

ADAPTING ADAPTATION

An Analysis of the Adaptation Discourse in the
Evolutionary Sciences of Religion

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NORWEGIAN ABSTRACT

Forskere som studerer religion i lys av evolusjon kan generelt deles i to skoler: En som ser religion som en evolusjonær adaptasjon (tilpasning), og en som ser det som et biprodukt av andre trekk. Denne oppgaven argumenterer for at konseptet adaptasjon er mer komplekst enn slik det har blitt presentert i religionsvitenskapen, og viser til temaer i den tilsvarende biologiske diskursen. Videre sammenlignes dette med debatten om religions adaptive status, og som følge av dette åpnes det for flere nye forskningsspørsmål. Spesielt anbefales det å studere evolusjonen av kultur i seg selv, og å legge mindre vekt på skillet mellom religion som adaptasjon og biprodukt. Avslutningsvis følger også en generell argumentasjon for en evolusjonær religionsvitenskap.

Stikkord: religion, adaptasjon, biprodukt, evolusjon

We are walking archives of ancestral wisdom. Our bodies and minds are live monuments to our forebears' rare successes. This Darwin has thought us. The human eye, the brain, our instincts, are legacies of natural selection's victories, embodiments of the cumulative experience of the past. And this biological inheritance has enabled us to build a new inheritance: a cultural ascent, the collective endowment of generations. Science is part of this legacy, and this book is about one of its foremost achievements: Darwinian theory itself.

—Helena Cronin, *The Ant and the Peacock*

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I

INTRODUCTION

Evolutionary approaches to the science of religion have in the past few decades started to re-emerge as a powerful paradigm and interdisciplinary field of research, although the taint of association to E. B. Tylor and J. G. Frazer's hierarchical cultural evolutionism still looms large. Far from suggesting a uniform movement from magic through religion to science, as Frazer had envisioned (Frazer 1900), evolutionary scientists of religion today generally appreciate the fact that evolution is a non-directional process. With the exception of the so-called 'new atheist' movement, operating on the fringes of the scientific study of religion (Geertz 2009), religion is no longer taken to be an intermediary stage on the way to scientific enlightenment, although the school of theorists claiming it to be a by-product of evolution might seem somewhat demeaning. And here lies some of the most interesting debate in the field: the question of whether or not religion is an evolutionary adaptation is arguably *the* question dividing scientists of this emerging paradigm. Very briefly, the question is whether religion has been produced by natural selection because it confers some or other kind of reproductive advantage (typically to genes), or if it is simply an accidental by-product of other traits. The present thesis purports to show that the discussion of adaptation concerning religion has not been sufficiently informed by the respective discussion in biology. In light of this, I will

attempt to re-analyse the arguments for and against religion as an adaptation, and see if some helpful insights can be gained through this.

To begin with, I will briefly present the current evolutionary science of religion, and then discuss the term adaptation itself. Chapter II presents issues related to adaptation as they appear in evolutionary biology, and Chapter III reviews the state of debate in the study of religion. Chapter IV will aspire to connect the dots between the two fields, before rounding off with my conclusions in Chapter V.

1.1: An Evolutionary Science of Religion

Darwin's realization that species evolve through natural selection stands today as one of the paramount discoveries of science, and not surprisingly, researchers in other fields were keen to incorporate his findings. Early forays proved far too simplistic, however, and the notion of religion as but an intermediary stage on the way to a scientific world view did not sit well with an increased awareness of the need for an emic perspective. Although simplistic, teleological models of evolution are unheard of and have been for a very long time, it would take almost a century for social and evolutionary sciences to cross paths again. Two important books were published in 1975: One was E. O. Wilson's *Sociobiology: The New Synthesis* (E. O. Wilson 1975), which marked the beginning of a new field studying social behaviour in light of evolution, and the other was Dan Sperber's *Rethinking Symbolism* (Sperber 1975), which foreshadowed the Cognitive Science of Religion (CSR), named after Stewart Guthrie's paper (Guthrie 1980). Sociobiology was a more general field, and its most important contribution to evolutionary sciences of religion seems to be in clearing the ground for new perspectives, such as evolutionary psychology. While sociobiology has been hailed as 'one of the scientific triumphs of the twentieth century' (Hagen 2005, 167), nothing much happened in CSR until the early 1990s, when a spate of books (Atran 1990; Lawson and McCauley 1990; Barkow, Cosmides, and Tooby 1992; Guthrie 1993; Boyer 1994) was published, launching the field in earnest.

Generally, these scientists advocate a move away from an understanding of the mind as an all-purpose problem solver, and rather view it as a patchwork formed by evolution gradually adding

purpose-specific modules. According to proponents of CSR, this combination of specialised subsystems prepares us for religion in several ways (Jensen 2009, 129). Already here there is a radical departure from more traditional ways of studying religion—in fact, it is not so much religion that is being studied as the mind itself (Jensen 2009; Saler 2008). Perhaps the most important claims concern so-called minimally counter-intuitive concepts (MCI, Boyer 2001) and hard-to-fake signalling (Irons 2001). MCI refers to what anthropologist Pascal Boyer claims is a cognitive optimum, that is, ‘a concept that is both attention-grabbing and that allows rich inferences’ (Boyer 2001, 86). By this he means that by slightly violating our expectations about how members of an ontological category (such as person, plant, or animal) should be, conceptions of gods and magical objects command our attention, so long as they are not so counter-intuitive that we cannot remember them. Hard-to-fake signals, on the other hand, expand on a concept well established in biology, namely costly signalling. The idea, very briefly, is that religious behaviour signals group commitment, which is assumed to be a requirement for cooperation to evolve in the face of possible exploitation by free riders, who do not contribute to the group. Limiting cooperation to those who display commitment to the group through extensive religious ritual is supposed to deter free riders, so that investments in the group is not squandered. This, too, is made possible by the way the brain works: faking commitment is hard, because merely going through the motions of religious ritual tend to make practitioners religious, and as such incorporate the group’s values of cooperation (Bulbulia 2008).

While CSR focuses on how biological evolution has prepared humans for religion, there is also a slowly increasing awareness that culture is as much capable of evolving as the biological substrate it depends on. Arguably, the most important work on this has been done on culture in general, rather than religion especially, but some traces can be found in studies of religion (D. S. Wilson 2002, 119; Boyer 2001, 273–287; Feierman 2009; Geertz 2010; 2011; Geertz and Markússon 2010; Jensen 2002). Cultural evolution is especially relevant when considering religion as an adaptation, as religion could turn out not to be a direct biological adaptation or by-product at all, but rather a cultural adaptation. I will argue that scholars studying religion need to pay more attention to cultural evolution. A note on terminology before we continue: I see the Cognitive Science of Religion as a subset of evolutionary approaches to studying religion. Some

theorists, perhaps more typically those who view religion as an adaptation, are rightly identified with evolutionary approaches, while not necessarily CSR. I will not pay much attention to the distinction here, as it is not at issue. Rather, I will speak generally of evolutionary approaches to (the study/science of) religion, unless the distinction is particularly relevant.

1.2: Adaptations

Though often equated with evolution, natural selection is not the only mechanism of evolutionary change. Three other prominent mechanisms are mutation, migration and drift (Freeman and Herron 2007, 141). Mutation is ‘the process by which genetic material undergoes a detectable and heritable structural change, or the result of such a change’ (Cammack 2006). As it pays no attention to evolved adaptations, is generally detrimental to fitness, although on average not by much (Freeman and Herron 2007, 151). Migration is ‘transfer of alleles from the gene pool of one population to the gene pool of another population’ (Freeman and Herron 2007, 225). Genetic drift is ‘irregular, random fluctuations in gene frequency in a (relatively) small population caused by statistical effects’ (Cammack 2006). In other words, it is the effect of random happenings on the gene pool, or more technically, sampling errors as a consequence of the gene pool being finite (Freeman and Herron 2007, 234). Genetic drift reduces variation and changes population gene frequencies from one generation to the next, and hence is an agent of evolution. In small populations, it can be a very significant agent, sometimes even overwhelming natural selection (Hedrick 2011, 187). The important lesson here is that neither drift, migration nor mutation correlate with performance; they will not favour a beneficial gene. Instead, only natural selection is capable of producing and refining adaptations (Of course, the very first stages of all adaptations are initially produced by mutation, but on the whole, mutation is not an adaptive process as most mutations are neutral or detrimental). Accordingly, a common definition is that a trait is an adaptation if it ‘performs a function that is of utility to the organisms possessing it and if the character evolved by natural selection for that particular function’ (Larson and Losos 1996). Note that functions are selected for utility in the first place, so

that this definition is really all about natural selection, but combining two elements: functionality and selective history.

Perhaps the concept of natural selection needs a bit of clarifying before we move on. Generally speaking, natural selection is the differential survival and reproduction of entities. I use ‘entities’ rather than the standard ‘alleles’ (genes competing for the same chromosomal slot) to allow for natural selection acting on more than just genes, such as cultural selection. Genes are not required for selection to work, but rather *variation, heredity* and *differential fitness* (Dennett 1995, 343). It is easy enough to understand what variation is, but an important point is that whatever variation exists must be linked to heredity and differential fitness. Heredity of course is the property of an entity to be able to pass its characteristics, largely intact, on to the next generation. Differential fitness means that the existing variation in characteristics is linked to performance, that is, some characteristics are better adapted to solve the problems posed by the environment. In other words, if a population of entities exhibit *heritable variation in fitness*, whether it might be a population of genes, groups, or elements of culture, the fittest entities will prosper at the expense of the least fit, and this is natural selection. However, the term ‘selection’ appears in several theoretical constructs, and it is perhaps necessary to point out that it is not used in the same way in all of these. The following list of four kinds of uses does not claim to be exhaustive, nor does it include all relevant subtypes. To begin with, there are concepts such as ‘artificial selection’ and ‘sexual selection.’ These are forms of natural selection, in that they speak of different selective regimes. Where in natural selection, nature sets the premise for what traits will be selected, these premises can also be artificial or sexual.¹ For example, in nature it might be advantageous to outrun a predator, whereas in artificial selection it is advantageous to outrun competing greyhounds, to be selected for breeding. Sexual selection will be treated in more detail below, but for now, it will suffice to say that it is a selective regime wherein mate choice determines which traits are fittest. Neither of these, of course, eliminate natural selection—sterility, for example, will always be selected against whatever the breeder or mate thinks about it.

¹ One might of course argue that artificial and sexual regimes are as much part of nature as anything else, but the terms provide clarity as the selective mechanisms are rather different.

Another use of ‘selection’ is in concepts such as ‘group selection’ and ‘cultural selection.’ Rather than specifying selective regimes, these terms are concerned with the *units of selection*. The term ‘natural selection’ does not specify this—most commonly, it is genes (or rather alleles), but as mentioned earlier, anything can in principle be selected; individuals, cells, groups, or cultural elements. Cultural and group selection are controversial processes, not in that the principle is in dispute, but in that they are often seen to be too weak to be of any significance (Williams 1966, 108; E. A. Lloyd 2007, 47). However, I aim to show that they are both viable (2.2 below), and that they may indeed play an important part in the evolution of religion (3.2, 3.4, 4.2, 4.4).

A third way to use selection is found in *patterns of selection*, such as ‘directional selection,’ ‘stabilising/balancing selection’ and ‘disruptive selection’ (Freeman and Herron 2007, 347). These can be distinguished by the outcome of selection, particularly on quantifiable traits, such as size and speed. Under directional selection, fitness is proportional (or inversely proportional) to the value of a trait, so that the value either increases or decreases over time. Trophy hunting leading to reduction of horn size is one example of this (Coltman et al. 2011). Stabilising selection refers to situations where intermediate values of a trait are the fittest, and disruptive selection is where extreme values are most fit, whether they are high or low, so that the population ends up divided in two opposite groups of roughly equal fitness. Stabilising selection can be found for example in birth weight, as smaller infants are less prepared for life outside the womb, and larger infants are more susceptible to birth trauma (Ulijaszek, Johnston, and Preece 1998, 367). An example of disruptive selection is where large and small, but not intermediate, bill sizes in birds are preferred, to specialise in different seeds (T. B. Smith 1993).

A fourth way to speak of selection, is in *mechanisms* such as ‘runaway selection’ and ‘frequency-dependent selection.’ These specify how selection operates in particular cases. Runaway selection is the positive feedback loop we get when a trait under selection influences the selective regime so that demand for that trait increases, often resulting in preposterously exaggerated traits. Runaway selection is often coupled with sexual selection, the canonical example being the peacocks’ extravagant tail (Zahavi 1975). This tail signals good health to

peahens, so that peahens with a preference for these tails will have fitter offspring. Because of the inherent feedback dynamic, this leads to runaway selection: Offspring of such couples inherit both the extravagant tail of their father and a preference for such tails from their mother, resulting in a genetic correlation between the two (Freeman and Herron 2007). As one trait increases in strength, so does the other—often with preposterous results, as in the two millimetre long bug *Micronecta scholtzi*, capable of underwater calls at just below 100 dB (Sueur, Mackie, and Windmill 2011). Frequency-dependent selection is where the fitness of a particular trait depends on how common it is in the population, and can be divided into negative and positive frequency-dependence. In the former, rare traits are selected for as long as they are rare, at which point selection favours competing traits. In the latter, traits benefit from being common. An astonishing example of negative frequency-dependence is found in the scale-eating cichlid of Lake Tanganyika, *Perissodus microlepis* (Hori 1993). These fish have an asymmetry in their jaw so that they prefer attacking from left or right, depending on the way their jaw twists. Their prey is generally alert, but particularly vigilant against attacks from the side where they have been attacked previously, that is, where the most common morph of cichlid attacks. This increases the fitness of the rarer morph, until their prey start looking to the other side, and the cycle repeats. In such situations, evolution cannot settle on an optimal trait, because as the trait approaches fixation, fitness decreases. Rather, such frequency-dependence leads to the evolution of what is called an evolutionary stable state (ESS: Maynard Smith 1982, 204). This state is an equilibrium where both (or all) competing traits have the same fitness. More will be said on evolutionary stable states and strategies in the treatment of the Prisoner's dilemma below (3.2). Positive frequency-dependence, on the other hand, is found for example in warning coloration. Such signalling is not really advantageous until it is so common that a significant number of would-be predators recognise it and stay away (Darst and Cummings 2006). The evolution of any kind of signalling, in fact, would be an example of positive frequency dependence, including the hard-to-fake signalling of commitment that will be discussed further below (3.2, 4.2).

It is worth pointing out that although selection is generally considered to give rise to adaptations, the extravagant traits formed by runaway selection and the compromises of

evolutionary stable states or strategies are generally suboptimal solutions. In a sense, they are examples of selection becoming too greedy and not quitting while it is still ahead. Still, these solutions are considered adaptations, because the optimal solutions are unstable. Peafowls would, on average, be fitter without their extravagant tail, but those peafowls who managed to signal fitness or detect such signals would be fitter still, and in this way handicaps are selected for; adaptations and maladaptations both, depending on your outlook. This will be discussed further in the chapter on biology (2.5), with implications for the evolution of religious cooperation later (4.2).

So, traits selected for their current function are adaptations, although they could still be suboptimal. But environments constantly change, and so do demands, so traits could well find new functions. Beneficial traits, when not considering their evolutionary history, are generally said to be adaptations, but for cases where a beneficial trait lacks a selective history for its current use, palaeontologists Stephen Jay Gould and Elizabeth Vrba coined the term 'exaptation' (Gould and Vrba 1982). Philosopher of biology Daniel Dennett, however, argues that the term is superfluous, as 'no function is eternal; if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all' (Dennett 1995, 281). Biologists John Endler and Tracy McLellan exclude the historical aspect altogether and call traits adaptations based on their current contribution to fitness, arguing that 'as soon as a new function for a trait occurs, natural selection will affect that trait in a new way and change the allele frequencies that generate that trait' (Endler and McLellan 1988, 409). When even biologists cannot agree on the definition of adaptation, scholars of religion should tread carefully when adopting the term, more so, I will argue, than they have thus far done.

