# The Origin and Evolution of Religious Prosociality

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We examine empirical evidence for religious prosociality, the hypothesis that religions facilitate costly behaviors that benefit other people. Although sociological surveys reveal an association between self-reports of religiosity and prosociality, experiments measuring religiosity and actual prosocial behavior suggest that this association emerges primarily in contexts where reputational concerns are heightened. Experimentally induced religious thoughts reduce rates of cheating and increase altruistic behavior among anonymous strangers. Experiments demonstrate an association between apparent profession of religious devotion and greater trust. Cross-cultural evidence suggests an association between the cultural presence of morally concerned deities and large group size in humans. We synthesize converging evidence from various fields for religious prosociality, address its specific boundary conditions, and point to unresolved questions and novel predictions.

Religious prosociality, or the idea that religions facilitate acts that benefit others at a personal cost, has many proponents. Indeed, religious texts of all major religions explicitly encourage prosociality in their adherents (*1*, *2*). Social science theories have long pointed to religion as a cultural facilitator of social cohesion and ingroup solidarity (*3*, *4*), often at the expense of rival groups. However, opinion, rather than careful observation, has dominated the debate on religion's role in prosocial behavior. Recent years have seen new developments in evolutionary explanations of religion, bolstered by a small but growing empirical base that unites several academic disciplines. Here, we critically examine and synthesize evidence from anthropology, sociology, experimental psychology, and experimental economics for religious prosociality. We also address empirical inconsistencies found in studies examining the association between religion and prosociality, offer possible resolutions, and point to remaining issues and future directions.

Various evolutionary theories of religion all predict that religious beliefs and behaviors have facilitated human prosocial tendencies, but there is no scientific consensus yet as to exactly how this might have occurred. Some argue that at least certain religious beliefs and behaviors are evolutionary adaptations for group-living in large communities that have maximized genetic fitness (*5*), perhaps even by multilevel selection (*4*). However, these accounts have difficulty explaining the differential cultural distribution and cultural change over time of religious beliefs and behaviors. Two additional evolutionary accounts, however, are compatible with such cultural variability. One proposes that religious content itself is a cultural by-product of a suite of psychological tendencies evolved in the Pleistocene for other purposes, such as detecting and inferring the content of other minds and sensitivity to one's prosocial reputation in the group (*6*, *7*). Religious beliefs, to the extent that they were compatible with these psychological tendencies, could then culturally spread through social learning mechanisms and could solve adaptive problems, particularly the problem of cooperation in large groups. A third evolutionary perspective, known as cultural group selection (*8*), maintains that competition among social groups may favor the spread of fitness-enhancing cultural beliefs and costly practices, such as religious prosociality (*4*, *9*, *10*). This last-mentioned view takes as its starting point that religious beliefs are cultural by-products of evolved psychology, but argues that reputation-sensitivity, although important, is not sufficient to explain the features of strong prosocial tendencies such as the ones found in religious behavior.

Despite these important differences, large agreement is emerging that selective pressures over the course of human evolution can explain the wide cross-cultural reoccurrence, historical persistence, and predictable cognitive structure of religious beliefs and behaviors. The tendency to detect agency in nature likely supplied the cognitive template that supports the pervasive belief in supernatural agents (*6*, *7*, *11*). These agents are widely believed to transcend physical, biological, and psychological limitations (*6*, *7*). However, other important details are subject to cultural variation. Although in many societies supernatural agents are not directly concerned with human morality, in many others, morally concerned agents use their supernatural powers to observe and, in some cases, to punish and reward human social interactions. Examples include the God of Abrahamic religions and Viracocha, the Incan supreme God, but also many morally concerned deities found in traditional societies, such as the *adalo*, ancestral spirits of the Kwaio Solomon islanders (*7*). These beliefs are likely to spread culturally to the extent that they facilitate ingroup cooperation. This could occur by conforming to individual psychology that favors reputation-sensitive prosocial tendencies, as the by-product account holds; by competition among social groups, as the cultural group selection account would suggest; or possibly by some combination of the two. Religious behaviors and rituals, if more costly to cooperating group members than to freeloaders, may have reliably signaled the presence of devotion and, therefore, cooperative intention toward ingroup members, in turn, buffering religious groups against defection from freeloaders and reinforcing cooperative norms. Religious prosociality, thus, may have softened the limitations that kinship-based and (direct or indirect) reciprocity-based altruism place on group size. In this way, the cultural spread of religious prosociality may have facilitated the rise of stable, large, cooperative communities of genetically unrelated individuals.

