Religion as an Evolutionary Byproduct: A Critique of the Standard Model
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ABSTRACT
The dominant view in the cognitive science of religion (the ‘Standard Model’) is that religious belief and behaviour are not adaptive traits but rather incidental byproducts of the cognitive architecture of mind. Because evidence for the Standard Model is inconclusive, the case for it depends crucially on its alleged methodological superiority to selectionist alternatives. However, we show that the Standard Model has both methodological and evidential disadvantages when compared with selectionist alternatives. We also consider a pluralistic approach, which holds that religion or various aspects of religion originated as byproducts of evolved cognitive structures but were subsequently co-opted for adaptive purposes. We argue that when properly formulated, the pluralistic approach also has certain advantages over the Standard Model.

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1 Religion as Evolutionary Explanandum
Religious belief and behaviour (collectively ‘religion’) are puzzling phenomena for evolutionary theorists, due to the combination of three key factors. First, religion is ubiquitous in human societies (Brown [1991]; Harris and McNamara [2008]), and has been so for tens of thousands of years.
Second, although religious traditions vary considerably, they exhibit striking parallels. Specifically, two recurrent themes emerge in cross-cultural studies of religion. One relates to representations of supernatural agents associated with rituals, artefacts, moral norms, and social identities (Boyer [2000]; Atran [2002]; Boyer and Bergstrom [2008]). The other concerns the structure of ritual (McCauley and Lawson [2002]; Whitehouse [2004]), shamanism, and other religious practices that exhibit remarkable similarities across disparate cultures and which appear to have common neuropsychological underpinnings (Winkelman [2000]; McClenon [2002]).

The result is a religious ‘morphological landscape’ that is vanishingly unlikely to result from stochastic processes alone (i.e. from many unrelated, complexly configured causes), and is therefore indicative of a common functional or structural cause. In contrast to the inertial dynamics of Newtonian physical systems, biological and cultural systems will tend to drift away from equilibrium or a pre-existing trajectory unless acted upon by a net evolutionary force (Brandon [2006]). It follows that the repeated clustering of religious morphology is the product of either selection or some pervasive structural–developmental constraint. Selectionist explanations and structural–developmental constraint explanations are both evolutionary explanations, in that they each purport to describe the mechanisms responsible for the non-random distribution of traits in a population over generational time. They differ, however, in offering competing causal accounts as to why there is not more variation in a given trait than we in fact observe.

Third, religious phenotypes are often extremely costly for individuals (in terms of the resources required to maintain them) without conferring any straightforward ecological benefit (Irons [2001]), and hence they are not readily amenable to conventional selectionist explanations. Acceptance of a religion typically involves commitment to a package of beliefs, norms, and rituals that is preserved and transmitted at great cost to its adherents and to no obvious fitness-enhancing end (Henrich [2009]; Sosis [2009]).

Cognitive scientists of religion often refer to ‘minimally counterintuitive agents’ to describe postulated beings that would be described more casually as ‘supernatural’. Although religions vary widely in the supernatural beings they posit, a common feature is that they involve properties that breach intuitive expectations for how entities in a particular ontological domain will behave: examples include a talking tree, a thinking mountain, or a person that floats through walls (Boyer and Ramble [2001]).

An alternative explanation of the recurrent similarities between different religious traditions is grounded in the assertion that they have a common historical cause (i.e. they are descended from a single common cultural ancestor). However, spatiotemporally disparate religions appear to be the result of rediscovery and reiteration, rather than diffusion from a single cultural ancestor (Winkelman [2000]). Even if all religions did have a common ancestor, some evolutionary force (such as selection or constraint) would still be needed in order to explain the maintenance of the original form for thousands of generations, particularly given the error-proneness of cultural transmission (see Section 5.2).
Whereas many aspects of human culture are clearly functional, such as tools, shelters, supermarkets, traffic lights, jobs, laws, etc., religion serves no similarly obvious utility. Taken together, the spatiotemporal ubiquity, recurrent morphology, and apparently maladaptive nature of religion cry out for evolutionary explanation.

Despite the predominance of selectionist explanations in the biological sciences, most scholars working in the cognitive science of religion reject selectionist explanations in favour of a structural constraints-based account of the evolution of religion. The now dominant view is that religion is an incidental byproduct of domain-specific cognitive adaptations that underwrite and constrain the universe of religious representations and their associated behaviours. According to Bering ‘[…] all but a handful of scholars in this area regard religion as an accidental byproduct of our mental evolution’ ([2011], p. 6). Evidence for the byproduct theory of religion is inconclusive (Richerson and Newson [2009]). Nevertheless, many of its proponents seem convinced that a byproduct theory is strongly preferable to any selectionist alternative, even while remaining evidentially uncommitted to any particular byproduct account (e.g. Dawkins [2006], pp. 179–90). The case for preferring the byproduct approach depends crucially on its alleged methodological, rather than evidential, superiority to adaptationist alternatives. In this article, we examine the methodological and empirical commitments of the standard byproduct account of the evolution of religion, and consider whether it is superior to selectionist alternatives. We will argue that it is not.

2 The Standard Model of the Origin and Evolution of Religion

Durkheim ([1965/1912], p. 62) famously argued that religious systems have the function of binding individuals into moral communities, although he did not couch his theory in evolutionary terms. Since then researchers have proposed numerous selectionist explanations of religion, although none has garnered broad-based support. Contemporary scholars in the cognitive science of religion tend to reject the selectionist approach, converging instead

3 It may surprise some readers to hear that Dawkins is an advocate of a byproduct account of religion given that he is a well-known advocate of memetics and that in The Selfish Gene he appears to endorse a memetic approach to explaining religion ([1976], pp. 198–9). Dawkins explicitly advocates a byproduct account in The God Delusion, with memetics relegated to shaping the details of particular religions ([2006], p. 190).

4 Hypotheses regarding the function of religion include the role it is alleged to play in strengthening social cohesion (Sosis and Bressler [2003]), forming a moral community (Graham and Haidt [2010]; Wilson [2002]), encouraging altruism and indirect reciprocity by serving as a badge of group membership (Sosis [2005]), enforcing social norms and suppressing free riding (Bering et al. [2005]; Norenzayan and Shariff [2008]; Atran and Henrich [2010]), attracting suitable mates (Slone [2007]), and producing reliable signals of cooperative intent (Bulbulia [2004]; Henrich [2009]).
on a strictly non-functional account of the evolution of religion, one that has become known in the field as the ‘Standard Model’ (‘SM’) (Boyer [2005]). The SM aims to describe the religious practices and representations that predominate in most oral societies, and which exist spontaneously in literate cultures that are otherwise characterized by ‘doctrinal’ modes of religiosity.

According to the SM, religion is not an adaptive mechanism ‘designed’ for generating religious representations and their associated behaviours, but rather an evolutionary side effect of various cognitive adaptations such as those responsible for agency detection, theory of mind, folk ontology, and other domain-specific conceptual architectures that have well-understood functions outside of the religious domain. The SM purports to deliver a ‘deflationary’ evolutionary explanation of religion (Boyer [2005]; Boyer and Bergstrom [2008]), in the sense that it takes religion to be wholly parasitic on other functional structures that would be present even if religion did not exist. According to many proponents of the SM (e.g. Boyer [2001]; Atran [2002]; Atran and Norenzayan [2004]), the structural byproduct description is superior to selectionist explanations because it allows researchers to account for the ubiquity of recurrent religious morphology, while avoiding the perceived methodological pitfalls associated with the use of functional explanation in the social and biological sciences.