Thus far, we have concentrated on selection. But as mentioned at the outset, selection is not the only force of evolution. One of the major controversies of evolutionary biology arose when Gould and Richard Lewontin, in their paper 'The Spandrels of San Marco' attacked 'the Panglossian paradigm,' claiming that selection had unduly been considered the sole mechanism of evolutionary change (Gould and Lewontin 1979). They agreed that it was the most important one (Ibid., 589), but stressed the importance of developmental constraints in limiting selection, to

the point where they ‘become much the most interesting aspect of evolution’ (Ibid., 594). A good three decades later, it appears that the adaptationist side has endured the ensuing controversy relatively unscathed, but with the new subject matter provided by expanding evolutionary approaches to the social sciences, another look might well be warranted.

1.3: The Adaptationist Program

The ‘Panglossian paradigm’ is more aptly called the adaptationist program, although it is not a unified group, but rather a catch-all for several different approaches to evolution that focus on adaptation as the most important evolutionary force. Peter Godfrey-Smith recognises three different kinds (Godfrey-Smith 2001), and Tim Lewens further divide these into seven (Lewens 2008). Arguably the most important difference is between merely pragmatic forms of adaptationism and making the claim that adaptation is in fact the correct explanation for most, or all existing traits.

Not accepting Gould and Lewontin’s allegations, defenders of the adaptationist program claimed the default assumption of adaptation as their strength. Philosopher David Resnik claims that assuming traits to be adaptations is not even a hypothesis that would be repudiated by finding other mechanisms to be more important, but rather a heuristic, the best way of examining traits (Resnik 1997). This is a slight modification of Elliott Sober’s claim that adaptationism should be viewed as a research program (Sober 2000, 132). Resnik disagrees ‘on how that research program should be characterised and justified’ (Resnik 1997, 41), arguing that even if it should turn out that most traits are not adaptations (a scenario, we should remember, not even Gould and Lewontin envisioned), we simply do not have any alternative research methods (Ibid., 43). What is also interesting to note, is that it has even been suggested that an adaptationist approach makes the best sense out of developmental constraints, the very problem that Gould and Lewontin were interested in (Orzack and Sober 2001, 84; Seger and Stubblefield 1996, 113; Dennett 1995, 232). As biologists David Stephens and John Krebs (1986, 212) point out, ‘[e]ven if they serve no other purpose, well-formulated design models are needed to identify

constraints: without a design hypothesis there would be no basis for postulating any kind of constraint!

Another aspect of the rebuttal of ‘Spandrels’ is the claim that natural selection is such a powerful force of evolution that the effect of developmental constraints or other complications are negligible (Sober 2000, 122). This does not mean that other forces do not exist, but rather, that adaptationism provides sufficient explanations (Ibid., 124). Dennett even argues that ‘not only do “over”-simplified models often actually *explain* just what needs explaining, but no more complicated model could do the job’ (Dennett 1995, 102, italics in original). Or, as put even more succinctly by John Ball, although not in quite the same context:

To make progress in understanding all this, we probably need to begin with simplified (oversimplified?) models and ignore the critics’ tirade that the real world is more complex. The real world is always more complex, which has the advantage that we shan’t run out of work. (Ball 1984, 159)

Resnik is open to the possibility that we one day might find adaptationism ‘foolish, but right now it is the best we can do’ (Resnik 1997, 43). While different in flavour, pragmatic approaches such as these seem to dominate evolutionary biology, rather than the stronger form of adaptationism claiming that most or all traits in fact are adaptations (Lewens 2008, 168).

There is an important caveat to all this, however. While the assumption of adaptation might be the optimal search strategy, we should not invoke adaptation when more basic explanations are available (Williams 1966; Dennett 1995, 247). Physics takes precedence over adaptation—leaves do not fall *down* because they have been selected to do so, but because of gravity. More interestingly, developmental constraints and by-products also take precedence over adaptation: If a trait can indeed be explained in terms of one of these, then it should not be explained as an adaptation. This does not conflict with using adaptationism as our initial hypothesis; rather, it means simply that *if* we find a more basic explanation, we should prefer it. Nor does it imply anything about the prevalence of developmental constraints or by-products, only that for the cases that are constrained, or by-products of something else, adaptation is irrelevant. Compare with Tim Lewens’ observation that while adaptationists explain ‘the non-appearance of form F* by pointing out that it is less fit than the actual F, [structuralists explain] this non-appearance by claiming that F* cannot arise (or is very unlikely to arise) by mutation from the existing system’

(Lewens 2008, 175). For any given trait where it happens that the structuralist explanation is correct, and the existing trait is the only available trait, we should not be calling it an adaptation.

Having made clear what an adaptation *is*, we now turn to the science that has studied it the longest, biology, in the hope that this can inform our further studies of religion.

II

ADAPTATION IN EVOLUTIONARY BIOLOGY

Whether one considers selection to be the only evolutionary force worth mentioning, or seek to challenge it by focusing rather on developmental constraints, it's hard to argue that adaptation isn't *the* central theme of evolutionary biology. The discussions pertaining to it are, however, quite different from those of evolutionary approaches to religion. The spandrel controversy did of course originate in biology, but now that the dust has more or less settled, the adaptationists seem mostly unscathed. Nevertheless, no treatment of adaptation would be complete without a review of this controversy, which will be found below (2.1).

A more pressing disagreement concerns multilevel selection, re-emerging in recent years as a viable alternative to the conventional view of the last decades, favouring selection at the level of genes. From the mid-sixties and onwards, the argument was driven home that only genes had the properties required to function as units of selection (Williams 1966; Dawkins 2006). The then-common assumption that selection could act for the good of the species was to be the subject of ridicule, with only a minority still investigating selection at the level of groups. With heredity centred on genes, higher levels were seen to be too unstable for selection on them to work. Multilevel selection has been gaining ground in recent decades, but note that the current theories are much more sophisticated than they used to be; groups need to meet certain requirements to be evolvable, and the entire species is never

seriously considered an adaptive unit, although commentators on television's nature shows don't quite seem to have caught up, as many biologists will complain (Bass 1994, 112; Carey 2003, 219; Breed and Moore 2011, 6).

A thorough examination of adaptation also requires clarification of a number of related terms, chief among them fitness. Roughly, biological fitness corresponds to a gene's relative success at spreading copies of itself. While often taken to be a property of individuals, as in the phrase 'survival of the fittest,' a closer look at the concept will show that fitness is not as easily defined as often assumed (Dawkins 1999, ch. 10).

Fourth, I will discuss constraints on optimality—mechanisms that limit evolution's ability to ascend the premier summits of adaptation. Optimality is constrained by the path evolution has thus far taken, and better solutions may be out of reach. Another constraint is time lag. The wheels of evolution grind slowly, and if the environment is changing too fast, the population cannot possibly be perfectly adapted. The adaptation of yesteryear may prove not merely inefficient in new environments, it could be positively maladaptive. There are several other ways evolution can produce suboptimal traits, to be presented below (2.4). I will also discuss mechanisms that balance these, such as genetic drift as a way to cross adaptive valleys.

In the final section of this chapter, I will examine processes where selection itself produces suboptimal traits, or maladaptive behaviour. Mechanisms that can produce such traits are arms races, runaway selection, evolutionarily stable strategies and extended phenotypes. Arms races and runaway selection are similar in that both keep raising the stakes without increasing the benefit, evolutionarily stable strategies are compromises where more cooperative solutions would be vulnerable to exploitation, and some forms of extended phenotypes are cases where an organism is being manipulated by another. The three first mechanisms can lead to maladaptive behaviour because evolution lacks foresight, and selects traits that are fittest of the current options, but in the long run detrimental. Extended phenotypes can be adaptations *par excellence*, but often not for the organism that possess the trait in question—another organism can be manipulating the former to its own benefit.

2.1: Spandrels

One major controversy in evolutionary biology during the final quarter of the twentieth century arose not from an organic life form, but rather architectural details of Venice's Basilica di San Marco. According to Gould and Lewontin, spandrels are 'the tapering triangular spaces formed by the intersection of two rounded arches at right angles' (Gould and Lewontin 1979, 581).¹ These were to haunt evolutionary biology for years, as a metaphor for 'a nonadaptive architectural by-product of definite and necessary form—a structure of predictable size and shape that then becomes available for later and secondary utility' (Gould



Spandrels, or pendentives, in San Marco di Venezia. Photo: Ricardo André Frantz. Licensed under the Creative Commons Attribution-Share Alike 2.5 Generic license. <http://commons.wikimedia.org/wiki/File:Venezia118.jpg>

1997, 10751). Concerning religion, spandrels are invoked by scientists claiming religion to be a by-product of other adaptations; In the chapter on religion, I will use 'by-product' when I might have used 'spandrel,' as the former term is more commonly used in that regard. Be that as it may, Gould and Lewontin proposed that spandrels were necessary by-products of mounting a dome on rounded arches, neglecting existing alternative designs demonstrating that spandrels are not necessary at all, but in fact adaptations (Dennett 1995, 273).

Perhaps we should ignore this arguably feeble metaphor and focus on the core of Gould and Lewontin's argument: That developmental constraints riddle nature with by-products, competing with natural selection for prominence in evolution. They argued that evolutionary biologists 'in their tendency to focus on immediate adaptation to local conditions, do tend to ignore architectural constraints and perform ... inversions of explanation [in the style of Voltaire's Dr.

¹ Dennett (1995, 272) disputes even the term's architectural origin, claiming that what Gould and Lewontin calls 'spandrels' are properly termed 'pendentives.' While the former term has evidently been used in both senses, Dennett seems to be correct in arguing that the three-dimensional spaces Gould and Lewontin are writing about are properly called pendentives, while spandrels are two-dimensional (Britton and Godwin 1838; C. M. Harris 1977; J. H. Parker 2004).

Pangloss, the preposterous eternal optimist]’ (Gould and Lewontin 1979, 583). However, even when disregarding the failed metaphor, the argument against ‘pervasive adaptation’ does not stand up to scrutiny.

A significant part of the critique in ‘Spandrels’ is levelled at what they call ‘just so stories,’ a term borrowed from Rudyard Kipling’s fanciful tales of the origin of various phenomena (Kipling 1902). ‘[P]lausible stories can always be told,’ they argue (Gould and Lewontin 1979, 588), suggesting that adaptationists just make up stories that seem to fit the fact and are content with that. But two can play at that game, and the error is just as easy to commit on behalf of spandrelism (Brandon 1990; Pigliucci and Kaplan 2000, 68). However, selection is easier to work with than non-selective forces, and an adaptationist hypothesis can provide a valuable and economical ‘first guess’ (D. S. Wilson 2002, 70). When the preliminary work has been done, Sober, following Parker (1992), has a suggestion: ‘*If optimality explanations are too easy to invent, let’s make the problem harder*’ (Sober 2000, 137, italics in original). The solution is to lay down a specific criterion of optimality for a given behaviour, rather than just ask why that behaviour takes place, and then get empirical support for the explanation. If a study can show that key variables are very near the optimum for some task, then it becomes difficult to say that natural selection has been constrained in that particular case, although the reverse is true as well. While this is true for particular cases, adaptationism itself, like Sober writes, ‘is testable only in the long run’ (Sober 2000, 131).

Other themes of ‘Spandrels’ are genetic drift, genetic correlations, developmental constraints and fitness landscapes with multiple adaptive peaks. These are all standard constraints to consider, and all Gould and Lewontin did, was to stress their importance. The relative significance of different evolutionary mechanisms is arguably what most disagreements in evolution are about, so ‘Spandrels’ is not unique in that regard. At any rate, these issues will be treated in the section on constraints, below (2.4).

One problem is that Gould and Lewontin are attacking a straw man: adaptationists are well aware of developmental constraints, which are ‘an integral part of (good) adaptationist reasoning’ (Dennett 1995, 270). Increased emphasis on constraints may well be warranted, but this would

not be the paradigm shift Gould and Lewontin might seem to think it would be. Even the style of argument has been criticised for being overly rhetorical, one-sided, and provocative, rather than stimulating constructive debate (Borgia 1994). One of the shortcomings of ‘Spandrels’ is particularly notable: according to Dennett, there are not even any official definitions of the term ‘spandrel’ as it pertains to biology (Dennett 1995, 275).² He charitably tries out a few possible definitions, none of which amount to any threat to adaptationism. As he comments, ‘it is never a mistake to *ask* the adaptationist’s “why” question, even when the true answer is that there is no reason’ (Ibid., 276). Ironically, none other than Richard Lewontin has expressed himself to much the same effect: ‘In a sense, then, biologists are forced to the extreme adaptationist program because the alternatives, although they are undoubtedly operative in many cases, are untestable’ (Lewontin 1978, 125).

Here we arrive at what in my opinion is the strongest defence against the ‘Spandrels’ article, namely that presented by David Resnik (1997). He argues that adaptationism is a heuristic, not a hypothesis, and as such that it is independent of the truth value of the adaptationist metahypothesis. A central point, similar to Lewontin’s, just quoted, is that evolution ‘is a very complex process and it may be useful to make some simplifying (though false) assumptions about this process in order to understand it’ (Resnik 1997). Perhaps, then, adaptationism with large strides and the occasional misstep is preferable to a spandrelist approach that is too complex to get anywhere at all.

2.2: Multilevel Selection

Theories of religion sometimes invoke selection at levels other than that of genes, such as groups or culture. This is not uncontroversial, and has been discussed thoroughly in biology. Early biologists often suggested that evolution works for the good of the species, a view heavily criticised by G. C. Williams (1966). This view was later to become the central theme of one of the best-selling books on biology, Richard Dawkins’ *The Selfish Gene* (1976/2006). Briefly, proponents of this gene-centred view of evolution argue that evolution works on genes and genes

² Note that Gould’s definition, cited above, was published *after* Dennett’s complaint, not in ‘Spandrels.’

only, because genes, unlike organisms and species, persist over evolutionary time. The composite entities which contain genes, such as individuals, groups, populations and species are all unique, and according to Dawkins, ‘you cannot get evolution by selecting between entities when there is only one copy of each entity!’ (Dawkins 2006, 34). Dawkins defines his selective unit, the gene, as ‘a piece of chromosome which is sufficiently short for it to last, potentially, for *long enough* for it to function as a significant unit of natural selection’ (Ibid., 35–36, italics in original). It must be short to minimise the chance that it’s split apart by crossing over during meiosis, which is the mixture of parental chromosomes during sexual reproduction (Freeman and Herron 2007, 306).

One example to show that evolution does not favour the good of the species can be found in sex ratios (Fisher 1930, 141–142). Since males are able to mate with a large number of females, and indeed in many species do, at the expense of weaker rivals, a species with a lower ratio of males would be able to keep up the same level of reproduction. If all the calories taken up by the excess males (who typically also consume more than females) could have been diverted to even more females, a species that could sustain a low ratio of males would seem to be favoured by selection, as the same resources would be divided among, on average, less resource-demanding individuals. The reason this does not happen, is that in such a group, it would pay to be male. Since each male statistically would have more offspring than any given female, genes that increased the ratio of males would spread, until the familiar equilibrium is reached. The example shows that the interests of the genes prevail over the interests of the species, since mutinous (‘selfish’) genes can invade a population, to its peril.

As this gene-centred view gained currency, it did so almost at the complete detriment of group selectionist views. A few persisted, however, and in recent years it has begun to seem that they were right after all, though their theories are far more refined than naïve ‘good of the species’ assumptions. Multilevel selection is a better approach than group selection, as no one disputes that genes can drive evolution, and groups of course exist at different levels, from cells to species (Alexander and Borgia 2011). To be fair, no one really disagrees that selection is possible at any level, but ardent gene selectionists hold that selection at the level of the gene is so powerful as to

cancel out all other selection. Pioneer of the gene selectionist view, George C. Williams writes that

Like the theory of genic selection, the theory of group selection is logically a tautology and there can be no sane doubt about the reality of the process. Rational criticism must center on the importance of the process and on its adequacy in explaining the phenomena attributed to it (Williams 1966, 108)

Dawkins' argument for the gene selectionist view is tied up with his interpretation of evolution as the differential survival of *replicators*. A replicator is 'any entity in the universe which interacts with its world, including other replicators, in such a way that copies of itself are made' (Dawkins 1978, 67). These entities have three qualities: (1) copying fidelity, (2) fecundity, and (3) longevity (Dawkins 2006, 17). In other words, they replicate (1) faithfully, with few errors—just enough to keep some variation on which selection can work. They also produce (2) more copies than are needed for simple replacement, so that a successful variant is able to spread, and they (3) last for long enough to replicate themselves. Dawkins argues that only genes are replicators (in biology, leaving the door open for memes in culture) (Dawkins 1999, ch. 6), and that organisms and groups are only *vehicles* in which replicators move about (Ibid., 82).

