

# The Evolution of Culture

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# The Evolution of Culture

## Volume IV

*Edited by*

**Stefan Linquist**

*University of Guelph, Canada*

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# Contents

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<i>Acknowledgements</i>	vii
<i>Series Preface</i>	ix
<i>Introduction</i>	xi

## **PART I THEORETICAL BACKGROUND**

1 F.T. Cloak, Jr. (1975), 'Is a Cultural Ethology Possible?', <i>Human Ecology</i> , <b>3</b> , pp. 161–82.	3
2 Luigi L. Cavalli-Sforza (1986), 'Cultural Evolution', <i>American Zoologist</i> , <b>26</b> , pp. 845–55.	25
3 William H. Durham (1990), 'Advances in Evolutionary Culture Theory', <i>Annual Review of Anthropology</i> , <b>19</b> , pp. 187–210.	37
4 Joseph Fracchia and R.C. Lewontin (1999), 'Does Culture Evolve?', <i>History and Theory</i> , <b>38</b> , pp. 52–78.	61

## **PART II THE PHYLOGENETIC APPROACH TO CULTURE**

5 Ruth Mace and Mark Pagel (1994), 'The Comparative Method in Anthropology', <i>Current Anthropology</i> , <b>35</b> , pp. 549–64.	91
6 John H. Moore (1994), 'Putting Anthropology Back Together Again: The Ethnogenetic Critique of Cladistic Theory', <i>American Anthropologist</i> , <b>96</b> , pp. 925–48.	107
7 Russell D. Gray, Simon J. Greenhill and Robert M. Ross (2007), 'The Pleasures and Perils of Darwinizing Culture (with Phylogenies)', <i>Biological Theory</i> , <b>2</b> , pp. 360–75.	131

## **PART III MEMETICS**

8 Daniel C. Dennett (1990), 'Memes and the Exploitation of Imagination', <i>Journal of Aesthetics and Art Criticism</i> , <b>48</b> , pp. 127–35.	149
9 Susan Blackmore (2001), 'Evolution and Memes: The Human Brain as a Selective Imitation Device', <i>Cybernetics and Systems</i> , <b>32</b> , pp. 225–55.	159
10 Mark Jeffreys (2000), 'The Meme Metaphor', <i>Perspectives in Biology and Medicine</i> , <b>43</b> , pp. 227–42.	191
11 Scott Atran (2001), 'The Trouble with Memes: Inference versus Imitation in Cultural Creation', <i>Human Nature</i> , <b>12</b> , pp. 351–81.	207
12 Kim Sterelny (2006), 'Memes Revisited', <i>British Journal for the Philosophy of Science</i> , <b>57</b> , pp. 145–65.	239

**PART IV DUAL INHERITANCE THEORY AND NICHE CONSTRUCTION**

- 13 Robert Boyd and Peter J. Richerson (1987), 'The Evolution of Ethnic Markers', *Cultural Anthropology*, **2**, pp. 65–79. 263
- 14 Joseph Henrich and Robert Boyd (2002), 'On Modeling Cognition and Culture: Why Cultural Evolution does not Require Replication of Representations', *Journal of Cognition and Culture*, **2**, pp. 87–112. 279
- 15 Kim Sterelny (2006), 'The Evolution and Evolvability of Culture', *Mind & Language*, **21**, pp. 137–65. 305
- 16 Kevin N. Laland, John Odling-Smee and Marcus W. Feldman (2000), 'Niche Construction, Biological Evolution, and Cultural Change', *The Behavioral and Brain Sciences*, **23**, pp. 131–46, 172–75. 335

**PART V PSYCHOLOGICAL MECHANISMS**

- 17 Christopher Boehm (1978), 'Rational Preselection from Hamadryas to *Homo Sapiens*: The Place of Decisions in Adaptive Process', *American Anthropologist*, **80**, pp. 265–96. 357
- 18 Joseph Henrich and Francisco J. Gil-White (2001), 'The Evolution of Prestige: Freely Conferred Deference as a Mechanism for Enhancing the Benefits of Cultural Transmission', *Evolution and Human Behavior*, **22**, pp. 165–96. 389
- 19 Dan Sperber and Lawrence A. Hirschfeld (2004), 'The Cognitive Foundations of Cultural Stability and Diversity', *Trends in Cognitive Science*, **8**, pp. 40–46. 421
- 20 Laureano Castro and Miguel A. Toro (2004), 'The Evolution of Culture: From Primate Social Learning to Human Culture', *Proceedings of the National Academy of Science*, **101**, pp. 10235–40. 429

**PART VI CULTURE IN NON-HUMAN ANIMALS**

- 21 Robert M. Sapolsky (2006), 'Culture in Animals: The Case of a Non-human Primate Culture of Low Aggression and High Affiliation', *Social Forces*, **85**, pp. 217–33. 437
- 22 Kevin N. Laland and Vincent M. Janik (2006), 'The Animal Cultures Debate', *TRENDS in Ecology and Evolution*, **21**, pp. 542–47. 455
- 23 Andrew Whiten, Victoria Horner, Carla A. Litchfield and Sarah Marshall-Pescini (2004), 'How Do Apes Ape?', *Learning and Behavior*, **32**, pp. 36–52. 461
- 24 Michael Tomasello (2001), 'Cultural Transmission: A View from Chimpanzees and Human Infants', *Journal of Cross-Cultural Psychology*, **32**, pp. 135–46. 479

*Name Index* 491

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# Series Preface

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The theory of evolution is one of science's great achievements. Though to those outside science, it may seem that the theory is controversial, within science there is no controversy at all about its basic form. Moreover, the theory of evolution plays a pivotal role in guiding new research. 'Nothing in biology makes sense except in the light of evolution', Theodosius Dobzhansky famously wrote; the theory of evolution unifies disparate subfields of biology and generates testable predictions for each. The success of the theory and its explanatory fecundity for biology cannot be doubted. But might the theory also be capable of illuminating phenomena outside the direct purview of biology?

