

Evolutionary Perspectives on Religion: An Overview and Synthesis

Zachary Smith
Holly Arrow

Department of Psychology, University of Oregon

ABSTRACT

Religion is a cultural universal that has puzzled evolutionists since Darwin. The moral, social, emotional, and explanatory components that make up complex religious systems offer both evolutionary benefits and costs. Evolutionists who propose functional accounts of religion argue that it offers adaptive benefits that outweigh the costs. Theorists who propose nonfunctional accounts view religion as a byproduct of interactions among nonreligious cognitive adaptations and environments. Others argue that religion evolved via memetic transmission, which allows maladaptive features to persist. These maladaptive features may be anachronisms that were functional in the past but are detrimental to fitness in modern contexts. A thorough review reveals that work guided by these different perspectives is driven by divergent research questions that ultimately complement one another to offer a more comprehensive evolutionary account of the complexity, variety, and durability of religious belief and behavior.

KEYWORDS

Psychology of religion; evolution of religion; cultural evolution; cognitive adaptation; cognitive byproduct; meme theory; multi-level selection; exaptation

INTRODUCTION

In the 1740s a small Protestant group known as the Shakers formed in Manchester, England. The Shaker creed emphasized equality between men and women in religious practices, the need for communal living, a literalist view of the Bible, and a strict moral code. Following their eventual migration to New England, the Shakers attracted nearly 20,000 converts throughout the nineteenth century

AUTHOR NOTE: Please direct correspondence to Zachary Smith, Small Groups Lab, Department of Psychology, 1227 University of Oregon, Eugene, OR 97403-1227. Email: zach.smith.71@gmail.com

(Garrett, 1987). Yet by 2006, there were only four Shakers left (Chase, 2006). How did this happen? Evidently, the survival of the group was difficult to maintain because of one major pitfall: they believed that men, to atone for women's original sin, should remain celibate for their entire lives, even in marriage. Thus, the group relied solely on conversion and adoption to maintain their ranks. This resulted in their eventual demise.

The story of the Shakers illustrates the power and complexity of religion. Their creed provided benefits to each individual and to the group by ensuring high levels of altruistic behavior within their communal living structure (Garrett, 1987). Yet these benefits came with the cost of extinguishing each individual's direct genetic line, resulting in an evolutionary dead-end. Evolutionarily, the initial popularity of the Shaker movement is puzzling because each follower willingly endured a significant detriment to their genetic survival and reproductive success. How could natural selection result in a willingness to sacrifice one's own reproductive fitness in the service of religion? Puzzles like this have challenged evolutionists since Darwin. Over the years, scientists have offered a variety of explanations to account for particular religious phenomena and to make sense of the universality, complexity, and variation among religions. Yet many questions remain unanswered. While one religion may directly promote within-group dynamics, another may be based on individual spiritual devotion devoid of group attachments. How did these very different manifestations of religion evolve? In the field of evolutionary religious studies, scholars examine possible underlying psychological mechanisms of religious belief and behavior, as well as their adaptive and maladaptive features, to seek scientific answers to these questions.

Thus far, evolutionists have formed three theoretical camps that view religion as nonfunctional, functional, or dysfunctional. Nonfunctional theorists hypothesize that religion is not an adaptation but instead an evolutionary byproduct of nonreligious adaptations. Functional theorists hypothesize that religion's benefits outweigh its costs in terms of survival and reproductive success. Work by such theorists focuses on identifying specific religious adaptations that serve particular functions. Dysfunctional theorists hypothesize that religious phenomena, particularly their maladaptive features, result from cultural evolutionary processes that are relatively independent of individual and group fitness. The three approaches also tend to differ in their favored level of analysis. Nonfunctional accounts tend to emphasize the role of genetics and the development of the brain in generating the various components of religious systems. Functional accounts tend to emphasize social and cultural influences on behavior with an explicit focus on religion's group-level features. Dysfunctional accounts tend to emphasize the role of cultural transmission and rapid environmental changes in preserving costly aspects of religion.

At first glance these perspectives appear incompatible. A thorough review, however, reveals that these theorists address divergent yet complementary research questions. Nonfunctionalists ask: What are the evolutionary origins of the religion's cognitive components? Functionalists ask: What adaptive functions does religion serve and how did it evolve to serve these functions? Dysfunctional theorists ask: How are religious concepts transmitted and maintained, and why do maladaptive features persist? Research and theory driven by different questions has

inspired divergent approaches and resulted in dissimilar conclusions. However, what appear at first to be incompatible results are actually more complementary than they seem. The review presented here is guided by the conviction that religion poses a set of evolutionary puzzles rather than a single puzzle to which different camps have offered contradictory solutions. By showing how the different perspectives complement one another, this article aims to sidestep the usual disputes and instead advance one step along the path to a more integrated, comprehensive evolutionary account.