Without too much controversy, we can admit some selective power to other levels as well. A study of yeast (*Saccharomyces cerevisiae*) showed that at the level of mitochondrial genomes within the cells, parasitic mitochondria are favoured over normal mitochondria because they replicate faster. At the level of yeast cells within a petri dish, however, selection favours the opposite (Taylor, Zeyl, and Cooke 2002). Without getting into biological technicalities well beyond the scope of this chapter, suffice it to say that the experiment confirmed that depending on the conditions, selection can and does operate at different levels. However, we are not concerned here with the levels of cells and mitochondria. Can selection at even higher levels also be a force significant enough that we cannot ignore it?

Yes, say a growing number of evolutionary scientists. The evolutionary mathematician Martin Nowak, in his recent, seminal work on cooperation and evolution, argues that the math behind group selection is sound (Nowak and Highfield 2011, ch. 4). Not only does he maintain that Dawkins' claim about selfishness as an important driving force behind evolution is irrelevant to group selection, which 'simply says that intense between-group competition will favour

mechanisms that blur the distinction between group and individual welfare if they improve performance or fitness at the group level' (Ibid., 93). Environmental scientist Peter J. Richerson and anthropologist Robert Boyd have developed a 'tribal social instincts hypothesis' (Richerson and Boyd 2005), arguing that pressures to conform decrease within-group differences while symbolic boundaries increase between-group differences, enabling groups to function as selective units rather than loose collections of individuals (Richerson and Newson 2008). Biologist David Sloan Wilson has a somewhat different angle, assuming that individuals take part in several different trait-groups, so called because they are founded on a specific trait shared among members (D. S. Wilson 1975). Within each of these groups, altruism has lower fitness than selfishness, but groups with more altruists have higher fitness than more selfish groups.

Whether selection is mostly confined to the genetic level, or if group selection is an important factor, too, is relevant for adaptation studies because adaptations at the level of genes will be markedly different from adaptations at the level of groups, as they may have conflicting interests. In cases where there is no conflict between levels, it is probably best to stick to a gene-centred model, even though group selection could explain the phenomena just as well (Williams 1966, 4). Note that a central point of *The Selfish Gene* was the claim that even though genes are favoured over organisms and groups, and even though these genes are best described as if they were selfish (without, of course, ascribing any real motivations to them), altruistic behaviour is still fully evolvable. We would, however, expect more cooperative behaviour from group selection than from gene selection (Bulbulia and Frean 2009, 189). There is a twist to this, though—altruism within the group often implies increased between-group competition (Bowles 2006). But even if we were all agreed as to what level or levels selection takes place, there is still another important lesson from multilevel thinking, implicit in the very debate. The only reason we can talk about different levels of selection is that they can select in different directions. As in the sex rate example above, genes and groups can have different 'interests.' For groups to prosper, the individuals composing it should be relatively altruistic, but selfish individuals are likely to outperform altruists. Generalising, we can probably say that for any given level of selection, it is advantageous that the parts composing a unit at that level are altruistic, while the unit itself is

selfish towards other units at the same level. We must be careful, when stating that something is an adaptation, to specify at which level, and remember that it can be quite maladaptive at another.

2.3: Fitness

Fitness is so integral to the debate on adaptation that it warrants its own section here. The two terms ‘adaptedness’ and ‘fitness’ are directly related, although not interchangeable. One could perhaps suggest that an increase in fitness is the function of evolution, and adaptedness is the means to attain the former. Another way to put it, is Elliott Sober’s observation that adaptation ‘looks to the past, reflecting the kind of history that a trait has had. [Fitness] looks to the future, indicating the chances that organisms have for survival and reproductive success’ (Sober 1984, 210). As such, one would expect the two to be correlated, and indeed they typically are. Exceptions are, for instance, when a foreign species successfully invades a habitat to which it is not historically adapted (Keller and Taylor 2008). Some traits experience increases in fitness as their host species escape natural enemies and parasites (Torchin et al. 2003), although to say that they are adapted to the environment in which they have just arrived is clearly false. Other examples are when adaptations in the long run are detrimental to fitness, as discussed below (2.5).

While the term ‘fitness’ does seem to have explanatory power, and consequently should be defined so that it can be used in precise measurements, Dawkins argues that it has done little more than to cause a great deal of confusion (Dawkins 1999, ch. 10). He describes no less than five different uses of the term (plus a brief mention of a couple more), and it is his main contention that even prominent scientists have been confusing these. The confusion surrounding fitness has led to demonstrable error, and furthermore, has led outside commentators to conclude that the entire theory of evolution is nothing more than a tautology (An objection which now seems limited to creationists). The five different formulations of fitness are, briefly: non-technical, population-genetic, classical, inclusive, and personal fitness.³

³ Dawkins does not give names for the first two types of fitness, and so I have given them my own, based on his text.

The first usage originates with Spencer, Wallace, and Darwin, and was not concerned with reproductive success as such, but rather with the traits required by specific habitats. For instance, if the selective environment requires a lot of running, fit individuals will be those with strong leg muscles. This is a non-technical usage that really is out of fashion, but it has similar disadvantages to classical fitness, discussed below.

A more precise usage is found in population genetics, where it 'may be regarded as a measure of the number of offspring that a typical individual of genotype Aa is expected to bring up to reproductive age, when all other variation is averaged out' (Ibid., 182). Note that with all other variation averaged out, it is really the trait's performance that is being measured, not the individual's. This is the sort of fitness one talks about when saying that a particular trait is fitter than another. Dawkins does not seem to have any particular misgivings about this usage, other than the criticism he levels at the term as a whole.

The most common association to biological fitness is probably the third usage, so-called classical fitness. Rather than a property of genes, it is a property of individuals, 'often expressed as the product of survival and fecundity' (Ibid., 183). This, of course, does not sit well with the gene selectionist Dawkins, rehearsing his famous argument that individuals do not reproduce. The gist of his criticism can be found here, in the tendency of 'fitness' to be concerned with individuals, rather than with genes. As he explains later, he believes 'that thinking in terms of individuals striving to maximise something has led to outright error, in a way that thinking in terms of genes striving to maximise something would not' (Ibid., 189).

The next two usages are inclusive fitness and personal fitness. I will conflate them here, as personal fitness is 'a kind of backwards way of looking at inclusive fitness.... [which] when properly used,... give[s] equivalent results' (Ibid., 187). The difference is not trivial, but too technical to be of interest here. Both usages stem from a paper by William D. Hamilton, observing that natural selection will favour not only genes conferring direct reproductive success, but also genes enhancing the reproductive success of other individuals carrying them (Hamilton 1964). Hamilton's paper provided a rigorous mathematical confirmation for J.B.S Haldane's famous comment that he would give his life to save two brothers, or eight cousins (McElreath

and Boyd 2007, 82), referring to the fact that two brothers or eight cousins would, on average, carry equal numbers of duplicates of a given gene (such as a gene for altruism). If, for instance, a gene induces its host to sacrifice its life to save four children, then for every one gene copy lost in this way, on average two copies would survive (a child has only a 50% chance of having a given gene from one parent), and as such, the sacrifice would be evolutionarily profitable. Compelling though the idea is, it comes with a trap; while properly conceived as a property of an organism's actions or effort, it was initially 'extremely common' to see it as a property of the organism itself (Dawkins 1999, 186). This implies the untenable conclusion that 'the inclusive fitness of a brother yet unborn would theoretically be increased by the birth of his elder nephew' (Ibid.). Hamilton himself saw this problem at the onset, and it seems to have all but disappeared from mainstream biology these days, but the scholars of the humanities adopting evolutionary approaches should take note of the confusion. At any rate, the confusion is avoided by remembering that fitness is a property of genes, but *not* individuals.

Recently, more serious criticism of inclusive fitness has been levelled by Nowak, Tarnita and Wilson, claiming it to be 'an unnecessary detour, which does not provide additional insight or information' (Nowak, Tarnita, and Wilson 2010) It also seems that 'members of social insect colonies cannot actually recognise their own degree of relatedness to their nest mates' (Nowak and Highfield 2011, 106), which they claim is a prerequisite for inclusive fitness to work at all. However, Nowak *et al.* find natural selection acting on genes to be quite sufficient for explaining what biologists previously thought required inclusive fitness. The findings of Nowak *et al.* seems to be in agreement with Dawkins, who argues that the findings 'expressed in terms of inclusive fitness [could] have been more simply derived in terms of Hamilton's "intelligent gene," manipulating bodies for its own ends' (Dawkins 1999, 188). This paper was heavily criticised in five letters to *Nature*, one of which had no less than 137 signatories, claiming that inclusive fitness has produced extensive results (Abbot et al. 2011; Strassmann et al. 2011). Furthermore, eusociality (the form of organisation found in social insects and naked mole rats) has only evolved in full-sibling families, strongly indicating that relatedness really matters (Boomsma et al. 2011).

Because of the possibility of confusing these different forms of fitness, and the possible confusion with inclusive fitness, Dawkins suggests doing away with the term altogether (Dawkins 1999, 193). Almost three decades later, however, the term persists, and it seems it is doing good service. Both Dawkins' and Nowak's critiques against inclusive fitness seem largely unfounded, and as long as we are careful about what sense we are employing when using 'fitness' in a technical way, we should probably be in the right doing so.

2.4: Constraints on Optimality

The main contribution of the spandrel debate was, arguably, in bringing more attention to the limits of evolution. Still, these constraints were not news to serious students of adaptation, and indeed, they represent a highly interesting part of evolutionary theory. A central metaphor for explaining adaptation is Sewall Wright's fitness landscape (Wright 1932), wherein adaptations are represented as peaks of high fitness. The horizontal distances represent genetic difference, so that the distance between two points in the landscape corresponds to the number of mutations it takes to get from one trait to another. The underlying assumption is that natural selection only allows populations to climb in this landscape, that is, evolve adaptations. In this way, evolution can be constrained by lack of viable options: In other words, natural selection cannot lead a population to be less adapted. Thus, populations at one adaptive peak may not reach a higher summit, because getting there would require descending into the adaptive valley in between. This is one of the many reasons no animal has evolved wheels—for legs to gradually evolve into wheels over generations requires intermediary variants that are hybrids of legs and wheels, with no conceivable selective advantage.

Other constraints abound, as well. My presentation here will be largely based on Dawkins' list of six constraints (Dawkins 1999, ch. 3). They are: (1) time lags, (2) historical constraints, (3) available genetic variation, (4) constraints of costs and materials, (5) imperfections at one level due to selection at another level, and (6) mistakes due to environmental unpredictability or 'malevolence.' The fifth of these were given separate treatment in the above section on multilevel selection, the rest will be discussed below, along with (7) developmental constraints, which is

missing from Dawkins' list, although it can be seen as an elaboration on (3) (Amundson 1994). We should also note that even though Dawkins is writing about constraints on genetic evolution, most, or even all of these, are with some modification applicable to cultural evolution. For example, substitute 'cultural' for 'genetic' in constraint (3).

The first constraint is especially relevant to studies of human culture, evolving as it does at a rate with which biological evolution can only dream to keep up. Time lags occur when the environment changes, so that previous adaptations are no longer helpful, and the organisms in question have not yet had time to readapt. Dawkins cites the example of the moth and the candle flame: For most of their evolutionary history, small sources of light in darkness would have been either small openings to escape through, or celestial bodies to manoeuvre after. The result is glaringly obvious if the moth assumes a candle to be an opening to fly through. A bit of geometry also shows that trying to keep a nearby flame at a constant angle results not in the straight flight we would have seen, had the candle been a distant star, but rather, the familiar spiralling towards immolation and a clear display of maladaptation (Ibid., 37).

While moths are maladapted to the occasional candle flame, we humans surround ourselves with cultures that can seem almost entirely novel, evolutionarily speaking. In a mere 10,000 years, or 400–500 generations, we have gone from hunter-gatherers to stock-market analysts. Modern lifestyles are radically different from those to which we have adapted (Freeman and Herron 2007, ch. 14.5). This is an important consideration when asking whether certain behaviours are adaptive. Dawkins, on the adaptedness of contraceptives, claims that 'the question, about the adaptive significance of behaviour in an artificial world, should never have been put' (Dawkins 1999, 36). He seems to be overreacting a bit, but there is a universal lesson here: take care to ask the right questions. Rather than asking if contraceptives are adaptive, we can ask what their adaptive basis might be. What traits do we possess that in modern environments manifest itself as a preference for contraceptives?

Both historical constraints and available genetic variation can be explained with reference to the above-mentioned fitness landscape. Historical constraints would be represented as a population's current position, and available genetic variation would be the ability to traverse certain paths. It should be obvious why the latter is a constraint: if genetic variation for a

particular trait does not exist, then that trait's location in the fitness landscape will be inaccessible, and the trait cannot evolve. Historical constraints are a bit less intuitive, and requires a more thorough presentation of the idea of a fitness landscape.

A fitness landscape is typically visualised as a three-dimensional landscape, where elevation represents differences in fitness,⁴ and horizontal movement represents differences in genotype or phenotype, depending on what is of interest to the present study. A more correct fitness landscape would have as many dimensions as the organism in question had genes, plus the standard 'height' dimension for fitness. This, of course, is entirely unfeasible, as well as unnecessary, with three dimensions being quite sufficient to get the point across.

As mentioned at the outset, the central assumption is that evolving organisms only will be able to rise in this landscape, because descending would mean selecting for less fit traits, which would imply a reversal of natural selection. As so often in science, assumptions of this kind prove upon closer inspection to be oversimplifications. Indeed there are mechanisms to cross adaptive valleys, two of the most prominent being drift and changes to the landscape itself. The latter was implied when we discussed time lags—if new circumstances change the fitness of traits, new opportunities for evolution present themselves. Lactose tolerance in adults, for example, could never have evolved in an environment without dairy farming, as the enzyme lactase would just be a waste of resources. Incidentally, lactose tolerance, needing only a single mutation, is one of the few clear examples of humans catching up with the time lag since making the shift from hunter-gatherers. People from areas of the globe without long traditions for dairy farming, however, are living examples of time lag, unable to metabolise lactose (Feldman and Laland 1996). There is also another way for the fitness landscape to change—if variation for a trait increases, the fitness landscape will be smoothed out 'because the population's mean fitness is determined by an average taken over a broader distribution of phenotypes' (M. Kirkpatrick 1996, 139).

The other important mechanism for crossing adaptive valleys is genetic drift (or just drift, to allow for other forms of evolution). Genetic drift is random changes in gene frequencies due to sampling error (Freeman and Herron 2007, 234). Though random, drift can be significant, as

⁴ Although the term 'fitness' was problematised in the previous section, it is used here in a non-technical sense. It does not matter how we measure fitness in this regard—the point is that some genotypes are fitter than others, and this restricts evolution as described above.

with the founder effect, which occurs when a small group settle in a novel habitat (Ibid., 236–238). As a small group, they will represent a biased sample of their group of origin, and so gene frequencies in the new group will be skewed. Unless maladaptive, traits that were rare in the original group can become fixed in the new group. In other situations, however, drift is of limited influence, and even for small groups to cross modest adaptive valleys can take an astounding number of generations (M. Kirkpatrick 1996, 137).

For examples of these two constraints, i.e. historical constraints and lack of genetic variation, we can return again to sex ratios. As mentioned above, the evolutionary stable ratio between sexes is unity, but there are exceptions to this. When the two sexes require different levels of parental investment, selection can indeed produce other ratios (Trivers and Willard 1973). However, the data shows that this is much more common in haplodiploid species, where fertilised eggs develop as female, and unfertilised eggs as male. It turns out that chromosomal sex determination, where all eggs are fertilised, is more costly to control, and thus requires a greater benefit to evolve (West and Sheldon 2002). Here, chromosomal sex determination is a historical constraint on sex ratio adjustment, reducing the chance that the latter will evolve—the ability to control sex ratios is partially dependent on the already evolved mechanism of sex determination. An example of selection constrained by available genetic variation is found in dairy cattle sex ratios. Cattle breeders would greatly value a bias towards female offspring, bulls being notoriously bad at producing milk. However, there seem to be no available genetic variation for sex ratio adjustment in cattle, which constrains artificial selection on this (Dawkins 1999, 43).