The volumes in this series are dedicated to exploring this question. They bring together some of the best writings of the past two decades which explore the relevance of evolution and evolutionarily-inspired thought to arenas of human life beyond the merely biological. Volumes focus on whether it is productive and illuminating to attempt to understand our most distinctive achievements and our most intimate features as evolved phenomena. Is the content of moral systems explained by evolution? To what extent are the processes of selection and reproduction that explain changes in gene frequencies also at work in explaining the reproduction of ideas? Can evolution shed light on why we think as we do, perceive as we do, even feel as we do? Might even our idea of God – and perhaps with it the perennial temptation to reject evolution in the name of religion – be explained by evolutionary thought?

Answering these questions requires not only a detailed grasp of the phenomena we aim to explain – the contours of religious thought, the features of morality, and so on – but also an understanding of the theory we aim to apply to the field. Though the theory of evolution is not itself controversial within science, there are lively controversies about its details. One volume of this theory is devoted to writings which illuminate these controversies and deepen our understanding of the mechanisms of evolution. It is only if we have an appreciation of how evolution works that we can begin to assess attempts to extend its reach to culture, to the mind, to morality and to religion.

The volumes are edited by experts in the philosophy of biology and include sensitive and thoughtful discussions of the material they contain. Naturally, in selecting the papers for inclusion, and given the large amount of high quality thought on the philosophy of biology, and on each of the topics covered by these volumes, it was necessary to make some hard choices. Each editor has chosen to focus on particular controversies within the field covered by their volume; on each topic, a range of views is canvassed (including the views of those who deny that evolution can contribute much to the understanding of non-biological features of human beings).

Evolution is our story; in coming to understand it, we come to understand ourselves. Readers of these volumes should be left with a deepened appreciation for the power and ambition of evolutionary thought, and with a greater understanding of what it means to be an evolved being.

NEIL LEVY

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# Introduction

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Recent decades have seen a renaissance in the study of culture from an evolutionary perspective. Since the early 1970s at least four theoretical frameworks have emerged that apply evolutionary concepts and models to cultural phenomena. This family of theories bears little resemblance to earlier, teleological accounts of cultural evolution that originated with Herbert Spencer and flourished during the late nineteenth and early twentieth centuries. Gone is the notion that societies can be ranked on a scale from ‘primitive’ to ‘advanced’ or the idea that cultural evolution requires technological or moral progress. Instead, contemporary accounts of cultural evolution are an extension of the same Darwinian tradition that informs the biological sciences. At the heart of this tradition are two principles that transformed prior conceptions about the nature of biological diversity. The first principle states that all earthly life forms share a common ancestor and are thereby related by descent. This insight gave birth to a new way of thinking about organisms and their parts. After Darwin, species were no longer seen as immutable types but instead as interbreeding lineages whose features are continually reshaped by changing environments. The second principle states that adaptiveness – the functional suitability of a species to its environment – arises automatically out of the intergenerational re-occurrence of variation, heritability and differential fitness. This is Darwin’s principle of natural selection.

Just as these two principles have revolutionized the study of biological diversity they are now having a similar impact on the study of culture. Recent Darwinian approaches to culture endorse (to varying degrees) the following two versions of these principles:

1. The principle of cultural descent: all human cultures share a common ancestor and are related by descent. Just as certain genetic and morphological structures are preserved among related organisms over successive generations, certain cultural traditions (for example beliefs, values, skills and tools) are preserved with fairly high fidelity as they are socially transmitted from individual to individual.
2. The principle of cultural selection: cultures adapt to local ecological and social conditions by a process of variation, heritability and differential fitness that is akin to natural selection.

Although these principles constitute the core assumptions of contemporary Darwinian approaches to culture, each member in this family places a unique spin on their meaning and significance. The phylogenetic approach prioritizes the principle of cultural descent, applying to cultural groups the same methods used in reconstructing ancestral relationships among species (see Part II). Meme theory places greater emphasis on the principle of cultural selection, viewing individual concepts or ‘memes’ as gene-like replicators that compete for control over human thought and behaviour (see Part III). Dual inheritance theory views culture as a second inheritance system that interacts with genetic evolution (see Part IV). Finally,

niche construction theory explores the ways that humans use culture to modify and adapt to their environments (see Part IV).

Proponents of these four approaches are engaged in ongoing debates over a set of key issues. For example, what are the units of cultural evolution? To what extent is cultural evolution constrained by genetic evolution? Is culture transmitted in fairly cohesive ‘chunks’ or are individual beliefs, norms, skills and so forth transmitted independently of one another? To what extent is culture transmitted horizontally (from individual to unrelated individual) and what does this imply about the biological cost and benefits of culture? Such questions are internal to the Darwinian tradition insofar as they accept the two central principles of cultural descent and cultural selection (although they sometimes disagree over the details). Many of the essays contained in this volume are concerned with just these sorts of internal questions.

Another set of external challenges question one or both of these principles. For example, a standard objection to the principle of cultural descent argues that cultural transmission is such a low fidelity process that, unlike genes or traits, there is no stable cultural entity that can be identified as a unit of evolutionary change. Another objection, directed more at the principle of cultural selection, states that concepts, beliefs and other cultural phenomena do not undergo variation and differential selection. Debates over these external challenges play out in different ways depending on which of the four perspectives one is considering (see below).