The acute human sensitivity to prosocial reputation (*12*) is a psychological mechanism, originally unrelated to religion, that evolved to facilitate strong reciprocal cooperative bonds within groups (*13*). In an intensely social, gossiping species, reputational concerns likely contributed to the evolutionary stability of strong cooperation between strangers. Individuals known to be selfish could be detected, subsequently excluded from future interaction, and even actively punished (*13*, *14*). The threat of being found out, therefore, became a potent motivator for good behavior. Accordingly, studies have repeatedly shown that experimentally reducing the degree of anonymity in economic games increases the rate of prosocial behavior (*15*). Exposure to photographic and even schematic representations of human eyes increases prosocial behavior in economic games (*16*) and decreases cheating in naturalistic settings (*17*). We argue that religion's effect on prosocial tendencies similarly depends on such reputational sensitivity. The cognitive awareness of gods is likely to heighten prosocial reputational concerns among believers, just as the cognitive awareness of human watchers does among believers and nonbelievers alike (*18*). However, supernatural monitoring, to the degree that it is genuinely believed and cognitively salient, offers the powerful advantage that cooperative interactions can be observed even in the absence of social monitoring.

This line of reasoning accounts for a wide range of empirical evidence linking religion to prosocial tendencies and predicts that this association ought to be context-sensitive, with clear boundary conditions. First, religious devotion, insofar as it involves habitual worship of morally vigilant deities, is expected to be associated with greater prosocial reputational concern. Second, religious situations, such as religious ritual performance or being in religious

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surroundings, would, in societies with morally concerned deities, activate thoughts of these deities and habitually facilitate prosocial behavior. Therefore, experimentally inducing religious thoughts would also increase prosociality even when the situation is objectively anonymous. But this should be the case only when thoughts of morally concerned supernatural agents are cognitively accessible in the moment when prosocial decisions are called for. Third, religious behavior that signals genuine devotion would be expected to mobilize greater cooperation and trust, and when internal and external threats to group survival are high, religious groups would be expected to outlast secular ones. Fourth, large societies that have successfully stabilized high levels of cooperative norms would be more likely than smaller ones to espouse belief in morally concerned gods who actively monitor human interactions. In the remainder of this paper, we critically examine the available empirical evidence in light of these four predictions.

### Self-Reports: Religiosity and Charitability

If religions centered around moralizing gods promote prosociality, it would be expected that individuals who report stronger belief in such gods would have stronger altruistic tendencies. Sociological surveys suggest that this is the case. Those who frequently pray and attend religious services reliably report more prosocial behavior, such as charitable donations and volunteerism (*1*, *19*). This "charity gap" is consistent across surveys and remains after controlling for income disparities, political orientation, marital status, education level, age, and gender. These findings have been much publicized as evidence that religious people are more prosocial than the nonreligious (*19*). However, it remains unresolved whether this charity gap persists beyond the ingroup boundaries of the religious groups (*1*). More importantly, these surveys are entirely based on self-reports of prosocial behavior. Psychologists have long known that self-reports of socially desirable behaviors (such as charitability) may not be accurate, reflecting instead impression management or self-deception (*20*). If, as we hypothesize, religious individuals are more motivated to maintain a prosocial reputation than the nonreligious, then the former may be more likely to engage in prosocial reputation management. Supporting this hypothesis, psychological research summarizing many studies has found that measures of religiosity are positively associated with tests of socially desirable responding, a common human tendency to project an overly positive image of oneself in evaluative contexts (*21*). This association raises questions about the validity of self-report measures of prosocial behavior. To address these methodological limitations, experiments with behavioral outcomes must be consulted.