Defining Religion

Perhaps because of the tendency to focus on one question rather than on a suite of questions, evolutionists have often used definitions of religion that fail to capture religion's complexity and encompass all of its possible forms and variations. To support a more comprehensive analysis, we define religion broadly as a set of myths, symbols, beliefs, and practices, of a supernatural quality, expressed and maintained by an individual or group and consisting of four often inter-related components: (1) morality, (2) social cohesion, (3) emotion, and (4) explanation.¹ Relative emphasis on the four major components varies across religions. So far, evolutionary theories of religion have also varied in their relative emphasis on these components. Religions can provide individuals and groups with systems for moral foundation and structure; social order, consistency, and cohesion; emotional comfort; and explanations for life's origins, harsh realities, puzzling natural phenomena, and an afterlife. The evidence, however, suggests that religious systems can be both beneficial and costly to individual and group fitness.²

The Evolutionary Theories of Religion

This multifaceted definition attests to the immense complexity of religion. As noted above, nonfunctional, functional, and dysfunctional approaches differ based on the three types of research questions they pose. Some of these perspectives have also generated different branches of theorizing, resulting in five competing evolutionary theories of religion. The nonfunctionalist perspective has generated byproduct theory. Byproduct theory posits that religion originates from psychological mechanisms that were nonreligious adaptations to evolutionary problems of our ancestral environment. The functionalist perspective has generated two theories: individual-level adaptation theory and multi-level selection theory. These theories posit that religion is adaptive at the individual and group level, respectively. The

¹ The first two components are more often group-level features while the latter two are more often on the individual level. The numbering does not represent any priority among these components.

² It is important to note that evolutionary 'success' is a context-dependent measure. What is costly to individual or group fitness in one context, may be beneficial in another, and vice-versa. Religions and the contexts in which they exist vary greatly. And, of course, the degree to which any religion is beneficial for any particular individual may be unrelated to "reproductive fitness" as defined by evolutionary logic.

dysfunctional perspective has also generated two theories: a memetic theory of religion and anachronism theory. Meme theorists propose that religion culturally evolves through a process of memetic transmission and retention, resulting in the production and persistence of its maladaptive features. Anachronism theorists, on the other hand, hypothesize that religion's maladaptive effects stem from significant changes to the human social environment in recent history that have rendered initially functional religious components dysfunctional.

Proponents of the five theories often argue against each other. Much less attention has been paid to the interesting ways these theories complement one another. An integrated perspective that synthesizes these theories can help us circumvent past arguments over religion's functionality and assemble a more comprehensive evolutionary account. In the review below, each theory is described in turn, with an emphasis on the features that make it distinctive. The paper concludes with suggestions of how the five theories might be integrated into a single overarching framework.

Byproduct Theory

Many evolutionists hypothesize that religious thought is a byproduct of the normal function of nonreligious psychological mechanisms that evolved in ancestral contexts. Supporters of byproduct theory propose that these nonreligious adaptive mechanisms are responsible for religion's incidental existence and generate the illusion of its ostensible design. This theory helps explain religion's universality and cross-cultural similarity by outlining its cognitive foundation in adaptations such as theory of mind and other features of social intelligence. It also provides a viable explanation for the evolutionary origins of religious thought.

According to byproduct theorists, one cognitive adaptation that plays a key role in generating religious cognition is theory of mind, the human propensity to attribute mental states such as beliefs and intentions to others. Theory of mind allows humans to understand that the mental states of others can be different from their own. This provides the foundation for skills critical to social functioning, specifically in identifying cooperators, defectors, and cheaters in human social groups. Some scientists believe that the capacities that comprise social intelligence, including perspective taking and the ability to manipulate others, probably set off an evolutionary arms race between cooperative, defective, and cheating dispositions (Orbell, Morikawa, Hartwig, Hanley, & Allen, 2004). This naturally led to the development of the cooperative behaviors, ethical instincts, and moral systems that humans exhibit today.

Theory of mind and social intelligence also gave humans a new perspective on *self* and *other*. In particular, *other* is redefined to potentially include *anything* that can be assigned agency (e.g. family members, friends, enemies, the deceased, supernatural entities, etc.). One cognitive device critical to this process is a hyperactive agency detection mechanism. This mechanism interprets unusual or ambiguous stimuli from our surrounding environment as signs of agency. This often makes us perceive human-like characteristics in nonliving objects. This originally nonreligious mechanism would have been a valuable asset in avoiding predators, especially other hostile humans. Anthropologists such as Stewart Guthrie (1995)

point to this systematic anthropomorphization of our environment (i.e. mistaking a shadow for an intentional spirit, seeing faces in the clouds, etc.) as the origins of supernaturalism and religious ideation. When coupled with a theory of mind, which readily assigns mental states and intentionality to these anthropomorphized objects, the resulting system incidentally generates thoughts of religious spirits and deities. Once humans developed these mechanisms, interactions among the mechanisms were inevitable, and the belief in the existence of immaterial, unverifiable, and supernatural entities with their own minds and intentions was a short cognitive step away.

Religion's complexity, however, indicates that a multitude of other mechanisms are also involved in generating religious cognition. As outlined by some cognitive anthropologists (Atran, 2002; Boyer, 2001, 2003; Boyer & Bergstrom, 2008), these mechanisms probably number in the hundreds. Byproduct theory proposes that modern humans are predisposed to think religiously because of interactions between these nonreligious cognitive adaptations and environments. Psychologist Lee Kirkpatrick (1999) organizes them into larger categories, including naïve physics and folk-biology, naïve psychology and theory of mind, intra-sexual competition, kin selection and nepotism, reciprocity and social exchange, attachment, and intergroup bias and coalitional psychology. All of the nonreligious mechanisms in these categories have been identified as serving critical adaptive functions in the evolutionary past.