In addition to these internal and external challenges, Darwinian approaches to culture encounter a third set of boundary issues concerning their relationship to neighbouring disciplines. One such issue is whether evolutionary accounts of cultural change conflict with non-Darwinian explanations offered by historians and anthropologists. It is often assumed that the Darwinian approach to culture undermines the standard model of explanation embraced within the social sciences (Barkow, Cosmides and Tooby, 1992). This assumption has led some social scientists to adopt a defensive stance towards theories of cultural evolution, focusing more on their limitations than on ways that those theories might be improved. However, it is often not clear whether Darwinian explanations do in fact conflict with historical or anthropological accounts of cultural change. This issue is addressed in the theoretical background section of this introduction and in Part I (see also Laland and Brown, 2002; Mesoudi, Whiten and Laland, 2006).

Other boundary issues arise at the interface between cultural evolution and empirical psychology. Typically, cultural evolutionists operate with a fairly thin description of the human mind. For example, a key theoretical concept in memetics is the idea of a ‘meme filter’. This psychological mechanism supposedly favours certain cultural variants over others and, in so doing, imposes a kind of selection pressure on memes. But it is not clear how this theoretical construct might be cashed out in psychological terms. This issue is discussed in more detail in what follows in the context of meme theory (see Part III and discussion below). Another boundary dispute between cultural evolution and empirical psychology concerns the extent to which culture is innately specified. Some critics of the Darwinian approach argue that it cannot explain the tendency for cultural representations to remain stable over successive generations. In particular, this objection has been raised by evolutionary psychologists who argue that if culture was transmitted primarily by social learning, as proponents of the Darwinian approach assume, then cultural traditions would rapidly degrade (Atran, Chapter 11; Sperber and Hirschfeld, Chapter 19). Thus, evolutionary psychologists offer an alternative perspective that views culture as the product of an innate psychological architecture. Such

boundary disputes between cultural evolution and empirical psychology are discussed in Part V and in what follows.

Finally, many of the theories discussed in this volume push the boundaries of our traditional concept of culture. It is often assumed that humans are a uniquely cultural species and, indeed, that it is culture which makes us 'special'. This view is challenged by the view that culture is simply socially transmitted information which, it turns out, is found in many species besides our own. Hence, another sort of boundary dispute concerns whether human culture is unique, and the extent to which it obeys the same evolutionary principles as culture in non-human animals. These issues are addressed in Part VI and below.

The six sections of this introduction offer a fairly self-contained summary of the six parts of this volume. As with any collection of its breadth, a considerable amount of hand wringing went into the selection process. Many significant publications had to be passed over because they are too technical for an introductory audience. Others were excluded simply because they already appear in existing collections. However, the essays that do appear in this volume offer, I think, a fairly balanced and comprehensive representation of recent trends in the study of cultural evolution.

### **Theoretical Background**

Darwinian theories of cultural evolution are relative newcomers to the intellectual landscape and their reception, especially within the social sciences, hasn't been overly enthusiastic. One reason why Darwinian theories of culture have encountered resistance is because of their association with previous, unsophisticated theories of human nature. The teleological theories of Spencer and his followers were not only misguided, they easily lent themselves to racist and imperialistic doctrines. More recently, the sociobiology movement of the early 1970s further contributed to Darwinism's bad name. Sociobiologists attempted to explain a broad spectrum of human behaviour as evolving by natural selection to promote inclusive (genetic) fitness. Everything from human mating preferences to the determinants of social status have been interpreted by sociobiologists as serving individual genetic interests. This emphasis on cross-cultural universality and the related idea that genes keep culture on a 'short leash' did not sit well with cultural anthropologists, many of whom were familiar with the diverse forms that human culture can take and with the central role of social learning in human development. (See Laland and Brown (2002) for an excellent discussion of the sociobiology movement and its influences on evolutionary approaches to culture.)

Proponents of modern Darwinian approaches to culture have therefore made an effort to distance themselves from the core assumptions of sociobiology. This concern is reflected in several of the essays appearing in this section of the volume. For example, in Chapter 1 F.T. Cloak emphasizes that a theory of cultural evolution must take into account the influence of learning constraints and social institutions on the direction of cultural change. Cloak also appears to have been the first to recognize that since cultural information is capable of rapid inter-organismic transmission (spreading, he notes, like a virus), culture will sometimes evolve in ways that are irrelevant or even destructive to the individuals who propagate them (the 'virus-like' nature culture was later seized upon and publicized by Richard Dawkins, and now forms one of the central tenets of meme theory). Although some of these principles have been developed considerably since the publication of Cloak's essay, many of his pioneering

ideas remain worthy of attention. Chapters 2 and 3 by Luigi Cavalli-Sforza and William Durham, respectively, advance a similar line of argument: Darwinian theories of cultural evolution address the origin and causes of cultural diversity – they in no way ignore it—and doing so requires making a distinction between cultural and genetic evolution. Written only a decade or so after Cloak’s influential work, these essays document the considerable amount of development that Darwinian theories of culture underwent during this productive period.

Chapter 4 offers a more sceptical assessment of recent theories of cultural evolution. Historian Joseph Fracchia and well-known evolutionary biologist Richard Lewontin argue that theories of cultural evolution lack the resources for explaining cultural change. These authors assume that evolutionary explanations of culture are either selectionist in nature (that is, they explain cultural change in terms of the principle of cultural selection) or else they are indistinguishable from standard historical explanations. The problem with selectionist explanations of culture, they argue, is that they adopt a ‘variational scheme’ – cultural change is attributed to variation and differential fitness among individual cultural variants. Fracchia and Lewontin note that many cultural changes do not follow this pattern of blind variation and selection. For example, historians sometimes appeal to things like a sense of national pride or cultural ethos when explaining why events unfold in particular ways and not others. Fracchia and Lewontin’s central argument is that these sorts of explanations, which appeal to shared cultural representations and communal goals, cannot be reduced to the variation and differential spread of ideas.