### Behavioral Evidence: In Search of the Good Samaritans

In several behavioral studies, researchers failed to find any reliable association between religiosity and prosocial tendencies. In the classic "Good Samaritan" experiment (*22*), for example, researchers staged an anonymous situation modeled after the Biblical parable—a man was lying on a sidewalk appearing to be sick and in need of assistance (Fig. 1). Participants varying in religiousness were led to pass by this victim (actually a research confederate) on their way to complete their participation in a study. Unobtrusively recorded offers of help showed no relation with religiosity in this anonymous context (*22*). Only a situational variable—whether participants were told to rush or take their time—produced differences in helping rates.

**Fig. 1.** In the parable of *The Good Samaritan* [painting by Jacopo Bassano, d. 1592, copyright 2006, The National Gallery, London], Christ preaches universal compassion and prosocial behavior. A similar message is found in many religions. Modern research from social psychology, experimental economics, and anthropology suggests, however, that religious prosociality is extended discriminately and only under specific conditions.

Other behavioral studies, however, have found reliable associations between religiosity and prosociality, but under limited conditions. In one study (*23*), researchers compared levels of cooperation and coordination between secular and religious kibbutzim in Israel. In this economic game, two members of the same kibbutz who remained anonymous to each other were given access to an envelope with a certain amount of money. Each participant simultaneously decided how much money to withdraw from the envelope and keep. Players only kept the money they requested if the sum of the requests did not exceed the total amount in the envelope. If it did, the players received nothing. The results showed that, controlling for relevant predictors, systematically less money was withdrawn in the religious kibbutzim than in the secular ones (*23*).

Thus, unlike studies such as the Good Samaritan, there were greater levels of prosociality among the religious in this study. One key difference is that reminders of God are likely to be chronically present in religious kibbutz, where religious prayer and attendance are a daily part of life. Another, is that prosociality in the religious kibbutz was clearly confined to the ingroup. In the kibbutzim study, highly religious men, who engaged in daily and communal prayer, took the least money, thereby showing the greatest amount of coordination and/or cooperation with ingroup members. It is also possible that regular, communal prayer involves public ritual participation, which, independent of religious devotion, might also encourage more prosociality.

Another approach to clarifying the nature and boundary conditions of religious prosociality is to investigate the altruistic or egoistic motivation underlying the prosocial act. One possibility holds that the greater prosociality of the religious is driven by an empathic motive to ameliorate the condition of others. Alternatively, prosocial behavior could be driven by egoistic motives, such as projecting a prosocial image or avoiding guilt (failing to live up to one's prosocial self-image). The preponderance of the evidence supports the latter explanation. Studies repeatedly indicate that the association between conventional religiosity and prosociality occurs primarily when a reputation-related egoistic motivation has been activated (*2*). In one experiment, for example, participants were given the option of volunteering to raise money for a sick child who could not pay his medical bills (*24*). Participants in one condition were led to believe that they would certainly be called upon if they volunteered. In

another, participants could volunteer although told that they were unlikely to be called upon. In the latter condition, participants could reap the social benefits of feeling (or appearing) helpful without the cost of the actual altruistic act. Only in the latter situation was a link between religiosity and volunteering evident. Many studies have corroborated that religiosity predicts prosocial behavior primarily when the prosocial act could promote a positive image for the participant, either in his or her own eyes or in the eyes of observers (*2*).

As insightful as these behavioral studies are, however, causal inference has been limited by their reliance on correlational designs. If religiosity is related to prosocial behavior under some contexts, it is possible that having a prosocial disposition causes one to be religious or that a third variable (such as dispositional empathy or being prone to guilt) causes both prosocial and religious tendencies. Recent controlled experiments have addressed this limitation by experimentally inducing thoughts of supernatural agents and then measuring prosocial behavior.

### Experimental Evidence: When Gods Are on Our Minds

In one such experiment (*25*), university students who were randomly assigned to a condition in which they were casually told that the ghost of a dead student had been spotted in the experimental room, cheated less on a rigged computer task. A different study conceptually replicated this effect—temporary, unconscious activation of God concepts lowered rates of cheating (*26*). Moreover, among those in the control condition, religiosity as an individual difference measure did not predict levels of cheating. In another experiment, children were explicitly instructed not to look inside a box, and then left alone in the room with it (*25*). Those who were previously told that a fictional supernatural agent—Princess Alice—was watching were significantly less likely to peek inside the forbidden box.

