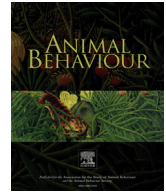




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special issue: Kin Selection

Inclusive fitness theory for the evolution of religion

Bernard Crespi^{a,*}, Kyle Summers^b^a Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada^b Department of Biology, East Carolina University, Greenville, NC, U.S.A.

ARTICLE INFO

Article history:

Received 11 October 2013

Initial acceptance 14 January 2014

Final acceptance 6 February 2014

Available online xxx

MS. number: ASI-13-00853

Keywords:

inclusive fitness

kinship

religious behaviour

We describe and evaluate an integrative hypothesis for the origin and evolution of human religious cognition and behaviour, based on maximization of inclusive fitness. By this hypothesis, the concept of God is represented by one's circle of kin and social salience, such that serving God and serving this circle become synonymous. The theory is supported by data from anthropology, evolutionary theory, psychology, neuroscience, psychiatry, endocrinology and genetics. It is largely compatible with, yet can subsume, previous theories of religion that are also based on adaptation and natural selection.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

There is something sacred about kinship, as most social anthropologists who have studied its operation in the field are prepared to admit (Myers, 1975)

W. D. Hamilton's (1964) inclusive fitness theory represents the foundation for studying social evolution, in the same way that Darwin's theory of natural selection forms the basis for understanding evolution itself. Hamilton's theory and its applications have focused in particular on the evolution of cooperation and altruism, behaviours that are challenging to explain because they represent the apparent antitheses of Darwinian competition for increased reproduction.

One human phenotype, religious behaviour, stands apart from all others with regard to its dominating emphasis on altruism and prosociality. This set of behaviours has yet to be analysed explicitly and comprehensively in the context of inclusive fitness theory, using the conceptual tools developed in Hamilton's wake for understanding its origins, maintenance and diversification. Like eusociality, or cooperative breeding, religion can be considered as a sociobehavioural system that has evolved in the contexts of genetic relatedness, parental manipulation (generalized here as asymmetries in control over phenotypes) and mutualism.

In this article we describe and analyse an integrative theory, based on inclusive fitness maximization, for understanding the origin and evolution of religious behaviour and the concepts of God and supernatural agents. The theory is based mainly on works by Hamilton, Alexander, Trivers, Lahti, Coe, Palmer and Steadman, and it draws together evidence from anthropology, psychology, neuroscience, psychiatry, endocrinology and genetics into a unified, testable framework. The theory is novel specifically in its integrative, synthetic and reconciliatory nature, and its central emphasis on the roles of genetic relatedness and inclusive fitness in the evolution of religion.

We first categorize and describe previous theories regarding the origins, bases and functions of the concept of God and other supernatural agents, and associated religious behaviour. Next, we present the theory, and discuss how it relates to, and can subsume, these earlier ideas without being strongly incompatible with any of them. We also discuss empirical evidence that bears upon the theory, and suggest opportunities for additional tests of its predictions.

PREVIOUS THEORIES

Previous ideas regarding the evolution of religion and concepts of God address diverse aspects of religious phenomena, at different levels of analysis, either proximate (dealing with mechanisms), or ultimate (dealing with selective pressures and other evolutionary causes). Moreover, studies of religion may focus on its supernatural components, its moralizing elements, or both in conjunction.

* Correspondence: B. Crespi, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

E-mail address: crespi@sfu.ca (B. Crespi).

Preconditions

Proximate factors in the origin of religion represent necessary preconditions that evolved along the human lineage for other reasons. Examples of such preconditions include: (1) causal inference and attribution, and agency detection; (2) social and emotional commitments to one's kin and other members of one's group, including capacity to establish, maintain and remember social relationships with other individuals even in their physical absence, or after their death; (3) imagination (ability to generate or form a mental image of someone or something that is not real or present), narrative formation and anxieties regarding mortality; (4) theory of mind, such that other humans, or other entities, are conceptualized as having thoughts, mental states, agency and motivations more or less comparable to one's own; (5) the evolution of indirect reciprocity (morality), with systems for repression or punishment of noncooperation and concern for one's reputation in the social group; and (6) the evolution of extensive social learning, whereby children effectively assimilate cultural beliefs that are presented to them. It is important to bear in mind that none of these factors represents, in any way, causal explanations for the origins of religious cognition, behaviour or cultural phenomena. Instead, they all apparently evolved for reasons unrelated to religion or concepts of God and other supernatural agents (i.e. complex social cognition in highly social groups) and are important only because they were either necessary for religious cognition and behaviour to evolve, or they facilitated its establishment by other means. Thus, although some or all of these phenotypes were certainly crucial to the later evolution of religion and concepts of God, other selective pressures must have actually underlain the evolutionary transition from nonreligious to religious thought and behaviour.

Maladaptive By-products

Proximate factors in the evolution of religion have been considered mostly in the context of by-products, whereby phenotypes that evolved adaptively under one set of conditions (such as social cognition) come to be expressed maladaptively in another (such as religious belief and behaviour; e.g. [Atran & Henrich, 2010](#); [Boyer & Bergstrom, 2008](#); [Dawkins, 2006](#); [Kirkpatrick, 1999](#); reviewed in [Powell & Clarke, 2012](#)). By-products involve selection for a highly advantageous trait that also leads to an increase in the expression of another, more or less deleterious, trait that is genetically, developmentally or environmentally tightly associated with it. In the case of religion, such deleterious effects could be considered as pathologies at the individual level (such as hyperdeveloped theory of mind in psychosis), or 'cultural pathologies', whereby cultural phenotypes that are maladaptive for members of the group (such as expending time and energy on costly rituals) can become established if the counterbalancing adaptive effects, in other contexts, are sufficiently strong ([Dawkins, 2006](#); [Powell & Clarke, 2012](#)). To the extent that some or all religious beliefs and phenomena are indeed maladaptive, with negative effects on inclusive fitness, one would expect selection against their cultural perpetuation and genetic underpinnings, which would be effective to the extent that maladaptive by-product effects can be separated from beneficial ones. This is an empirical question that has not yet been directly addressed: to be considered valid, hypotheses of maladaptation require demonstration of the proximate mechanisms that prevent or constrain adaptation ([Crespi, 2000](#)), rather than arguments based on circumstantial evidence. Personal religiosity exhibits substantial heritability at least in some recent environments (e.g. [Bradshaw & Ellison, 2008](#); [Kandler & Riemann, 2013](#)), which indicates potential responsiveness to selection.

More generally, evolutionary theory predicts that any phenotypic feature of humans that, like religion, is both culturally

universal and costly, is precisely the sort of trait that is least likely to represent a maladaptive by-product of selection in some other domain, unless ancestral and current environments are fundamentally mismatched or pleiotropy is exceedingly strong. One would also not expect, under hypotheses of maladaptive by-products, to be able to substantially explain religious phenotypes and the concept of God from hypotheses based on adaptation and inclusive fitness.

Adaptations

Hypotheses based on ultimate factors postulated to explain the evolution of religion have centred on roles for religious practices in facilitating cooperation within human groups. Such behaviours may be beneficial in either or both of two circumstances: (1) survival and reproduction within groups (e.g. in ecological contexts, and for reducing within-group competition especially as group sizes increase) and (2) competition between groups over fitness-limiting resources, or enhanced survival under challenging ecological conditions. These hypotheses have mainly posited cultural group selection as the primary driving force for the evolution and maintenance of religion, with important effects from pre-emption and repression of within-group competition by adoption and enforcement of stringent moral rules (e.g. [Atkinson & Bourrat, 2011](#); [Atran & Henrich, 2010](#); [Bulbulia, 2004](#); [Johnson, 2005](#); [Palmer, Steadman, Cassidy, & Coe, 2008](#); [Roes & Raymond, 2003](#); [Rossano, 2007](#); [Sosis & Alcorta, 2003](#); [Wilson, 2005](#)).

By most of these hypotheses, religion and the concept of God are seen as being adaptive in cultural, group-wide contexts (whereby the cultures with the 'best' religious cultural variants outcompete others, increase in frequency faster, or survive intact for longer periods, and the best variants are preferentially adopted by group members), and in the context of individual benefits from enhanced cooperative behaviour. [Pagel \(2012\)](#) termed such phenotypes 'cultural survival vehicles', because they represent group-level phenotypes that enhance fitness for both groups and their constituent members. A complementary view, described below, is that culturally expressed traits like religion are expected to be adopted and maintained to the extent that doing so consciously or unconsciously increases the inclusive fitness of the individuals or groups that control trait expression ([Alexander, 1979, 2013](#)). In this context, it is important to note that group-level selection, and inclusive fitness maximizing (kin selection), represent two valid, complementary and mathematically equivalent perspectives on the same processes ([Queller, 1992](#)).