A detailed treatment of Fracchia and Lewontin’s argument is beyond the scope of this introduction. In fact, most of the essays contained in this volume either expand on features of this argument or attempt to demonstrate why it is flawed. (Of particular interest are the essays contained in Part II where the phylogenetic analysis of culture is defended. These essays demonstrate that not all evolutionary explanations of culture are selectionist in character.) Rather than attempting to survey all of the issues raised by the essays appearing in Part I, the remainder of this section focuses on three common issues: (1) how should ‘cultural evolution’ be defined, (2) what are the units of cultural evolution and (3) how is cultural selection akin to natural selection? A brief review of these general questions will set the stage for more specific topics addressed in following parts.

### *Defining ‘Cultural Evolution’*

Many researchers consider it important at the outset of an investigation to precisely define their subject matter. This is a challenging task in the study of cultural evolution because both ‘culture’ and ‘evolution’ are vague and ambiguous terms. The concept of culture operative within the social sciences is what philosophers would call a ‘family resemblance’ concept: it refers to a broad range of practices, traditions, artefacts and beliefs that exhibit some overlapping similarities, but which do not share an essential set of defining characteristics. Some cultural phenomena, like novel works of art, probably do not lend themselves to an evolutionary analysis. While other cultural practices, like tool-making or language, are especially good candidates for an evolutionary investigation. The term ‘evolution’ is problematic for a different reason. In common parlance, ‘evolution’ often connotes progressive change towards some end or goal. Biologists have made an effort to strip the term of such teleological implications. However, the standard textbook definition of evolution as *a change in gene frequencies over*

*successive generations* is obviously too narrow for theories of cultural evolution, and arguably too narrow for biology. An alternative definition of ‘evolution’ as *descent with modification*, though vague, is perhaps better suited to current purposes. This phrase captures what is essential to most of the objects that evolutionary theorists study: these are entities (in a loose sense of the term) that preserve many of their features as they are transmitted from individual to individual, but which undergo slight modifications in structure that are retained and become salient over large time scales. Importantly, evolution is not to be confused with the Darwinian mechanism of natural or cultural selection. Selection – which involves variation, heritability and differential fitness – is just one of several mechanisms that can drive the evolutionary process.

Ideally, it would be possible to specify from the outset which sorts of cultural phenomena admit of an evolutionary analysis and which ones do not. However, as Luigi Cavalla-Sforza notes in Chapter 2, attempting to define the scope of evolutionary theories of culture would be premature at this early stage of their development. A more productive strategy is to begin with a vague definition of culture that captures a range of cultural phenomena that lend themselves to an evolutionary analysis. This definition can then be refined as the discipline matures. To this end, Cavalli-Sforza defines culture as the range of phenomena that involve learning and transmission. He clarifies this working definition to some extent by providing prototypical examples of culture found in both human and non-human organisms.

In Chapter 1 F.T. Cloak points out that ‘culture’ is used ambiguously to refer both to the set of internal mental instructions that guide behaviour (‘i-culture’, as he calls it) and also to the set of material artefacts, social relations and institutions that reside outside the individual mind (or ‘m-culture’). These two forms of culture interact in several ways. I-culture both propagates itself from individual to individual and tends to give rise to m-culture. In turn, m-culture influences the development of both i-culture and other m-cultural artefacts. However, Cloak argues that, from an evolutionary perspective, i-culture is more fundamental than m-culture. Although i-culture is capable of replicating itself without m-culture, he claims, m-culture requires i-culture to persist indefinitely. For example, a clay pot will degrade and disappear over time, but the instructions for making pots can survive indefinitely. Cloak concludes that m-culture will tend to evolve in ways that promote the spread and maintenance of i-culture, but not vice versa. Thus, in order to identify the evolved function of a tool or piece of pottery it is necessary, on this view, to determine how these artefacts contribute to the maintenance and spread of the instructions that code for their production. On this view, artefacts have the evolved function of promoting the instructions that generate them in the same way that, according to some evolutionary biologists, phenotypic traits have the function of propagating the genes that contribute to their development (Williams, 1966; Dawkins, 1976).

In drawing this distinction between i-culture and m-culture, Cloak appears to be searching for something within the domain of culture that corresponds to the genotype/phenotype distinction in biology. He also accepts uncritically the view that packets of information and not their physical manifestations are the ‘fundamental units’ of evolution. According to this line of reasoning, an entity must be capable of surviving indefinitely in order to qualify as a unit of evolution (Williams, 1966). Information encoded in either genes or mental instructions are supposedly ‘immortal’ while the physical products of information, like phenotypic traits or material artefacts, are considered ephemeral.



This argument touches on a controversial subject within evolutionary biology that is too involved to discuss here (see Sterelny and Griffiths, 1999). Restricting ourselves to cultural phenomena, however, the claim that all forms of i-culture can persist indefinitely without m-cultural manifestations is mistaken. It is hard to imagine how one would convey certain tool-making strategies or pottery techniques without constructing one of these artefacts. Nor, for that matter, is it likely that someone could glean the requisite craftsmanship from just a close inspection of the finished products. Rather, it appears that both i-culture and m-culture play essential, reinforcing roles in the maintenance and propagation of certain traditions. Contrary to Cloak's claim, neither type of culture necessarily evolves to promote the propagation and maintenance of the other.