A complete evolutionary explanation of religion, as with any phenotypic trait, must describe not only the proximate cognitive-developmental mechanisms that generate religious representations and behaviours during the human lifetime, but also the evolutionary causes of the differential propagation of the mechanisms described in the proximate explanation (Mayr [1993]). If the SM endeavours to provide a reasonably complete evolutionary explanation of religion, it must do more than simply cite the relevant proximate mechanisms. It must also link-up its structural byproduct hypothesis with a theory of cultural evolution, since religious phenotypes are not generally understood as being genetically transmitted or pre-specified (but see Section 5.1). This allows the SM to account for the repeated independent origination of similar

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5 The term ‘Standard Model’ was coined, as far as we can tell, by Boyer ([2005]), who uses it to refer to a growing body of work in the cognitive science of religion, including (inter alia): (Boyer [2001], [2000]; Atran [2002]; McCauley and Lawson [2002]; Atran and Norenzayan [2004]; Barrett [2004], [2000]; Kirkpatrick [2006]; Bloom [2009]).

6 Whitehouse ([2004], pp. 65–70) states that religion in the ‘doctrinal mode’ refers to post-Neolithic forms of religion that contain a standard centralized creed that is policed for orthodoxy by authoritative leaders, involve large inclusive communities, and are characterized by repetitious rituals with low levels of arousal.

7 According to the SM, religion is a spill-over of some subset of discrete (local or distributed) neocortical systems associated with (e.g.) agency detection, theory of mind, pattern recognition, memory, moral judgement, intuitive ontology, social exchange, contamination and contagion avoidance, coalition formation, childhood gullibility, attachment, and dualism.
religious phenotypes, their effortless acquisition within the human lifetime, and their persistence across generations.

Many proponents of the SM rely heavily on Sperber’s ([1996]) ‘epidemiological’ account of cultural transmission, which explains the differential proliferation of cultural variants in terms of their tendency to resist distortion given their relative ‘psychological fitness’ (Boyer [2001]; Whitehouse [2004]). According to the SM, religious phenotypes proliferate and withstand degradation over time, not because of their utility to or the fitness benefits they confer on individuals who acquire them, but because human cognition is highly specialized and not neutral with respect to acquiring, retaining, and transmitting cultural representations. The differential proliferation of religious variants can be explained by the degree to which they comport with human psychological biases (Boyer [2005], p. 4; Whitehouse [2004], p. 146), including their mnemonic and inference-generating properties and the ways in which they figure in folk reasoning, intuition, and perception (Boyer and Ramble [2001]). These pervasive psychological biases act as structural–developmental constraints, or ‘canalizing agents’, that create attractors in the cultural evolutionary landscape (Atran [2002], p. 248). Taken together, the compartmentalized architecture of the human mind and the ‘psychological properties’ of religious variants are purported to explain why religious phenotypes remain ubiquitous at the population level despite their significant costs to fitness.

3 Elaborating on the Standard Model: Modules and Spandrels

Proponents of the SM cite ‘massive modularity’ theorists, such as Sperber ([1996]) and Cosmides and Tooby ([1994]), in arguing that the comparative success of religious variants is determined by their psychological properties which enable them to spread between ‘brains with massively similar conceptual architectures, composed of functionally distinct capacities specialized in different types of objects and problems’ (Boyer [2005], p. 5). SM theorists tend to avoid using the term ‘module’ in their description of the relevant proximate cognitive mechanisms, perhaps hoping to evade criticisms that have beleaguered traditional modularity theories. Despite the proliferation of module constructs in cognitive science, there are few if any uncontroversial examples of ‘Darwinian cognitive modules’, or highly specialized units of mind produced by natural selection (Fodor [2001], chapters 4–5; Machery [2007], p. 827; Robbins [2010]).

For example, Boyer ([2001]) argues that the minimally counterintuitive agency embodied in supernatural concepts constitutes a memory optimum. He offers preliminary evidence to suggest that minimally counterintuitive entities are psychologically salient because they violate some intuitive expectations that otherwise hold true over a folk ontological domain.
Modularity has been the subject of intense debate in cognitive science and the philosophy of mind ever since the publication of Fodor’s ([1983]) classic work. Almost all modularity theorists, Fodor included ([2001]), have backed away from the highly specified structures that Fodor originally envisaged: namely, cognitive processes that are fast, automatic, cognitively impenetrable, informationally encapsulated, and domain specific. In particular, modern modularity theorists have weakened the requirements that modules must be informationally encapsulated and domain specific (Barrett and Kurzbar, [2006], pp. 631–2). Given the broad range of modularity theories that are currently available, it is not entirely clear what commitments advocates of the SM make when drawing on contemporary massive modularity theorists. At the very least, though, commitment to modularity involves a commitment to specialized, isolable subsystems that are fast, opaque to introspection, insulated in significant ways from central or higher level processing, and optimized by natural selection for a given function. Advocates of the SM need not be committed to modularity as a thesis about the overall structure of the human mind. For the SM to succeed, only those cognitive processes specified in the proximate byproduct explanation of religion must be module-like (see footnote 7 for a list of popular candidates).

As discussed above, the SM interprets costly religious phenotypes as the straightforwardly maladaptive consequence of cognitive biases imposed by the modular (or module-like) architecture of mind. These cognitive biases are thought to be the result of evolutionary constraints on the optimization of cognitive function—in particular, the ineluctable trade-off between accuracy and generality in the fashioning of complex cognitive adaptations. It is not possible in practice for natural selection to produce a cognitive mechanism that is general enough to solve a wide range of ecological problems, such as the detection of predators, prey, mates and conspecifics, and accurate enough to avoid potentially maladaptive outcomes, such as mistaking rustling leaves for the presence of one of the former.

Moreover, some degree of cognitive error is not only evolutionarily tolerable, but also ecologically desirable. Consider the supposed ‘module’ responsible for detecting agents in the environment (which we will return to in greater detail in Section 4). Cognitive functions that maximize the accuracy of agency attribution are not optimal from the standpoint of natural selection, given the asymmetrical fitness costs associated with two types of attribution error: false negatives (e.g. failure to detect a predator or prey when it is present) and false positives (e.g. erroneous detection of a predator or prey when it is absent). False positives may result in an unnecessary expenditure of time and energy or lost opportunity costs, but the consequences of false negatives can be much more severe, as they can result in death or grievous bodily injury. As early hominins co-evolved with large cats, bears, and other megascopic predators,
including and especially other hominins, and since they relied heavily on hunting to meet their protein intake requirements, it was advantageous to have a device that overattributed agency and avoided false negatives, even at the cost of allowing more false positives (Barrett [2000]). In real-time ecological scenarios, where fight-or-flight decisions need to be made and executed rapidly on the basis of input from these detection systems, extremely high levels of accuracy, which can only be achieved by increasing the cognitive-behavioural resources that are devoted to perception, can be fitness-reducing particularly when the costs of false negatives are so high. As a result, cognitive faculties that produced representations that approximated the world to an ecologically sufficient degree were generally more adaptive than those that aimed to get it exactly right all of the time (Perlman [2002]).