Adaptive hypotheses for religion based on cultural group selection are supported most directly by evidence suggesting that direct and indirect (e.g. ecological) competition among human groups, delineated and motivated in part by cultural traits, have represented pervasive selective pressures in human evolution ([Alexander, 1979](#); [Bowles, 2009](#); [Dawkins, 2006](#); [Pagel, 2012](#); [Rossano, 2010, p. 50](#)). However, cause, effect and process remain unclear: did increased among-group competition drive enhanced, cooperative within-group religiosity, vice versa, or both? How did religion actually originate and evolve, step by small step, with Darwinian continuity and explicable selective pressures mediating each stage? And how might religious cognition and behaviour have been advantageous to individuals, and to their small social groups of kin and nonkin, during its crucial early stages prior to presumed larger group-level effects?

THE INCLUSIVE FITNESS THEORY OF RELIGION

We propose an integrative theory for the origin and evolution of religion and the concept of God that is based on inclusive fitness

maximizing by individuals or groups in control of religious phenotype expression. Religion is considered here as a sociocultural belief and behaviour system involving both supernatural ideas and morality, each to some degree. 'Belief' can be studied like any other self-report human psychological or cognitive phenotype (Johnson, 2009), as well as with methods from neuroscience such as functional imaging (e.g. Kapogiannis et al., 2009; Saver & Rabin, 1997). The theory includes elements of inclusive fitness (i.e. gene-level selection), parental manipulation (and power asymmetries more generally) and mutualistic benefits (direct and indirect reciprocity, and joint cooperative benefits), and it can provide continuity in selective pressures from the earliest stages of religious thought to the development of religious institutions. It is predicated on the supposition that religion represents an aspect of culture that has originated, and is perpetuated and elaborated, because of inclusive fitness benefits, to varying degrees, to grandparents, parents, children, other kin, social groups of varying sizes in relatively small-scale societies, and religious figures and leaders, in the context of the power exerted by individuals or groups at each level in this hierarchy.

By the hypothesis, religion and the concept of God originated and are maintained in the context of maximizing inclusive fitness through serving the interests of one's circle of kin and one's larger-scale social and cultural groups (Alexander, 2006, 2013). Synonymy between religious and inclusive fitness meanings of life has thus provided the foundation for the origins, persistence, growth and elaboration of religious beliefs, behaviours and institutions, as described by Alexander (2006):

An appropriate initial question about God might be "What if God were, in some way, all of us?" In practical terms, and across all of human history right to the present day, "all of us" could mean all of us in some particular cooperative or unified group, which could be our nuclear family, our clan or circle of relatives, our immediate community, our church membership, our culture, our nation, everyone in our particular religion all across the earth, or everyone in an alliance of nations or of religions. For some purposes it could mean several or even all of these units; humans have the unique ability to "belong to," and serve and gain from, a large number of different groups at the same time.

Suppose the concept of God is attached to a "circle of social significance," in the way suggested above. Perhaps most often, across human history, this would be the circle of kin, because there are good reasons for the prevailing opinion among anthropologists that across most of their history humans lived primarily in kin groups of up to 200–250 individuals, including "in-laws." If so, then serving God becomes, at least historically, serving the kin circle or kindred.

To the extent that the concept of God actually arose as a metaphor for the kindred, or circle of kin, then – perhaps surprisingly, at first – the evolutionary version of the meaning of life becomes synonymous with the religious version of the meaning of life. In both cases the meaning of life is to serve God. (Alexander, 2006)

Given Alexander's (2006) premise, how would religious thought and behaviour evolve from nonreligious phenotypes, originally in the context of circles of kin and their dynamics? Cooperation and conflict within nuclear families centre on interactions between parents and offspring, and among offspring themselves. Because genetic relatedness between each of these pairs of interactants is equal to one-half (for numerically dominant autosomal genes), parents, especially mothers, maximize inclusive fitness by investing equally in offspring. However, each offspring maximizes their inclusive fitness by soliciting more resources from the mother than

she is selected to provide, because the offspring will be more closely related to their own children (with $r = 0.5$) than to the children of their siblings (with $r = 0.25$; Bossan, Hammerstein, & Koehncke, 2013; Trivers, 1974, 1985). The result is conflict between parents and offspring, which parents are, of course, under selection to win, and conflict between siblings, which parents are under selection to repress, pre-empt, or alleviate. Much more generally, parents, grandparents and other sets of kin gain inclusive fitness benefits from increased cooperation among their descendent (as well as collateral) relatives, because copies of their alleles are thereby interfering with each other's transmission to a lesser extent (Coe, Palmer, Palmer, & DeVito, 2010).

The upshot of these relatedness considerations is that grandparents and parents should seek to inculcate prosocial, mutualistic and altruistic behaviour among their descendants, over whom they exert pervasive psychological influences during early child development. Moreover, to the extent that such prosocial inculcation is perpetuated culturally, and adopted by descendants who learn and copy it from ancestors, each progressive generation of parents, grandparents and other kin is expected to benefit in terms of inclusive fitness (Coe & Palmer, 2013; Palmer et al., 2008). Such family and local-group based indoctrination is expected to focus specifically on 'proper' social interactions, especially with regard to kinship. The resultant teachings, stories and moral prescriptions for descendants may provide benefits through a combination of at least four effects: (1) fostering of altruism towards kin (to the proper degrees for maximizing inclusive fitness, at least for the teacher), (2) enhanced mutualism among kin, (3) cooperative behaviour among kin that reduces exploitation in prisoner's dilemma or local public-goods situations, and (4) enhancement of beneficial reciprocal interactions among nonkin (including affine 'in-laws') through more effective establishment of cooperation and trust among interactants who treat each other as 'fictive' or 'psychological' kin (Bailey & Wood, 1998; Coe, Aiken, & Palmer, 2006; Jones, 2000; Palmer & Coe, 2010; Steadman & Palmer, 1997).

Despite the partial fragmentation of relatedness structure by exogamy and dispersal in humans, and low average relatedness among adults in hunter-gatherer groups (Hill et al., 2011), kinship-associated benefits would still accrue to the extent that within-group relatedness (at any cultural group level) was higher than relatedness between groups, which must have been the case for at least the vast majority of human ancestry (e.g. Bowles, 2006; Langergraber et al., 2011). Similarly, although each individual's circles of kin and social salience differ, the overlapping interests of closer kin are greater, and all individuals in a group can still, under our model, benefit from religious thought and behaviour. Kin 'groups' are conceptual, as well as behavioural, and need not exist in discrete spatial form, as witnessed most clearly by the importance and nature of kinship relationships in small-scale societies. Theory and research also suggest that humans parse their perception of, and interactions with, other humans into kinship 'groups' or 'categories' in a way that is influenced by overall levels of relatedness within groups, and that these categories strongly influence human social interactions (Jones, 2000). Furthermore, there is substantial evidence that human cognition itself is strongly influenced by the hierarchical kinship structures and patterns of interaction with kin that have been prevalent across the course of human evolution (Jones, 2004, 2011).

We consider the situation described above to hover at the cusp of the transition from nonreligious to religious thought and behaviour, and to serve as the central context for the addition of supernatural beliefs to moral sentiment. A key point here is that parents and grandparents die, but their influence can persist; as described by Lahti (2009, p. 78):

I suggest that the crucial cultural step in the evolution of religion was not the sudden recognition of previously unknown spiritual entities, but rather a subtle psychological slide from remembrance of and reference to the dead, to the concept of an afterlife. The conceptual distinction between 'Grandfather would have wanted you to do this' and 'Grandfather wants you to do this' would not only have been slight in a linguistically simple culture, but community norms would be much more effectively upheld by the stronger latter claim. As soon as elders began to be perceived as remaining powerful and offering advice postmortem, the society can be considered to have entered upon parochial religion by the definition offered here (Steadman et al. 1996). This development would have further strengthened the community not only by ensuring the maintenance of traditional rules with reference to a past leader, but also by rooting them in a person who was to some extent superhuman. Thus I argue that religion has not co-opted moral norms, as some social theorists claim; rather, moral norms themselves favored the evolution of religion. (Lahti, 2009)

This inclusive-fitness context for the origin and early evolution of religion is, as described below, consistent with diverse, independent lines of evidence from anthropology, psychology, psychiatry, neuroscience, endocrinology and genetics.

Ancestor Worship, Totemism and Shamanism

Ancestor worship, and belief in some form of immortality of the dead, occur in virtually all human cultures (Rossano, 2006, 2007; Steadman, Palmer, & Tilley, 1996), suggesting that they are ancestral, and nearly or fully universal, with regard to human cultural evolution. These beliefs and behaviour are foundational to the connections between kinship and God, and service to one's circle of kin, because initially it was ancestors who apparently became the first supernatural agents and gods: they were absent, of human form, morally powerful, immutable and mysterious yet comforting by virtue of warm, supportive bonds of kinship. Religious rituals focused on ancestors also necessarily strengthen kinship links (Rossano, 2010, p. 148; Steadman et al., 1996) and foster cooperation more generally (Fischer, Callander, Reddish, & Bulbulia, 2013). Other forms of traditional religion, such as totemism (which involves the assignment of 'tags' to kinship-associated lineages), also generate and maintain links to common ancestors, thus serving as 'cultural mechanisms aimed at building and sustaining social relationships between close and distant kin', by encouraging 'family-like cooperation between relatively distant kin' (Palmer et al., 2008). This sociocultural system connecting the wisdom, ethics and supernatural power of dead ancestors with living descendants was mediated, in many traditional societies, by shamans, who served as repositories of cultural, religious and moral knowledge and helped to solve social problems through non-self-serving interpretation of ancestral values (Rossano, 2007; Steadman & Palmer, 1994).