Next up are constraints of costs and materials. These are simply cost-benefit calculations, and the main point is that traits that would seem to be obvious improvements will not evolve unless the benefits outweigh the costs. In Dawkins' words, 'any design that achieves "better" than the specified criterion performance is likely to be rejected, because presumably the criterion could be achieved more cheaply' (Ibid., 46). Outrunning your predators with a large margin is obviously 'better' than just outrunning them, but selection is unlikely to produce much above the bare minimum for survival and reproduction. This is the reason our big brains present us with such a conundrum—they obviously evolved for a purpose, but what necessitated brains so hugely out of proportion with our body size? Bigger brain are obviously 'better' from at least one perspective,

but selection will generally not produce anything exceeding the demands posed by the environment. In a way, this is not a real constraint, as it is not a mechanism by which organisms perform suboptimally, but rather one by which they avoid ostensibly good solutions because they would not be worthwhile. Dawkins cites an interesting study where digger wasps (*Sphex ichneumoneus*) seemed to commit the so-called Concorde fallacy, by valuing a resource according to prior investments, rather than actual profitability (Dawkins and Brockmann 1980). It turned out that the wasps' choices were the best ones they could make, given the available information. A better assessment of the situation could lead to better strategies, but at too a high cost. Dawkins comments that the discovery was made by *post hoc* modification to suit the hypothesis of optimization, but in defence quotes Maynard Smith, writing that 'in testing a model we are *not* testing the general proposition that nature optimises, but the specific hypotheses about constraints, optimization criteria, and heredity' (Maynard Smith 1978, 43). Note that this argument is in agreement with the defence against 'Spandrels' that adaptationism is a research program, not a hypothesis.

Then there are mistakes due to environmental unpredictability or 'malevolence.' This is simply a constraint of complexity—evolution prepares organisms for statistically likely scenarios, but cannot foresee every minute detail. This is mainly a problem when it comes to behaviours, as the short time spans to which behaviours relate are especially susceptible to unpredictability (Dawkins 1999, 53). Malevolence, in this regard, pertains to directly competing organisms, to which the unlucky subject organism has not had occasion to adapt.

Finally, there are the developmental constraints. This sort of constraint is perhaps the one closest to Gould and Lewontin's spandrels. They are biases 'on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system' (Maynard Smith et al. 1985). In other words, a constraint on available variation due to how traits are produced. According to Gilbert, developmental constraints can be further divided into physical, morphogenetic, and phyletic constraints (Gilbert 2006, 744). However, phyletic constraints are really the same as historical constraints, yet Gould and Lewontin see it the other way around; for them, developmental

constraints are a subgroup of phyletic constraints (Gould and Lewontin 1979, 594). Whatever the ordering, the important point is the different ways in which adaptation can be constrained.

Physical constraints are quite simply limitations imposed on evolution by physics. Here, we see another reason animals do not come with wheels: physics will not allow blood to circulate to a rotating organ (Gilbert 2006, 744). Morphogenesis is the process of organisms developing their shape, and this can be constrained in a number of ways. Constraints can define the initial parameters of a trait, its development, or how and when this development ends (Bard 1990, 251). An example is found in some freshwater turtles (*Chrysemys picta* and *Deirochelys reticularia*), unable to produce eggs large enough to achieve the optimal balance between egg size and number of eggs produced (Congdon and Gibbons 1987).

This presentation of constraints is far from exhaustive. There are also a number of constraints arising from the mechanisms of Mendelian genetics, but these are probably too technical to be of interest here. They include pleiotropy, where a single gene codes for multiple phenotypic traits (Freeman and Herron 2007, 496), overdominance and heterozygote inferiority (Sober 2000, 125–130). Overdominance means that fittest gene combination for a given trait is a heterozygote, meaning that it consists of two different alleles. In such a case, the optimum cannot ‘breed true,’ because two heterozygotes might well have homozygote offspring, with equal copies of the allele in question. With heterozygote inferiority, the population will evolve towards one of the homozygotes, but not necessarily the fittest one—that depends on which one is most common to begin with.

2.5: Selecting for Inferiority

There are also other ways that selection itself can produce suboptimal results. Most notably, these are arms races, evolutionarily stable strategies, and runaway selection. These are not generally seen to be constraining evolution in the same way as the mechanisms described above, but they are connected in that they produce costly traits, ones that would not evolve if evolution was prescient or maximally cooperative. Furthermore, traits can be maladaptive for the host organism if they are produced by another organism, such as a parasite. The different themes

mentioned here have some overlap; exploitation of one organism by another, for instance, will typically lead to an arms race between the two. I will endeavour to show later (4.2) that mechanisms such as these threaten the cooperation that hard-to-fake signalling is supposed to establish.

Runaway selection and evolutionarily stable strategies should have been amply treated in the introductory chapter, under mechanisms of selection, but it is worth reiterating. In runaway selection, the feedback dynamic inherent in genetic correlations between a particular signal and mating preference for that same signal may evolve both these well beyond the optimum from a survival perspective. To return to the peacock's tail, having the longest tail of the population would confer the same fitness benefit before the evolution of splendid tails took off, at a lower cost, since a shorter tail would be less of a handicap. The importance of handicap signals is not absolute handicap, but rather relative handicap. The problem arises when peacocks are selected for the longest tail for successive generations: The benefit of having a relatively long tail stays the same, while in absolute terms, tail length becomes an increasing liability. However, if survivability is significantly reduced, and not offset by increased reproduction, selection should favour less ornamental tails (Feldhamer 2007, 423). Overall, though, the process is evidently a costly one.

The problem with evolutionarily stable strategies is that they are typically a compromise between optimal, cooperative solutions, and the need to defend against exploitation. If a population consisted entirely of cooperators, every one of them would likely stand to benefit from synergy. However, in response to invasion by non-cooperating organisms, indiscriminate cooperation will be selected against. For example, if all trees could restrict their growth to a set limit, they could all grow to that height and get equal amounts of sunlight, without spending too much resources on growth. However, since such a strategy would be susceptible to trees cheating by growing ever so slightly more to gain a little more sunlight, trees grow to preposterous, wasteful heights to outcompete each other (Vincent and Brown 2005, 95–96). The theoretically optimal strategy of not wasting energy on an unproductive trunk thus loses out to the evolutionarily stable strategy of growing ever taller.

This last example could serve just as well for arms races, but a more specific example will illustrate how peculiar effects selection can produce. Locusts of the genus *Magicicada* have a very distinct life cycle—they live as underground nymphs for either 13 or 17 years, depending on species, before emerging for but a few weeks to reproduce (M. Lloyd and Dybas 1966). In a given location, all but a negligible few cicadas are exactly the same age, so that for most of the time, the area appears entirely locust-free. While severely limiting reproductive capacity in this way might not seem like much of an adaptation, it turns out to have a very definite advantage: The more time these periodical cicadas spend as underground nymphs, the less basis there are for specialised above-ground parasites to thrive on them. Lloyd and Dybas hypothesised that the cicadas had evolved longer and longer cycles in a race against some parasite that eventually could not keep up, and went extinct (Ibid., 479). Predators with shorter, overlapping cycles are avoided by the cycles being of a prime number of years (Ibid., 482).

Arms races can also be found in the case of extended phenotypes, which are traits in the external environment to the individual. Phenotypes in general are observable traits, in contrast to genotypes, the genetic constitution of organisms. An organism's phenotype depends both on its genotype and the environment, and it has been one of Dawkins' major contributions to point out the degree in which other organisms are part of that environment, and conversely, that the effects of a given gene stretch well beyond that gene's host organism (Dawkins 1999). The classic examples of this are beaver dams, manipulating the terrain well beyond the beaver cells, where the genes that control for dam-building sit (Ibid., 59). The element of arms races becomes apparent when one organism influences features of another. Dawkins cites reports of correspondence between thicker snail shells and parasite infestations (Cheng 1986), claiming that ability to manipulate shell thickness may well be an adaptation on the parasite's part (Dawkins 1999, 210). If this is true, it leads to a conflict of interest: For the snail, shell thickness is likely to be a trade-off between thick, protective shells, and thinner shells, which could, conceivably, free up resources to be invested in reproduction. For the parasite (a fluke), however, the snail's reproductive success does not matter; rather, the parasite is dependent on a safe environment. Dawkins' case is hypothetical, and it does not really matter exactly what the requirements of the

snail and fluke are, respectively—what is important is that the optimum shell thickness is hardly likely to be the exact same from both points of view. As long as that is true, there will be selection pressure on both snails and flukes on ability to reach optimum shell thickness. An interesting consequence of this, Dawkins notes, is that the flukes in this way will affect shell thickness even in unparasitised snails—if flukes are sufficiently common that snails are compensating by making thinner shells, unparasitised snails will have shell thicknesses *below* the optimum (Dawkins 1999, 212).

Examples such as these show that suboptimality does not necessarily imply that adaptation has been constrained. Rather, it can be the case that adaptation itself is the constraining factor, in that resources are wasted on competition because cooperation is hampered by opportunism. Or it could mean that the adaptation is not where we expect it to be, and that another organism has succeeded in manipulating the trait we are examining to its own benefit. Conversely, knowing that these mechanisms are powerful in certain situations, we should be alert when they seem not to work as expected.

2.6: Summary

Having examined spandrels, multilevel selection, and constraints on optimality, a pattern should be evident. Evolution can be seen as a competition between different evolutionary units, and the competitive element is pervasive. So pervasive, in fact, that nearly all disagreements concerning evolution are to do with the relative importance of mechanisms. As West and Sheldon point out, ‘More generally, understanding the relative importance of different potential constraints on adaptation remains one of the biggest problems for evolutionary biology’ (West and Sheldon 2002, 44). ‘Spandrels’ were indeed criticised for several concrete errors and on rhetorical grounds, but the debate concerning the main notion has been confined to how pervasive by-products are, or how limiting constraints are. No one disagrees that there are constraints on optimality; some just assume that selection is such a powerful force that other factors can be ignored. The same goes for multilevel selection—opponents do not question the principle, only the assumption that

selection at any other level than the gene can be a strong enough force to override their preferences.

Where does this leave us regarding the evolutionary science of religion? We have seen that by-product theories are viable, but require just as much empirical support, if not more, as adaptationist theories. We should also be open to the idea of group selection, or indeed selection of any kind, possibly in conflict with standard natural selection operating at genes. We turn now to the evolutionary approaches to religion, to examine problems of adaptation there.

III

ADAPTATION IN THE SCIENCE OF RELIGION

While multi-disciplinary approaches to any science are much appreciated and needed, it is a venture best undertaken with great care. As shown in the previous chapter, the biological concept of adaptation is fraught with complications, most of which have gone largely unnoticed in the evolutionary science of religion. Nonetheless, adaptation is arguably *the* central distinction between different evolutionary theories of religion—on the one hand, there are those who argue that religion is an adaptation, and on the other, those who argue that it is a by-product. What an adaptation is, is more or less taken for granted, and the discussion seems not to have incorporated the theoretical advances made in biology.

In this chapter, I will present the discussion on adaptation as far as religion is concerned. I open with a section on the issue of how religion is to be defined, that old chestnut of studying religion. I argue that the matter is especially pertinent for evolutionary approaches to religion, and that it is time to embrace family resemblance definitions. Second, I examine the chief argument for religion as an adaptation, namely the theory of hard-to-fake signals of group commitment. This is a theory with easily missed caveats, and I present some mechanisms that might make it work. Third are by-product theories of religion, where I will investigate concepts such as hyperactive agency detection and minimally counter-intuitive concepts. Fourth, the arguably underestimated approach of seeing religion as an

evolvable entity in its own right is presented. I will argue that the question of religion's adaptedness probably is best answered by employing a mix of the three viewpoints, and that they are not at all as incompatible as they may perhaps at first appear.

3.1: Defining Religion

The question of how to define religion is as old as the science of religion itself, and still undecided. Sociologist of religion James A. Beckford even claims that 'an all-purpose, universally acceptable definition of religion is unattainable' (Beckford 2003, 20) This is no small matter—Russell McCutcheon calls definitions 'theories in miniature' (McCutcheon 2001, 13), so that not having a definition is not far shy of not having a theory. In an evolutionary framework, a definition arguably becomes more important still, as the question of whether religion is adaptive cannot very well be settled unless one knows what religion *is*. Or at least what one assumes it to be—as anthropologist Marvin Harris once suggested, '[r]ather than employ concepts that are necessarily real, meaningful, and appropriate from the native point of view, the observer is free to use alien categories and rules derived from the data language of science' (M. Harris 1979, 32). With religion being notoriously difficult to define, this is valuable advice. If redescribing religion in this way sounds too drastic, Benson Saler offers an alternative: Perhaps it is time to revive Wittgenstein's old concept of family resemblance (Wittgenstein 1953, §66–71), and see religion as related 'by similarities that differentially overlap and criss-cross, not by sharing some essence' (Saler 2008, 222). His suggestion should have appeal to proponents of evolutionary approaches, as gradual evolution means that things are related by degree, rather than separated by essence, the latter word being frowned upon by evolutionary scientists (Dennett 1995, 36–39). Saler quotes biologist and evolutionary theorist Ernst Mayr as saying that 'Darwin showed that one simply could not understand evolution as long as one accepted essentialism' (Mayr 2001, 83), arguing that the same is likely to be true for religion (Saler 2008, 224).

Turning first to current definitions in the Cognitive Science of Religion, we seem to be back where we started. Tylor famously defined religion as 'the belief in spiritual beings' (Tylor 1871, I:383), a modern version of which could be Guthrie's 'systematic application of human-like

models to non-human, in addition to human, phenomena' (Guthrie 1980, 181). E. Thomas Lawson and Robert N. McCauley are also close, seeing a 'religious system as a symbolic-cultural system of ritual acts accompanied by an extensive and largely shared conceptual scheme that includes culturally postulated superhuman agents' (Lawson and McCauley 1990, 5), and Harvey Whitehouse even accepts Tylor's definition outright (Whitehouse and Martin 2004, 230). But other than this, definitions of religion are curiously absent from most of the major works in the Cognitive Science of Religion. Lee A. Kirkpatrick plainly refuses to define it, claiming that he means 'pretty much what most people mean by the term' (L. Kirkpatrick 2005, 15). Ilkka Pyysiäinen does not see the point in defining religion, because definitions 'only reduce the defined concepts to undefined ones without that much benefit from the point of view of empirical study (sic)' (Pyysiäinen 2004, 54). Boyer, in *The Naturalness of Religious Ideas*, sees definitions as 'the outcome, rather than the starting point, of particular research programs' (Boyer 1994, 33), and also denies giving a precise definition—in *Religion Explained*, he ignores the question altogether. Justin L. Barrett does not define religion in his book *Why Would Anyone Believe in God?*, but he does define gods as 'broadly any number of superhuman beings in whose existence at least a single group of people believe and who behave on the basis of these beliefs' (Barrett 2004, 21). D. Jason Slone, not about to uproot received wisdom, concedes that 'religion is centrally about dealings with postulated superhuman agents' (Slone 2004, 5), but makes a much more interesting suggestion in saying that perhaps religions ought to be 'construed prototypically rather than classically' (Ibid., 71).

A prototypical definition posits a standard with which other entities can be loosely compared, rather than listing a set of necessary condition, all of which a definiendum must meet to qualify. The qualities of such an prototype can be seen as a set of family resemblances, so that the more of those resemblances the case shares with the prototype, the better it fits the definition. For example, orthodox *Theravāda* Buddhism would be a very good fit with most prototypical, or family resemblance, definitions of religion, except of course that it lacks worship of gods.¹ When employing a prototypical definition, one might for example decide that subjects would be

¹ That some *Theravādins* no doubt worship gods is beside the point, which is that some demonstrably don't, and still are seen by most researchers as interesting subjects for a science of religion.

weighed according to their fit with the prototype, or to split analysis in parts, so that each trait making up the prototype would be considered by itself (Martin 2008, 351; Bering 2005).