Consistent with the evolutionary trade-off scenario described above, byproduct theorists hold that religion is produced by the ‘misfire’ of various error-prone cognitive structures (e.g. Guthrie [1993]). On this view, religion is a reliable effect, but not a selected effect, of the normal operation of other cognitive components. In other words, it is a ‘spandrel’ (sensu Gould and Lewontin [1979]), or a structurally constrained side effect, of the functional architecture of mind. Before discussing evolutionary spandrels, it is helpful to clarify the more fundamental notion of adaptation. ‘Adaptation’ refers to the fit between an organism and its environment due to the cumulative operation of natural selection. To say that trait $T$ of organism $O$ is an adaptation, is to be committed to the causal-aetiological claim that $T$ has proliferated under cumulative selection because of its tendency to produce a certain effect—its ‘function’—which increased the chances that $O$’s ancestors would survive and reproduce. The fact that $T$ has an aetiological function does not imply that $T$ is currently contributing to the reproductive success of $O$. Assessments of aetiological function are entirely retrospective judgements regarding the $a$ $posteriori$ probability of selection: to say that $T$ is an adaptation is to say nothing about its present contribution to fitness or its current causal capacities (Brandon and Rausher [1996]). Thus, even if religion is largely maladaptive in the modern selective environment, this does not rule out the possibility that it is an adaptation.

Of course, not all organismic traits are adaptations. In a seminal paper, Stephen Jay Gould and Richard Lewontin ([1979]) critiqued what they viewed as the tendency of evolutionists to assume that all biological traits are optimized by natural selection for a given function. They introduced the term spandrel into the evolutionary lexicon to refer to the non-adaptive consequences of ontologically prior structural adaptations. In the architectural realm, spandrels refer to the roughly triangular spaces unavoidably created by resting a dome on top of contiguous arches. Gould and Lewontin argued that, analogously, many biological characters arose as structural byproducts of

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other adaptive features. The term spandrel has since been broadened to refer to all incidental side effects of other adaptations, whether properly structural or not.

Although spandrels are non-functional in their origin, they may nonetheless be co-opted for a functional role. In order to avoid confusion regarding the possibility of functional spandrels, following Buss et al. ([1998]) we will speak instead of ‘byproducts,’ or features that play no role in functional design although they may be causally associated with traits that do. Unlike the functional properties of adaptations, the intrinsic properties of byproducts are not causes of their population-level success. The fact that oxygen-carrying blood cells are red or that vertebrate bones are white are both properties of light diffraction which play no role in the oxygen transport and rigidity functions of these respective materials, and hence are incidental to, rather than a cause of, their evolutionary proliferation.

To hold that \( T \) is a byproduct of adaptation \( A \) in organism \( O \), is to say that \( T \) is an effect of \( A \), but not one that is causally related to the differential reproduction of \( O \). While there is a positive statistical relationship between the presence of \( T \) and the differential reproductive success of \( O \), this relationship is not directly causal, but rather grounded in a common cause—namely, \( A \). To assert that \( T \) is an evolutionary byproduct of \( A \) is to be committed to a causal-aetiological story regarding the origins and proliferation of \( A \), a causal-mechanical account of the link between \( A \) and \( T \), and the proposition that \( T \) has never subsequently contributed in any significant way to the survival and reproduction of \( O \).

This is a considerable evidentiary burden to shoulder. In order to persuade us to accept it, advocates of the SM rely on the crucial claim that the byproduct approach has certain methodological advantages over competing selectionist explanations. In the next section we consider whether the SM does in fact enjoy the methodological advantages that some of its proponents suppose. In the final section we consider (inter alia) the potential advantages of a pluralistic approach that draws upon the SM, but relaxes the latter’s restriction on the contributions of religious byproducts to fitness.

### 4 A Methodological Comparison of Functional and Byproduct Explanation

It may be surprising to some that the SM has become dominant in the cognitive science of religion, given that the adaptationist explanatory alternatives

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9 More precisely, to establish that \( T \) is a functionless byproduct of adaptation \( A \), we need to show (1) that \( A \) and \( T \) covary because \( T \) is the direct causal consequence of \( A \), and (2) that manipulations in the value of \( T \), while holding other effects of \( A \) constant, have no statistical bearing on the differential reproduction of \( O \).
that its proponents eschew are so influential elsewhere, and given that there are often said to be methodological reasons for preferring adaptationist to non-adaptationist alternatives. In an influential paper, Godfrey-Smith analyses various types of adaptationism and identifies a specifically methodological variant, which involves endorsing the following policy recommendation: ‘the best way for scientists to approach biological systems is to look for features of adaptation and good design. Adaptation is a good “organising concept” for evolutionary research’ ([2001], p. 337).

Godfrey-Smith interprets Gould and Lewontin’s ‘Spandrels’ paper ([1979]) as offering important challenges to methodological adaptationism. Gould and Lewontin argue that because evolutionary theorists who adopt methodological adaptationism are overly focussed on the search for adaptive explanations of individual traits, they are liable to commit three sorts of error. First, they are liable to fail to distinguish the current utility of traits from the reason that traits have originated. Secondly, they are liable to rely on plausibility alone as a criterion of explanatory acceptability, and in so doing become advocates of speculative ‘just so stories’; and thirdly, they are liable to fail to consider explanations that appeal to factors other than adaptation. While Godfrey-Smith reads Gould and Lewontin simply as critics of methodological adaptationism, Lewens ([2009], p. 161) argues that the ‘Spandrels Paper’ points towards a genuinely non-adaptationist methodology, one which involves prioritizing the search for ‘explanations of form in terms of broad structural constraints on the development of the whole, integrated organism’ (p. 173).

Many proponents of the SM hold that there are methodological grounds for favouring byproduct explanations over adaptationist alternatives, and their reasoning is broadly parallel to Gould and Lewontin’s case against adaptationism. However, this parallel is somewhat obscured because SM theorists typically direct their criticisms at ‘functionalism’ in the social sciences, rather than adaptationism in the biological sciences (e.g. Sperber [1996], pp. 47–9; Boyer [2001], pp. 28–31). Functionalism was a methodological approach that was particularly influential in the social sciences before the 1960s, and which involved the programmatic explanation of the existence and persistence of social institutions by appeal to the current function of those institutions (Boyer [2001], p. 29).

Some common criticisms of functionalism are not criticisms of the use of functional explanation per se, but of other commitments that functionalists are alleged to make. For example, Boyer criticizes functionalists for implicitly assuming that every social institution has a function ([2001], p. 29), and Sperber ([1996], p. 48) and Needham ([1972]) criticize functionalists for failing to identify and employ systematic typologies of social-functional kinds. Functionalists also stand accused of close correlates of the failings that Gould and Lewontin ([1979]) ascribe to adaptationists. They are criticized
for confusing the explanatory task of accounting for the current utility of social institutions with the task of accounting for the emergence of those institutions (Little [1991], p. 92); they are criticized for advocating speculative just so stories instead of warranted explanations (Sperber [1996], p. 47; Boyer [2001], p. 29); they are criticized for ignoring important aspects of societies that have no clear function and for advancing ad hoc functional explanations, rather than considering non-functional explanations of cultural institutions (Boyer [2001], p. 29).