From a research standpoint, byproduct theory offers an effective method for cognitively analyzing religious phenomena. In general, byproduct hypotheses require the identification of the byproduct's underlying adaptations and the reason for its coupling with those adaptations (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Tooby & Cosmides, 1992). The byproduct theory of religion focuses on psychological mechanisms that can be empirically examined in laboratory settings. Scientists can form testable hypotheses regarding specific cognitive, behavioral, and cultural tendencies based on these adaptive mechanisms which have been theoretically explained using evolutionary theory (Kirkpatrick, 1999). Psychologists Jesse Bering and Lee Kirkpatrick both empirically explore the nature of religious belief using this approach. Bering (2005, 2006) focuses on the complex development of afterlife beliefs resulting from interactions among mechanisms for causal attribution, moral judgment, theory of mind, concept acquisition, and teleological reasoning. Kirkpatrick (2005) investigates the role of an attachment mechanism in generating person-God relationships.

Boyer (2001) also notes how this theory is capable of reversing many assumptions made by functionalists by reducing religion to its cognitive components. For instance, theologians and sociologists have often argued that religion's function is to provide the moral basis to our decision making. However, the evidence suggests that humans have an innate moral system (see Hauser, Young, & Cushman, 2008) and that religious systems based on this foundation are a byproduct of these moral and ethical faculties interacting with other social mechanisms. Thus, morality is a predictable component of religious systems because of these underlying mechanisms. Similarly, rather than exist as an adaptation to enforce social order or promote group cohesion, religion is partially a byproduct of innate mechanisms that drive us to form coalitions and groups as well

as organize and categorize other people. Clearly, byproduct explanations turn these functional assumptions upside-down.

Many scientists, however, have pointed out that this theory may overemphasize the role of genetics and the development of the brain (e.g. Wilson, 2002). Thus, byproduct theory fails to answer critical evolutionary questions. For example, culture is an influential aspect of modern human environments and in reality genetics *and* culture influence the production, acquisition, and maintenance of religious concepts. So, how do religious systems, as innately social phenomena entailing individual and group-level components, change when we factor in these cultural influences? Although byproduct theory offers an effective cognitive approach, it fails to adequately address this question because it does not attend to religion's social and cultural evolution. Fortunately, this oversight is rectified by functional theories that more effectively address social and cultural processes in explaining how religious traditions and institutions change over time. We turn next to the functionalist theories, starting with individual-level adaptation theory.

Individual-level Adaptation Theory

Supporters of this theory hypothesize that religiousness enhanced the fitness of individual ancestors and still enhances individual fitness today. In their attempt to answer questions regarding religion's ostensible functionality, many proponents of this theory have stressed religion's role in promoting cooperation and altruism, traits that have been shown to be individually adaptive by Hamilton's kin-selection equation and Trivers' reciprocal altruism theory (Hamilton, 1964; Trivers, 1971). Individual-level theorists often argue that religion was specifically an *adaptation* to increase cooperative and altruistic behavior between non-kin. Essentially, individuals displaying higher levels of religiousness gain the benefits of reciprocal support from other religious individuals (Dennett, 2006). If these benefits were significant enough, and the fitness costs associated with religiousness were low enough, then selection pressures would have favored religiousness. According to these theorists, evidence that the majority of individuals alive today are religious, or at least self-identify as religious, supports this hypothesis. Recently, several research programs have arisen that are seeking empirical support for this theory. Individual-level adaptation theory helps highlight potential selective pressures that may have contributed to religion's social and cultural evolution. This helps address questions left unanswered by byproduct theory.

This functional approach can be taken in many different directions. Many religious theorists examine specific aspects of religion and subject them to a functional analysis. For example, anthropologist Richard Sosis (2004) developed a costly signaling theory of religious rituals based on studying many different religious groups, including Jewish kibbutzim in Israel. Sosis proposes that religious rituals often effectively display an individual's religious devotion and fitness, which increases his or her within-group status and reproductive opportunities. Likewise, this behavior can indirectly provide individual benefits to everyone in the group, as group solidarity tends to increase with higher levels of costly signaling behavior. Using this type of functional analysis, particular religious traditions and institutions can be examined from an individual-level perspective.

Jainism, a tradition that emerged in India around the same time as Buddhism, can serve as an example. Traditionally, Jains have occupied a distinguished position within the Indian economy as successful jewel traders. The ascetic values of Jainism are incredibly strict. The most devoted followers, called renouncers, often wear masks to filter the air they breathe, have extremely strict diets, are homeless, and travel completely naked. “Some even accomplish the ultimate ascetic act of fasting themselves to death” (Wilson, 2005, p. 436). However, Jain renouncers “constitute a tiny fraction of the Jain religion.” In reality, most lay Jains are impressively wealthy and follow a different set of doctrinally approved and more functional behaviors (p. 440). Fasting rituals are important aspects of their community, yet a lay Jain would rarely die as a result. Wilson notes that “fasting in young women demonstrates mastery over their appetites and increases their marriage prospects,” while “men compete for the privilege of supporting community activities.” Essentially, “the more extreme these demonstrations of religious devotion, the more they are publicized and raise the status of the family” (p. 438). Increased marriage prospects and higher family status would most likely entail a boost to individual reproductive success within this community. This example illustrates one of many modern manifestations of religion’s individual-level functionality.