The example of *Theravāda* Buddhism is but one of the many familiar examples demonstrating that religion is an ambiguous category that does not lend itself to precise, yet all-encompassing definitions. Saler argues that religion is not even a specific thing, but rather ‘variable congeries of different elements [that] did not all evolve together; rather, they arose as spandrels in the evolution of certain capacities and dispositions that offered adaptive advantages’ (Saler 2008, 215–216) The assumption of spandrelism may well be premature, and we should stay open to the possibility that religion might be a conglomerate of spandrels *and* adaptations, but the quote hints that family resemblance definitions are well suited for religion in general, and the question of adaptation in particular. And in fact, the few cognitive scientists of religion who don’t settle for one-sided superhuman definitions or overlook the question altogether seem rather open to the concept of family resemblance (below, see also: S. Atran and Norenzayan 2004; Alcorta and Sosis 2005; Bulbulia 2005; Whitehouse 2008). This approach could even explain the reluctance of some scholars to define religion, for as Barrett writes,

Rather than specify what religion is and try to explain it in whole, scholars in this field have generally chosen to approach ‘religion’ in an incremental, piecemeal fashion, identifying human thought or behavioral patterns that might count as ‘religious’ and then trying to explain why those patterns are cross-culturally recurrent. If the explanations turn out to be part of a grander explanation of ‘religion’, so be it. If not, meaningful human phenomena have still been rigorously addressed. (Barrett 2007, 768)

Tom Sjöblom follows anthropologist Donald Brown (1991, 48) in calling religion a ‘universal of classification’ as opposed to an ‘universal of content,’ writing that these universal of classification ‘share common patterns but not necessarily individual components’ (Sjöblom 2007, 293), which arguably seems like family resemblance. Sperber is explicitly supportive of family resemblance, although ‘a different kind of family resemblance from the one Wittgenstein and Needham (1975) had in mind’ (Sperber 1996, 17). He writes that ‘the resemblance involved is a resemblance in meaning among all the notions rendered by means of the terms, rather than a resemblance among the things referred to by these terms’—an ‘interpretative resemblance’ (Ibid.) Sperber’s distinction may be well worth mentioning, but for the present discussion, the most important point is that he is one of many advocates of family resemblance definitions.

There is good reason for cognitive scientists of religion to be more open to family resemblance definitions than other scholars of religion. Both groups have the problem of religion being a fuzzy category, but in light of adaptation, there is yet another issue. Even if a particular species of animal is well defined, separated from its closest relatives by too many generations for any doubts about delimitation, one cannot well ask if that species is an adaptation. Religion is not only a fuzzy category, it is also an immensely complex one. And the question of adaptation should be asked on a trait basis, not for a whole collection of traits, like religion. We should not expect to discover whether religion is an adaptation, but whether it is composed of traits which are themselves adaptations, by-products, or a mix of the two. While this could well amount to a definition of several necessary traits found in all religions, I think the open-ended approach of family resemblance is better suited still. Family resemblance definitions of religion helpfully shift the imagination away from religions as entities with essences that can be adaptive or not, over to a loose conglomeration of different traits, some of which may be adaptations, some of which may serve largely different purposes but be exploited for religious purposes, and some of which may be cultural, and have an evolutionary trajectory quite apart from our DNA. In other words, endorsing a family resemblance definition is an admission that the subject demands a pragmatic approach, an admission I am entirely comfortable with.

3.2: Religion as an Adaptation

The debate on whether or not religion is an adaptation is fundamentally similar to the old question of functionalism, which has been with scholars of religion at least since Durkheim's day. An interesting difference, perhaps, is that while functionalists have been thought by many to reduce religion to a mere profane matter, their modern counterparts, the adaptationists, now form religion's defence against those critics of religion who see it as a by-product. They claim that religious people live longer, healthier lives, are better socialised, but most importantly, that religion solves the so-called free rider problem. This is what occurs when society as a whole is better off if everyone cooperates, but individuals who cheat, are even better off. Adaptationists

usually argue that religion inhibits cheating by making group participation so costly that would-be cheaters are deterred.

We will first examine the adaptationist side of the argument, which in fact is an elaborate version of the handicap principle. This is the principle that explains the magnificent peacock's tail as a deliberate handicap to demonstrate quality to potential mates, because only a high quality peacock would be able to avoid predation in spite of such a tail (Zahavi 1975). Hence, the disadvantage to survival is offset by signalling that the peacock is still very fit, and hence a suitable partner. Probably the most common argument for religion as an adaptation is William Irons' theory about hard-to-fake signs of commitment (Irons 1996a; 1996b; 1996c; 2001), which has been elaborated upon by several scholars (e.g., Berman 2000; Cronk 1994; Iannaccone 1992; 1994; Sosis 2003; Sosis and Ruffle 2003; Sosis and Bressler 2003). It progresses along much the same lines as the standard handicap argument, and sees rituals as costly endeavours, which only confer individual fitness advantages through signalling commitment. The adaptive problem that a signal of commitment is most commonly supposed to solve can be analysed in the prisoner's dilemma. Arguably the most famous implementation of game theory, this dilemma presents two prisoners who are given the choice of testifying against the other for a reduced penalty, or remaining silent. If both remain silent (mutual cooperation) they will receive a relatively mild sentence because there is not enough evidence for a full conviction. This outcome is called R for Reward for mutual cooperation, and is the best outcome when averaged for both prisoners. For an individual prisoner, however, there is an even better outcome: T, or Temptation to defect. Here, the defecting prisoner testifies against the other, and gets the mildest possible sentence, while the cooperating prisoner gets the hardest possible sentence, the Sucker's payoff, or S. The last outcome is P, Punishment for mutual defection, where both prisoners defect, and get a relatively hard sentence, but with some reward for testifying. For a true prisoner's dilemma, the sentences must be set so that $T > R > P > S$, and for repeated prisoner's dilemma, $2R > T+S$ (Hofstadter 1983). This is to ensure that the optimal averaged outcome is mutual cooperation, although there is a temptation for an even higher reward for lone defectors.

This dilemma is related to the aptly-named tragedy of the commons (Hardin 1968). If cooperation could be ensured, long-term optimality would ensue, but evolution being a myopic

process, defecting opportunists abound. A population of co-operators would have a high fitness, but would be susceptible to invasion by a defecting mutant, who would have an even higher fitness until his descendants would dominate the population so there would be too few co-operators left to free-ride on. An adaptation securing cooperation against this predicament, it seems, would be most welcome.

Alternatively, the problem of cooperation can be interpreted as a stag hunt (Bulbulia 2009a; Bulbulia and Frean 2009), after the thought experiment proposed by Rousseau (1755). He proposed that hunters could choose to hunt for either stag or hares. Stag hunting would benefit everyone the most, but only on the condition that everyone cooperated, because stag are difficult game to hunt. If a hunter suspects that any other hunter is unwilling to cooperate, he has the option of hunting hare. In this case, he will reap a lesser bounty, but one that is not dependent on his hunting party. This scenario is fundamentally different from the prisoner's dilemma, because here, there is no longer any incentive to cheat. Rather, the threat to cooperation is the fear of any other member defecting, which of course will grow the larger the group becomes. Modelling religious cooperation on the stag hunt, rather than the prisoner's dilemma, is an interesting endeavour with potentially far-reaching implications, but that presupposes that cooperative problems for which religion is a candidate to solve, in fact does resemble a stag hunt. For the present thesis, I will concentrate on the prisoner's dilemma, as it seems to be the most common model of cooperative problems in adaptive theories of religion. And if religion or religiousness is a solution to the prisoner's dilemma, then the problem is one of cheating.

This is where signals of commitment come in. An act of cooperation in itself is, by the prisoner's dilemma, detrimental to the fitness of the performer, and as such dependent on the favour being returned. It is in the cooperators' interest to form groups with other co-operators, but how can they ensure that other group members are not defecting invaders? The main adaptive theory of religion suggests that observing costly, hard-to-fake rituals serve as signs of being committed to the group. If they are taken as a requisite for receiving cooperation, it is supposed that free riders will be deterred by the high cost of entering the group, and only true cooperators will remain.

However, this is clearly insufficient. Handicaps work because they demonstrate a surplus of the resource or trait *that is being sought after*. When a peacock grows a splendid tail, or a deer grows great antlers, they are able to do this because they have energy left after living expenses have been paid. If the tail or antlers are symmetrical and spotless, this is an indication that the owner is disease-free, because many diseases would have interfered with this. But when *Haredi* Jews spend most of the day in prayer, dressed in clothing hardly suitable for a Middle Eastern climate, they demonstrate a number of traits, from persistence to compliance, but not necessarily commitment to cooperation. There seem to be nothing stopping a would-be free rider from paying lip service to the rituals, while still avoiding the cost of cooperation.

Richard Sosis suggests that what makes this signalling of commitment work is a combination of differing perceptions of costs and the psychological effects of performing rituals (Sosis 2003). He claims that believers will perceive costs of ritual as less than would non-believers, while simultaneously exaggerating the benefits. Furthermore, merely taking part in ritual stimulates belief. In this way, religious groups tend to be dominated by believers rather than free riders, and these can then more or less embrace an entire set of values, which include cooperation. Sosis mentions two theories that might explain how belief is formed when performing rituals: self-perception theory (Bem 1972) and cognitive dissonance theory (Festinger 1957; 1964). The former claims that people can acquire attitudes and beliefs by observing themselves, and the latter claims that the discomfort of a conflict between attitudes and actions may lead to a change of attitudes. As Sosis notes, the argument does not depend on which one of these is correct, so long as studies demonstrate that beliefs are in fact affected by actions. He gives several arguments and examples that this is in fact so (Sosis 2003, 98–100), one of the most telling being the Unification Church's attraction of members through involving them in a number of activities for months on end before even introducing them to the teachings of the Rev. Sun Myung Moon (Pesternak 1988). If these assumptions are correct, and participation in ritual catalyses belief in group values, so that religious displays act as reliable markers for willingness to cooperate, then this again can be strengthened through group selection. Richerson and Boyd argue that when 'reliable symbolic markers exist, selection will favor the psychological propensity to imitate and interact selectively

with individuals who share the same symbolic markers' (Richerson and Boyd 2005, 212). This, in turn, strengthens the group as unit of selection by reducing within-group variation while reinforcing differences between groups. If then also 'cultural rules arise that cause individuals to sacrifice their own interests for the good of the group, group selection can cause the frequency of individually costly but group-beneficial traits to increase' (Ibid., 162). In the case of hard-to-fake signalling, the demand of such cultural rules is obviously already met.

Richerson and Boyd are writing about culture in general, but on this topic, their theory converges with Sosis', and the two theories reinforce each other. Hard-to-fake signalling can arise because it is a reliable signal of willingness to cooperate, and thus, those who exhibit such signals, i.e. religiousness, will increase their own fitness as they become beneficiaries of the cooperative efforts of their co-religionists. As all this signalling creates well-demarcated groups, group selection begins to act, further increasing the opportunity for cooperation.

But, as group cooperation grows stronger, so does the incentive to cheat. One solution to the problem of cheating is punishment, to remove the cheaters' benefit. However, punishing cheaters entail opportunity costs, and punishers thus face the so-called second-order free-rider problem (Guttman 1978; Yamagishi 1986; Heckathorn 1989). This is the same problem as the regular, first-order free-rider problem, only that now, the public good that cheaters will avoid paying to provide is punishment. The solution that religion is proposed to contribute, is the threat of supernatural punishment (Bering and Johnson 2005; Schloss and Murray 2011). Thus, religious belief not only explains what motivates cooperation in the first place, but also why people abstain from cheating when widespread cooperation would seem to make such cheating profitable. It is as if punishment has been outsourced to gods. Of course, this means that cheating really is no more costly than it would be without the threat of punishment, it only appears as if it is to would-be cheaters.

In contexts where people cannot rely on supernatural punishment of cheaters, we can expect them to be as averse to people who do not punish cheaters as they are to cheaters themselves. This is because the existence of nonpunitive 'suckers' is a threat to cooperation, as 'they make cheating a viable strategy' (Boyer 2001, 186). Perhaps more unexpectedly, it has also been found that also overly unselfish group members are looked at with suspicion. Psychologists Craig D.

Parks and Asako B. Stone (2010) found that members contributing generously to the group, without taking their full share of the benefits, were unwanted in the group by fair members, who felt that the generosity of the former made the latter look bad. It would perhaps be an interesting study to repeat the experiment while controlling for religiosity, to see if that makes any difference.

It should be apparent that the selective problem of cooperation is fraught with difficulties, and not only because it seems to be a mix of individual and group selection. We need to take great care to understand exactly what mechanisms are at work. In the example of the peafowl, there is a strict correspondence between the desired trait (good health) and the signal (splendid tail). It need not be entirely impossible to grow a splendid tail while in poor health, but what matters is that the signal is reliable enough to offset the cost. No conscious effort is required—the peahen may well choose her mate only for his dazzling colours, with no concern for offspring, as long as this preference leads to her mating with a fitter mate than without it. The peacock, on the other side, will grow his tail whatever he thinks of it. But religious beliefs are not so simple. Many may uncritically adopt the religion of their parents, but belief is at least potentially open to conscious decision. Does it make a difference if belief is just the result of blind selection, or if each practitioner consciously evaluates what she stands to gain by adopting the group's beliefs? This is a question that needs to be taken seriously when considering religion to be adaptive, to which we will return later (4.2).

3.3: Religion as a By-product

The main by-product hypothesis of religion concerns the 'hyperactive agency detector,' or HADD for short. This is a purported mind module that anthropologist Justin L. Barrett (2004), following Stewart Guthrie (1980; 1993), argues evolved to avoid predators, but now mainly serves to induce religious belief. This is supposed to work because throughout most of our evolution, it has been adaptive to over-detect agency in our surroundings, because while over-detecting agency is not especially costly, under-detecting it in an environment where other agents might well have a good mind to eat you is an evolutionary nonstarter. Furthermore, minds prone to detecting

agency where there is none, are, according to Barrett, likely to attribute that unseen presence to gods.

The second most important component of by-product-theories is the idea of minimally counter-intuitive concepts (MCI). This idea stems from Sperber and Atran in the early 1980s, and was presented in its current form by Boyer a decade later (Bulbulia 2009b). He writes that ‘certain combinations of intuitive and counter-intuitive claims constitute a cognitive optimum, in which a concept is both learnable and nonnatural’ (Boyer 1994, 121). A potentially religious idea that violates too many ontological expectations becomes impossible to learn, but if it violates too few, it is ‘*ipso facto*, nonreligious and has little attention-demanding power’ (Ibid., 122).

Neither of these are unproblematic assumptions. Barrett himself, writing about HADD in 2008, asserts that ‘no experimental evidence exists in support of this agency detection device playing any role in religious belief formation or transmission, let alone the role that context effects might impact the relative sensitivity or accuracy of this device’ (Gibson and Barrett 2008, 334). In fact, Geertz and Markússon note that ‘repeated, demonstrated false alarms from HADD should equally reinforce beliefs in non-theistic, natural explanations’ (Geertz and Markússon 2010, 157) MCI concepts, on the other hand, have been demonstrated to be less memorable than intuitive ones (Atran 2002, 103), however they do seem to play a role in drawing attention to belief sets mostly composed of intuitive ideas (Ibid., 106). But, can they motivate religious commitment and costly behaviour?

By-product theories of religion in particular face ‘the Mickey Mouse’ problem (Atran 1998, 602). That investigative, talking little rodent is surely as counter-intuitive as most gods, yet no one seems to worship him. Apparently, he is not the first character that comes to mind when people are out operating their hyperactive agency detectors, either. Lest you think worshipping a cartoon mouse is too ridiculous a proposition to consider, the problem has also been posed as the Zeus problem (Gervais and Henrich 2010).² If god concepts are cognitively optimal, what is it that makes different concepts optimal for different people? Both these problems demonstrate that however relevant HADD and MCI might be to the development of religious ideas, they are not

² Not to be confused with the Zeus problem of classical studies, discussed in Conacher, D.J., *Aeschylus’ Prometheus bound: a literary commentary*. Toronto: University of Toronto Press, 1980.

the whole story. Social psychologist Will M. Gervais and anthropologist Joseph Henrich stress the importance of context, criticising cognitive approaches for a one-sided focus on content (Ibid.). Religious context will be further elaborated on in the section on cultural selection, below (4.4).