Our target is not the SM’s criticisms of functionalism per se, but the specific methodological criticisms of adaptationist alternatives to the SM that are bound up with it. The criticism that functionalists implicitly assume that every social institution has a function and that functionalists fail to identify and employ systematic typologies of social-functional kinds are not methodological problems for users of functional explanation in general, so they do not apply to adaptationists who employ functional explanations without subscribing to functionalism. The three lines of criticism that correlate with Gould and Lewontin’s criticisms of adaptationism do need to be considered carefully. However, two of these do not seem to apply or are of low relevance in the context of debates about the evolution of religion. One is the charge that adaptationists are liable to confuse current utility with reasons for origin. Scholars working in this area are usually very careful to stress that the ‘imaginistic’ religious practices of preliterate societies that are relevant to explaining the origins of religion have social and ecological effects that are very different from those associated with contemporary ‘doctrinal’ religions (Whitehouse [2004]). Similarly, the charge that scholars working in the cognitive science of religion are liable to fail to consider alternatives to adaptationist explanations is not apropos here, given that the dominant evolutionary approach to religion appeals heavily to structural–developmental constraints.

The one significant criticism of users of functional explanation that can clearly be detached from broader criticisms of functionalism and which is relevant here is that these users are alleged to be peculiarly liable to advocate speculative ‘just so’ stories instead of warranted explanations. Functional explanations can be warranted, but in many cases social scientists, evolutionary psychologists, and some ‘adaptationists’ in the biological sciences have been content to identify particular uses that an entity or trait happens to have and then proceed as if they have identified the functions that have caused those particular entities or traits to come into being and proliferate. Gould and Lewontin express this criticism in the context of the biological sciences as follows:

Often, evolutionists use consistency with natural selection as the sole criterion and consider their work done when they concoct a plausible
story. But plausible stories can always be told. The key to historical research lies in devising criteria to identify proper explanations among the substantial set of plausible pathways to any modern result ([1979], p. 588).

A just so story is a speculative ‘how possibly’ explanation and the mistake that we are liable to make is to presume that it has higher evidential standing than is warranted. The most egregious form of this mistake is to assume that a just so story has the status of a well-formed instance of inference to the best explanation, a form of inference that is considered legitimate across the various sciences and which can warrant truth claims (Psillos [1999]; Lipton [2004]).

The charge that many actual applications of functional explanation in the social sciences, in evolutionary psychology, and in the biological sciences are not warranted is well taken, but this is not a charge that is properly directed against all uses of functional explanation. We should not conclude from this observation that functional explanations cannot be warranted, or that scientists are unable to determine when particular functional explanations are warranted. The problem of determining when particular functional explanations are warranted should be no more difficult to solve than the problem of determining when other similarly complicated causal explanations are warranted.

If the evidential standards that we insist on before accepting functional explanations are the general standards of evidence in science, then these same standards should be applied to byproduct explanations (cf. Sosis [2009], p. 325). Do byproduct explanations in the cognitive science of religion need to face up to a version of the just so charge levelled so often against attempted functional explanations? We will argue that byproduct explanations must face two (closely related) forms of the just so charge. To develop this argument we will offer general conceptual considerations as well as criticisms of a well-known byproduct explanation of religion. However, our claim is a methodological one. We are not arguing that proponents of religious byproduct explanations can have no effective response to our criticisms.

10 According to some critics of the use of functional explanation in the social sciences, the key to overcoming the just so problem is to identify the mechanisms by which the postulated beneficial effects of functional traits ensured that those traits were reproduced (Little [1998], pp. 6–7). While the identification of such mechanisms can help overcome the just so problem, it should be obvious, given the persistence of the just so problem in the biological sciences (where natural selection serves as a generic mechanism for the origin and proliferation of functions), that the identification of a mechanism does not guarantee that a functional explanation will overcome the just so problem. Moreover, if the postulated mechanism of reproduction is speculative, and there are different possible mechanisms available that might be invoked to underpin a particular functional explanation, then we have created an additional just so problem at the level of mechanism rather than dealt with the just so problem that we set out to solve (cf. Steel [2005], p. 947).

11 For more on the relationship between just so stories and inference to the best explanation see (Holcomb [1996]).
Our point is that, like others who face the just so charge, they need to provide a response.

Religious byproducts, if there are such things, are the byproducts of functional cognitive structures. Because explanations that involve religious byproducts also involve appeals to functional cognitive structures, they necessarily entail appeals to functions, and so they are necessarily vulnerable to the just so charge as are all explanations that involve appeals to functions. Religious byproduct explanations are also vulnerable to the just so charge in virtue of the fact that they appeal to the existence of modules or module-like cognitive structures and such appeals may be ad hoc. The just so charge can apply to appeals to the existence of structures and the putative constraints imposed by those structures as much as it can to appeals to functions—a much neglected point that has been made by Williams ([1985], p. 20) (see also Lewens [2009], pp. 174–5).

The degree to which byproduct explanations are susceptible to the just so charge depends on the epistemic standing of the functional structures that are appealed to in those byproduct explanations. If these are well established, then appeals to such structures can be defended from the just so charge. To determine how vulnerable standard cognitive science of religion explanations are to the just so charge, we need to know more about the status of the underlying science of cognition that they rely upon.

As we noted earlier, advocates of the SM are committed to the existence of cognitive modules or module-like structures. But modularity theses are controversial in the cognitive sciences, and hence it is difficult to see how the just so charge could be evaded by advocates of the SM. If it could be evaded, it would be in virtue of the fact that the case for the existence of particular modules was warranted by well-formed uses of inference to the best explanation. But if this were the case, then we would expect that massive modularly, or some other modularity thesis, would have come to predominate in cognitive science and this has not happened. Many critics of modularity theories currently concede that there is evidence for modularity in a few components of the mind, such as language and perception (Samuels [1998], p. 576). Others, however, question whether even these aspects of cognition are genuinely modular (e.g. Churchland [1988]; Prinz [2006]).

But suppose that a modularity theory came to predominate in cognitive science on the basis of reliable evidence. Would that render byproduct explanations in the cognitive science of religion invulnerable to the just so charge? Not in and of itself. If we only know that the mind is significantly modular, but do not have a precise catalogue of the particular modules contained therein, then appeals to particular possible modules are ad hoc. Consider Justin Barrett’s influential Hypersensitive Agency Detection Device (HADD) hypothesis ([2004], pp. 31–44). Barrett makes a plausible case for the
conclusion that having a HADD would be evolutionarily advantageous for us. But establishing that it would have been evolutionarily advantageous for us to have a HADD is a far cry from establishing that a HADD has actually evolved and that it is disposed to cause religious byproducts, even if we are able to establish that the human mind is suited to containing modular structures like the HADD. One cannot reliably infer from a particular adaptive pattern of behaviour (such as hypersensitive agency detection) that there is a specific organ or cognitive mechanism ‘designed’ by natural selection to produce that behaviour (cf. Lloyd [1999]).