### *The Units of Cultural Evolution*

The previous subsection hit on a question that is often raised in the context of evolutionary theories of culture: what are the objects or 'units' that evolve by cultural evolution? As Cavalli-Sforza notes, it is extremely difficult to identify a cultural unit of transmissible information that corresponds to the biologist's favourite unit of evolution: the gene. What cultural evolutionists are apparently looking for is something that is both preserved with high fidelity across generations and capable of undergoing something akin to genetic mutations. Most often, cultural evolutionists will speak of ideas or 'memes' (as Richard Dawkins has dubbed them) as the units of cultural evolution. However, we have already seen that mental states are not the only sorts of cultural entities that undergo descent with modification – cultural artefacts evolve as well. Moreover, it is often difficult in practice to tease apart the respective roles that material artefacts and ideas or memes play in their continued maintenance and propagation. Some cultural evolutionists adopt the more neutral term 'cultural variant' to describe the vast range of entities capable of undergoing cultural evolution (Boyd and Richerson, 1985). It remains to be seen whether this concept can be further refined to provide a cultural analogue to the evolutionary gene or, indeed, whether identifying such an entity is important for developing a theory of cultural evolution (see Part III and discussion of memetics below). For purposes of clarity, throughout this introduction the term 'tradition' will be used when speaking in general terms about material objects, mental representations or social practices that are structured primarily by culturally transmitted information. The word 'trait' will be reserved for objects, representations or social practices that are influenced primarily by biologically (for example genetically) transmitted information. Note, however, that these are not exclusive categories. The development of many behavioural dispositions, for example, involves both genetically and culturally transmitted information.

### *Cultural Transmission and Cultural Selection*

There are some obvious differences between the ways that biological and cultural information gets passed on. Since traits are inherited genetically they are restricted to a *vertical* mode of transmission (from parent to offspring). This constraint limits the rate at which traits can evolve. Cultural traditions, by contrast, are potentially also transmitted *horizontally* (from individual to unrelated individual in the same generation) or *obliquely* (from an individual in the  $n$  generation to unrelated individual in the  $n+1$  generation). These additional transmission



pathways influence the rates at which culture evolves. As Cavalli-Sforza explains in Chapter 2, cultural traditions evolve most rapidly when they are transmitted horizontally from one-to-many individuals. However, horizontal transmission can also retard the rate of cultural evolution, such as when a tradition is transmitted non-vertically from many-to-one. Traditions that are enforced by peer pressure (for example etiquette norms) are likely to follow this pattern. The fact that traditions can spread horizontally and obliquely also allows for the evolution of maladaptive behaviours. A behaviour is maladaptive when it decreases the reproductive fitness of its bearer in comparison to some alternative course of action. Enforcement of the one-child policy in some cultures is an example of a horizontally transmitted tradition with maladaptive consequences.

Such talk of traditions that are favoured by one's cultural circumstances but maladaptive at the biological level can generate confusion, especially when it comes to distinguishing cultural transmission from cultural selection. In biology, heritability (or parent-offspring transmission) is just one component of natural selection. For natural selection to occur there must also be variation and differential fitness among traits. However, in cultural evolution theory the distinction between transmission and selection is often blurred. Consider a tradition that spreads rapidly through a population because of its obvious utility, such as the controlled use of fire. Should we say that this tradition is favoured by cultural selection? Or, is the increase in popularity due to what some theorists call a 'transmission bias'? What, if anything, is the difference between these two characterizations? To make matters more complicated, a tradition like this one will undoubtedly enhance the reproductive fitness of those who adopt it. Assuming that fire-making techniques are passed on from parent to offspring, their increase in frequency will therefore be driven to some extent by natural selection in addition to cultural factors.

A certain amount of progress could be achieved in this domain if cultural evolution theorists could agree on a single conceptual framework for categorizing cultural phenomena. Unfortunately, different theorists currently use 'transmission', 'cultural selection' and 'learning bias' to describe different sorts of processes. Perhaps the simplest option is to abandon the analogy between cultural and natural selection and view culture strictly as a mechanism for transmitting information (Boyd and Richerson, 1985). On this view, selection occurs only at the biological level, namely, when a behaviour (influenced either by culturally or genetically inherited information, or both) impacts the *reproductive* output of its bearer. In some cases selection will be the primary force driving the spread of a behaviour, such as when an adaptive tradition is transmitted exclusively from parent to offspring. In other cases selection will be overwhelmed by cultural factors, such as when a maladaptive tradition evolves rapidly by horizontal transmission. From this perspective it makes no sense to describe a tradition as being culturally selected. This notion conflates the factors that influence the rate and direction of inheritance with the process of differential reproduction.

