. *Journal of Personality and Clinical Studies, 3*, 135–138.

Singh, M. (2018). The cultural evolution of shamanism. *Behavioral and Brain Sciences, 41*, 1–62.

Sinha, R., & Jastreboff, A. N. (2013). Stress as a common risk factor for obesity and addiction. *Biological Psychiatry, 73*, 827–835.

Smith, A. P., & Zentall, T. R. (2016). Suboptimal choice in pigeons: choice is primarily based on the value of the conditioned reinforcers

rather than overall reinforcement rate. *Journal of Experimental Psychology: Animal Learning and Cognition, 42*, 212–220.

Solt, F., Habel, P., & Grant, J. T. (2011). Economic inequality, relative power, and religiosity. *Social Science Quarterly, 92*, 447–465.

Sosis, R. (2009). The adaptationist-byproduct debate on the evolution of religion: five misunderstandings of the adaptationist program. *Journal of Cognition and Culture, 9*, 315–332.

Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Oxford: Blackwell.

Strenze, T. (2007). Intelligence and socioeconomic success: a meta-analytic review of longitudinal research. *Intelligence, 35*, 401–426.

Swaffield, J., & Roberts, S. C. (2015). Exposure to cues of harsh or safe environmental conditions alters food preference. *Evolutionary Psychological Science, 1*, 69–76.

Tek, C., & Ulug, B. (2001). Religiosity and religious obsessions in obsessive-compulsive disorder. *Psychiatry Research, 104*, 99–108.

Tinbergen, N. (1951). *The Study of Instinct*. Oxford: Oxford University Press.

Tomie, A., Badawy, N., & Rutyna, J. (2016). Sign-tracking model of loss of self-control of drug-taking. In: Recent Advances in Substance Abuse. *AvidScience*, pp. 2–64.

Torres, C., Glueck, A. C., Conrad, S. E., Moron, I., & Papini, M. R. (2016). Dorsomedial striatum lesions affect adjustment to reward uncertainty, but not to reward devaluation or omission. *Neuroscience, 332*, 13–25.

Torrey, E. F. (2017). *Evolving brains, emerging gods. Early humans and the origins of religion*. New York: Columbia University Press.

van Balen, J. H. (1980). Population fluctuations of the great tit and feeding conditions in winter. *Ardea, 68*, 143–164.

Volkow, N. D., Wang, G. J., Fowler, J. S., Logan, J., Jayne, M., Franceschi, D., Wong, C., Gatley, S. J., Gifford, A. N., Ding, Y. S., & Pappas, N. (2002). "Nonhedonic" food motivation in humans involves dopamine in the dorsal striatum and methylphenidate amplifies this effect. *Synapse, 44*, 175–180.

Witter, M. S., & Cuthill, I. C. (1993). The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society B, 340*, 73–92.

Yamamoto, K., & Vernier, P. (2011). The evolution of dopamine systems in chordates. *Frontiers in Neuroanatomy, 5*, 21.

Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience, 7*, 464–476.

Zuckerman, M., Silberman, J., & Hall, J. A. (2013). The relation between intelligence and religiosity: a meta-analysis and some proposed explanations. *Personality and Social Psychology Review, 20*, 1–30.