As we have seen, advocates of the SM are not better off than proponents of selectionist explanations when it comes to addressing the just so charge. We will now show that proponents of the SM are actually worse off (methodologically speaking) than advocates of traditional functional explanations because they incur two additional explanatory burdens. Both of these result from the complexity of byproduct explanations in comparison to simpler selectionist alternatives. The first of these explanatory burdens is that of demonstrating the causal ontogenetic relation between a mental module and its religious byproduct (see (1) in footnote 9). It is easy to claim that a particular aspect of religious belief or behaviour is the product of a postulated mental module, but it is another thing to demonstrate an actual causal relationship. Suppose we can establish that the HADD exists. We know that people are disposed to believe in supernatural agents, and it might seem simple enough to attribute such beliefs to the activity of the HADD; but without making a credible case for the conclusion that the operation of the HADD actually causes people to believe in supernatural agents, we are not entitled to this inference. Indeed, the lack of evidence for the role of a specialized HADD in generating religious phenotypes is acknowledged by Barrett and some of his recent collaborators (Knight et al. [unpublished]).

To establish that the HADD causes belief in supernatural agents, we need an explanation of how and why we come to attribute supernatural rather than natural agency. We also need an explanation of how and why people continue to believe in the existence of supernatural agents. The HADD hypothesis may explain why we tend to infer agency when we hear rustling in the grass, but it does not account for belief in the ongoing existence of the agents that we (mis)attribute. In cases of ordinary agency, we are able to correct our initial attributions: we hear rustling in the grass and turn around expecting to be met

12 The actual evidence that Barrett ([2004]) and Knight et al. ([unpublished]) provide does not seem to go beyond that of the persistent tendency of people to attribute causality and animacy to geometric shapes on screens, as reviewed by Scholl and Tremoulet ([2000]). This is far removed from the claim that people’s brains contain a device that tends to overattribute agency in the real world and as a result throws off religious byproducts.
by an agent, but when we fail to see an agent and instead observe wind moving the grass around, we typically correct our initial overattribution (Barrett [2004], pp. 40–2). In contrast, it seems that attributions of supernatural agents are highly resilient and rarely corrected for. This is not a knockdown case against a HADD-based explanation of religion, as its proponents may be able to fill in the explanatory gaps that we have identified. But advocates of byproduct explanations need to do the work required to demonstrate a credible causal connection between a module and its putative byproduct. This is not a task that proponents of simpler selectionist explanations need to undertake.

The second problem for those who appeal to byproduct explanations of religion is that we are owed an explanation of why religious byproducts continue to exist over generational time, despite the fact that, by the lights of the SM, they make no causal contribution to fitness and in fact will often be fitness-reducing. If there were no barriers to humans evolving cognitive mechanisms that could function without also creating religious byproducts, which are ex hypothesi costly (in evolutionary terms) to maintain, then one would expect that evolution would select for cognitive mechanisms that did not create religious byproducts. In some cases it is easy to see why byproducts are not selected against. Architectural spandrels are the byproducts of placing contiguous arches under a dome. They are geometric features that are necessary to this structural arrangement and cannot be eliminated. Belief in supernatural agents, in contrast, may be a byproduct of the operation of the HADD and other modules, but it is not obviously a structurally constrained by-product: that is to say, it is not evident why selection would be unable to produce a functioning HADD that did not misfire so as to lead to persistent belief in supernatural agents. The same reasoning applies to participation in onerous religious rituals, fear of supernatural retribution, and the like.

If the HADD could be incrementally modified (or reliably overridden) in such a way that it produced an overattribution of belief in natural agents but not in supernatural agents—and this seems plausible enough, given the degree

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13 How might one go about finding evidence for this causal connection? One possibility would be to test whether the degree of agency detection sensitivity (appropriately operationalized) correlates with strength of belief in supernatural agents. If the HADD causes belief in supernatural agents then, all things being equal, a particularly active HADD should cause more belief in supernatural agents than a less active one. Another possibility is to look for ways in which deficits in the function of the HADD might limit the types of supernatural agency attributed. For example, an individual with an impaired HADD might be disposed to attribute supernatural agency to discrete entities such as rivers and trees but not to omniscient supernatural agents that are present in many or all locations, such as the Judeo-Christian God. In a similar vein, Whitehouse suggests that theory of mind (ToM) deficits associated with autism may lead to a reduced propensity among autistics to attribute forms of supernatural agency that make greater demands on ToM, such as spirit possession which involves tracking two mental entities: a possessing spirit and a host ([2008], pp. 38–9).
of informational flexibility in the underlying cognitive processes—then it is hard to see why selection wouldn’t have produced such an outcome, assuming it was fitness-enhancing. Given their commitment to the maladaptive character of religion, the employer of standard byproduct explanations owes us an account as to why evolution has not done away with, or at least minimized the influence of, the byproduct being appealed to. This might be done by demonstrating that the byproduct is somehow structurally tied to the module that generates it, as spandrels are to arches under a dome, or it might be done by showing that once a particular byproduct was created, there was no mutationally feasible evolutionary pathway to eliminating it. Our point is not that this cannot be done, but that it is work that needs to be done. The defender of byproduct explanations has once again incurred an explanatory debt that needs to be paid off, one that does not burden the proponent of more straightforward selectionist explanations.

5 Selectionist Alternatives to the Standard Model

The discussion thus far has glossed over an important aspect of the adaptation-byproduct debate, namely the level-specific nature of adaptation. Adaptations are traits that evolve through the cumulative operation of natural selection, and evolution by natural selection is possible (but never guaranteed due to ever-present stochasticity) whenever there is heritable variation among members of a reproducing population that is causally related to the expected differential survival and reproduction of its members. In theory, adaptation can occur at any level of biological organization, including genes, cells, organisms, groups, colonies, cultures, and clades, provided that the conditions for natural selection obtain (cf. Lewontin [1970]).

As Dennett cautions ([2006], p. 56), in claiming that a trait is an adaptation we should be careful to ask ‘cui bono?’ A trait may be maladaptive (or neutral) at one level of selection, and fitness-enhancing at another. For example, representations of supernatural agents may be highly fit at the level of cultural variants themselves (due to their mnemonic and inferential properties), but maladaptive from the organismic perspective when viewed as part of the extended phenotype. When authors claim that religion is adaptive, they are asserting that religion has propagated due to its history of fitness-enhancing effects relative to non-religious evolutionary units at a particular level of organization. Meme theorists, such as Blackmore ([1999]) and Dennett ([2006]), tend to emphasize antagonistic co-evolutionary interactions between levels of selection, especially between the organism and the invisible particulars of genetic and cultural inheritance. Dennett for instance views religion as a cultural parasite that proliferates at the direct evolutionary expense of individuals and groups—much as the ‘zombifying’ lancet fluke hijacks the
neurological and motor functions of ants, placing its stricken host in a position exquisitely tailored to further its parasitic life cycle ([2006], pp. 3–4).