It is also important to remember that not all religious concepts are minimally counter-intuitive. Some are full-on bizarre, 'extremely hard to learn and pass on.' Anthropologist Harvey Whitehouse suggests that both these forms of religious belief are important, using a slightly modified form of Michael Tomasello's 'ratchet effect' (Tomasello 1999). A ratchet does two things: it holds the bolt in its place, and turns it around. By analogy, Whitehouse suggests that the 'holding' function is fulfilled by MCI beliefs, which are easily enough attained to serve as a more or less constant background in religious traditions. The 'turning' effect corresponds to 'those aspects of religion that build up, cumulatively, over time... essentially an evolutionary process' (Whitehouse 2008, 37). Contributing to this category are the religious innovators, with their complex revelations. This agrees with Boyer's 'tragedy of the theologian,' which is that people misunderstanding religious ideas will distort them and add new ones, and 'that the only way to make the message immune to such adulteration renders it tedious, thereby fuelling imagistic dissent and threatening the position of the theologian's guild' (Boyer 2001, 285).

It is interesting to note in this context that Whitehouse's theory of 'modes of religiosity' describes three ways, consecutively evolved, in which religion is acquired that seem roughly to correspond to the three first sections of this chapter. The first, 'species-typical and more or less invariable, consisting of naturally "catchy" concepts' (Whitehouse 2008, 38) seems to agree with the idea of MCI concepts as a by-product of evolution. The second, the 'imagistic mode' corresponds with intense social cohesion, exclusivity, low uniformity and complex, typically esoteric revelations, seemingly compatible with religion as an adaptation for group cooperation (Whitehouse 2002, 309). The third and final mode he calls the 'doctrinal mode,' characterised by high transmissive frequency, large-scale and rapid spread, and learned ritual meaning (Ibid.). This, arguably, has a strong ring of the third alternative of the present chapter, namely religion evolving by itself. This indicates that the three approaches are not so incompatible as perhaps some assume.

3.4: By-product for Us, Adaptive Unto Itself?

As mentioned earlier, one of the most important considerations when studying adaptations is the level at which adaptation is supposed to operate. An obvious example is adaptations at an individual level that are detrimental to group welfare, but adaptations can also happen at the level of religion itself. Richard Dawkins coined the term *meme* for a unit of culture (Dawkins 2006, ch. 11), behaving in principle like a gene. The basic idea is that memes that are better at getting copied will predominate—for instance, a religion that contained a proselytizing element, or meme, would spread better than a religion where missionary activity was looked down at, and all else being equal, would eventually ‘win out.’ These memes need host organisms, but otherwise are mainly independent of selection at the gene level. In this way, religious memes can exploit mental preferences that evolved for entirely unrelated purposes, to facilitate their own spread. As such, our adoption of religion would be a by-product of big brains capable of culture, but it would still be wrong to say that religion was not adaptive, because it would indeed be, unto itself. According to memeticists, religion’s purpose is for the religious memes to replicate.

When Dawkins proposed the idea in 1976, he meant it more as a thought experiment, and it took almost twenty years before the idea was taken seriously. Then, from 1997 to 2005, an online *Journal of Memetics* was published (Best et al.), but when no significant progress was made after eight years, the journal was discontinued, and memetics is generally considered a failed endeavour today (Edmonds 2005). However, it is worth mentioning that it is not the basic premise of memetics that was in dispute. Memetics is a fairly straightforward extension of natural selection, well compatible with what Dennett has called ‘the Darwinian Algorithm’ (Dennett 1995, 48–51). The problem was mainly that no one was able to properly operationalise the concept, as memes elude definition in several respects. And whereas genetic evolution is mediated through the brilliantly adapted DNA molecule, a meme too vague even for definition seems only to allow for very weak selection at best. A related objection to memetics is that cultural transmission is of too low fidelity—for instance, every time a story is retold, it changes, and presumably too much for evolution to work (Benítez-Bribiesca 2001).

Nevertheless, memetics is not the only candidate for a theory of cultural evolution. One of the more intriguing is Robert Boyd and Peter J. Richerson's cultural selectionism, or dual inheritance theory, as it emphasises the importance both of genetic and cultural transmission (Boyd and Richerson 1985; 2005; Richerson and Boyd 2005). They claim that because of the particularities of culture, it can evolve even without a unit of selection, and thus their theory avoids the main problem of memetics. To understand this, we need to remember that genetic evolution depends on the particulate inheritance of traits. Save for mutations, genes are passed down intact from parent to offspring—for any given locus, you are likely to inherit either your father's gene or your mother's. If instead genes had been mixed, so that each of your genes had been an average of your father and your mother, this averaging process would 'use up' the variation required for evolution. It is worth noting that because of the DNA molecule's extraordinary copying fidelity, mutation rates are generally surprisingly low: research on the roundworm *Caenorhabditis elegans* has revealed mutation rates as low as 2.1×10^{-8} per site per generation, which amounts to 2.1 new mutations per worm (Denver et al. 2000). Mutation rates vary among species, but not by much (Freeman and Herron 2007, 148). Boyd and Richerson's theory elegantly lets the two main flaws of memetics cancel each other out. No unit could be found, and variation was too high. But a unit of selection is only required when mutation rates are too low to maintain variation by itself. Errors of transmission, abundant in culture, will 'keep pumping variation into a population as blending bleeds it away' (Richerson and Boyd 2005, 88).

Whatever the mechanics of cultural evolution, it is likely a force to be reckoned with, and the possibility that religion exists at least partly for its own sake, should be seriously considered. Note that this scenario is a true combination of both the by-product and adaptationist view. If religion exists for its own sake, then it could not be our adaptation, but rather our willingness to embrace religion would be a by-product of some or other mental predisposition. At the same time, just as genetic evolution produces adaptations, so does cultural evolution. And as a product of cultural evolution, religion would likely be adapted to us, its hosts. To see how this might work, we will examine a few examples of religion as an evolving entity in itself.

Long-time critic of religion Richard Dawkins wrote a short paper on what he saw to be ‘Viruses of the Mind’ (Dawkins 1993), referring to what he saw as a pathological spread of religious memes. He emphasises the human mind’s susceptibility to memetic infections. Like with cells and hard disks hosting viruses, brains have two qualities in particular that allow for this: ‘firstly, a readiness to replicate information accurately, perhaps with some mistakes that are subsequently reproduced accurately; and, secondly, a readiness to obey instructions encoded in the information so replicated’ (Ibid., 19). Dawkins also shows runaway selection to be at work in religion: He cites a rabbi taking pride in keeping kosher precisely because they are meaningless (Ibid, 22), and a televangelist claiming that ‘God really appreciates a donation... only when that donation is so large that it hurts’ (Ibid, 24). Note that runaway selection works in a slightly different way here than in the standard adaptationist view of religion. On that view, excessive ritual is to display group commitment, so that other members know that cooperation will not be wasted. According to the memetic view, however, it is more of a kinship function: excessive ritual demonstrates that religious memes are present. Then, if there is a religious meme instructing its hosts (practitioners) to help other religious practitioners, then this will confer a fitness benefit to likely carriers of that same meme. For example, such a meme might cause a religious person to sacrifice his life for those of two of his faith. As they likely carry that same meme, one would be sacrificed to save two. This would be adaptive behaviour on the part of the meme, although not necessarily on the host’s genes.

While primarily a proponent of a more standard by-product theory, Pascal Boyer’s hypothesis about religious guilds (Boyer 2001, 273–285) is clearly concerned with cultural evolution. Boyer suggests that as literacy arose, so did a class of scribes. These scribes, Boyer argues, became involved in the production of religious texts and formed guilds to protect their interests and control the market. However, unlike other guilds, the religious guilds sold services which could be imitated by outsiders. They compensated for this by trying to gain political influence. Note that according to Boyer’s argument, this need not be an inherent preference for religious groups, but rather, those who happen to seek political influence are those that prevail—or, in more evolutionary terms, political influence is selected for. In other words, when considering guilds,

religiousness is not an adaptation of people, for political power, but an adaptation of religions, for outcompeting other religions.

3.5: Summary

I have examined the problem of defining religion, and three approaches to the question of its adaptedness. For the evolutionary science of religion to thrive, I believe a number of issues pertaining to these must be addressed. First off, we need to be explicit about what it is that is being studied. A trait cannot be said to be an adaptation if we are not sure what that trait is. Second, we need to examine what mechanisms of selection are operative, and where. Does blind selection decide for us whether or not we should believe, or are we mediators of cultural selection, evaluating whether or not religions are beneficial for us? Third, if not adaptations, then what? Merely suggesting that religion is a spandrel is not enough, without positing some alternative force that keeps the spandrels in their place. Something so complex and influential as religion can hardly expect to be untouched by selection, unless some stronger force outweighs it.

IV

DISCUSSION

Having surveyed the debate in both biology and the science of religion, it is now time to follow the threads, and see what new insights we can glean based on the presentation of the biological adaptation debate. I believe several points have been missed in the discussion so far, and need to be taken seriously by future research.

First of all, we can do well to be clearer about what we are studying. Just claiming religion to be an adaptation or not is too simplistic—we need to investigate thoroughly what the relevant traits are, and only then ask about their adaptive status. Second, if selection is so good at undermining cooperation, and religion is an adaptation for cooperating, why aren't cheaters outnumbering believers? Does not an adaptive theory of religion require the help of fortunate constraints? Third, if religion is not an adaptation, but a by-product, is it not too significant for selection to ignore it? What constraining forces do by-product theories of religion assume, if any? Fourth, for a cultural science, surprisingly little attention has been paid to the possibility that there might be selection acting on different cultural variants. If this was to be given serious thought, what might the implications be for a science of religion? And finally, are adaptations 'good'? Is there any danger of confusion when discussing the benefit of religion? Is the benefit to us, our genes, or to religion itself?

4.1: What's a Trait?

Philosopher of biology Tim Lewens has argued that ‘one of the most significant lessons that the Spandrels paper teaches is about the importance for evolutionary biology of an empirically grounded account of what is, and what is not, a trait’ (Lewens 2008, 180). With all the debate about how to define the subject matter, this is a problem easily applicable to the evolutionary science of religion.

First of all, we need ask what we are looking for—is it religion or religiousness? However religion is defined, it is not a trait that people can have. One can adhere to a religion, but one cannot ‘have religion.’ Religions are sets of culturally specific practices and beliefs, with a far greater variance than can be explained by genes alone (cf. Aunger 2002, 41–46). Religiousness, on the other hand, is more likely to be a biological phenomenon (although it need not be, if religion is a cultural phenomenon altogether). In other words, if there is something biologically adaptive to religion, it is the tendency to acquire it, namely religiousness. If, on the other hand, we are considering cultural adaptation (as we will return to in 4.4), then ‘religion’ is what we’re after. The most pressing concern, however, is the near-universal human propensity for religiousness, so we will start there.

Thus, we need to identify the different aspects of religiousness in humans, and examine whether they might be independent traits, or aspects of the same trait. Lewens suggests a complication: Some traits might be so strongly linked through developmental constraints that they cannot really be considered separate traits at all, although they seem to be (Ibid: 166). His example is a scenario where it would be optimal to have short forelimbs and long hind-limbs, but where linkage reduces the available traits to long or short limbs, period. Perhaps also in religion, some practice which in itself is entirely maladaptive is so intricately linked to an adaptive practice that they must be considered two aspects of the same trait. This is the old by-product argument again, but we should remember that it can be valid for adaptive religious traits as well—for example, private rituals might just be a by-product of public ‘signalling’ rituals.

Furthermore, we should seriously consider whether some traits commonly assigned to religiousness might be adaptations while other traits are not. This is implicit in Sosis’ assumption

that 'cognitive, emotional, and behavioral elements were exapted for use in a complex system of communication, cooperation, and coordination, namely the religious system' (Sosis 2009, 323). Here, a by-product such as HADD is a fundamental component of an adaptive system of commitment signalling. There is no need to commit to a view of religion as either an adaptation or a by-product.

There is a possibility, however, that religion does exist as an adaptive system—a collection of traits where the collection itself is an adaptation (Purzycki, Haque, and Sosis forthcoming). Purzycki *et al.* compares religion to the immune system, which they claim no one would argue 'is not an adaptation, yet we find no one claiming that there is a particular locus of this adaptation since the system is composed of a number of interacting units and they must function together to maintain the defensive capabilities of organisms against infectious microorganisms' (Ibid., 4). This is certainly a possibility, yet it cannot be taken for granted in the way adaptationists seem to have done in the past. And again, one does not exclude the other—different religions may have different evolutionary trajectories. When it comes to religiousness, however, the situation is different. The human genome is 'remarkably poor in polymorphism' (Bertranpetit et al. 2004, 81), and we should perhaps not expect the *biological* trait of religiosity to vary much—although that question possibly warrants a study in itself.

To sum up, then, the adaptive status of *religion*, as a cultural phenomenon, may vary from case to case, and even within each case: a religion may consist of adaptive and non-adaptive traits both, or it may be an adaptive system. The same is the case with *religiosity*, construed as a biological trait, although here, the answer seems less likely to vary between populations. In other words, if the tendency for religiousness is found, for example, to be an adaptive system in one group, it is likely to be an adaptive system in all groups. At the same time, different religions may well differ in adaptive status. The take-home lesson, at any rate, is that the question 'is religion adaptive?' is far too simplified and need to be refined by distinguishing between religion as a cultural trait and religiousness as a biological trait, and opening up for the possibility that both may be composed of sub-traits of varying adaptive status.

4.2: Adaptive Constraints

Although commonly considered in opposition to selection, constraints can have an adaptive element, too. If, as shown in chapter 2.5, selection can produce suboptimal traits, then it follows that constraints acting on such selection are beneficial. A typical victim of untimely selection is cooperation: Although, under the right conditions, everyone would benefit by cooperating, free riders would benefit even more, and outcompete cooperators. But cooperation is just the thing adaptationist explanations claim that religion promotes—thus, assuming that religion exists to promote cooperation and free riders would have an advantage over true believers, something has to constrain the evolution of free riders. However, an adaptive, widespread constraint seems too good to be true. Unlike adaptations, constraints cannot proliferate on account of being adaptive, which makes it hard to explain how religious cooperation can be so ubiquitous as it might seem. If the natural tendency of evolution is to select for free riders in the face of cooperation, and religions all over the world are centred on cooperation, how is it that free riding is constrained in all of them? It is hard to see how something so obviously beneficial as free riding could be subject to a constraint that would apply to all of the world's religions (or most, if religion-as-costly-signalling only explains a subset of all religions).

Let us examine again our list of seven constraints, to see if any of them might explain how free riding does not arise in religious communities, or at least arises seldom enough to make hard-to-fake signalling of commitment a significant explanation of religion. These are: (1) time lags, (2) historical constraints, (3) available genetic variation, (4) constraints of costs and materials, (5) imperfections at one level due to selection at another level, (6) mistakes due to environmental unpredictability, and (7) developmental constraints. To begin with, examining (2), (3), and (7) cannot be explored in this thesis, but it is hard anyway to see how they could work against free riding, which evidently, at least in other settings, is within the range of human phenotypes. Constraints (1) and (6) seem highly unlikely given the already long history of human religiousness, and (4) is also implausible—how can paying less for group benefits be constrained by cost? Sosis' claim that believers perceive costs differently (Sosis 2003) could well explain why

believers are constrained from free riding, but it cannot explain why unbelief is not more common.

The final sort of constraint is in fact selected for, although not by virtue of its constraining element. The lack of free rider evolution could be seen as (5) imperfections on one level due to selection at another level, if we see the group as that other level. If in fact free riding is constrained by group-level selection for altruism, as particularly David Sloan Wilson argues, then strong group selection pressures could explain why such a constraint is so widespread as signalling theories of religion apparently requires it to be. In fact, the fit with the data might be very good—while under other constraints (2, 3 and 7 in particular), the constrained genotype is often entirely unavailable, constraint (5) merely implies that it will be selected against on another level. In the case of free riding, although group-level selection for altruism will constrain it, there could still be some selection for it on the level of genes. This agrees with Sloan Wilson's claim that selfish behaviour will be selected for within groups, while between-group selection will promote altruism (D. S. Wilson 1975). Even though religion in general might be strongly cooperative, one easily imagines new atheists such as Dawkins having a field day looking for examples of free riders in religion—certain televangelists with double standards come to mind.