However, many theorists prefer to view cultural selection as a separate, analogous process to natural selection. In Chapter 3 William Durham offers one of clearest statements of this perspective. He begins by distinguishing two general 'forces' that impact cultural evolution. *Non-conveyance forces* introduce cultural variation into a population. Included in this list are innovation, diffusion, migration and chance effects. *Conveyance forces* affect the direction and rate of cultural evolution. Of these latter forces Durham identifies three different types which supposedly vary in strength. The first type of conveyance force is what Durham calls

‘transmission’. He offers no general description of this process, providing instead just a single example: all things being equal, the rate at which a tradition spreads through a population increases as its frequency increases. It is not entirely clear why this process qualifies as a form of transmission as opposed to the cultural analogue of what is known in biology as frequency-dependent selection. Nor is it obvious what else would qualify as a transmission force for Durham. For instance, Cavalli-Sforza notes that in societies where children have little exposure to non-family members during the sensitive period when certain skills and values are acquired, the amount of horizontal transmission is minimized and culture evolves relatively slowly. We are left wondering whether such social influences qualify as transmission forces or, alternatively, as a form of cultural selection on Durham’s view. The second kind of conveyance force is natural selection, or the dissemination of a tradition by the differential reproduction of its bearers. Durham views both transmission and natural selection as having only minor influences on cultural evolution. The third and supposedly most powerful conveyance force according to Durham is cultural selection. Included in this category are the decision rules and values that affect individuals’ choices between alternative cultural traditions. Durham notes that these values can be either ‘primary’, arising from genetically encoded preferences, or ‘secondary’, themselves inherited by cultural transmission. He assumes that most of the decision rules and values that exert a selective force on culture will be of the secondary variety – that is, they are themselves culturally inherited traditions – but Durham admits that this is little more than a hunch.

This is not the place for a detailed analysis of the distinction between cultural transmission and cultural selection. It is noteworthy that one of the primary externalist objections to Darwinian theories of culture states that this distinction cannot be drawn. Critics like Fracchia and Lewontin argue that the analogy between cultural and natural selection is deeply misleading: since cultural traits do not undergo blind variation and selection they do not undergo selection in the strict Darwinian sense. Whether the idea of cultural selection can be made tenable remains a hotly debated question that will re-emerge in our discussion of memetics (Part III). In the mean time, it remains an interesting question whether it is possible to develop an evolutionary theory of culture without endorsing the principle of cultural selection. The tradition that comes closest to such an approach is the phylogenetic approach, which will now be discussed in some detail.

### **The Phylogenetic Approach to Culture**

Most people are familiar with the phylogenetic tree diagrams that biologists use to represent relationships of descent among species. These *cladograms* usually follow a branching pattern with the most ancestral species situated at the base of the tree and its extant descendants located at the tips. Branch points in a cladogram represent likely speciation events where one ‘parent’ species has diverged into two ‘daughters’. In biology, cladograms play a central role in testing evolutionary hypotheses as well as in the classification of species. Recently, this technique has been employed as a tool for reconstructing human cultural evolution. Fundamental to this approach is the assumption that most cultural traditions follow a similar branching pattern to species. Presumably, when a human group diverges into two subpopulations each of the daughters will initially share most of their traditions, having recently inherited them from a common ancestor. But as those populations go their separate ways they will each adopt unique

traditions and become increasingly distinct over time. Those novel or *derived* traditions are in turn passed on to the respective daughter populations. Thus, by comparing the number of shared derived traditions among a group of cultures it should be possible to reconstruct their ancestry. All things being equal, the greater the number of shared derived traditions among two given cultures, the more closely they are related.

However, when conducting this sort of analysis it is important to distinguish two different sources of cultural similarity. Some shared traditions are inherited from a common ancestor while others are independently invented by a process analogous to convergent evolution. Only shared derived traditions carry information about ancestral relationships; convergent traditions are a source of noise that can generate overestimates of the relatedness among cultures. For example, indigenous cultures who lived in the Chatham Islands shared numerous technological similarities with early inhabitants of north-western Tasmania (Sutton *et al.*, 1982). Both groups used bone harpoons, awls, watercraft and flake stone tools that were suited to their coastal lifestyles. Based on such similarities it appears that these populations shared a direct cultural ancestor from whom their technologies were inherited. However, Douglas Sutton and his colleagues argue that a careful analysis of the archaeological record suggests that these technologies were independently invented by each population. Although this is a controversial example, it illustrates the nature of the difficulties associated with the construction of cultural phylogenies. To avoid mistaking cases of cultural convergence for cultural inheritance, phylogeneticists draw upon numerous sources of information (when available) in constructing cultural phylogenies including linguistic, archaeological and genetic data (Cavalli-Sforza *et al.*, 1988). However, different types of information can sometimes point towards different phylogenetic trees. One of the main methodological debates in this domain is over which traits and traditions render the most accurate cultural phylogeny.

Once a cultural cladogram has been constructed for a particular group it is extremely useful for evaluating functional hypotheses. When two or more populations inhabiting similar environments converge on the same tradition, as appears to be the case among indigenous Chatham Islanders and Tasmanians, this can suggest that those shared traditions serve some function in the local environments. In Chapter 5 Ruth Mace and Mark Pagel employ this method to test a variety of functional hypotheses. These authors convincingly argue that the phylogenetic approach is superior to alternative comparative methods used by anthropologists. Specifically, they argue that the phylogenetic approach is uniquely suited to avoiding 'Galton's Problem'. Francis Galton, nephew of Charles Darwin, was the first to point out that there is a danger lurking in the inference from cultural similarity to functional significance. Cultural similarities can be due either to functional convergence or to common descent. Notice that Galton's Problem arises in the evaluation of functional hypotheses. It is the logical converse of the problem that researchers encounter when constructing cultural phylogenies. When constructing a cultural phylogeny, cases of convergence are a potential source of noise because they masquerade as shared derived traditions. However, when testing a functional hypothesis, instances of cultural convergence carry the desired signal while similarities due to common descent are a potential source of false positives.