SM theorists have generally preferred epidemiological accounts of cultural evolution to ‘memetic’ ones because of the deep theoretical difficulties associated with memetics. These include the problem of individuating memes and the fact that these do not (usually) replicate digitally. Cultural representations are transformed and intelligently manipulated during acquisition, and they are amalgamated from disparate social sources. As a result, they typically fail to form discernable lineages in the way that genes do (Sperber [1996]; Atran [2002]). In this article, we focus on individual and group-level selectionist explanations of religion and set aside problematic memetic approaches. We will look in particular at three lines of selectionist research and consider whether these offer any evidential advantages over the SM. These are: (i) that religion is an adaptation with a genetic basis; (ii) that religion is a non-genetic adaptation of cultural groups, and (iii) that religion arose as a byproduct à la the SM and was subsequently co-opted for adaptive functions (which we will call the ‘pluralist’ view).

5.1 Religion as an adaptation with a genetic basis

Several researchers argue that religion is a genetically mediated adaptation of individuals or groups (e.g. Johnson and Bering [2006]; Harris and McNamara [2008]; Wilson et al. [2008]; Haidt [forthcoming]). This claim is based on evidence that religion is spatiotemporally universal and/or cross-culturally robust, that it emerges relatively early in ontogeny, and that it is pleasurable in its own right—all supposed hallmarks of genetic adaptation. However, because there is little direct evidence that religiosity is a genetically mediated disposition, selectionist explanations of religion are often dismissed (e.g. Kirkpatrick [2006]; Pinker [2006]). We will argue below that the process of adaptation need not be tied to genetic transmission. But first we will address a theoretical criticism commonly levelled at the gene-based adaptationist approach to religion: that given the relatively recent origins of religion, there has not been enough time for natural selection to generate the complex suite of genetic traits that comprise religion and drive them to fixation in human populations. This conclusion is based on long-standing assumptions about the tempo of human evolution that have been called into question by the recent explosion of genome-wide association studies purporting to identify positive selection in human populations since the agricultural revolution (Vallender and Lahn [2004]). As we noted earlier, religion has been around for tens of millennia, presenting a sufficient timeframe for genetic adaptation, even on conservative estimates. Even if genetic dispositions towards religion did not become adaptive until the formation of larger post-Neolithic human
groups, as Shariff et al. ([2010]) contend, this may still provide sufficient time for genetic selection.14

Advocates of the genetic adaptation hypothesis need not insist that religion was generated de novo via genetic mutation, as is often presupposed. Paralleling Baldwinian accounts of the evolution of deep grammar structure, they can maintain that religious dispositions were initially learned but became increasingly genetically assimilated over time, making religious dispositions easier to acquire. This may have happened through the proliferation of genes associated with ‘promiscuous teleology’ and other cognitive biases that facilitate acculturation to religion (for a similar suggestion, see Bering and Johnson [2005]). The possibility that religious dispositions were partially genetically assimilated in the process of gene-culture coevolution offers a potential rejoinder to criticisms of the genetic adaptation approach that rely on the prevalence of atheism and other environmentally induced variation in religiosity to show that the genetic hypothesis is implausible (e.g. Shariff et al. [2010]). While we agree with the scholarly majority that the evidence for selection on genes associated with religiosity is not substantial, this possibility should not be dismissed on theoretical grounds.

5.2 Religion as an adaptation of cultural groups

Researchers sympathetic to selectionist explanations of religion are often motivated to explore genetic adaptation hypotheses because they are not convinced that cultural processes can produce Darwinian adaptations.15 This scepticism arises from the recognition of several key differences between biological and cultural evolution. In biological evolution, mutation is random with respect to adaptation, whereas in cultural evolution variation is generated by intentional actors and hence may be directed towards its anticipated effects. On most accounts of Darwinian evolution, directed variation does not in and of itself pose an obstacle to the creation of adaptations.

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14 Shariff et al. ([2010]) attack the genetic adaptation approach to religiosity, pointing to the absence in pre-literate religions of omniscient, moralizing high gods. They reason that since these features are only present in larger, post-Neolithic societies, and since ~10,000 years is not a sufficient window of time for selection to produce a complex genetic adaptation for religiosity, the genetic adaptation claim fails. This argument hinges on questionable conservative assumptions regarding rates of human genetic evolution (see main text). It also presumes that the socio-functional effects of moralizing high Gods are the only fitness-enhancing effects of religion, and thus it overlooks the effects of ritual (which has existed for ~40,000 years) on intra-group cohesion and cooperation. Moreover, while we recognize that the link between pre-literate religion and ordinary morality remains controversial (for a discussion see Winzeler [2008], p. 38), it may be significantly stronger and relatively more frequent than the sceptics of genetic adaptation allow (cf. Johnson and Bering [2006], p. 222).

15 This scepticism may underlie a methodological tension that arose in our earlier discussion of the SM: the willingness of its proponents to entertain selectionist stories regarding underlying cognitive modules (such as the HADD), while being reluctant to embrace non-genetic selectionist explanations of religion.
(Henrich et al. [2008]). But other features of cultural transmission are more problematic, rendering the products of cultural evolution at best loose approximations of paradigmatic Darwinian adaptations. If individuals deliberately filter cultural variants that are constructed from disparate information sources—in particular, from unrelated individuals of the same or preceding generation, resulting in non-vertical transmission—then the heritability of cultural traits is diminished (Godfrey-Smith [2009]).

Notwithstanding these complexities, there are good reasons to hold that cultural and adaptationist explanations are not mutually exclusive. Cumulative adaptation can be produced by any reliable mode of inheritance that transmits fitness-relevant variation. The key question is whether cultural transmission in humans is sufficiently reliable to allow for the accumulation of adaptive information. Over the past few decades, population-dynamic models of cultural evolution have provided quantitative support for the view that robust social learning in humans is a complex system of developmental resources with the meta-level function of carrying adaptive behavioural phenotypes across generations.16 Richerson and Boyd ([2005]) have shown how the significant noise and parasite threat associated with non-vertical, inference-modulated cultural transmission can be overcome through (inter alia) conformity and success biases, allowing for heritable, fitness-enhancing cultural variability at the population level.17 Evolution by natural selection does require a certain degree of heritability, but it does not require replicators in the high-fidelity Dawkinsian ([1976]) sense.18

16 Some have queried whether behaviours that arise from the complex interaction of cognitive mechanisms in the human brain are sufficiently isolatable or ‘mosaic’ to be malleable targets of selection (see Sterelny and Griffiths [1999], p. 321; for a critique of this view, see Driscoll [2004]). Sterelny and Griffiths argue that genetic changes that modify the mechanisms underlying specific complex behaviours will tend to have selectively prohibitive collateral consequences for other important aspects of the phenotype. Yet if we accept that high levels of phenotypic plasticity combined with a robust system of social learning can allow for the origin and reliable transmission of a wide range of adaptive behaviours, then the non-independence critique loses whatever force it might carry in the sociobiological realm. Genetic changes in underlying cognitive mechanisms are not necessary to produce behavioural adaptations, and non-genetic adaptations are not susceptible to the aforementioned critique.