According to individual-level theorists, the beneficial effects of religiousness have been documented elsewhere as well. Recent studies have outlined correlations between religiousness and higher happiness, sociability, community involvement, lower anxiety, less emotional distress, and generally enhanced individual health (Jacobs-Pilipski, Winzelberg, Wilfley, Bryson, & Taylor, 2005; King, Welch, Nazroo, Blizard, & the EMPIRIC team, 2006; Kirby, Coleman, & Daley, 2004; Maselko & Kubzansky, 2006; Saroglou, Pichon, Trompette, Verschueren, & Dernelle, 2005; Wink & Scott, 2005). Some scholars question the efficacy of this correlational research when applied to evolutionary theorization (e.g. Tooby & Cosmides, 1990), as current correlations with fitness do not necessarily reveal longer term, past selective pressures. Instead (according to this critique) the appropriate role for evolutionary explanations is to explain why a feature exists in the first place (Buss, et al., 1998, p. 540; Symons, 1992; Tooby & Cosmides, 1990).

According to individual-level theorists, these correlational data *do* reflect religion’s function and *do* reveal past selective pressures. They believe the dispute will be resolved in the near future through an expansion of more *evolutionarily based* research programs such as the interdisciplinary Evolution of Religion project (2009). The researchers in this program are collaborating to experimentally test the hypothesis that religious beliefs and behaviors offer effective solutions to important evolutionary problems and confer adaptive advantage to the individuals involved.

Although often seen as incompatible, the functional approach can also be viewed as supplementing byproduct theory. Essentially, even though religion has *functionality*, it need not be an *adaptation* per se. Byproduct theory effectively addresses religion’s evolutionary and cognitive origins. The functional approach can provide insight into how byproducts that were originally generated by the interaction of nonreligious adaptations may be co-opted to serve new adaptive functions, even if they were initially nonfunctional. The next theory we address adds another layer of

complexity to this model, addressing questions regarding religion's potential functionality "for the good of group" (Wilson & Wilson, 2008).

Multi-level Selection Theory (MLST)

In their quest to answer questions regarding religion's functional purpose, multi-level selection theorists, led by David Sloan Wilson (2002, 2005, 2007), hypothesize that religion is primarily a group-level adaptation that promotes social cooperation and cohesion and thereby benefits social groups in comparison to other less cooperative social groups. In fact, many past attempts to support individual-level adaptation theory can be viewed as supporting group-level adaptations (Wilson, 2002, 2005). For instance, individual-level researchers in the Evolution of Religion project (2009) have, in the past, attempted to address religion's group-level components from an individual-level perspective. Their findings have generally supported the hypothesis that religion is adaptive at the group level by helping groups in "overcoming collective action problems, promoting cooperation, suppressing within-group conflict, and surviving inter-group competition" (para. 2). Religion, by definition, entails group-level components, making it an inherently social phenomenon. In many cases, this social phenomenon appears to serve group-level functions. MLST offers a viable explanation for how this group-level functionality can emerge when selection between groups based on group-benefiting social and cultural features outweighs individual-level selection within groups.

Multi-level theorists conceptualize human groups such as religious congregations as group organisms that function in competition with other group organisms. When applied to religion, MLST posits that selection can take place at the individual *and* group level because cultural evolution operates differently than genetic evolution in human groups. Cultural information can quickly and easily infiltrate an entire group organism relative to genetic mutations. Indeed, this theory places heavy emphasis on the power of learning, development, and culture in influencing human behavior. When included in this field's theoretical integration, MLST helps illuminate the group-level selective pressures partially responsible for religion's co-opted functionality.

In *Darwin's Cathedral: Evolution, Religion, and the Nature of Society* (2002), Wilson uses several extended examples to argue that religion specifically functions to unify social groups and solve problems encountered at the group level. He sees Calvinism, for example, as a group-level reaction to perceived injustices of the Catholic Church and the resulting civil unrest in sixteenth-century Geneva. The Calvinist Church successfully resolved some of the problems specific to that environment. A system of checks and balances among the clergy, a strong belief in predetermination, and a belief in a personal relationship with God for each follower helped eliminate corruption, comfort the lower classes, and rebuild the social order that had dissolved under Catholic rule. From this perspective, religious systems socially evolve on short timescales via between-group competition. Systems that effectively display secular utility, that address and resolve group-level conflicts, and that promote individual and group fitness are thus socially selected and retained until inevitable environmental changes provoke another social movement.

Wilson (2002) argues that cultural factors have greatly altered humans' evolutionary landscape, making group-level selection more feasible in explaining complex social phenomena. Although many evolutionary biologists reject the idea of group selection based on logical errors in the original formulation by Wynne-Edwards (1962), the new conception embedded in MLST deserves a thorough reexamination given new developments in the evolutionary sciences (Wilson & Wilson, 2008; see also Pigliucci, 2009). In fact, MLST has applications in biological evolutionary processes as well as cultural ones, as exemplified by Herron and Michod's (2008) analysis of the evolution of single celled organisms into multicellular algae colonies.