At a more fundamental level, anthropological kinship systems themselves, and human names and body decoration as symbols for identifying kin and lineages, can be seen as originating in the context of cultural traditions for maximizing inclusive fitness (Coe & Palmer, 2013; Steadman & Palmer, 1997). Ancestors simply carry such tags into the supernatural realm.

Stories and Enculturation

Traditional stories concerning behaviour, culture and one's group are, like religion, universal, and centre on precisely the sorts of moral and kinship-focused prescriptions, especially to children,

that are postulated to drive the origin of religious cognition and behaviour (Coe et al., 2006; Coe & Palmer, 2013; Steadman & Palmer, 1997). Such stories concern 'remote unverifiable events' and provide guidance concerning how to behave socially, especially with regard to kin (e.g. with sacrifice, restraint and moral virtue). In most cultures, it is the mother who tells stories to her children, such that they perpetuate vertically; but stories (especially effective and memorable ones) have presumably also spread horizontally within and across extended families and local cultural groups (Coe et al., 2006; Coe & Palmer, 2013).

Religious stories (such as those regarding local gods, the origins of one's group and appropriate behaviour as indoctrinated by supernatural agents) are meant to be considered as literally true (although they are supernaturally based, and hence impossible to validate). As such, they may serve at least two inclusive fitness purposes. First, similar to magical rituals, they can promote cooperation through shared metaphor uncritically taken as fact (Palmer, Steadman, Cassidy, & Coe, 2010). Second, they should increase the 'good behaviour' of children and other group members, through modelling of appropriate behaviour to kin and other group members, and generating fear of retribution, for improper conduct, from both omniscient supernatural agents and relatively powerful members of the group, including the mother (Coe et al., 2006, 2010; Coe & Palmer, 2008, 2013).

In contrast to religious stories, fanciful stories (fiction), which also provide social, moral, and often kin-based lessons, come to be regarded as untrue narrative creations as children become older, but are nevertheless effective in teaching patterns of behaviour that benefit the teller and listener. According to the framework described here, religious stories should focus mainly on kin and group-based moral inculcation and enculturation. Nonreligious stories should more specifically involve social scenario building (Alexander, 1979, 2013), whereby individuals learn about how to succeed in socially complex situations through assembling a mental collection of plausible narratives that serve as potential models or components for their own behaviour. In the vast majority of such stories, of course, good, God, moral virtue and individuals showing proper behaviour triumph; a satisfying conclusion and lesson given that we normally identify, personally, with the protagonists.

Social Learning and Psychological Kinship

With regard to the social evolution of religion, it is of fundamental importance that children are told (i.e. socially learn) who their kin are, as this process directly affects their unconsciously perceived behavioural mechanisms for maximizing inclusive fitness (Alexander, 1979; Steadman & Palmer, 1997). As such, psychological kinship (the perception of kinship and kinship-like bonds that are not necessarily mediated by close or actual biological links; e.g. Bailey & Wood, 1998; Jones, 2000) may be no less important than biological kinship as ascertained by an omniscient geneticist. Indeed, psychological kinship may be more important because of its flexibility and conditionality in changing fitness-related contexts, its ability to generate solidarity groups with broadly overlapping inclusive fitness interests (Jones, 2000), its applicability even to individuals who are not friends or even known personally, and its vulnerability to manipulation that may be either beneficial or deleterious to the individual concerned (Qirko, 2004). Moreover, psychological kinship commonly exhibits a well-defined spatial group structure (of kin and nonkin delineated by cultural phenotypes and spatial distributions of human groups), whereas kinship itself will tend to be more spatially dispersed, at least locally, because of exogamy.

For both biological and psychological kin, groups are fundamentally hierarchical and structured by pedigrees, phylogenies and cultural identities from families to tribes and beyond; psychological

kinship may thus apply at any level. Historically, for human adaptation, the levels of families, clans, bands and tribes should have been most important as selective contexts, and extensions to much higher levels are evolutionarily recent and hence prone to expression of environment–adaptation mismatches and maladaptation (Dawkins, 2006).

A key facet of hierarchical human population structure for the evolution of religion is that ancestors, and other kinship figure gods, may serve to unify groups through psychological kinship at increasingly higher levels as human populations increase, given that larger population sizes generate more within-group conflicts, as well as leading to larger-scale group-against-group conflict (e.g. van den Berghe, 1981; Vanhanen, 1999). To the extent that among-group conflicts involve coincidence of whole-group interests with the interests of each constituent circle of kin, individuals may continue to gain in inclusive fitness from religious beliefs and behaviour, and from acceptance of religion-based psychological kinship as a motivation for adaptive behaviour.

Religious beliefs, institutions and associated moral behaviour may, of course, also themselves drive among-group human competition, as amply demonstrated by human history (e.g. Alexander, 2013; Dawkins, 2006). Such conflicts develop in part because the competing groups are, in a psychological sense, threatening or threatened circles of kin each supported by different supernatural forces, and in part because of proselytizing, conquest and attempted or successful religicide by faiths that become more widespread through adoption of such doctrines and practices. Immutable moral, religious group-specific rules and laws, as taught in stories to children and maintained in adults, may foster and fuel conflicts, or at least reinforce or exacerbate clashes that start for other reasons, as noted by Alexander (2006):

Most religions teach that God is the power that watches over and guides their particular group. Gods apparently began as tribal gods (which we can consider as “kin circle” gods), and it is obvious but unfortunate that they have never ceased being such, even if particular religions (in effect, large and sometimes fragmented tribes) have become huge and widely distributed (that is, God was, and still is, a way of winning by promoting a particular kind of collective good feeling that makes a group a more formidable force against threatening or competitive human groups).

Most (but not all) religious people think there actually is but a single God, and that achieving world harmony is mainly a matter of people in other religions coming to realize that. Typically, however, such realization is viewed as coming to understand that the only real God is the one that looks out for one’s own group’s interests. Worse, as religions (or cultures) become more extensive, and stronger, and the numbers of different religions and nations correspondingly diminish, the situation actually becomes more dangerous and less likely, not more likely, to eventuate into a concept of God acceptable to all people, and to yield some semblance of world-wide harmony. (Alexander, 2006)

Strong links of cultural, religious and racial heterogeneity with ethnic conflicts have been documented by Vanhanen (1999) in a cross-cultural study, although the independent contribution of religious divisions was not addressed.

Magic, Morality and Immutable Law

A supernatural, magical component to religion can be beneficial to the origin and maintenance of kinship-related benefits of religion because it provides apparent immutability, objectivity and impartiality to moral precepts in three contexts: (1) pre-emption or

reduction of social conflicts regarding moral decision making within groups; (2) provision of relatively group-beneficial ‘causal’ explanations (irrationalizations, as it were) for virtually any event impacting the group, and (3) a simple cultural and conceptual vehicle and mechanism (acceptance of a magical claim or participation in a magical ritual) for uncritically accepting the beliefs and influence of individuals and groups with whom one cooperates (Palmer et al., 2010). Religious beliefs and behaviour can thus greatly strengthen moral precepts, cooperation and group unity in ways that serve the interests of one’s self and circle of kin, and in the larger milieu of overlapping, intermingled kin circles of other individuals within a clan, band or tribe.

We strive to make law and morality – that is, what we see as right actions, as opposed to wrong ones – into forms such that they can be timeless and unchanging; we recognize that there is a strong potential for injustice in the mere possibility that laws and rules can be altered too readily, for example as a result of the whims of powerful individuals or cliques. This attitude tends to cause people to view anything associated with morality and the concept of God as hallowed, divine, and sacrosanct. From this it translates easily to the concept of a supernatural power that determines and maintains laws and rules, over-riding human failings, therefore is not to be challenged. (Alexander, 2006)

In brief, ‘the authority of living persons is partial and subject to challenge; that of ancestors is pervasive and absolute’ (Calhoun, 1980).