17 It is critical for all theories of cultural evolution that cognitive biases modulate cultural acquisition and transmission, lest culture become completely decoupled from genetic evolution, eliminating the fitness benefits associated with this defining feature of Homo sapiens. Although both sociobiological views of culture and gene-culture co-evolutionary models view cultural evolution as to some degree reined in by a genetic leash (so to speak), the crucial difference between them is that the latter emphasize population-level statistical learning biases that channel cultural variation in adaptive directions, a division of labour between genes and culture in transmitting ecologically valuable information, and the mutual interaction of culture-shaped environments and genetic selection regimes.

18 The fact that cultural representations are not gene-like does not mean that they cannot be the stuff of cumulative adaptive evolution, especially when there are many cognitive attractors in the social learning landscape (Henrich et al. [2008]). A small number of very powerful psychological attractors in social learning would undermine cumulative adaptive cultural evolution, since cultural transmission must be sufficiently unconstrained for the gradual optimization of
In addition to the problem of identifying discernable lineages in non-vertical inheritance systems, the transmission of information between unrelated individuals entails a significant degree of altruistic behaviour, since teaching often involves the time-consuming provision of ecologically valuable informational resources (Sterelny [2006]). Institutionalized information sharing requires cooperative norms and other cultural scaffolds that are only likely to evolve through cultural group selection, as these are liable to be undermined by defectors at the individual level. Group selection theory initially fell out of favour after prominent theoretical and methodological critiques (especially Williams [1966]; Maynard Smith [1976]). Recently, however, the case for group selection has overcome the ‘possible in principle but insignificant in practice’ mantra which dominated selectionist thinking in the second half of the 20th century.

The debate was reinvigorated by Sober and Wilson ([1998]) who proposed ‘intrademic’ models of group selection which largely avoided the earlier critiques, since these do not require reproductively isolated, spatially discrete and/or long-lived groups that differentially give rise to daughter groups in organism-like fashion (for a detailed discussion, see Okasha [2009]). A recent review of multi-level selection theory by E.O. Wilson and D.S. Wilson ([2007]) has advanced group selection theory a step further, with the (former) pre-eminent defender of individual-level selectionist explanations, and the leading proponent of group selection, jointly proclaiming that ‘four decades of research since the 1960s have provided ample empirical evidence for group selection, in addition to its theoretical plausibility as a significant evolutionary force’ ([2007], p. 334). Wilson and Wilson defend the relative importance of interdemic group selection—that is, group selection proper, rather than the watered down version of Sober and Wilson—not only in eusocial insect but also human evolution. For interdemic group selection to occur, it is not necessary that between-group genetic variation be high, so long as there is substantial phenotypic plasticity in the traits exhibited by competing groups. In the human case, the effects of phenotypic plasticity on between-group variation are amplified by mechanisms of cumulative cultural transmission, which allow for the rapid spread of fitness-enhancing cultural variants within groups, thereby increasing the fitness-relevant phenotypic differences between them.

Cultural group selection is now a widely accepted explanation of many cultural phenomena, and probably critical for understanding the full extent of human prosociality and its origins (cf. Atran and Henrich [2010]; Sterelny [forthcoming]). Although social learning is quite unlike the exquisitely artefacts and behaviours to be possible. But as Driscoll ([2011]) points out, the epidemiological model of cultural evolution is not necessarily committed to this stronger claim.
accurate mechanisms of DNA replication, it does underwrite the origin, incremental improvement, and reliable transmission of complex, ecologically valuable phenotypes—the *sine qua non* of a Darwinian process. There are many clear-cut examples of non-genetic adaptations that increased the fitness of cultural groups, including the manufacture of fire (Wrangham [2009]) and the construction of sea-faring vessels (Richerson and Boyd [2005]), as well as the development of moral norms, military hierarchies, and sophisticated social exchange networks that were built gradually by ‘invisible hand’ mechanisms that are closely analogous to paradigmatic natural selection (Sterelny [2007]). Religion may be a less functionally obvious case than these, but there is nothing inherently problematic about it being an adaptation of cultural groups. One may quibble over whether culturally transmitted traits in the genus *Homo*, such as fire and hand axes, are adaptations in the traditional evolutionary theoretical sense of the term—but this semantic issue is not central to the debate that occupies us here. For in conceding that religion is akin to fire or tools in its historical utility to human individuals or groups, the SM theorist would effectively forfeit the crucial byproduct claim.

Many group-oriented adaptive hypotheses have been proposed to explain religion (see footnote 4 for a sampling), and it is reasonable to think that at least some of these were critical for the success of small hunter–gatherer groups, while others may have played an important role in the transition from kin groups into larger, more inclusive societies of reputationally anonymous, distantly related individuals organized under abstract social identities such as religion, nationality, and other badges of fictive kinship. The capacity of religion, through rituals and supernatural representations, to bind individuals into moral communities, increase group cohesion, encourage within-group altruism, and foster inter-group hostility is likely to have enhanced phenotypic variation among groups and hence to have affected their comparative performance and survival.

Evidence has been mounting in favour of these adaptationist hypotheses, with a range of studies directly or indirectly linking religion with reproductive fitness. Religious societies have been shown to out-persist (Wilson [2002]; Sosis and Bressler [2003]), produce more individual offspring (due to reproductive norms and the link between religiosity and fertility) (Sanderson [2008]), and cooperate more effectively than comparable non-religious societies (Henrich *et al.* [2010]). Religious primes enhance prosocial tendencies in cooperative games (e.g. Shariff and Norenzayan [2007]), religiosity correlates strongly with adaptive assortative sociality (Fincher and Thornhill [forthcoming]), and ritual attendance is positively associated with self-sacrificial behaviour (Ginges *et al.* [2009]) and increased cooperativeness (Sosis and Ruffle [2003]) within groups. Larger, more complex and harder-to-police
societies are more likely to worship omniscient deities that are preoccupied with group morality and to punish norm violations harshly (Johnson [2005]). In our view, these findings add up to a *prima facie* case against one of the central propositions of the SM—namely, that religion has never contributed in any significant way to the survival and reproduction of human individuals or groups.

Two features of religion that advocates of the SM have a particularly difficult time explaining, and which cultural group selectionist explanations seem to account for much better, are (i) the close connection between religion and folk morality (see footnote 14), and (ii) the great personal consequenti- ality of religious belief. The first feature is demonstrated by cross-culturally robust representations of postulated supernatural entities that encourage norm following via threat of punishment in small-scale groups, and which are elaborated on in post-Neolithic societies to include ‘full-access’ supernatural agents who are concerned with mundane matters of group morality, coordinate group action, and enhance within-group altruism. Even cognitive scientists of religion who are sceptical of selectionist explanations tend to agree that religion plays an important role in defining social identity, facilitating indirect reciprocity, and enforcing moral norms (Atran [2002]; Boyer [2001]; Norenzayan and Shariff [2008]). As to the second feature, it is important to distinguish between the role of psychological properties in the spread of religious representations, and the powerful *motivations* that people have to preserve and transmit those beliefs (cf. Henrich [2009]). While the SM goes some way towards explaining the former (see discussion in Section 2), the enormous personal commitment individuals have to religion is a major explanandum left untouched by the SM.