According to Wilson, religious systems function at a higher level than other socially unifying features of culture in producing prominent beliefs in sacred things. He recognizes supernaturalism and beliefs in 'the sacred' as natural supportive forces that developed to better implement moral order and group solidarity. For this purpose, Wilson (2005) expounds an idea of individual-level proximate mechanisms. He argues that these mechanisms ultimately motivate adaptive behaviors for the group. For instance, individual meditative practices elicit group-level benefits by building cooperative dispositions within practitioners despite their emphasis on introspection and mental isolation. Wilson argues that these practices, and the religions that support them, require a functionalist approach because they exhibit clear adaptive benefits for groups. In fact, he asserts that all otherworldly beliefs motivate practical behaviors that provide these benefits. One detailed example he provides is Jainism.

Wilson (2005) believes that a functional analysis of Jainism supports this group-level hypothesis. As touched on before, Jain rituals among lay followers provide individual fitness enhancements. However, the institution of Jainism also has features specifically designed for group-level functions, such as enforcement mechanisms that maintain the system of inequity between Jain renouncers and the Jain laity as well as between the in-group and the out-group. In addition, Jain rituals, which display the intense spiritual devotion of group members, increase group solidarity. Moral standards within the group are paramount and members of the out-group receive differential treatment, further reinforcing group unity. Jainism appears to provide individual *and* group-level benefits to its lay followers, while many of its dogmatic prescriptions are particularly functional for the group as a whole. Thus, Wilson argues that this example provides support for MLST.

Many evolutionists have criticized this approach as disregarding religion's individual-level components and cognitive foundations. Boyer (2001) argues that the need for social cohesion and morality cannot be isolated as the root cause of religiousness or the creation of institutions. Rather, anthropologists and psychologists have discovered that, *by nature*, humans are social creatures with social intelligence. The study of this more fundamental social mind can "show us why people have particular expectations about social life and morality and how these expectations are connected to their supernatural concepts" (p. 27). Other nonfunctionalists view Wilson's theory as "mind-blind" (Atran, 2002) as it ignores the possibility that religious tendencies can be reduced to more fundamental, naturally selected social cognitive mechanisms.

These criticisms of the MLST approach to religion are less problematic if MLST is seen as supplemental to the nonfunctional account. Essentially, MLST adds another layer of complexity by effectively addressing questions concerning religion's apparent functional design. From a broader, more integrated perspective, nonfunctional and functional accounts can be viewed as complementing one another to form a more comprehensive account that addresses both the evolutionary and cognitive origins of religion *and* the selective pressures that have shaped religion's apparent functionality. The final step in this integration incorporates concepts from the dysfunctional perspective, which addresses those features and effects of religion (such as the celibacy requirement of Shakerism) that are maladaptive.

Meme Theory

Meme theory explains both the rapid transmission of religious concepts and the persistence of maladaptive religious features. A *meme* is an "element of culture that may be considered to be passed on by non-genetic means, especially imitation" (Atran, 2001, p. 3). In *The Selfish Gene*, Richard Dawkins (1976) used a gene-meme analogy to help explain the evolution of cultural phenomena problematic to selfish gene theory. This analogy not only shows similarities between genes and memes but also outlines key differences. While the selfish gene perspective views bodies as the vehicles for genes, the *memetic* perspective views minds as the vehicles for memes (Atran, 2001). Memes can survive and replicate vertically *and* horizontally in a lineage. For example, the religious ritual of circumcision travels vertically from parent to child but memes can also travel horizontally from an unrelated individual to another via the dissemination of ideas. Memes are "selfish," just like genes or parasites: they need not confer any benefits to their hosts. Meme theory conceptualizes one potential system of cultural transmission underlying the fast propagation of religious concepts, and also helps explain how and why maladaptive features of religion can persist despite evolutionary costs to individual and group fitness.

A reexamination of Jainism can help clarify these ideas. Meme theorists interpret Jainism as a memplex (i.e. a group of memes or meme complex) that entails specific dogmatic prescriptions. In extreme cases, the memplex might kill a devout follower (a Jain renouncer). Yet Jainism can replicate *horizontally* via the spread of interest in Jainism even if some followers die. Among the Jain laity, followers who have a less "virulent" devotion to the sect can pass on this memplex vertically from generation to generation within their tight community *and* horizontally to new members or converts. Although Jainism may seem to be based on irrational concepts and behaviors, its followers receive benefits such as economic security and a supportive community. They may also endure costs as the Jain community remains a small minority in India, which limits reproduction opportunities for followers. The costs are worst for the most devout members, the renouncers. According to meme theory, Jainism, as a memplex, competes with other memes and memplexes for survival. As long as it does not directly kill most of its "hosts" before it is transmitted, it will survive. The beneficial aspects of Jainism help this memplex "fit" within the minds of group members. Its costly aspects persist

because it is designed via a memetic evolutionary process that is relatively independent of individual and group fitness.

Of course, memes are not autonomous agents per se. The language used simply helps illuminate the argument. Some theorists (e.g. Dawkins, 2006) appear to believe that many or most religious memeplexes entail an ultimate evolutionary cost. However, memes and memeplexes can also be neutral or beneficial for their host. For example, early Christians vowed to care for sick members of the in-group during the plague. This commitment helped ensure the survival of both Christians and the Christian faith (the memeplex) in a hostile environment. Some meme theorists have offered an interpretation of religious memes that accommodates this sort of mutually beneficial result.