Given that Gods do not directly impose their moral precepts, enforcement falls upon several human agents, each of whom is expected to benefit from doing so at least in many or most circumstances. These agents include: (1) shamans and priests, who mediate between the secular and supernatural worlds with regard to interpretations and applications of divine law (Rossano, 2007; Steadman & Palmer, 1994), (2) solidarity groups of kin, who enforce ethical principles through socially imposed rights and obligations that represent extensions of parental inculcation and manipulation (Jones, 2000), (3) individuals themselves, who should be selected to ‘self-police’ through sincere belief in the immutable and supernatural nature of religious precepts, at least in appropriate conditions, and (4) leaders within groups, who will have commonly gained this position through having many kin in the group (thus serving as central, focal points in local kinship networks) as well as some degree of more general benevolence, or ability to more or less gently coerce, across group members. The most successful such individuals should also have been especially likely to eventually transmute into local and tribal gods, because they have most closely shared the interests of the largest proportion of the group (Alexander, 2006; Chagnon, 2013; Hughes, 1988). Such individuals are indeed like fathers, in a general way, as explained by Alexander (2006):

In virtually any coordinated group, from family to nation, or even alliances of nations, a single individual is often recognized as most influential, or most powerful. It is reasonable to suppose that such an individual tends to be the one regarded as most effective in serving the interests of the entire group – or at least of a large enough portion to acknowledge (create, grant, maintain) the influence. It is clear that we socially cooperative (and competitive) humans tend to appoint (or accept) such individuals, either formally or informally, in both the smallest and the largest groups. Unless their power somehow becomes prohibitive to the wishes of the main portion of the group, that main portion is likely to seek to remove them whenever strong and widespread beliefs arise that such leaders are no longer serving the interests of the group.

*No one lives forever, and when a recognized and revered leader dies, there may be unusually severe social disruption. Consider the case when a father dies, leaving behind a wife and children of varying ages. Who should now be regarded as most likely to serve the interests of the whole family, in the particular way that it was served by the father? Presumably, the individual or individuals most likely to share and therefore continue the father's interests is that one whose personal interests are most likely to coincide with those of all the other individuals in the family, and who has the power, influence, and acumen to cause those interests to be realized. Whenever women are allowed to be dominant and influential, this person would surely be the wife; in other situations it is likely to be the oldest son or the wife's male sibling. Any impression that such individuals most nearly share the interests of all other family members can be enhanced by a successful claim not only of sharing the father's interests, but of having an ability to keep on understanding his interests through a continuing communication with the deceased spouse or ancestor. This is why I said in 1979 (*Darwinism and Human Affairs*, p. 249) that, "I do not regard it as an accident that God should have come to be regarded as a 'Father in Heaven'."*

This general situation characterizes not only small groups such as the family and the kin circle, but every level at which the interests of a cooperative group can best be served when someone (or some subgroup, including tribal gods, saints, angels, and all such) takes on a managerial or coordinating role. (Alexander, 2006)

Phylogenetic Expansion of Biological and Psychological Kinship

Morality and religious belief and behaviour may spread vertically and horizontally from nuclear and extended families, to sociocultural groups with varying degrees of more distant kin and nonkin, because the inclusive fitness benefits that accrue to individuals, and kin, also accrue to the increasingly large levels of culturally or religiously defined groups. This expansion process should, at least in traditional societies such as hunter-gatherers, horticulturalists or pastoralists, be largely seamless, because kinship associations of humans within the groups where they reside and interact (nuclear families, extended families, clans, bands and tribes) decline more or less smoothly, with a transition from more closely related biological kin to more distant kin and psychological kin (Bailey & Wood, 1998), and benefits of favouring cooperation are gained at each level. The primary discontinuities in the expansion would come at two levels: where marriages are no longer arranged or otherwise conducted among groups, such that contact and kinship take a marked biological and psychological drop, and where groups become states that are sufficiently heterogeneous in ethnic composition that psychological kinship becomes difficult to maintain.

Parochial, group-level altruism and mutualism at all levels appear to be the result of this phylogenetic expansion process (van den Berghe, 1981; Lahti, 2009), which is selected for in several contexts: (1) favouring one's inclusive fitness within a group, through enhanced cooperation between one's kin and associated affines and allies, and (2) fostering unity and social-emotional solidarity for enhanced success in conflicts with other groups, and (3) generating larger, more competitive religion-based groups themselves. As described by previous authors, among-group conflict is expected to strongly select for within-group unity, cooperation and altruism (Lahti, 2009; Lahti & Weinstein, 2005), in part through extension of psychological kinship bonds within the group such that all members are considered and treated as relatives (Bailey & Wood, 1998; Lahti, 2009; van den Berghe, 1981). This process, and group-level nepotism that socially enforces 'an ethic of

unidirectional altruism towards kin' (Jones, 2000), should consolidate religion as a primary mechanism for maintaining social cooperation and parochial morality.

Common Endocrine and Psychological Mechanisms Mediating Kinship and Religion

To the extent that religion originated in the context of kinship bonds, parent-child associations, childhood development of social cognition and imagination and human bonding more generally, its proximate genetic, neurological and hormonal mechanisms should overlap broadly with those that mediate kinship and sociality (Grigorenko, 2011; Kirkpatrick, 2005). Human parent-child and adult affiliative bonds are mediated to a considerable degree by the neuropeptide oxytocin, which has also been demonstrated to influence trust, generosity, tend-and-defend behaviour, social persuasion, ingroup-outgroup-related decision making and parochial altruism, and kinship recognition (Bryant & Hung, 2013; De Dreu, 2012; De Dreu, Greer, Van Kleef, Shalvi, & Handgraaf, 2011; De Dreu, Shalvi, Greer, Van Kleef, & Handgraaf, 2012; Fischer-Shofty, Brüne, et al., 2013; Fischer-Shofty, Levkovitz, & Shamay-Tsoory, 2013; Stallen, De Dreu, Shalvi, Smidts, & Sanfey, 2012). Oxytocin appears to be more important for female behaviour, whereas vasopressin exhibits comparable effects on sociality more commonly among males (e.g. van Anders, Goldey, & Kuo, 2011). Oxytocin has also been linked to participation in social rituals, dance and enjoyment of music, all central aspects of many religious activities (Chanda & Levitin, 2013; Zak, 2012). These considerations, and the strong female biases to religious behaviour reported across human cultures (Flere, 2007; Trzebiatowska & Bruce, 2012) suggest central roles for oxytocin in religious cognition, experiences and behaviour, as well as in motivation of kinship and group-related behaviours that specifically affect inclusive fitness (Grigorenko, 2011). Indeed, the Latin root of the word 'religion' is considered by many etymologists as 'religare', which means 'to bind'. The only human genetic disorder that has been associated with substantial overproduction of oxytocin is Williams syndrome (Dai et al., 2012); this syndrome is also characterized by love of music (Lense, Gordon, Key, & Dykens, 2013), hypersociality and unselective friendliness (Järvinen, Korenberg, & Bellugi, 2013), and high levels of religious belief and participation (Plesa-Skwerer, Sullivan, Joffe, & Tager-Flusberg, 2004).

The two primary human psychological conditions associated with alterations to sociobehavioural cognition (autism and schizophrenia) both exhibit clear links to religious thought, but in opposite directions from typicality. Thus, individuals with autism, and nonclinical individuals who score high on scales of autistic cognition, both exhibit and endorse lower levels of religious cognition, apparently because of reductions in theory of mind, mentalistic cognition, societal enculturation, empathy and social bonding that characterize the autism spectrum (Badcock, 2009; Bering, 2002; Marsh, Pearson, Ropar, & Hamilton, 2013; Norenzayan, Gervais, & Trzesniewski, 2012). By contrast, schizophrenia and its nonclinical manifestations in schizotypy involve heightened levels of some core components of religiosity, including magical ideation and unusual cognitive-perceptual experiences of, for example, hearing voices and perceiving animacy and agency in nonhuman phenomena (Diduca & Joseph, 1997; Gray, Jenkins, Heberlein, & Wegner, 2011; Maltby, Garner, Lewis, & Day, 2000; Murray, Cunningham, & Price, 2012). These psychological phenotypes can be interpreted in terms of hyperdeveloped mentalistic cognition, the opposite to the pattern seen in autism (Badcock, 2009; Crespi & Badcock, 2008). Numerous major historical religious figures have also shown clear signs of schizotypal phenotypes as diagnosed by neurological and behavioural symptoms (Brewerton, 1994; Devinsky & Lai, 2008; Murray et al., 2012; Previc,

2006), and religious belief has been positively associated with schizotypy in present-day nonclinical populations (e.g. MacPherson & Kelly, 2011). Moreover, to the extent that hyperdeveloped theory of mind involves accurate and enhanced sensitivity and responsiveness to the emotional and cognitive states of others (e.g. Dinsdale & Crespi, 2013; Oakley, 2007), and ability to manipulate these states, it may also have fostered the development of religious followings. These findings and inferences suggest overlapping genetic and developmental trajectories towards schizotypal and religious cognition during human evolutionary history (Dein & Littlewood, 2011; Previc, 2006).