We have proposed that the cultural spread of religious prosociality may have promoted stable levels of cooperation in large groups, where reputational and reciprocity incentives are insufficient. If so, then reminders of God may not only reduce cheating, but may also increase generosity toward strangers as much as reminders of secular institutions promoting prosocial behavior. These hypotheses were supported in two anonymous economic game experiments, one with a sample of university students and another with nonstudent adults (*27*) (Fig. 2).

Thoughts of God, activated without conscious awareness (*28*), thus caused greater generosity between anonymous strangers. One explanation for this finding is that the imagined presence of a morally concerned supernatural watcher reduced the anonymity of the situation and heightened prosocial reputational concerns, thereby increasing prosocial behavior. Alternatively, it is possible that thoughts of God and thoughts of charity or benevolence are cognitively associated; thus, priming the former concept increased behavioral tendencies consistent with the latter (*27*). This explanation, however, begs the question as to why God concepts are mentally associated with charity in the first place. These alternative explanations await further experimental investigation. In either case, the effect occurred only to the extent that thoughts of a morally concerned divine agent were activated in the moment of decision-making. Self-reported belief in God or self-reported religious devotion was, as has been found before, not a reliable predictor of generous behavior in anonymous settings.

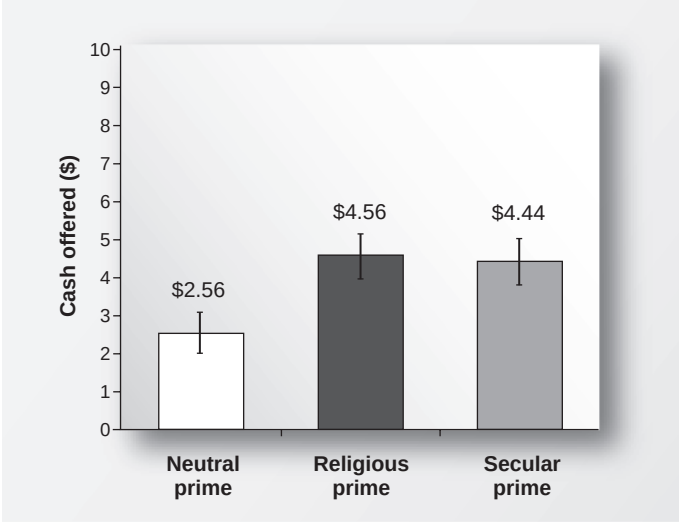


**Fig. 2.** Implicit activation of God concepts, relative to a neutral prime, increased offers in the one-shot, anonymous Dictator Game, $t(48) = 2.47$, $P = 0.02$, SE = 0.81, $d = 0.71$. (*27*). Priming secular concepts indicating moral authority had a similar effect, $t(48) = 2.29$, $P = 0.03$, SE = 0.82, $d = 0.67$. The results showed not only a quantitative increase in generosity, but also a qualitative shift in social norms. In the control group, the modal response was selfishness, a plurality of players pocketed all $10. In the God group, the mode shifted to fairness, a plurality of players split the money evenly ($N = 75$). It remains to be seen, however, whether these effects would occur if the recipient was clearly marked as an outgroup member.

### Religious Prosociality, Costly Signaling, and Trust

In the absence of reputational information about a stranger's prosocial inclinations, outward evidence of sincere belief in the same or similar morally concerned gods may serve as a reliable cooperative signal. But a signal is only reliable to the extent that it is difficult to fake by potential freeloaders. Because professions of religious belief can be easily faked, theorists of religion have recognized that evolutionary pressures must have favored costly religious commitment, such as ritual participation and various restrictions on behavior, diet, and life-style, that validates the sincerity of otherwise unobservable religious belief (*5*, *29*). However, for costly signals to evolve as a stable strategy, religious behaviors ought to be more costly for cooperators than for freeloaders, and variation in costliness should predict degree of intragroup trust and cooperation. Mathematical models question the possibility that costly signaling as an individual fitness-maximizing strategy extends to nondyadic collective cooperation as in the case of religion (*9*, *10*), and models of costly signaling applied to religious behavior, with or without cultural group selection, are currently in their infancy (*30*). Nevertheless, qualitative and quantitative evidence is emerging, that, although not yet definitive, addresses parts of these predictions.

