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Inclusive fitness theory for the evolution of religion

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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.

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.

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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 preemption 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

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