To evaluate the hypotheses that social neuropeptides mediate religious beliefs, we conducted a preliminary test for effects of genetic variation in four genes associated with social bonding (oxytocin and arginine vasopressin genes) on the religion-associated components of autism and schizotypy (Imagination, Magical Ideation, Unusual Perceptions and unusual Cognitive-Perceptual experiences) in a nonclinical population of undergraduates (Table 1). Statistical evidence of such association was found in all four genes (bearing a total of six single nucleotide polymorphisms), for one or more of these correlates of religious cognition. Replication across the 2 years of data was limited. Our results are concordant, however, with the only comparable study conducted to date, which found that the G allele for the polymorphism rs1042778 in the oxytocin receptor OXTR gene was associated with higher creative abilities, and that intranasal oxytocin led to enhanced 'holistic processing, divergent thinking, and creative performance' but reduced analytic reasoning (De Dreu et al., 2013). For this polymorphism, we found that individuals (of both sexes) with the GG genotype tested in 2010–2011 showed statistically higher levels of self-report imagination and substantially lower performance on a test of mental rotation than GT and TT individuals (Table 1) (Thompson et al., 2013). For rs1042778, the G allele has also been associated with higher plasma oxytocin

(Feldman et al., 2012). Similarly, for rs2254298 in the OXTR gene, the T allele is associated with higher plasma oxytocin (Feldman et al., 2012), and in our data, males with this allele showed significantly higher scores on the Unusual Perceptions scale. For rs3796863 in the CD38 gene, females with the high-oxytocin T allele (Feldman et al., 2012) had significantly higher scores for Magical Ideation (Table 1). These findings are thus suggestive of links between religion-associated cognitive phenotypes and genetically based (and physiologically and socially induced) high levels of oxytocin, but further tests (currently in progress) are clearly required, especially with closer metrics of religiosity. We predict in particular that individuals bearing high-oxytocin OXTR and CD38 genotypes will endorse and experience higher levels of religiosity, as well as closer attention to social relationships that involve kin.

It is indeed a remarkable gap in the scientific literature that oxytocin and related hormones have yet to be studied in direct relation to religious thought, behaviour and experiences. As described by Alexander (2006):

The concept of God may be hypothesized to derive from a particular set of feelings that we share with members of our group: warm, pleasant feelings of good will, agreement, cooperativeness, commitment – and power as a result – power associated directly with the cooperativeness of the group. Because everyone in an integrated group tends to share these feelings, all members of such a group can accept God as denoting a unifying force so real that the collective agreement upon which the concept is based can easily be expanded to symbolize a superhuman entity. (Alexander, 2006)

We suggest that such warm, pleasant, cooperative, trusting and powerful feelings are uniquely functions of oxytocin, and that analysing this endocrine system in the context of inclusive fitness considerations will lead to important new insights into religious cognition and behaviour.

Table 1
Associations of polymorphisms in oxytocin and arginine vasopressin genes with self-report psychological correlates of religious cognition*

Gene	SNP (years)	AQ: Imagination	SPQ: Magical Ideation	SPQ: Unusual Perceptions	SPQ: Cognitive-Perceptual experience
OXTR	rs2254298 (2010–2011)	0.023 (M)	0.077 (M)	0.031 (B) 0.050 (M)	0.048 (B) 0.078 (M)
OXTR	rs2254298 (2011–2012)				0.11 (M) 0.11 (F)
OXTR	rs1042778 (2010–2011)	0.043 (B) 0.015 (F)			
OXTR	rs1042778 (2011–2012)		0.088 (M)	0.11 (F)	
CD38	rs3796863 (2010–2011)	0.073 (B)	0.048 (F)		0.16 (F)
AVPR1A	rs11174811 (2010–2011)	0.13 (B) 0.14 (M)	0.064 (B) 0.020 (F)		0.078 (F)
AVPR1A	rs11174811 (2011–2012)	0.18 (F)		0.017 (B) 0.002 (F)	0.10 (B) 0.038 (F)
AVPR1A	rs10877969 (2010–2011)	0.09 (B) 0.17 (M)			
AVPR1A	rs10877969 (2011–2012)			0.073 (B) 0.026 (F)	
AVP	rs2740204 (2010–2011)	0.051 (B) 0.011 (M)	0.0508 (B)	0.12 (F)	0.024 (B) 0.10 (M) 0.09 (F)
AVP	rs2740204 (2011–2012)	0.175 (M)	0.04 (B) 0.015 (F)	0.12 (B) 0.12 (F)	0.013 (B) 0.004 (F)

SNP: single nucleotide polymorphism; M: male; F: female; B: both.

* We used standard metrics of autism (autism quotient, AQ) and schizotypal cognition (schizotypal personality questionnaire, SPQ). Cognitive-Perceptual experience represents a higher-level scale, derived from summing values from Magical Ideation (aspects of supernatural beliefs), Unusual Perceptions (altered perceptions of reality) and Ideas of Reference (excessive beliefs that events relate to the self). P values between 0.05 and 0.20 are shown in bold to aid in assessment of replication across years. The population and methods are described in Leach et al. (2013).

Individual Variation in Religious Cognition and Behaviour

Evolutionary analyses of religion have concentrated mainly on its postulated benefits, although costs in terms of 'free-riding' and apparent energetic ecological wastefulness have been discussed by various authors. Consideration of such costs is important in the context of the commonplace nature of apathy, rejection, ambivalence and antipathy regarding religious beliefs and actions, and the clear correlates, such as female–male differences (Flere, 2007; Norenzayan & Gervais, 2013; Trzebiatowska & Bruce, 2012), in such psychological and behavioural variation. Indeed, if religion is adaptive for individuals and at least for relatively small social groups, especially in such an evolutionarily central domain as inclusive fitness, why is it not universally adopted, like other cultural universals such as language or incest avoidance? We suggest four potential reasons.

First, by the hypothesis described here, religious belief and behaviour develop in part from, and engender, manipulation and conflicts within groups (Coe et al., 2010; Coe & Palmer, 2013; Qirko, 2004; Trivers, 1974). At the smallest scale, although mothers are selected to inculcate children with prosocial, religiously based teachings, their children are selected to at least partially and conditionally resist, as it may often be in their personal inclusive fitness interests to do so. It is power and information asymmetries, combined with substantial benefits to children from uncritical social learning of a diversity of cultural beliefs and practices (most of which are fundamental to survival and reproduction), and benefits from conformity and tradition themselves (Palmer, 2010), that can maintain phenotypes that are deleterious to individuals in some contexts and conditions. More generally, conflicts between, as well as within (Haig, 2011) individuals, can maintain variation to the extent that they remain unresolved across evolutionary time. Are such processes also reflected by links of imprinted genes with magical ideation (Leach, Prefontaine, Hurd, & Crespi, *in press*), altruism (Tsang et al., 2013) and oxytocin production (e.g. Champagne, Curley, Swaney, Hasen, & Keverne, 2009; Muscatelli et al., 2000; Villanueva, Jacquier, & de Roux, 2012)?

Second, cooperative social systems are vulnerable to exploitation by individuals who garnish their benefits while reducing their costs to inclusive fitness. The benefits of such 'cheating' or 'free-riding' behaviours should decline as their frequencies increase, but one still expects some proportion of such individuals, whose religious cognition and behaviour would be hypocritical if not heretical (e.g. Johnson, 2009). Despite such considerations, religion would appear especially resilient in the face of free-riding, given the difficulties of avoiding detection in small-scale societies or relatively small socioreligious congregations, the apparent roles of costly signalling in maintaining the honesty of religion-associated altruism and mutualism (Henrich, 2009), and the historically high magnitudes of punishment imposed on detected unbelievers or free-riders, which include social exclusion or death.

Third, the relative strengths of selection within human groups, compared to between groups, is expected to have fluctuated substantially both within and across generations (Alexander, 2013; Lahti & Weinstein, 2005). To the extent that between-group selection represents a major driver of religion and its tightly associated within-group unity and cooperation, and individuals can gain inclusive fitness from within-group competition through more or less unconscious exploitation of religious beliefs and practices or superficiality of religious behaviour, variation among individuals in religious cognition and commitment should be maintained. This situation is directly comparable to the maintenance of other phenotypes by frequency-dependent selection, spatiotemporal heterogeneity in selection and variation across levels of selection.

Fourth, religious cognition, which is fundamentally mentalistic in ascribing supernatural omnipresence, omniscience, omnipotence to magical, imaginary agents with human properties, is expected to trade off among individuals with cognition that is mechanistic, based on physical, material, observable cause and effect (Badcock, 2009; Crespi & Badcock, 2008; Haig, 2011). This trade-off may be reflected in some cognitive differences between females and males (small, average differences, associated with both genetic and environmental causes), as well as in a spectrum between schizotypal and autistic cognition, with typical cognition at the centre (Crespi & Badcock, 2008; Dinsdale, Hurd, Wakabayashi, Elliot, & Crespi, 2013). Cognitive trade-offs can be detected and characterized using genetic data, in that some genetic polymorphisms (e.g. in genes linked to autism or schizophrenia risk, religious or social cognition, or oxytocin levels or responsiveness) are expected to associate inversely with mentalistic compared to mechanistic skills or endorsed beliefs: at a locus, one allele or genotype should be associated with more mentalistic, and the other allele or genotype with more mechanistic, cognition or abilities, as described above for rs1042778 in the *OXTR* gene. Such apparent trade-offs are represented on a large scale in the contrasts between relatively autistic individuals, who appear to be less religious but show enhanced mechanistic, systematic, visuospatial and perceptual accuracy and precision skills, with relatively schizotypal individuals, who tend to show more religious phenotypes but notably reduced abilities in this same set of traits, and an increased incidence of imaginary and empathic cognition and perception (Brosnan, Ashwin, Walker, & Donaghue, 2010; Gray et al., 2011; Thompson, Hurd, & Crespi, 2013). Genetic and psychological tests of these hypotheses should be simple and direct at the individual level. Culturally, mechanistic, material cause-and-effect cognitive abilities should be favoured by a broad swath of ecological and social circumstances, especially as human survival and reproduction have come to depend more and more upon aspects of technology since the first stone tools were crafted.