Daniel Dennett (2006), for example, distinguishes between wild memes and domesticated memes, and uses the analogy of the dairy cow to illustrate the latter. Reliance on humans has been functional for the dairy cow, ensuring its survival and reproductive success. Its human stewards, for their part, have artificially selected dairy cows to serve their human caretakers. Religious memes, Dennett argues, evolved in this manner. Wild memes, or the religious thoughts and concepts of folk religions, originate within the confines of our cognitive structure and then evolve based on their relative success at being transmitted both vertically and horizontally. As these wild memes become domesticated, they are shaped and designed by humans to provide benefits for individuals and groups.

Psychologist Donald Campbell (1975) offered a somewhat less cynical account. He argued that religious traditions often promote beneficial cognition and behavior. Campbell stressed that religious systems culturally evolve via between-*meme* competition.³ Religious memes that infiltrate groups compete, and the traditions that have the best chances of survival within human cultures are those that are functional for their followers. From this perspective, the most successful memeplexes live in harmony with their hosts, providing benefits for followers.

Memetics in general has remained largely theoretical, and has yet to garner much empirical support (Aunger, 2000, 2002). Some scientists have called it “pseudoscientific dogma” (Benitez-Bribiesca, 2001, p. 29). Others view it as a valuable framework to help conceptualize cultural information, but note a lack of evidence for treating these units as replicators (Atran, 1998). These criticisms need to be addressed if memetics is to progress as a scientific field. Aunger (2000) suggests that the meme may occupy a metaphorical position similar to that of Darwin’s original units of inheritance in the nineteenth century or genes in the twentieth century, before these units were empirically discovered. Meme theory’s primary conceptual utility may be as an impetus to continue grappling with the challenges of studying cultural evolution and transmission. Although the conceptions of memes and memeplexes as either cultural parasites or domesticated tools of social engineering may ultimately prove to be unsatisfactory, meme theorists have highlighted critical research questions about religion’s cultural transmission and

³ ‘Meme’ as noted before is Dawkins’s term. Campbell developed his theory around the same time that Dawkins wrote *The Selfish Gene*, and would not have used this specific word. For the purposes of this discussion, however, it is conceptually useful for Campbell’s argument.

persistence and developed a conceptualization of culture that can help explain both adaptive and maladaptive religious phenomena. These are useful conceptual tools that more complex evolutionary models of religion can incorporate into their toolbox.

Anachronism Theory

Anachronism theorists, who focus on religion's modern dysfunctionality, have pointed out a fascinating phenomenon: on short historical timescales, environmental and social changes can dramatically alter the utility of religious beliefs, behaviors, practices, and traditions. In essence, what was beneficial about a particular feature of religion yesterday may be costly today, and vice-versa. The disparity between ancestral and modern contexts (see Badcock, 2000; De Waal, 2002) plays a key role in this approach to evolutionary theory. Essentially, adaptations to ancestral environments do not necessarily have the same effects on fitness in novel environments. Examples of this phenomenon include the human sweet tooth. Humans living in hunter-gatherer tribes when food was scarce developed a significant, instinctual desire for high-caloric foods. Unfortunately, this ancestral adaptation has led to maladaptive behavior in modern fast-food environments (Buss, et al., 1998; Wilson & Green, 2007). Similarly, religion can be viewed as an ancestral adaptation that has become modernly maladaptive, making it an evolutionary anachronism. Like memetics, anachronism theory adds to our understanding of the cultural evolution of religious systems and explains how religion can become dysfunctional.

For example, some cultural psychologists have proposed that religion is an anachronism based on a human propensity for warfare (Kitayama & Cohen, 2007). This war hypothesis posits that religion was adaptive in an environment defined by between-group conflict. Recent evidence has shown that inter-group conflict could have played a critical role in human evolution (Keeley, 1997; LeBlanc 1999). Although mostly theoretical at this point, the war hypothesis highlights the critical role that short-timescale environmental changes, such as the shift from tribal societies to massive technologically advanced nations, can play in determining religion's beneficial or costly impact on individual and group fitness.

As already noted, studies have also found correlations between religiousness and psychological well-being and physical health (e.g. Kirby, Coleman & Daley, 2004; Maselko & Kubzansky, 2006). Some theorists argue that these benefits would have increased individual survival and reproductive success in ancestral contexts by reducing anxiety and distress, promoting cooperative behavior, increasing group solidarity, and increasing success during group conflicts (Kitayama & Cohen, 2007).

As evidence for a rapid change in functionality, anachronism theorists offer many examples of currently dysfunctional religious traditions. For instance, in an environment without modern food preservation technology, but with growing populations and expansive trade networks, certain foods become dangerous carriers of disease. Under these historical conditions, many religions developed doctrinal prescriptions to avoid certain foods (e.g. pork). Boyer & Bergstrom (2008) note that certain cognitive capacities define the way "religious institutions are built, work, and perpetuate themselves" (p. 123). In this case, fears of contagion and

pathogen avoidance mechanisms *guided* doctrinal modifications that were *instigated* by selective pressures in the social and cultural evolutionary process. Many food avoidance traditions that are still maintained are anachronistic and unnecessary given modern preservation techniques and could be maladaptive in food scarce environments.