We think that the ‘social-functional’ approach to religion, which dates back to Durkheim and has been significantly developed by (e.g.) Wilson ([2002]), Graham and Haidt ([2010]), and Haidt ([forthcoming]), offers a promising avenue for explaining the two features of religion discussed above. Religion can enhance in/out-group effects in a number of ways that go beyond the simple delineation of group boundaries. It can supply positive and negative incentives to cooperate with members of the in-group and to compete aggressively and self-sacrificially with members of the out-group. Religion also facilitates intra-group cooperation and coordination through the psychologically powerful effects of communal ritual, which lead to a convergence in mood, identity, mutual affection, and a sense of belonging in convening co-believers (Marshall [2002]). Similar psychological effects are produced by synchronic movements (Wiltermuth and Heath [2009]), rhythmic dance, and music (Atran and Henrich [2010])—all cultural universals that are strongly associated with religion, and which are likely to be fitness enhancing in the ecological competition between groups.
5.3 A pluralist view

The evolution of religion debate is often cast as a forced choice between byproduct and selectionist theories of religion, but this is a false dichotomy. It is incorrect to claim, as some byproduct theorists have done (e.g. Atran and Norenzayan [2004], p. 757), that to establish a selectionist account of religion, one must rule out the possibility that religion was produced as a byproduct of other features. To show that religion arose as a structural byproduct is not to show that religion is merely a byproduct—that is to say, it does not exclude the possibility that religion’s subsequent proliferation and preservation in human populations for tens of thousands of years was due to one or more of its effects. The byproduct origin hypothesis is thus entirely consistent with religion, or at least some aspects of it, having been ‘exapted’ (or subsequently co-opted by selection). Indeed, some authors now explicitly defend a byproduct origin account of religion but suggest that it subsequently proliferated at the population level in accordance with principles of selection (e.g. Atran and Henrich [2010]; Pyysäinen and Hauser [2010]).

To clarify the byproduct/exaptation distinction and its relation to selection, we will follow Godfrey-Smith ([2009]) in distinguishing ‘origin explanations’ from ‘distribution explanations’. Debates over the evolution of religion have tended to conflate these distinct categories of evolutionary explanation, and as a result they have been hampered by cross-purpose dialogue. Selection is not necessary for origin explanations, as simple mutations, novel combinations of genes, or structural/developmental processes can suffice to generate a given effect (although selection may be necessary to explain its distribution in a population over time). However, functionally complex structures call for selectionist explanations of their origins since, barring saltations, they can only arise after many rounds of selection on their various interrelated features and character dimensions.

Sanderson ([2008]) argues that religion exhibits a level of complexity that calls for selectionist explanation. As tempting as this conclusion may be, it is important to recognize that complex traits may arise as incidental structural byproducts of other complex functional arrangements, and hence that complex configuration should not be equated with adaptive configuration (Gould [1997]). This caveat is especially apropos in relation to the human mind which is likely to be bursting with intricate mental spandrels. Nevertheless, religious systems appear to incorporate too many developmentally orthogonal components (such as rituals, supernatural representations, social norms, etc.) in an ecologically relevant manner to be accounted for parsimoniously by a simple byproduct origin explanation. As Sosis puts it,

Systems that can do what the religious system does are extremely low-probability arrangements. By an unimaginably large margin, most
biologically possible arrangements cannot unite unrelated organisms under common purpose, achieve extraordinary self-sacrifice, and motivate large-scale cooperation and coordination. All of this suggests that the religious system is an adaptation. ([2009], pp. 328–239)

The crucial point is not that religion is a low-probability arrangement per se, but rather that very few complex structural configurations could realize the package of beneficial ecological effects that religion produces. A recurrent homeostatic cluster of orthogonal features that in combination produce important ecological effects is strongly indicative of functional complexity, which in turn is strongly indicative of selection. This is not to deny that important aspects of religious systems can be accounted for through byproduct origin explanations. Since religious representations and behaviours make use of, but are not fully explained by, more evolutionarily primitive cognitive pathways, such as agency detection, theory of mind, social exchange, coalitional psychology, folk ontology, language, memory, vision, and so forth, any successful adaptive explanation of religion is likely to involve co-optation of pre-existing functional elements. But even so, the religious phenotype per se could not be said to have arisen as a byproduct, if by religious phenotype we mean the individuated functional complex of cognitive and cultural components that are referred to in most definitions of religion. If religion is composed of a suite of co-opted byproducts that were gradually organized and improved over time through cumulative selection, then it looks less like an exaptation and more like an ordinary adaptation.

As we saw in Section 4, advocates of the SM assume the burden of explaining why a byproduct that systematically detracts from fitness has not been selected against. Because the pluralist does not insist that byproducts are never subsequently co-opted, she does not incur this explanatory burden. A pluralist approach to the evolution of religion can avail itself of explanatorily powerful selectionist hypotheses, while retaining elements of the byproduct origination story.\textsuperscript{19} The psychological biases on cultural transmission described by the SM could work synergistically with cultural group selection by channelling variation so as to make it more likely that certain fitness-enhancing forms of religion are arrived at independently and frequently—a pattern that is consistent with anthropological observation (e.g. Winkelman [2000]; McClendon [2002]) and parallels the ‘positive’ interaction between

\textsuperscript{19} Whether any successful component co-optation explanation is likely to advert to modular architecture, or rather to cognitive structures with a less restricted range of input, remains an open question. We see no clear theoretical advantage to postulating domain-specific cognitive adaptations as opposed to more general information-processing mechanisms that generate adaptive learned behaviours, particularly given the widely acknowledged ecological value of behavioural plasticity in the case of human beings (see Lloyd [1999] for a discussion). Indeed, an advantage of pluralist theories and of selectionist approaches in general is that they can remain agnostic to the causal structure of the underlying proximate mechanisms.
developmental constraints and selection in the evolution of animal form (Gould [2002], p. 84).

6 Conclusion

The SM does a reasonable job of identifying some of the proximate cognitive mechanisms that factor into the comparative fitness of religious phenotypes. It also makes a credible case for the functionless origin of certain components of religion. However, it does a poor job of explaining a wide range of religious phenomena, including the close connection between religion and morality, the great personal significance of religious beliefs, the effects of religious ritual on group dynamics, and the existence of robust social scaffolding necessary to ensure that complex religious traditions are reliably transmitted over generational time.

Defenders of the SM might be inclined to argue that even though the evidence in favour of the byproduct theory and against its selectionist competitors is far from telling, the SM has clear methodological advantages over adaptationist alternatives. However, we have shown that there is no reason to accept this claim. The SM actually suffers from methodological disadvantages in comparison to more straightforward selectionist explanations of religion and pluralistic alternatives. These methodological burdens could be overcome, given sufficient evidence of the existence of cognitive modules or module-like structures, sufficient evidence that these structures cause religious byproducts and cannot be modified so as to eliminate them, and sufficient evidence that religious byproducts have not been co-opted for functional purposes. However, such evidence is not currently available. In its absence there is no good reason to prefer the SM to selectionist or pluralistic alternatives.

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