CONCLUSIONS

We have described and evaluated an integrative hypothesis for the origin and evolution of human religious cognition and behaviour, based on maximization of inclusive fitness and consideration of the concept of God as represented by one's circle of kin and one's higher-level groups of social salience (Alexander, 2006, 2013). The theory is derived from foundational work mainly by Hamilton, Alexander, Trivers, Lahti, Coe, Palmer and Steadman, which we have synthesized more explicitly into a unified inclusive fitness framework, and extended through consideration of genetic, endocrine and psychological dimensions to religious cognition and behaviour. Most generally, the analysis has proceeded along Tinbergian, animal behavioural lines, in that we have addressed four questions: (1) function (adaptation) of religion in maximizing inclusive fitness of those in control of the relevant phenotypes, mainly older and relatively powerful individuals, and especially mothers, in a social group, but expanding to benefits for extended kin groups, clans, bands, tribes and groups of psychological kin; (2) phylogeny (evolution), whereby religious cognition and behaviour have, over evolutionary time, grafted upon moral sentiments that evolved through kin selection and direct and indirect reciprocity; (3) development (ontogeny), through socially learned inculcation of deeply impressionable children with religious, moral beliefs that teach them 'proper' social behaviour towards kin and others; (4) mechanism (causation), whereby religious thought and behaviour is hypothesized to centre on the oxytocin and arginine vasopressin systems that mediate expression of social bonding, altruism, ingroup–outgroup cognition and perception of kinship.

Hypotheses at all four of these levels are falsifiable, with anthropological, psychological, neurological, endocrinological and genetic data. We suggest that direct and especially useful tests will come from: (1) historical and anthropological data on conflictual interactions (and their outcomes) between pairs or sets of cultural groups that differ in their religious and kinship-associated traits (e.g. Jones, 2011; Rossano, 2010, p. 50; Vanhanen, 1999); (2) comparative studies of coevolution between kinship systems and religious systems; (3) analyses of how religious and moralistic inculcation of children influence their cooperative interactions with kin and non-kin, especially mothers, sibs, and more distant kin; (4) neuroimaging studies that localize and quantify religious cognition and belief in brain networks (Kapogiannis et al., 2009; Saver & Rabin, 1997) and can thus test whether cognitive systems subserving religious belief and experiences overlap with cognitive systems underlying kinship, psychological kinship and social group interactions; and (5) genetic and experimental studies to determine the degree to which the oxytocin and vasopressin systems (and interacting neurotransmission systems involving dopamine and serotonin; e.g. Sasaki et al., 2013; Topp et al., 2014) jointly mediate religious beliefs and behaviour and kin-based and group-based interactions. Our genetic data are consistent with roles for polymorphic oxytocin and vasopressin genes in some important aspects of self-endorsed, religion-associated traits, but behavioural genetics, personality genetics and experimental studies that focus more specifically on religion will provide direct and more robust tests of these hypotheses.

A central feature of our hypothesis is that it is notably compatible with virtually all previously described theories for the origin and evolution of religion that invoke adaptation and natural selection in some way, yet it grounds the process in foundational theory of behavioural evolutionary biology: maximization of inclusive fitness. In this regard, the contentious interfaces of religion with evolutionary biology can be considered in new light (Alexander, 2006):

Religions contend that God created humans. Viewing God as the collective moral sense within (or characterizing) any group that functions as a social unit – as a real or surrogate kin circle – is, surprisingly, not contrary to that contention. God as collective moral sense is a term for a collective spirit (or its effects) arising entirely within the realm of everyday “natural” causation, and leading to morality and social harmony. In this version, there need be no incompatibility between evolutionary biology and religion because (1) God (as the moral capability that spread across our evolving species) is the “creator” of human life, (2) the evolutionary meaning, or function, of human life is the same as the religious one – to serve God (as kin circle), and (3) even if different cultures or religions serve God in somewhat different ways because of different histories and different conditions of existence, God as collective moral sense evidently has the same single origin as humanity, and is at base the same trait or tendency in all human societies.

I have found that if I interpret the concept of God in the way just described, a wide diversity of uses of it in human sociality (indeed, virtually all such uses) make sense – even to people who think of God as a wise and powerful individual humanoid of supernatural origin.

God is just (in the above arguments, justice means fairness within cooperative human groups); God is all-powerful (in fact, the source of all justice and power exerted within the kin group is that of the kin group itself, mediated by power differentials among competing aspiring leaders); God is eternal (because for all practical purposes the concept lasts as long as the group, and to us individuals that either makes the kin group “eternal” or creates the wishful thinking that it will or must be so, especially if we can work at helping this to

come true); God is all-seeing (so many liars and deceivers forget that they are being watched almost continually by essentially the whole group to which they belong – which, during most of human history, would have been small groups in which everyone is likely to be familiar with the traits and tendencies of everyone else within the primary social groups; in such small kin groups, deception and chicanery must have taken forms somewhat different from their expressions in today’s huge modern urban societies largely made up of virtual strangers); God (our surround of kin) will take care of us.

In other words, the collective morality of the cooperating group – the actions and capabilities of the kin group – can probably account for all of the most important characteristics we attribute to God, without requiring a supernatural force in the form of a humanoid creator or overseer.

One can be either a fundamentalist or a prior atheist yet accept or tolerate others who see God as the collective moral sense that, originally within the kin circle, now leads to the more widespread cooperativeness and beneficence and patriotism that we use the concept of God to promote. In terms of justice and morality, essentially the same ends are sought by people with both beliefs. So God as the vision and power of the community causes some of the reasons for controversies about religion and evolution to diminish or disappear. (Alexander, 2006)

The hypothesis described here demonstrates in a new context how cooperation can evolve from competition, when the interests of genetically and phenotypically more or less interdependent parties overlap. In this way, the origin of religion resembles a major transition in evolution (Maynard Smith & Szathmáry, 1997), whereby a new level of organization is reached through suppression of lower-level conflicts. This phenomenon differentiates humans from other primates in a manner comparable to language, but like other major transitions it is directly concerned with cooperative, and competitive, behaviour, and it generates new conflicts as well as suppressing previous ones. To the extent that inclusive fitness theory can help to explain religion and its prosocial, magical and moralistic dimensions, it should also prove useful in developing better methods to ameliorate its deleterious, conflictual effects on human societies and wellbeing.

Acknowledgments

We are grateful to Richard Alexander, Kathryn Coe, Steve Frank and David Lahti for helpful comments and discussion, to Joan Strassmann for inviting us to contribute this article, and to the Natural Sciences and Engineering Research Council of Canada for financial support. We especially thank Richard Alexander for allowing us to use material from an unpublished essay.

References

- Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle, WA: University of Washington Press.
- Alexander, R. D. (2006). The concept of God and the meaning of life. Unpublished manuscript.
- Alexander, R. D. (2013). Religion, evolution and the quest for global harmony. In K. Summers, & B. Crespi (Eds.), *Human social evolution: The foundational works of Richard D. Alexander* (pp. 384–425). Oxford, U.K.: Oxford University Press.
- van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The steroid/peptide theory of social bonds: integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, 36, 1265–1275.
- Atkinson, Q. D., & Bourrat, P. (2011). Beliefs about God, the afterlife and morality support the role of supernatural policing in human cooperation. *Evolution and Human Behavior*, 32, 41–49.