Anthropologists who employ the comparative method have developed various sampling procedures in an effort to overcome Galton's Problem. For example, Murdock and White (1969) carefully selected a sample of 186 geographically disparate populations exhibiting minimal amounts of linguistic and cultural overlap. Mace and Pagel object that this approach

fails to control for similarities that have a 'deep' phylogenetic ancestry. Also, this technique cannot be applied at a fine level of grain to closely related cultures. An alternative sampling method relies on statistical procedures to identify the portions of cultural variance that are thought to be due to common descent (for example Dow, 2007). Mace and Pagel object that this alternative is highly sensitive to the individual researcher's assumptions about how sets of traditions tend to cluster. They go on to argue that the phylogenetic approach is superior to these alternatives because of its signal emphasis on identifying shared derived traditions and distinguishing them from cases of convergence. Moreover, Mace and Pagel argue that the phylogenetic approach can potentially be applied to any group of cultures whose ancestry can be reconstructed, regardless of their geography or degree of relatedness.

In their list of the 'pleasures' associated with cultural phylogenetics, Russell Gray, Simon Greenhill and Robert Ross (Chapter 7) identify several additional applications of this technique that go beyond the testing of functional hypotheses. These authors cite studies where cultural cladograms are used to test theories about the homeland or origin of a cultural group, to trace population movements and expansions, to test theories about the rates of cultural change and to date divergence events. In most of these examples cultural cladograms are based in linguistic evidence. The key assumption here is that linguistic data provides a fairly reliable picture of cultural evolution because grammatical mutations are preserved with high fidelity and passed on primarily in a vertical direction, from parent to daughter populations. Therefore, linguistic data is regarded as a fairly pure source of information about patterns of cultural descent. However, Gray *et al.* note that drawing inferences about a culture's homeland, its movements, divergence events and so on often requires correlating linguistic cladograms with other forms of evidence, including genetic, archaeological and anthropological data (see Cavalli-Sforza *et al.*, 1988).

Although phylogenetic techniques appear more rigorous than alternative comparative approaches to culture, some anthropologists and evolutionary biologists object that this approach relies on a faulty analogy between cultural groups and species. Whereas species tend to remain reproductively isolated once they have diverged, it is argued that a considerable amount of 'hybridization' occurs among cultures. Human populations tend to borrow useful technologies from their neighbours when they come into contact. In addition, when formerly isolated populations merge or immigrate to a common location there tends to be a mixing of languages and social practices. These problems are exacerbated by the high degree of mobility and sociality characteristic of our species. For example, in Chapter 6 John Moore cites a case study by Thomason and Kaufmann (1988) where large sectors of phonetic and grammatical information have been horizontally transmitted among language groups. If such cultural and linguistic admixture is common among human populations, then, Moore argues, it is impossible to construct a reliable cultural cladogram for groups that have come into frequent contact. For many prehistoric populations, Moore adds, the extent of their interactions with neighbouring groups is unknowable. Therefore he thinks that the phylogenetic approach should be applied only with the utmost caution and in conjunction with alternative approaches.

A second respect in which cultures arguably differ from species is in their rates of change. Moore argues that unlike the genetic and phenotypic traits used to construct species phylogenies, which remain relatively stable over time, cultural traditions are highly plastic and adaptable to local environments. He cites an example of a group of North American Indians who adopted radically different modes of subsistence as they migrated across the

central plains. If a population's core traditions undergo such dramatic changes each time the environment changes, this effectively erases the historical signal on which cultural cladograms are based.

Cultural phylogeneticists acknowledge that a certain amount of hybridization occurs as a result of intergroup contact and that populations sometimes undergo rapid adaptations to new environments. However, it is argued on both theoretical and empirical grounds that the extent and frequency of these events are exaggerated by critics like Moore. In an influential paper, Mace and Holden (2005) argue that cultural hybridization events do not pose a significant threat to the phylogenetic approach. Drawing on the anthropological record, these authors note that large-scale merging events tend to occur only when a group is undergoing rapid depopulation. For example, cultural merging occurred among North American Indian groups as a result of depopulation due to epidemics and armed conflicts with seventeenth-century Europeans. Mace and Holden also note that in cases where populations are expanding they tend to split and diverge rather than merge with neighbouring groups. If splitting is the typical response to population growth and merging is usually associated with population decline, it is argued, then the majority of extant cultures will be the products of divergence events and thereby conform with a phylogenetic model. Mace and Holden further argue that languages cannot undergo rapid evolutionary change because this would make intergenerational communication impossible. Thus, due to its inherent conservatism, linguistic information is an especially reliable source of data for constructing cultural phylogenies. In support of this claim, Mace and Holden cite several studies documenting a high degree of overlap between linguistic and genetic phylogenies. Against this background of empirical evidence the results reported by Thomason and Kaufmann appear highly exceptional. Mace and Holden further note that if a reliable cultural cladogram can be constructed out of linguistic data, then evidence of horizontal transmission (for example the adoption of one culture's traditions by another) can provide useful information about prehistoric contacts among groups.

In Chapter 7 Gray *et al.* also take issue with the alleged disanalogy between species and culture. The assumption that only a small amount of horizontal genetic transmission occurs among biological lineages is, they argue, biologically naive. In fact, a considerable amount of horizontal transfer is common among bacteria and also occurs on a large scale during such major transition events as the evolution of eukaryotes. Biologists have developed statistical techniques for constructing cladograms that allow for high rates of horizontal transmission, and Gray *et al.* propose that these techniques can be applied to cultural systems as well. Thus, if the occurrence of horizontal transfer (even fairly large amounts of it) is not an impediment to the construction of biological cladograms, then it shouldn't be regarded as a barrier to the construction of cultural phylogenies either.