Whatever the exact mechanism of constraint, this is an area where adaptationist theories of religion have failed. While they do explain how religion can be adaptive, they do not properly explain how free riding whilst merely faking religious commitment is not common enough to thwart religion's adaptive function. Saying that belief is generated merely by performing rituals (Sosis 2003) might well be a step in the right direction, but what is needed is an explanation for why no 'defence' against this mechanism has evolved—an ability to fake commitment when needed, while avoiding paying the costs of co-operation whenever it is possible.

4.3: Alternatives to Selection

If lessons from biology have been disregarded in incorporating an evolutionary framework to the study of religion, arguably the greatest neglect concerns by-product theories. There is some irony here: The same error that Gould and Lewontin accused adaptationists of is brazenly committed

now in the name of by-products. But as the ‘spandrels’ controversy showed, claiming traits to be by-products requires *more* work than assuming them to be adaptations. No such discussion is found concerning religion as a by-product, rather, religiousness is seen simply as a secondary property of other, adaptive traits. But something as significant as religiousness is hardly likely to be without fitness effects—if these are positive, it hardly makes sense to call them by-products, and if they are negative, what constraints are limiting selection working against them?

A look at biological by-products might be instructive. When a gene has more than one phenotypic effect, it is called pleiotropy. Its secondary effects may be detrimental—this is antagonistic pleiotropy. The classic example is senescence, or biological ageing (Williams 1957). Traits that are beneficial at a young age may well have deleterious side effects in old age, i.e. senescence is the late onset by-product of adaptations. For example, the gene labelled p53 is integral to the body’s defence against cancerous cells, but also has the adverse effect of depleting stem cells, leading to ageing (Rodier, Campisi, and Bhaumik 2007). Antagonistic pleiotropy of this kind is possible because selective pressures are stronger around an individual’s reproductive peak than later in life—genes that cause their hosts to die before raising progeny will not last, but genes that only cause death later in life might (Freeman and Herron 2007, 494). If the benefits outweigh the cost, antagonistically pleiotropic genes can spread. As such, pleiotropy is yet another cause of suboptimality, in addition to the constraints and maladaptations mentioned in Chapter II. But, while these mechanisms in many cases effectively rule out evolving optimal traits, pleiotropy may only be a delaying factor. Even though a selected-for gene has deleterious side effects, the possibility is still there for modifier genes to cancel out these (Dawkins 1999, 35). This does not always happen, as is evident from the depletion of stem cells by the p53 gene, mentioned above. Still, the possibility of modifier genes show that it is not a necessary by-product, but one that could conceivably be selected away. If this does not happen, we are left with the possibility that the evolution of modifier genes has been constrained.

Whether by-products such as religiousness caused by HADD or MCI qualify as pleiotropic effects might depend on your outlook,¹ however, the principle is the same—there’s no particular

¹ Typically, pleiotropy refers to two or more effects of a single gene, which is unlikely to be the case for religion (L. B. Koenig and McGue 2011). A case where several genes have an aggregate by-product, as is more likely here, does seem analogous, but I’m not certain that such a case warrants the use of the term ‘pleiotropy.’

reason modifier genes should not evolve, unless (a) religiousness is either adaptive or neutral, or (b) evolution of modifier genes is constrained. If religiousness is adaptive, it is hard to show that it has not also been selected for, and as such, it makes no sense to speak of it as a by-product. To my knowledge, no one has demonstrated religiousness to be adaptively neutral, and given the significance of religion, it hardly seems likely that it is. To claim that religion is a by-product, then, would seem to necessitate an examination on what factors might be constraining the evolution of modifier genes. Again, this seems to be lacking from the literature.

It is not inconceivable that religiousness really is a by-product, but it is a tall claim that needs to be rigorously tested. In particular, time lags and lack of genetic variation seem viable candidates for constraints on modifier genes, perhaps coupled with low selection pressure. Also, we should keep in mind that even though religiousness might be linked to other traits that are adaptations, religiousness could be an adaptation all the same. As Dennett writes, ‘every adaptation is one sort of exaptation or the other—this is trivial, since no function is eternal; if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all’ (Dennett 1995, 281). In other words, if a trait is adaptive, it will be selected for its adaptive function, and in time, be indistinguishable in this regard from any adaptation.

4.4: Biologically or Culturally Evolved Adaptations?

With few exceptions, evolutionary and cognitive scientists of religion have focused on the question of biological adaptation. It is my contention that this is unfortunate, and that a lot is to be gained by adding cultural evolution to the mix. This changes the question of adaptation radically: While a biological adaptation outperforms the alternatives in spreading certain genes, a cultural adaptation spreads (thus far loosely defined) bits of culture. The relationship between the two might well be symbiotic, but it need not be; In particular, memeticists have been fond of seeing culture in terms of viruses (Dawkins 1993; Brodie 1995). Richerson and Boyd put the matter succinctly, writing that ‘if we fail to find the predicted sorts of maladaptations that derive from the Darwinian theory of cultural evolution, the whole theory is suspect’ (Richerson and

Boyd 2005, 151). By this they mean that since genes and culture are transmitted differently, their criteria of success are different too, and we should expect that in some cases, conflicts will arise. If cultural evolution really is a significant force, then, we should expect it to have serious implications for any evolutionary theory of religion.

Here, I am concerned mainly with adaptive theories of religion. I mentioned earlier (3.2) that whether selection for belief is conscious or not is important, and this is what I had in mind. Imagine on the one hand that the cost-benefit analysis of whether to believe is made purely by selection acting on genes, and on the other hand that we are equipped with a capacity for making cost-benefit calculations in questions of religious affiliation. These are distinct scenarios. The first in particular faces the free rider problem, because natural selection is blind to perceived benefits. It is not inconceivable that, coupled with actual belief, religiosity can be selected for on a genetic level, but perhaps it is easier to assume that humans assess the costs and benefits of joining a religion? In this case, it suddenly becomes entirely plausible that the benefit of joining a religion is wrongly evaluated. This need not happen on a conscious level, what is important is that the mechanism for selecting a religion is divorced from the actual benefits it is supposed to confer. In standard natural selection, this is not the case: If the selective environment calls for sharp teeth, sharp teeth will be selected for the benefit to their owners. The alternative is a kind of selection by proxy: A mental cost-benefit evaluation module of sorts is selected for its general prowess in identifying adaptive strategies, but as long as it works well enough on average for continued selection, any strategy that can fool the module will be just as likely to be chosen as a correctly identified good strategy. A strategy, on this view, is a unit of cultural selection, selected not for its direct benefit to genes, but rather its fit with a genetically evolved bias. In this context, a religion is such a strategy. Religions promise that by paying certain costs, benefits will be obtained, and while the benefits are typically inflated (eternal life in heaven, &c), the costs are played down, for example by presenting them as virtues.

On this view, the free rider problem becomes less pressing. Because cultural selection can operate much faster than biological selection, time lag becomes a perfectly acceptable explanation for why free riders do not appear in greater numbers. Remember that on this view, a religion's criterion for success is not any of the biological ones that free riding would optimize, but rather

the fit with a mechanism of detecting good strategies. In other words, a religion that promises great benefits can be selected over a religion that actually delivers such benefits.

The costs of group membership imposed by religions may in fact suggest cultural evolution in yet another way. Richerson and Boyd (2005, 183), using the Amish as an example, point out that the high standard of asceticism in fact acts as a cultural defence against ‘the flow of ideas from the world of the flesh.’ In other words, costly signals might not be signals at all, but rather cultural adaptations of religions to keep its adherents preoccupied with that religion. As with so many of the scenarios presented in this thesis, however, one does not preclude the other, and cultural selection and religious signalling may well exist in a symbiotic relationship.

There is another context where cultural evolution will be relevant. In scenarios where religion benefits a powerful minority, such as in Boyer’s hypothesis of the religious guilds (Boyer 2001, 273–285; 3.4 above), it is unlikely that the benefit is to genes, because religious affiliation is not transmitted genetically. Adopted children do not preserve the culture of their biological parents, but the one they are brought up in (Richerson and Boyd 2005, 39). That religious leaders in fact do benefit from their position is not necessarily relevant, as long as a significant portion of them are celibate, or otherwise hold positions that are not hereditary. Some cases, where religious positions are hereditary, could perhaps be explained biologically with reference to this benefit, but for the rest, the evolutionary benefit of religious power and influence seems to be to the religions themselves. Whether the beneficiary is a lineage of priests or a religion, the parallel to extended phenotypes is worth pointing out: Dawkins demonstrated that traits may well be produced by forces extrinsic to the host organism, and there is no reason to assume that the same process cannot operate with respect to religion.

The idea that culture evolves in its own right is far from new, but unfortunately, it has not received the attention it deserves. Even if the hypothesis outlined above should turn out to be mistaken, the possibility of a kind of evolution not predicated on gene reproduction drastically changes our understanding of what is going on. The apparent failure of memetics should not deter us from investigating other ways in which culture might evolve. At any rate, we should recognise that culture is a force to be reckoned with when it comes to human evolution, even if it should turn out—and I hazard it won’t—that mapping the evolution of culture itself is futile.

4.5: Who Needs Adaptation?

As mentioned, scholars favouring a by-product approach to religion tend to be more critical of religion than adaptationists. It is worth reminding that although we are all products of evolution, by now we have reached a level of complexity such that we need no longer share evolution's 'goal' of mere proliferation. Indeed, we have attained a level of fitness so extreme that we might soon overpopulate the earth, if we have not already. Our genes might act as if it was in their interest to proliferate indefinitely, but it certainly is not in ours. That said, adaptive behaviour often, perhaps ordinarily, coincides with our interests, and it is not absurd to suggest that there is, at least, some loose correlation between how adaptive religion is, and how good it is for *us*. But these *need* not be linked. It is worth examining endorsements of religion to see if the traits in question are really adaptations, or just incidentally good for us. It is also worth examining the apparent linkage between critique of religion and assuming it to be a by-product, on the one hand, and approval of religion and seeing it as an adaptation, on the other hand.

A common argument is that religiousness is conducive to improved mental health (Grinde 1998, 25; Sanderson 2008, 150; McGuire and Tiger 2009, 133). While the point can well be made that this might improve individual fitness (Grinde 1998, 24), we should remember that religion also creates a significant amount of anxiety (Boyer 2001, 20; L. Kirkpatrick 2008, 64), and also that mental health problems are likely to be a fairly recent phenomenon, evolutionarily speaking (E. O. Smith 2002). General claims about religion's positive health effects have also been made (Ferriss 2002; H. G. Koenig, McCullough, and Larson 2001; H. G. Koenig and Cohen 2002), but here, too, we should be careful to make inferences from a longer post-reproductive life to adaptation (L. Kirkpatrick 2008, 64)—a possible, but not necessary connection.

We should perhaps remember to look at this from the other side, as well. Some adaptations can, however good they are for spreading genes, be bad for society. Cooperation might sound like something we cannot get enough of, but armies, crime syndicates and terrorist organisations rely on cooperation, too. As Matt Ridley, following George Williams, puts it, 'preferring the morality of group selection to the ruthlessness of individual struggle is to prefer genocide to murder It

is a rule of evolution to which we are far from immune that the more cooperative societies are, the more violent the battles between them' (Ridley 1998, 193).

Another possibility is that adaptive traits of religions used to be good for us, but are not any longer. That religion at least has the potential to increase fertility is well documented (e.g., Janssen and Hauser 1981; Heaton 1986; Sosis 2003; Frejka and Westoff 2007), and that might have been a desired effect in the past. But at seven billion people, struggling with inequality and an escalating climate crisis, more fertility is arguably the last thing we need now.

It might be that not very many confuse adaptation and what is good for us psychologically, morally, &c, but it should be worth pointing out that the two are at best loosely connected. Religion might be a by-product and true at the same time, as observant Christian and by-product theorist Justin L. Barrett would testify (Henig 2007), or it might be adaptive, yet false and bad for us. Nature, it seems, does not care one way or the other.

4.6: Summary

If my analysis has been correct, a close examination of the adaptation discourse in biology has indeed been fruitful, and a number of questions warrant closer inspection. First, the very question of religion's adaptedness needs refinement; Are we talking about religion as a cultural phenomenon, or the biological trait religiousness? And can these be further subdivided—is religiousness a single trait, or is propensity to perform ritual one and belief another, for instance? Second, why do not cheaters thwart religious cooperation? If belief is a group-level adaptation, then unbelief should be the individual's optimal reply. Is this happening? Third, if religions or religiousness does not serve an adaptive purpose, what constraints hinder selection's removal of them? Fourth, can studying cultural evolution bring new insights to the study of religion? Is religiousness biologically adaptive, or is it merely religion that is a cultural adaptation, which by chance happens to be adaptive for us as well? Is it a mix of the two? And fifth, are we taking the requisite care to avoid confusing adaptive benefit with benefit to *us*? These are all questions the evolutionary science of religion needs to take seriously. With any luck, pursuing them will lead to new insights into our fascinating subject.

CONCLUSION

Surveying the literature on adaptation has prompted several hopefully interesting questions, but what are the broader implications of all this? The evolutionary approach to religion is still only a minority endeavour, so for most students of religion, the questions posed here are not even considered relevant. I argue in the following that the evolutionary framework should be the natural choice for future studies of religion, and that this will greatly improve compatibility with other sciences. Second, I argue that the strong division in the evolutionary sciences of religion is ill-advised, and call for a synthesis between the two views.

5.1: The Need for an Evolutionary Approach

A good century ago, the promising project of applying the already successful concept of evolution to the humanities and social sciences was tainted by an overly simplistic approach, and the implication of primitive societies as inferior. One is tempted to speculate that the association with social Darwinism and the massive collective trauma of World War II did not help that project's esteem, either. But the continued reluctance of social scientists to adopt evolutionary approaches can be hard to understand. Darwinism is arguably the greatest success story of modern science, and human beings are undeniably Darwinian subject matter. At the same time, possibly the greatest threat to public acceptance of science

(aside from the dreadful denial of climate change) is found in opposition to the theory of evolution. But how can we expect the man in the street to take evolution for a fact, when not even scientists can agree on its applicability? Can we really blame people for questioning evolutionary theory if there is disagreement among scientists as to whether it is *the* theory that explains human nature? Granted, arguing that human nature is too complex for evolutionary studies to be at all feasible is not the same as arguing that evolution is irrelevant, but that distinction may well be lost on those without scientific training who are weighing arguments of evolutionary theory versus creationism. In the worst case, by not studying the humanities in an evolutionary framework, not only are we missing out on valuable insights, but we are potentially undermining public respect for scientific findings.

Evolutionary approaches to religion have been criticised, sometimes with good reason, for being arrogant and hostile to other perspectives (Rydving 2008). While this could go some way in explaining why they have not been more successful, it is of course entirely irrelevant to the validity of the theories. One might also add that an even graver sort of arrogance is being committed by those who reject evolutionary explanations—denying the relevance of the theory that accounts for the origin of our subject matter (at least for the social sciences in general) is not to be done lightly. So why this reluctance?

The critique seems to have a handful of reasons, none of which amount to any reason to shy away from evolutionary approaches. I will call them (1) genetic determinism, (2) territoriality, (3) nothing new, (4) erroneous research, and (5) applicability. By ‘genetic determinism,’ I’m thinking of the belief that an evolutionary approach necessarily reduces everything to genes, greatly simplifying the issues at hand. ‘Territoriality’ refers to the fear that biologists might encroach on the social sciences. ‘Nothing new’ is the claim that evolutionary approaches don’t add any new insights, but merely frame them in a new way. ‘Erroneous research’ concerns critique against findings, and ‘applicability’ refers to whether these approaches can be utilised in all relevant questions.