- Atran, S., & Henrich, J. (2010). The evolution of religion: how cognitive by-products, adaptive learning heuristics, ritual displays, and group competition generate deep commitments to prosocial religions. *Biological Theory*, 5, 18–30.
- Badcock, C. (2009). *The imprinted brain: How genes set the balance between autism and psychosis*. London, U.K.: Jessica Kingsley.
- Bailey, K. G., & Wood, H. E. (1998). Evolutionary kinship therapy: basic principles and treatment implications. *British Journal of Medical Psychology*, 71, 509–523.
- van den Berghe, P. L. (1981). *The ethnic phenomenon*. New York, NY: Elsevier.
- Bering, J. M. (2002). The existential theory of mind. *Review of General Psychology*, 6, 3–24.
- Bossan, B., Hammerstein, P., & Koehncke, A. (2013). We were all young once: an intragenomic perspective on parent–offspring conflict. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122637. <http://dx.doi.org/10.1098/rspb.2012.2637>.
- Bowles, S. (2006). Group competition, reproductive leveling, and the evolution of human altruism. *Science*, 314, 1569–1572.
- Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, 324, 1293–1298.
- Boyer, P., & Bergstrom, B. (2008). Evolutionary perspectives on religion. *Annual Review of Anthropology*, 37, 111–130.
- Bradshaw, M., & Ellison, C. G. (2008). Do genetic factors influence religious life? Findings from a behavior genetic analysis of twin siblings. *Journal for the Scientific Study of Religion*, 47, 529–544.
- Brewerton, T. D. (1994). Hyperreligiosity in psychotic disorders. *Journal of Nervous and Mental Disease*, 182, 302–304.
- Brosnan, M., Ashwin, C., Walker, I., & Donaghue, J. (2010). Can an 'extreme female brain' be characterized in terms of psychosis? *Personality and Individual Differences*, 49, 738–742.
- Bryant, R. A., & Hung, L. (2013). Oxytocin enhances social persuasion during hypnosis. *PLoS One*, 8, e60711.
- Bulbulia, J. (2004). The cognitive and evolutionary psychology of religion. *Biology and Philosophy*, 19, 655–686.
- Calhoun, C. (1980). The authority of ancestors: a sociological reconsideration of Fortes's Tallensi in response to Fortes's critics. *Man*, 15, 304–319.
- Chagnon, N. (2013). *Noble savages: My life among two dangerous tribes: The Yanomamo and the anthropologists*. New York, NY: Simon & Schuster.
- Champagne, F. A., Curley, J. P., Swaney, W. T., Hasen, N. S., & Keverne, E. B. (2009). Paternal influence on female behavior: the role of *Peg3* in exploration, olfaction, and neuroendocrine regulation of maternal behavior of female mice. *Behavioral Neuroscience*, 123, 469–480.
- Chanda, M. L., & Levitin, D. J. (2013). The neurochemistry of music. *Trends in Cognitive Sciences*, 17, 179–193.
- Coe, K., Aiken, N. E., & Palmer, C. T. (2006). Once upon a time: ancestors and the evolutionary significance of stories. *Anthropological Forum*, 16, 21–40.
- Coe, K., & Palmer, C. T. (2008). The words of our ancestors: kinship, tradition, and moral codes. *World Cultures eJournal*, 16, Article 1.
- Coe, K., & Palmer, C. T. (2013). Mothers, traditions, and the human strategy to leave descendants. In M. L. Fisher, J. R. Garcia, & R. S. Chang (Eds.), *Evolution's empress: Darwinian perspectives on the nature of women* (pp. 115–132). Oxford, U.K.: Oxford University Press.
- Coe, K., Palmer, A. L., Palmer, C. T., & DeVito, C. L. (2010). Culture, altruism, and conflict between ancestors and descendants. *Structure and Dynamics*, 4, 1–17.
- Crespi, B. J. (2000). The evolution of maladaptation. *Heredity*, 84, 623–629.
- Crespi, B., & Badcock, C. (2008). Psychosis and autism as diametrical disorders of the social brain. *Behavioral and Brain Sciences*, 31, 241–260.
- Dai, L., Carter, C. S., Ying, J., Bellugi, U., Pournajafi-Nazarloo, H., & Korenberg, J. R. (2012). Oxytocin and vasopressin are dysregulated in Williams Syndrome, a genetic disorder affecting social behavior. *PLoS One*, 7, e38513.
- Dawkins, R. (2006). *The god delusion*. Boston, MA: Houghton Mifflin.
- De Dreu, C. K. (2012). Oxytocin modulates cooperation within and competition between groups: an integrative review and research agenda. *Hormones and Behavior*, 61, 419–428.
- De Dreu, C. K., Baas, M., Roskes, M., Sligte, D. J., Ebstein, R. P., Chew, S. H., et al. (2013). Oxytonergic circuitry sustains and enables creative cognition in humans. *Social Cognitive and Affective Neuroscience*. <http://dx.doi.org/10.1093/scan/nst094>. Advance online publication.
- De Dreu, C. K., Greer, L. L., Van Kleef, G. A., Shalvi, S., & Handgraaf, M. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 1262–1266.
- De Dreu, C. K., Shalvi, S., Greer, L. L., Van Kleef, G. A., & Handgraaf, M. J. (2012). Oxytocin motivates non-cooperation in intergroup conflict to protect vulnerable in-group members. *PLoS One*, 7, e46751.
- Dein, S., & Littlewood, R. (2011). Religion and psychosis: a common evolutionary trajectory? *Transcultural Psychiatry*, 48, 318–335.
- Devinsky, O., & Lai, G. (2008). Spirituality and religion in epilepsy. *Epilepsy & Behavior*, 12, 636–643.
- Diduca, D., & Joseph, S. (1997). Schizotypal traits and dimensions of religiosity. *British Journal of Clinical Psychology*, 36, 635–638.
- Dinsdale, N., & Crespi, B. J. (2013). The borderline empathy paradox: evidence and conceptual models for empathic enhancements in borderline personality disorder. *Journal of Personality Disorders*, 27, 172–195.
- Dinsdale, N. L., Hurd, P. L., Wakabayashi, A., Elliot, M., & Crespi, B. J. (2013). How are autism and schizotypy related? Evidence from a non-clinical population. *PLoS One*, 8, e63316.
- Feldman, R., Zagoory-Sharon, O., Weisman, O., Schneiderman, I., Gordon, I., Maoz, R., et al. (2012). Sensitive parenting is associated with plasma oxytocin and polymorphisms in the *OXT* and *CD38* genes. *Biological Psychiatry*, 72, 175–181.
- Fischer, R., Callander, R., Reddish, P., & Bulbulia, J. (2013). How do rituals affect cooperation? An experimental field study comparing nine ritual types. *Human Nature*, 24, 115–125.
- Fischer-Shofty, M., Brüne, M., Ebert, A., Shefet, D., Levkovitz, Y., & Shamay-Tsoory, S. G. (2013). Improving social perception in schizophrenia: the role of oxytocin. *Schizophrenia Research*, 146, 357–362.
- Fischer-Shofty, M., Levkovitz, Y., & Shamay-Tsoory, S. G. (2013). Oxytocin facilitates accurate perception of competition in men and kinship in women. *Social Cognitive and Affective Neuroscience*, 8, 313–317.
- Flere, S. (2007). Gender and religious orientation. *Social Compass*, 54, 239–253.
- Gray, K., Jenkins, A. C., Heberlein, A. S., & Wegner, D. M. (2011). Distortions of mind perception in psychopathology. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 477–479.
- Grigorenko, E. L. (2011). Closeness of all kinds: the role of oxytocin and vasopressin in the physiology of spiritual and religious behavior. In A. E. A. Warren, R. M. Lerner, & E. Phelps (Eds.), *Thriving and spirituality among youth: Research perspectives and future possibilities* (pp. 33–60). Hoboken, NJ: John Wiley.
- Haig, D. (2011). Genomic imprinting and the evolutionary psychology of human kinship. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 10878–10885.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour, I and II. *Journal of Theoretical Biology*, 7, 1–52.
- Henrich, J. (2009). The evolution of costly displays, cooperation, and religion: credibility enhancing displays and their implications for cultural evolution. *Evolution & Human Behavior*, 30, 244–260.
- Hill, K. R., Walker, R. S., Bozicević, M., Eder, J., Headland, T., Hewlett, B., et al. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331, 1286–1289.
- Hughes, A. L. (1988). Kin networks and political leadership in a stateless society, the Toda of South India. *Ethology and Sociobiology*, 9, 29–44.
- Järvinen, A., Korenberg, J. R., & Bellugi, U. (2013). The social phenotype of Williams syndrome. *Current Opinion in Neurobiology*, 23, 414–422.
- Johnson, D. (2009). Beyond belief [Review of *The Supernatural and Natural Selection: Religion and Evolutionary Success* by L.B. Steadman & C. T. Palmer]. *Evolution and Human Behavior*, 30, 225–228.
- 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.
- Jones, D. (2000). Group nepotism and human kinship. *Current Anthropology*, 41, 779–809.
- Jones, D. (2004). The universal psychology of kinship: evidence from language. *Trends in Cognitive Sciences*, 8, 211–215.
- Jones, D. (2011). The matrilineal tribe: an organization of demic expansion. *Human Nature*, 22, 177–200.
- Kandler, C., & Riemann, R. (2013). Genetic and environmental sources of individual religiousness: the roles of individual personality traits and perceived environmental religiousness. *Behavior Genetics*, 43, 297–313.
- Kapogiannis, D., Barbey, A. K., Su, M., Zamboni, G., Krueger, F., & Grafman, J. (2009). Cognitive and neural foundations of religious belief. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 4876–4881.
- Kirkpatrick, L. A. (1999). Toward an evolutionary psychology of religion and personality. *Journal of Personality*, 67, 921–952.
- Kirkpatrick, L. A. (2005). *Attachment, evolution, and the psychology of religion*. New York, NY: Guilford Press.
- Lahti, D. C. (2009). The correlated history of social organization, morality, and religion. In E. Voland, & W. Schiefelhövel (Eds.), *The biological evolution of religious mind and behavior* (pp. 67–88). Berlin, Germany: Springer-Verlag.
- Lahti, D. C., & Weinstein, B. S. (2005). The better angels of our nature: group stability and the evolution of moral tension. *Evolution and Human Behavior*, 26, 47–63.
- Langergraber, K., Schubert, G., Rowney, C., Wrangham, R., Zommers, Z., & Vigilant, L. (2011). Genetic differentiation and the evolution of cooperation in chimpanzees and humans. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2546–2552.
- Leach, E., Hurd, P., & Crespi, B. (2013). Schizotypy, cognitive performance and genetic risk for schizophrenia in a non-clinical population. *Personality and Individual Differences*, 55, 334–338.
- Leach, E. L., Prefontaine, G., Hurd, P. L., & Crespi, B. J. The imprinted gene *LRRTM1* mediates schizotypy and handedness in a non-clinical population. *Journal of Human Genetics*. in press
- Lenze, M. D., Gordon, R. L., Key, A. P. F., & Dykens, E. M. (2013). Neural correlates of cross-modal affective priming by music in Williams syndrome. *Social Cognitive and Affective Neuroscience*. <http://dx.doi.org/10.1093/scan/nst017>. Advance online publication.
- MacPherson, J. S., & Kelly, S. W. (2011). Creativity and positive schizotypy influence the conflict between science and religion. *Personality and Individual Differences*, 50, 446–450.
- Maltby, J., Garner, I., Lewis, C. A., & Day, L. (2000). Religious orientation and schizotypal traits. *Personality and Individual Differences*, 28, 143–151.
- Marsh, L., Pearson, A., Ropar, D., & Hamilton, A. (2013). Children with autism do not overimitate. *Current Biology*, 23, R266–R268.