In this way, aspects of anachronism theory can add some additional complexity to evolutionary models of religion by building on concepts of religion's dysfunctionality. In sum, the dysfunctional perspective, including meme and anachronism theory, helps answer questions left unanswered by nonfunctional and functional theorists. They effectively address how religious phenomena are socially and culturally transmitted and how maladaptive features of religion may arise and persist despite their dysfunction. While meme theory explains religion's dysfunction in terms of between-meme competition that is relatively independent of individual and group fitness, anachronism theory highlights how short-timescale environmental changes can render initially adaptive features maladaptive. By incorporating aspects of each theory into a complex evolutionary model, evolutionists can enrich their ability to address multiple research questions using a broadened perspective. We close the paper by briefly sketching out what a more integrated model might look like.

THE INTEGRATED MODEL

An integrated synthesis of nonfunctional, functional, and dysfunctional perspectives on religion would be beneficial for several interrelated reasons. First, they address different questions regarding the evolution of religion and religious systems: What are the evolutionary origins of religion's cognitive components? What adaptive functions does religion serve and how did it evolve to serve these functions? How are religious concepts transmitted and maintained, and why do maladaptive features persist? In their attempt to answer different questions, evolutionists from each perspective have developed different theoretical accounts and conclusions. Incompatibilities between theories arise when they offer conflicting conclusions regarding the *same* research question. An integrated model would incorporate all three sets of questions by incorporating the five complementary theories into a comprehensive account.

Second, each perspective emphasizes a different aspect of religion's evolutionary development. The nonfunctional perspective emphasizes the influence of cognitive dispositions, innate mechanisms, and genetics. Functional explanations emphasize the power of learning, development, and culture in influencing human behaviors. The dysfunctional perspective focuses on how short-timescale cultural transmission and environmental change can influence the evolution of cultural features. Evolutionary theory as a whole has progressed beyond disputes over which component requires more emphasis. In reality, each piece is critical to evolutionary explanations. In fact, the evolutionary sciences are currently undergoing a paradigm shift, called the "Extended Synthesis," partially based on the transition to more complex models (see Pigliucci, 2009). Recent evidence suggests that there are "four, not just one, systems of inheritance that affect the evolution of

biological organisms: the standard genetic one, an epigenetic component, a behavioral one, and a symbolic one” (Jablonka and Lamb, 2005; Pigliucci, 2009, p. 223). The “epigenetic component” refers to inherited changes in phenotypes caused by mechanisms other than changes to the underlying DNA sequence. It remains unclear what role epigenetics plays in the evolution of religious systems. The “behavioral” and “symbolic” components, on the other hand, denote imitative behavior and symbolic transmission that seem extremely influential in the process. According to the ES perspective, scientists should incorporate all four systems of inheritance into evolutionary models to effectively explain complex phenomena like religion.

Synthesizing the five strands of evolutionary theorizing about religion would take the first step in this direction by integrating non-genetic systems with genetic ones. First, byproduct theory evolutionarily explains the genetic inheritance of cognitive mechanisms underlying religion. Second, individual-level adaptation theory outlines selection pressures that may add design to the byproducts of these mechanisms. Third, MLST factors in the rapid behavioral and symbolic inheritance within groups that may also functionally design these byproducts at the group-level. This occurs when between-group selection pressures outweigh pressures within the group due to cultural uniformity and identification with a tradition or institution. Fourth, meme theory adds to the model by offering a useful conceptualization of how this behavioral and symbolic inheritance might occur. In fact, according to Wilson (2007) memes may form the social physiology of the human group organism. Meme theory also helps explain how memetic evolution may result in the persistence of religion’s maladaptive features. And fifth, anachronism theory accounts for another way that the complex inheritance of religious systems can lead to maladaptive outcomes. When synthesized, these theories complement one another to build a complex model that accounts for non-genetic systems that, according to the Extended Synthesis, should be included in evolutionary analyses.

An integrated perspective is based on a previously refuted hypothesis that we believe merits reexamination: the *exaptation* or *co-opted byproduct*⁴ hypothesis of religion. Stephen Jay Gould (1991) first proposed this hypothesis nearly twenty years ago. It was, for the most part, rejected seven years later because it did not meet certain standards of evidence (Buss, et al., 1998). It now offers a viable alternative to purely nonfunctional, functional, and dysfunctional accounts. Buss and colleagues faulted Gould’s arguments as failing to adequately specify “(a) the original adaptations or byproducts that were co-opted to produce religion; (b) the causal mechanism responsible for the co-opting;” and (c) “the manner in which

⁴ An *exaptation* is a “feature that now enhances fitness, but was not built by natural selection for its current role” (Gould, 1991, p. 47). Buss, et al., (1998) make the necessary distinction between two types of exaptations: co-opted adaptations and co-opted byproducts. In the former, the mechanism being co-opted for a new function was an adaptation and selection is required to explain the original adaptation being co-opted (e.g. fish fins, adapted for swimming, being exapted for walking on land). In the latter, the mechanism being co-opted was not an adaptation but rather an incidental byproduct of an adaptation (e.g. reading, a byproduct of many adaptive mechanisms in the brain, being exapted for many functional purposes).

religion contributes to the solution of an adaptive problem of survival or reproduction” (p. 542). Over the past decade, however, evolutionary research and theorization has built up evidence where it was previously lacking. Byproduct theory helps specify (a) “the original adaptations or byproducts,” while individual-level adaptation theory, multi-level selection theory, and memetics help outline (b) “the causal mechanism” and (c) religion’s exapted function. Meme and anachronism theory also help explain how this exapted function can rapidly change, even becoming maladaptive, given memetic evolution and novel environments.