Attitudinal surveys show that religious individuals are perceived to be more trustworthy and more cooperative (*31*). From behavioral evidence, ethnographic examples such as the spread of Islam in Africa, which preceded the flourishing of wide-scale trade among Muslim converts (*32*), and the trade networks of Medieval Jewish Maghrebi merchants (*33*) are consistent with this idea. Costly commitment to the same supernatural deity may have lowered monitoring costs and fostered cooperation in communities spread across geographic and even ethnic boundaries. However, it is disputable whether membership in these religious groups was costlier than commitment to local deities or whether costliness was directly associated with greater intragroup trust; therefore, the ethnographic data are open to other interpretations, for example, that religious conversions led to greater access to preestablished trade networks along these religious lines.

To address these limitations, quantitative analyses are needed. Sociological analyses are consistent with the idea that religious groups imposing more costly requirements have members who are more committed. Controlling for relevant sociodemographic variables, "strict" Protestant (e.g., Mormon) and Jewish denominations (Orthodox) show higher levels of church and synagogue attendance and more monetary contributions to their religious communities (despite lower average income levels) than less strict ones (Methodist and Reform, respectively) (*30*). However, these findings do not demonstrate that strictness predicts community survival and growth. One systematic attempt to do so examined religious and secular communes in 19th-century America, whose survival de-

pended upon solving the collective action problem. Religious communes were found to outlast those motivated by secular ideologies, such as socialism (Fig. 3) (*29*). A further quantitative analysis of 83 of these religious and secular communes (*34*) for which more detailed records are available found that religious communes imposed more than twice as many costly requirements (including food taboos and fasts, constraints on material possessions, marriage, sex, and communication with the outside world) than secular ones. This difference emerged for each of the 22 categories of costly requirements examined. Importantly for costly religious signaling, the number of costly requirements predicted religious commune longevity ($R^2$ = 0.38) after the study controlled for population size and income and the year the commune was founded, although the number of costly requirements did not predict longevity for secular communes. Finally, religious ideology was no longer a predictor of commune longevity, once the number of costly requirements was statistically controlled, which suggests that the survival advantage of religious communes was due to the greater costly commitment of their members, rather than other aspects of religious ideology. However, these findings are correlational, making causal conclusions premature. They collectively imply, but do not definitively demonstrate, that the greater longevity of religious communes with costlier requirements was due to greater intragroup cooperation and trust levels, which have not been measured directly. These results also imply that greater costly commitment is at best a partial explanation as to why religious communes outlasted secular ones. Other aspects of religion that might promote greater community stability are open for investigation.

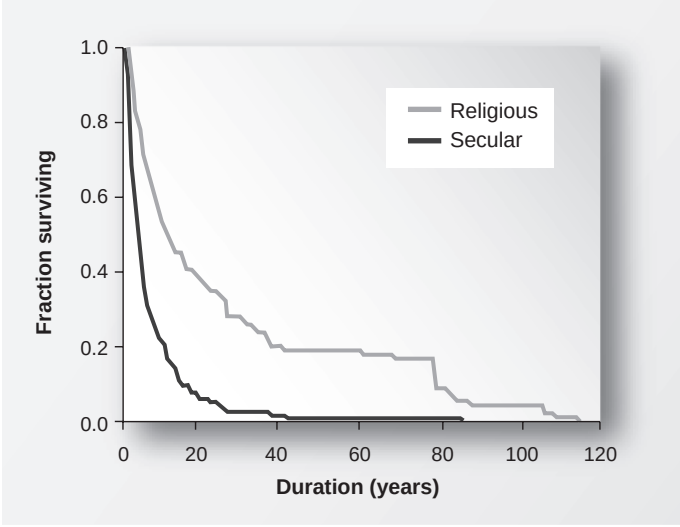


**Fig. 3.** Life expectancy of religious versus secular communes. An analysis of 200 religious and secular communes in 19th-century America (*29*), for every year of their life course, religious communes were about four times as likely to survive than their secular counterparts, log rank $T$ statistic = 40.14, df = 1, $P <$ 0.00001. This difference remained after statistically controlling for type of commune movement, year founded, and year at risk of dissolution (the last control assesses major historical trends that may independently impact commune dissolution). [Copyright 2003, reprinted from (*29*) with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.]