- Maynard Smith, J., & Szathmáry, E. (1997). *The major transitions in evolution*. New York, NY: Oxford University Press.
- Murray, E. D., Cunningham, M. G., & Price, B. H. (2012). The role of psychotic disorders in religious history considered. *Journal of Neuropsychiatry and Clinical Neurosciences*, 24, 410–426.
- Muscattelli, F., Abrous, D. N., Massacrier, A., Boccaccio, I., Le Moal, M., Cau, P., et al. (2000). Disruption of the mouse *Nesdin* gene results in hypothalamic and behavioral alterations reminiscent of the human Prader–Willi syndrome. *Human Molecular Genetics*, 9, 3101–3110.
- Myers, M. G. (1975). *Kinship, religion, and the transformation of society: The 1975 Karl G. Maeser Distinguished Teaching Award address*. Provo, UT: Brigham Young University. Retrieved from: <http://speeches.byu.edu/?act=viewitem&sid=1134>.
- Norenzayan, A., & Gervais, W. M. (2013). The origins of religious disbelief. *Trends in Cognitive Sciences*, 17, 20–25.
- Norenzayan, A., Gervais, W. M., & Trzesniewski, K. H. (2012). Mentalizing deficits constrain belief in a personal god. *PLoS One*, 7, e36880.
- Oakley, B. (2007). *Evil genes: Why Rome fell, Hitler rose, Enron failed, and my sister stole my mother's boyfriend*. Amherst, NY: Prometheus Books.
- Pagel, M. (2012). *Wired for culture: Origins of the human social mind*. New York, NY: W. W. Norton.
- Palmer, C. T. (2010). Cultural traditions and the evolutionary advantages of non-innovation. In M. J. O'Brien, & S. J. Shennan (Eds.), *Innovation in cultural systems: Contributions from evolutionary anthropology* (pp. 161–174). Cambridge, MA: MIT Press.
- Palmer, C. T., & Coe, K. (2010). From morality to law: the role of kinship, tradition and politics. *Politics and Culture*, 1. Retrieved from: <http://www.politicsandculture.org/2010/04/29/from-morality-to-law-the-role-of-kinship-tradition-and-politics/>.
- Palmer, C. T., Steadman, L. B., Cassidy, C., & Coe, K. (2008). Totemism, metaphor and tradition: incorporating cultural traditions into evolutionary psychological explanations of religion. *Zygon*, 43, 713–729.
- Palmer, C. T., Steadman, L. B., Cassidy, C., & Coe, K. (2010). The importance of magic to social relationships. *Zygon*, 45, 317–337.
- Plesa-Skwerer, D., Sullivan, K., Joffe, K., & Tager-Flusberg, H. (2004). Self concept in people with Williams syndrome and Prader–Willi syndrome. *Research in Developmental Disabilities*, 25, 119–138.
- Powell, R., & Clarke, S. (2012). Religion as an evolutionary byproduct: a critique of the standard model. *British Journal for the Philosophy of Science*, 63, 457–486.
- Previc, F. H. (2006). The role of the extrapersonal brain systems in religious activity. *Consciousness and Cognition*, 15, 500–539.
- Qirko, H. (2004). Altruistic celibacy, kin-cue manipulation, and the development of religious institutions. *Zygon*, 39, 681–706.
- Queller, D. (1992). Quantitative genetics, inclusive fitness, and group selection. *American Naturalist*, 139, 540–558.
- Roes, F. L., & Raymond, M. (2003). Belief in moralizing gods. *Evolution and Human Behavior*, 24, 126–135.
- Rossano, M. J. (2006). The religious mind and the evolution of religion. *Review of General Psychology*, 10, 346–364.
- Rossano, M. J. (2007). Supernaturalizing social life: religion and the evolution of human cooperation. *Human Nature*, 18, 272–294.
- Rossano, M. J. (2010). *Supernatural selection: How religion evolved*. Oxford, U.K.: Oxford University Press.
- Sasaki, J. Y., Kim, H. S., Mojaverian, T., Kelley, L. D., Park, I. Y., & Janusonis, S. (2013). Religion priming differentially increases prosocial behavior among variants of the dopamine D4 receptor (DRD4) gene. *Social Cognitive and Affective Neuroscience*, 8, 209–215.
- Saver, J. L., & Rabin, J. (1997). The neural substrates of religious experience. *Journal of Neuropsychiatry*, 9, 498–510.
- Sosis, R., & Alcorta, C. (2003). Signaling, solidarity, and the sacred: the evolution of religious behavior. *Evolutionary Anthropology: Issues, News, and Reviews*, 12, 264–274.
- Stallen, M., De Dreu, C. K., Shalvi, S., Smidts, A., & Sanfey, A. G. (2012). The herding hormone oxytocin stimulates in-group conformity. *Psychological Science*, 23, 1288–1292.
- Steadman, L. B., & Palmer, C. T. (1994). Visiting dead ancestors: shamans as interpreters of religious traditions. *Zygon*, 29, 173–189.
- Steadman, L. B., & Palmer, C. T. (1997). Myths as instructions from ancestors: the example of Oedipus. *Zygon*, 32, 341–350.
- Steadman, L. B., Palmer, C. T., & Tilley, C. F. (1996). The universality of ancestor worship. *Ethnology*, 35, 63–76.
- Thompson, G. J., Hurd, P. L., & Crespi, B. J. (2013). Genes underlying altruism. *Biology Letters*, 9, 20130395.
- Tops, M., Koole, S. L., Ijzerman, H., & Buisman-Pijlman, F. T. (2014). Why social attachment and oxytocin protect against addiction and stress: insights from the dynamics between ventral and dorsal corticostriatal systems. *Pharmacology Biochemistry and Behavior*, 119, 39–48.
- Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist*, 14, 247–262.
- Trivers, R. L. (1985). *Social evolution*. Menlo Park, CA: Benjamin/Cummings.
- Trzebiatowska, M., & Bruce, S. (2012). *Why are women more religious than men?* Oxford, U.K.: Oxford University Press.
- Tsang, S. Y., Zhong, S., Mei, L., Chen, J., Ng, S.-K., Pun, F. W., et al. (2013). Social cognitive role of schizophrenia candidate gene *GABRB2*. *PLoS One*, 8, e62322.
- Vanhanen, T. (1999). Domestic ethnic conflict and ethnic nepotism: a comparative analysis. *Journal of Peace Research*, 36, 55–73.
- Villanueva, C., Jacquier, S., & de Roux, N. (2012). DLK1 is a somato-dendritic protein expressed in hypothalamic arginine-vasopressin and oxytocin neurons. *PLoS One*, 7, e36134.
- Wilson, D. S. (2005). Testing major evolutionary hypotheses about religion with a random sample. *Human Nature*, 16, 382–409.
- Zak, P. J. (2012). *The moral molecule*. New York, NY: Penguin/Dutton.