Claims of genetic determinism have plagued evolutionary biology (Dawkins 1982, ch. 2), and there is every reason to believe that scepticism against evolutionary sciences are based at least

partly on beliefs that they reduce all explanation to genes. As Dawkins and others have noted, this is simply not true—Richerson and Boyd suggest that rather than looking at genes as blueprints, we should think of them as recipes where ‘the ingredients, cooking temperature and so on are set by the environment’ (Richerson and Boyd 2005, 9). But there is a broader, more interesting point here: Reductionism. For someone studying the complexities of the humanities, wariness of reductionism is understandable, but I argue rather that reductionism be embraced enthusiastically. Recall the arguments about adaptationism—although other forces than selection undoubtedly are operable at times, investigating them is often so difficult, that headway can only be made with the simplifying assumption of adaptation. Economical first guesses are just that—they don’t burn any bridges, and we can revise our findings later, if new evidence comes to light. E. O. Wilson neatly sums up the issue, writing that ‘[c]omplexity is what interests scientists in the end, not simplicity. Reductionism is the way to understand it. The love of complexity without reductionism makes art; the love of complexity with reductionism makes science’ (E. O. Wilson 1998, 59).

It is easy to argue that territoriality shouldn’t be a problem, but the fear is perhaps harder to assuage. Quite simply, if evolutionary approaches turn out to be the best tool to studying religion, then we should welcome the change, and adapt accordingly. Psychologically, of course, it might not be so easy for scholars well set in their ways. I can think of no better way to persuade such scholars to adapt evolutionary approaches than to demonstrate that they produce convincing results, accommodate complexity, and not least, are extraordinarily interesting. But most of all, territoriality isn’t a real argument—one must hope that in the end, the fittest alternative prevails.

So what about those who claim that incorporating evolution accomplishes nothing new? Here I say only that translating findings about religion into a language shared with biology and other disciplines is hardly ‘nothing new.’ Even if really novel discoveries haven’t turned up yet—and I daresay they have—unifying the sciences, or trying our best to do so, is a worthy achievement in itself. Interdisciplinarity and unification should be a goal of all science, and for the science of religion, indeed all social sciences, biology and evolution seem the most natural allies.

The final two points are taken in particular from Håkan Rydving's (2008) critique of the cognitive science of religion (surely an evolutionary approach), and I will conflate them here—not because they are identical, but because the solution is. First, he points out several methodological problems with a number of studies, and then he argues that cognitive theories are inadequate for investigating a number of issues. From what I can see, there is nothing fundamental with either of these complaints, and the solution is simply to work harder. Rydving even gives very specific suggestions as to how the studies in question can be improved—hardly something he could do if the discipline was fundamentally flawed. When it comes to applicability, we have yet another reason to study cultural evolution; I think it would provide the flexibility needed to tackle the questions Rydving supposes cannot be answered with a cognitive approach alone, such as how Pentecostal movements vary so much in success in different Latin-American countries. At any rate, for a discipline still in its infancy, the evolutionary science of religion seems to be doing remarkably well, although that's not a defence we can keep rehearsing indefinitely.

In the end, I think a shift is inevitable, but if that is for the better, as I think it is, then it is the responsibility of the scientific community to speed up that shift. Evolution has been one of the greatest discoveries of science, and it produces staggering results. Biologists Scott Freeman and Jon C. Herron aptly comment on the theory's predictive power: 'If we had a theory that worked like that for picking stocks or race horses—well, we could have retired years ago' (2007, 196). Granted, they were commenting flour beetles; human culture is likely to be orders of magnitude harder to untangle. It is very amusing when Pascal Boyer complains that it takes several chapters even to 'approach a question that many people, in [his] experience, can solve to their satisfaction in a few seconds of dinner-table conversation' (2001, 50), only to produce 'the full history of all religion (ever)' in two and a half short pages (*ibid.*, 326-8), but of course it is not that simple. Evolution is a powerful tool, but not a magic bullet—yet more than good enough, I think, to embrace wholeheartedly. Incidentally, for those who might be worried that evolutionary approaches will focus on genetics and biology to the detriment of culture, studying cultural evolution offers the prospect of giving culture its due within that framework. And what's more, if one considers that a constraint is really any force that counteracts natural selection, then

evolutionary theory easily accommodates rival theories—if a scholar thinks that evolutionary approaches are irrelevant because theory *x* explains religion much better than natural selection does, then *x* should be fairly easy to recast as a constraint on selection. In other words, rival theories can be construed as showing how selection has *not* been able to create the behaviour we would expect. Or: if selection has produced a given trait, then surely an evolutionary explanation is required; if, on the other hand, the trait in question is not an adaptation, evolutionary theory fully accommodates an explanation of the trait's origin by examining how selection was constrained in that particular case. Not only does this have the benefit of increasing consilience, by presenting the theory in a scientific language that can and should be common to the social sciences and biology, but it is also a good way of confronting evolutionary theories. Evolution's role in the origin of humanity is universally accepted,¹ so a theory that claims that religion arose otherwise should at least account for how selection had no say in the matter of the origin of religion, not to mention why other evolutionary mechanisms such as constraints are disregarded.

In short, I can see no reason to stray away from an evolutionary approach to studying religion, and several reasons to adopt one. Perhaps the most important of these is that an evolutionary framework seems our best shot at making social and biological sciences commensurable, which is a worthy goal in itself. If I am right that existing non-evolutionary theories of religion could be recast as constraining selection in various ways, then the evolutionary approach should be an obvious choice.

5.2: Can We Get Along?

This thesis has presented a number of controversies, from the adaptationist/spandrelist debates in biology and the science of religion, respectively, to levels of selection, and whether to adopt an evolutionary approach to studying religion. I think in fact that the differences are not as critical as we might assume. As has been mentioned earlier, most debates in evolutionary biology

¹ In response to the Discovery Institute's list of 700 scientists doubting evolution, the National Center for Science Education launched 'Project Steve,' a tongue-in-cheek list of supporters of evolution where only scientists named Steve were allowed to sign. That list is currently at well over 1100 scientists, which should indicate a support for evolution at well above 99% in the scientific community. See <http://ncse.com/taking-action/project-steve>

concern quantitative differences—the degree to which particular mechanisms affect the outcome of evolution, rather than whether or not they exist at all. This of course means that they are not matters of us or them, from which a clear-cut winner will eventually emerge. As we have seen, both sides in the biological adaptationist/spandrelist debate to a large degree recognise the other—clearly constraints exist, and clearly adaptations are a prominent, even perhaps the most prominent, mechanism of evolutionary change. It is almost—almost—so that we can say that the two sides are in perfect harmony, and scientists can more or less choose sides based on research interests, rather than evaluating who is right. Granted, the at times heated debate indicates otherwise, but to a large extent, they are two sides of the same coin, rather than different denominations.

I think this point is all the more valid for the science of religion. Perhaps most obviously, adaptationist accounts do not rule out the possibility that religiousness is based on traits that in the first place appeared as by-products, such as HADD and MCI. I hope furthermore I have been able to show convincingly that cultural evolution, most often assumed to arise as a by-product,² is entirely compatible with adaptationist theories of religion.

This is the main reason I choose to argue for a family resemblance definition of religion—I do not think religion is a single thing at all. Adaptationists have produced many a convincing study of cooperative religious societies, but how do they account for the utter seclusion of some religious specialists, such as the forest monks of Sri Lanka (Carrithers 1983), or the ten years of self-mummification endured by the *Sokushinbutsu* (Jeremiah 2010)? Extreme cases such as these might be rare, but a complete theory of religion will have to account for them nonetheless. Since, for individuals as these, however few, religious practice amounts to such extremely maladaptive behaviour, we have to allow at the very least that the spread of some religions is a by-product. On the other hand, in some communities, such as the Hutterites (Sosis 2003), religion seems to serve a strong adaptive purpose. Yet, while it makes no sense to ask whether or not all religiousness is an adaptation, or if all religion is adaptive, we could well ask what came first, or what is most common. I am not aware of any theories about how religion arose as an adaptation—rather, what adaptationists of religion are concerned with, is how religion functions adaptively, while the

2 Although culture could well be an adaptation in its own right, see Richerson and Boyd 2005, ch. 4

question of origin is left unanswered. If we can assume for the time being, then, that religiousness' *origin* as a by-product is not seriously challenged, then the interesting question becomes what the ratio of adaptive religions to non-adaptive religions is. This question unifies both adaptationist and by-product theories, and I think it is the question we should be asking. The scenario I am proposing, is this: Evolution has endowed us with adaptive mental modules such as HADD and a propensity to remember MCI concepts, which in turn, as a by-product, predispose us to religious beliefs. Some of these beliefs, quite by accident, are structured so that they foster cooperation through costly or hard-to-fake signalling. These beliefs will be cultural adaptations and are likely to be spread at greater rates, if not directly through proselytising, then indirectly through the fitness benefits they confer upon believers. Still, non-adaptive religions may persist either because they are selectively insignificant, or because selection against them is constrained in some way. Thus, we end up with a host of entirely different, not necessarily related religions—some culturally transmitted, some adaptive, some pure by-products, but with no need anywhere for a biological adaptation for religiousness. Dennett explains how culture reduces the need for adaptive explanations of human behaviour, while at the same time showing that similar phenomena may well be unrelated:

The very considerations that in other parts of the biosphere count *for* an explanation in terms of natural selection of an adaptation—manifest utility, obvious value, undeniable reasonableness of design—count *against* the *need* for any such explanation in the case of human behavior. If a trick is that good, then it will be routinely rediscovered by every culture, without need of either genetic descent or cultural transmission of the particulars. (Dennett 1995, 487, italics in original)

There is no reason to assume that religion is any different. As long as we agree that humans have a general propensity for religiousness, and we do, and that religion-as-an-adaptation can be explained through cultural selection, and I think we should, then it follows that adaptive religions will appear at different places, unrelated to each other. Incidentally, remember that the main problem adaptive religion is supposed to solve, is non-kin cooperation (kin based cooperation is understood fairly easily, as seen in kin selection and exemplified by the eusociality of insects such as ants, termites and bees). Candace Alcorta (Alcorta 2009, 118) writes that

[w]hen there is no need for non-kin cooperation, or when other institutions more efficiently or effectively meet that need, then religion and adolescent rites of passage should be absent or greatly attenuated because the time

and energy costs these entail are not offset by the benefits religion confers. Recent declines in religious participation in modern European nation-states suggest such a trend.

In other words, even if religion is one of Dennett's 'good tricks,' we should not be surprised to see nonadaptive forms of religion as well, perhaps particularly in modern societies. With all this in mind, does it make sense to speak of religion? Only, I think, insofar as we employ a family resemblance definition. Some religions may be by-products, and others adaptive, and the adaptive ones will likely solve the problem of cooperation in different ways. There is no essence to speak of here, and we needn't look for one. What we need is a theory to account for religion, and I think if we work together, then we have that. And I think that gives the evolutionary science of religion a solid application for acceptance among more traditional scholars of religion.

5.3: Conclusion

With this thesis, I hope to have shown that adaptation has been treated in the evolutionary science of religion somewhat more simplistic than the subject deserves, and that a closer look at how it is studied in biology can shed light on issues pertaining to religion. I conclude that the prevailing dichotomy between religion as an adaptation and religion as a by-product is somewhat misleading, and that religion is best understood as a mix between the two, preferably with the spread of particular religions studied as cultural evolution. At the same time, neither adaptationist or by-product theories of religion fully explain the phenomenon. Adaptationist theories explain how religion can evolve as a system of hard-to-fake signals of commitment, but they do not explain how an ability to fake such signals has not evolved in response. By-product theories, on the other hand, do not explain how selection has been constrained from removing such by-products. These theories seem to demand such explanations, respectively.

To paraphrase Dennett (1995, 270), good evolutionary reasoning makes use of adaptations and constraints both. For a phenomenon as complex and multifaceted as religion, I find it hard to see how an explanation can be produced without both these being integral to it. Furthermore, I hope I have shown how different religions can both have common elements and still be either distantly

related or not related at all, through a combination of cultural evolution and selection producing similar adaptations under similar conditions.

Perceiving religion in this way as a mix between two, or even multiple, partly related, but distinct phenomena, opens up for a family resemblance definition of our subject. I think this thought can be taken further still—if religion is not taken as something *sui generis*, then perhaps we should do well to blur the distinction between religion and culture in general, in the hopes that it will smooth interdisciplinary work, and emphasise the importance of cultural evolution. Scientists of religion will still know what their main interests are, but I think it will be helpful to pay more attention to the fact that religion is just one part of our magnificent cultural tapestry. Then perhaps we would not need to bother about questions such as are rock concerts and football matches modern day religions—who cares if they are, but we've got the tools to study them as if they were. Consilience works both ways; not only should scientists of religion reach out to biology, we should blur the distinction with other social sciences as well. In the end what counts is the scientific tools we apply, not what we apply them to.

GLOSSARY

- adaptation.** A trait, whether biological or cultural, produced by natural selection.
- adaptive.** A trait x is said to be adaptive in environment y if it confers a fitness benefit in that environment. That trait may, but need not, be an **adaptation**.
- allele.** One of two or more variants of a gene.
- altruism.** The tendency of one organism to promote the welfare of another, to its own detriment. Opposite of selfishness.
- by-product.** A trait, or aspect of a trait, that is not itself an **adaptation**, but a consequence of one.
- consilience.** Compatibility between different scientific disciplines.
- constraint.** A mechanism or effect which limits the ability to evolve an **adaptation** in a certain context.
- eusociality.** A form of organisation found particularly in the social insects and naked mole rats. Characterised by sterile workers assisting the reproduction of the queen. Enables cooperation through intricate kinships.
- evolutionarily stable strategy (ESS).** A strategy that, once common in a population, cannot be invaded by a competing strategy. A mix of two or more stable strategies is also possible in some cases. Compare with an evolutionarily stable state, a state to which a population will return to after a disturbance.
- frequency-dependent selection.** Selection where the fitness of a phenotype is determined by how common it is. Can be negative or positive: In the former, rare traits are selected for, while in the latter, being common is beneficial.
- gene.** The biological unit of heredity and selection.
- genetic drift.** Chance variations from one generation to the next in gene frequencies.
- genotype.** An organism's genetic constitution. Compare with **phenotype**.
- hard-to-fake.** A signal about an organism's internal state or intentions considered reliable to the extent that producing a false signal of the same kind would be difficult or very costly.
- heterozygous.** A trait that is produced by different alleles at a particular locus in a chromosomal pair, as when different alleles are inherited from each parent. Opposite of **homozygous**.
- homozygous.** A trait that is produced by similar alleles at a particular locus in a chromosomal pair, as when the same allele is inherited from each parent.
- hyperactive agency detection device (HADD).** A theoretical mental module evolved to detect agents in the environment, to avoid ambushes and the like. Hypothesised to produce belief in superhuman agents as a by-product when triggered erroneously.
- locus.** A particular spot on a chromosome. Can be inhabited by only one gene per individual—competitors for the same locus are said to be **alleles** of each other.
- meiosis.** The process by which new sex cells are produced. A cell division where the chromosomal pairs are reshuffled. Two new cells are produced, each with only one

chromosome per original pair, the new chromosomes being blends of the original pairs.

meme. A hypothesised cultural unit of heredity and selection. Compare to **gene**.

minimally counter-intuitive concepts (MCI). A concept that includes just enough of a breach of expectation to be maximally memorable. Hypothesised to account for the prevalence of religious ideas.

mutation. A change in genetic code, typically occurring during **meiosis**. The source of new **alleles** and new **genes**.

optimality. The theoretical point of maximum adaptation for a trait or individual. May not be reachable, either because of **constraints** or competing selection pressures.

phenotype. The observable characteristics of an organism, produced by **genes** interacting with the environment.

pleiotropy. The property of a gene to have multiple **phenotypic** effects. Can be a constraint on optimality in that an adaptive trait is coupled genetically with a less favourable one, possibly outweighing the benefit.

replicator. A generalised unit of heredity and selection. Replicators have (1) fecundity, (2) fidelity, and (3) longevity, that is: ability to (1) reproduce frequently with a (2) high degree of precision and (3) last for long enough to be selectively significant. **Genes** are said to embody these traits, **memes** are controversial in this regard, particularly in regard to fidelity.

runaway selection. A selective process in which traits are exaggerated over time. Often the result of sexual selection where (typically female) preference for high values of a quantitative trait is coupled with traits of such values (typically in males), resulting in a feedback dynamic where both are amplified.

spandrel. A **by-product** of an **adaptation** that takes a necessary shape or form due to developmental **constraints**. May serve a secondary adaptive function, but is not selected for this purpose.

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