The few relevant laboratory studies corroborate that there is an empirical association between religion and trusting behavior. Trust can be operationalized as a costly investment in a person or entity, with the future expectation of return. In one well-researched laboratory game of trust (*35*), participants were randomly assigned to be a proposer (truster) or a responder (trustee). In the first step, the proposer decides how much money to forward to the responder, which gets multiplied. In the second step, the responder decides how much money to send back to the proposer. By transferring money to the responder, the proposer stands to gain, but only if the responder can be trusted to reciprocate. In a variation of this trust experiment (*36*), researchers measured individual differences in the religiosity of the proposer and the responder. In addition, in some trials, proposers knew about the level of religiosity of the responder in an anonymous context. Results indicated that more money was forwarded to responders perceived to be religious, and this was particularly true for religious proposers. Furthermore, religious responders were more likely to reciprocate the proposer's offer than less religious responders. These findings are consistent with the idea that outward evidence of religious devotion may engender more trust, although two issues remain unresolved: They do not show that costly religious behavior elicits more trust and cooperation than less costly behavior under controlled conditions, as required by costly signaling explanations of religion; or that members of religious groups that impose more costly requirements are more trusting and less likely to take advantage of others, particularly ingroup members, as would be expected from cultural group selection accounts.

The relation between religion and trust is, therefore, an area ripe for more research. Experimental studies and alternative mathematical models of costly religious behavior (either as a stable strategy characteristic of individuals or as a stable strategy that takes into account intergroup social competition) will place these theoretical predictions on firmer empirical ground. The existing evidence, however, suggests the possibility that religious belief, to the extent that it could be advertised with sincerity, may enhance within-group interpersonal trust, lower monitoring costs, and so further reinforce intragroup prosocial tendencies. Belief in morally concerned gods may stabilize prosocial norms even in the absence of social monitoring mechanisms. This, in turn, would be expected to expand the reach of such norms, facilitating the emergence of larger cooperative communities which otherwise would be vulnerable to collapse. We examine this hypothesized association between moralizing gods and large group size next.

### Big Groups, Big Gods: Cross-Cultural Evidence

From large village settlements at the dawn of agriculture to modern metropolises today, human beings are capable of living in extraordinarily large cooperative groups. However, extrapolating from cross-species comparisons of neocortex size, it has been estimated that human group sizes cannot exceed 150 individuals before groups divide or collapse (*37*). Although this specific number has been disputed (*38*), and whereas some Pleistocene foragers possibly lived in large villages, it is apparent that the size of human settlements since the end of the Pleistocene far exceed the limitations that kin-based and reciprocity-based altruism place on group size.

Cultural evolution, driven by between-group competition for resources and habitats, has favored large groups. However, large groups, which until recently lacked institutionalized social-monitoring mechanisms, are vulnerable to collapse because of high rates of freeloading (*13*). If unwavering and pervasive belief in moralizing gods buffered against such freeloading, then belief in such gods should be more likely in larger human groups where the threat of freeloading is most acute. Because there is considerable variability in the cultural distribution of morally concerned deities, researchers could measure whether this variability correlates with group size across cultures. In a quantitative cross-cultural analysis of the 186 societies in the Standard Cross-Cultural Sample, this prediction was confirmed. The larger the group size, the more likely the group culturally sanctioned deities who are directly concerned about human morality (*39*). Although most cultures in the world do not promote morally concerned deities, those that do tend to have disproportionately larger populations. As a consequence, the majority of religious adherents in the world worship moralizing gods.