A useful analogy helps illustrate the idea of a co-opted byproduct. Religion may have developed more like a closet underneath a staircase: a separate system with separate functionality, despite its origins in the structure and function of the staircase itself. The structure of the staircase incidentally creates a byproduct (the space under the stairs) that can be adapted for functional purposes (e.g. a storage closet). Essentially, the underlying structure is co-opted to solve problems for which it was not initially designed. Imagine human psychology and all of its functional components (i.e. psychological mechanisms, cognitive adaptations, etc.) as the staircase. This staircase is built out of many individual boards that form its steps and allow humans to solve a variety of cognitive and social problems. Each represents one of these functional components which combine to form a functional apparatus: the staircase. The triangular space underneath the staircase emerges as an unintended creation that lacks design and function. This represents religion as an incidental byproduct.

However, this incidental creation can be transformed into something functional, such as a closet. This closet can serve many purposes and be used by individuals and by groups, perhaps an entire family. Similarly, religion can evolve to serve the needs of individuals and those of an entire social group, society, or civilization. Evolutionarily, the closet endures because *the staircase* serves adaptive functions. Yet closets also serve functions and can be socially and culturally shaped and developed. The structural requirements of a particular closet as dictated by the architecture of the staircase can also determine how, and within what limits, it functions. Thus, the closet is subject to the constraints of its architectural features. In religion’s case, these limits represent the constraints established by the human cognitive niche. Over time the closet’s function changes based on individual and group level pressures, but only within these constraints. If the closet compromises the staircase’s integrity, the system collapses. In religion’s case, the demise of Shakerism exemplifies this phenomenon. Thus, although initially created as an incidental byproduct, the closet develops over time into a structurally constrained, socially designed, functional byproduct. Evolutionarily, this is commonly referred to as an exaptation or “co-opted byproduct” (Buss, et al., 1998; Gould, 1991).

Exiting the storage closet and returning to reality, we can tell an analogous evolutionary story. Byproduct theory offers a viable explanation for the evolutionary origins of the cognitive components of religion. Religious cognition incidentally results from the everyday functioning of nonreligious cognitive adaptations and interactions among these mechanisms and environments. The human cognitive niche predisposes us to form supernatural and religious ideations. Once humans generate religious byproducts, these byproducts propagate through systems of behavioral imitation and symbolic transmission. Meme theory helps conceptualize

these systems. These byproducts can be co-opted for many different individual and group-level benefits, including better reproductive opportunities for group members and increased group solidarity and success in inter-group conflict. Individual-level adaptation and multi-level selection theories help evolutionarily explain this co-opting process. As societies and environments change on short timescales, maladaptive outcomes can result as certain functions become anachronistic and detrimental to evolutionary fitness.

A reevaluation of Jainism can once again help elucidate many of these points. Jainism, just like all other religions, is innately a byproduct of functional cognitive capacities interacting with each other and environments. However, Jainism also displays co-opted functionality and exapted design. For example, Jain renunciators publicly display their devotion and transmit this memplex horizontally to potential converts. Different dogmatic prescriptions for Jain laity demonstrate this memplex's development in the group. Jain rituals appear to promote the fitness of individual group members through costly signaling behaviors. They have also helped form a unified, tight-knit community in which each devoted member is treated like kin. These beneficial outcomes have contributed to the group's longevity and economic success relative to other religious groups in India.

Thus, a multitude of interrelated cognitive byproducts that make up religious systems are co-opted for individual, group, *and* meme-level functionality through a process of *multi-level social and cultural selection*. Following this logic, we have theoretically addressed each of the requirements to explain religion as a co-opted byproduct. First, nonfunctional research offers evidence for a wide range of cognitive adaptations that interact to create religion. Second, the multi-level social and cultural selection of religion works as the causal mechanism responsible for the co-opting of the religious byproducts generated by these adaptations. And third, a multi-level analysis and complex evolutionary model, which incorporates selective pressures at the individual, group, and memetic levels along with non-genetic systems of inheritance, demonstrates that religion fulfills a multitude of exapted functions.

Of course, this is just a brief sketch of how the theories might be integrated, anchored on the idea of a co-opted byproduct exaptation. The main purpose of the illustration is not to offer a full-fledged synthesis, but to suggest the value of integration as opposed to denouncing different approaches and promoting one's preferred model on the grounds that it is addressing a set of problems the others ignore. With the emergence of the Extended Synthesis in evolutionary theory, evolutionists have the tools to broaden their perspective and to synthesize the leading theories of religion as well. Energy currently being expended on intramural disputes could be focused instead on empirically investigating the multiple evolutionary processes at work in the complex and multifaceted phenomenon of religion.

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