One alternative explanation is that Christian and Muslim missionary activity may have caused both more belief in the moralizing Abrahamic God and may have favored larger group size. Another, is that because large societies are more socially stratified, belief in moralizing gods serves to preserve political and economic inequality. However, although missionized societies and caste-stratified societies were indeed more likely to endorse a moralizing God, the association between large group size and the prevalence of

moralizing Gods remained strong even after statistically controlling for missionary activity and for two indicators of societal inequality, as well as for population density and geographic region. Similarly, controlling for the cultural diffusion of moralizing Gods via Christian and Muslim missionary activity, society size, population size, and societal inequality, moralizing gods are more likely in societies with high water scarcity—where the threat to group survival, and the need to minimize freeloading, is also pronounced (*40*). The cross-cultural evidence suggests that moralizing gods are culturally stabilized when freeloading is more prevalent or particularly detrimental to group stability. However, further empirical research is needed to clarify causal direction and to distinguish between alternative explanations for these associations.

## Conclusions, Outstanding Questions, and Future Directions

Many religious traditions around the world explicitly encourage the faithful to be unconditionally prosocial (*1*, *2*); yet, theoretical considerations and empirical evidence indicate that religiously socialized individuals should be, and are, much more discriminating in their prosociality (*2*). Although empathy and compassion as social-bonding emotions do exist and may play a role in prosocial acts of religious and nonreligious individuals some of the time (*41*), there is little direct evidence to date that such emotions are systematically implicated in religious prosociality.

The preponderance of the evidence points to religious prosociality being a bounded phenomenon. Religion's association with prosociality is most evident when the situation calls for maintaining a favorable social reputation within the ingroup. When thoughts of morally concerned deities are cognitively salient, an objectively anonymous situation becomes nonanonymous and, therefore, reputationally relevant, or alternatively, such thoughts activate prosocial tendencies because of a prior mental association. This could occur when such thoughts are induced experimentally or in naturalistic religious situations, such as when people attend religious services or engage in ritual performance. This explains why the religious situation is more important than the religious disposition in predicting prosocial behavior.

Although religions continue to be powerful facilitators of prosociality in large groups, they are not the only ones. The cultural spread of reliable secular institutions, such as courts, policing authorities, and effective contract-enforcing mechanisms, although historically recent, has changed the course of human prosociality. Consequently, active members of modern secular organizations are at least as likely to report donating to charity as active members of religious ones (*42*). Supporting this conclusion, experimentally induced reminders of secular moral authority had as much effect on generous behavior in an economic game as reminders of God (*27*), and there are many examples of modern, large, cooperative, and not very religious societies (such as those in Western and Northern Europe), that, nonetheless, retain a great degree of intragroup trust and cooperation (*43*).

Any one study we have discussed can be subject to alternative accounts; therefore, specific evidence should be interpreted with caution. Nevertheless, convergent evidence is emerging from several disciplines using different methods and procedures that supply different pieces of the religious prosociality puzzle. Despite the recent scientific progress in explaining the effects of religion on prosociality, open and important questions remain. In particular, more research is needed to address the costliness of religious and nonreligious rituals, and few studies have attempted to quantify these costs in relation to prosocial behavior. The finding that religiosity evokes greater trust underscores the need for more experimental and theoretical research, including mathematical modeling, to establish the specific conditions under which costly religious commitment could evolve as a stable individual strategy and whether these models need to take into account intergroup competition. More broadly, the extent to which religion is implicated in human cooperation, and the precise sequence of evolutionary developments in religious prosociality, remain open to lively scientific debate. Further progress on these issues will require concerted collaboration among historians, archaeologists, social scientists, and evolutionary biologists.

In recent years, moral psychology has received a great deal of scientific attention (*44*), and although most of the studies reviewed here concern behavioral outcomes, the relation between religious prosociality and moral intuitions and reasoning is ripe for further investigation. More direct research on the possible role of prosocial motivations, such as empathy and compassion, in religious prosociality are needed. Finally, we have seen that religious prosociality is not extended indiscriminately; the "dark side" of within-group cooperation is between-group competition and conflict (*45*). The same mechanisms involved in ingroup altruism may also facilitate outgroup antagonism. This is an area of no small debate, but scientific attention is needed to examine precisely how individuals and groups determine who are the beneficiaries of religious prosociality, and who its victims.

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