Instead of relying on theoretical arguments about the amount of horizontal transfer or cultural adaptation that may or may not occur among human populations, Gray *et al.* insist that these questions can only be confronted empirically. As a way of framing the available evidence these authors present a multidimensional possibility-space that identifies three axes along which cultures might vary. The first axis,  $R_x$ , is the rate at which vertically transmitted traditions change. If  $R_x$  is extremely high (as suggested by Moore's Plains Indians example) then the historical signal will be lost and cultural phylogenies are impossible to reconstruct. However, Gray *et al.* cite several case studies suggesting that, especially in the case of language,  $R_x$  is within acceptable boundaries for conducting phylogenetic analyses. The



second dimension,  $R_h$ , is the rate of horizontal transfer of traditions among populations. Provided that  $R_h$  is low for at least some traditions, it should be possible to construct cultural cladograms that accurately represent the histories of particular populations. This condition appears to hold for language and arguably for other cultural phenomena. The final dimension,  $C$ , is the extent to which cultural traditions come ‘packaged’ together. In the limiting case of extreme atomism, where each tradition follows its own transmission trajectory and rate of change, researchers will be unable to generalize across cladograms. For example, a cladogram based on linguistic features will not resemble a cladogram based on tool dimensions or pottery design. Such a predicament would make it difficult to use phylogenetic methods for drawing certain historical inferences, such as the homeland of a population or the point at which two communities diverged, because such inferences require convergence among multiple sources of evidence. Gray *et al.* argue that in fact many cultural traditions are ‘packaged’ together into a cohesive unit, such as when they are functionally related to one another. However, even in the limiting case where  $C$  is low, it is arguably not impossible to apply the phylogenetic approach to individual traditions. On this view, particular traditions rather than cohesive cultural groups become the unit for phylogenetic analysis.

The scenario just envisioned, where each cultural tradition follows its own evolutionary trajectory, is not one that most cultural phylogeneticists tend to favour. Typically, the phylogenetic approach to cultural evolution takes the cultural group (a population of individuals with a core set of traditions) as its focal unit of analysis. The idea that individual ideas are the focal unit of cultural evolution is more commonly associated with memetic approaches, to which we now turn.

## Memetics

To understand the central tenets of memetics as well as the reasons why this doctrine has attracted such a large and devoted following it helps to consider the context in which the meme concept was introduced. Richard Dawkins’ popular book *The Selfish Gene*, (1976) is best known for its defence of gene centrism. This is the theory that individual genes, not organisms or groups, are the primary units of biological evolution. Central to Dawkins’ view is his distinction between replicators and vehicles. A replicator is any entity whose structure is reliably copied (and therefore preserved) over indefinitely many copying events. DNA, or more precisely the information encoded in a strand of DNA, is a prototypical replicator. A vehicle (or ‘interactor’ as they are also called) is the entity that houses a replicator and facilitates its transmission. Organisms are prototypical vehicles. One of Dawkins’ central arguments states that only replicators and not their vehicles are candidates for evolutionary change. Following G.C. Williams (1966), Dawkins argues that in order to be a candidate for evolution an entity must enjoy a certain kind of immortality: it must be capable of surviving for indefinitely many generations. Replicators have this property by definition; vehicles by definition lack it. Therefore, Dawkins concludes, evolution occurs primarily at the level of the replicator or gene. An implication of this view is that our traditional way of thinking and talking about adaptation requires a subtle revision. We tend to speak of adaptations as having evolved to promote the survival and reproduction of the *individual organisms* that possess them. Thus, the drive to feed, fight, flee or mate (or ‘the four F’s’ as they are sometimes called) are conventionally described as having evolved to help *the organism* obtain calories, defend

territories, avoid predators and so on. Strictly speaking, Dawkins argues, these claims are false. Adaptations cannot evolve to benefit organisms, because these vehicles exist for just a single life cycle. This is too short a time for cumulative evolution to occur. Instead, Dawkins proposed that adaptive traits evolve to benefit replicators, for example genes, because only they are able to accumulate and benefit from those adaptations through their continued existence.

Dawkins and other advocates of the gene's eye view argue that much of evolutionary biology can be understood in terms of selection acting on genes. However, the final chapter of *The Selfish Gene* contains an important qualification to this view. The gene's eye perspective is limited, Dawkins claims, when it comes to explaining large components of human thought and behaviour. Although some of our basic drives are undoubtedly under genetic control, Dawkins argues that many beliefs, desires and actions run counter to our genetic interests. He thereby distinguishes himself from advocates of the sociobiology movement who view the human mind as being on a 'short genetic leash'. Instead, Dawkins proposes that most human actions are under the control of another sort of replicator. This is the role that Dawkins assigns to memes.

A meme according to Dawkins is a concept or idea that influences an individual's actions in ways that promote the meme's own replication. A catchy tune, a recipe, a popular phrase, even the concept of the meme itself promote self-perpetuating behaviours like singing, cooking, speaking in certain ways or even writing about memes. Not only are memes similar to genes in their 'immortality', it also appears that some memes compete with one another for brain space. There are only so many tunes you can hum or recipes that you can try. This arguably imposes a type of selection pressure favouring the most memorable or appealing memes over those that are less attractive or easily forgotten.

Just as adopting the gene's eye perspective involves revising some common-sense views about what adaptations are for, so does the meme's eye perspective require a shift in thinking about the ultimate purpose of our actions. We tend to rationalize our actions in terms of goals or beliefs supposedly emanating from deep within our psyches. From Dawkins' perspective, however, the ultimate explanation for many of our actions is that they are meme's way of replicating itself. The reason that we cherish certain beliefs, resist some temptations and fight for particular ideals is, on this view, because we are under the grip of some highly adapted memes. While critics of the meme idea sometimes find this view demoralizing, others consider it highly insightful and even excitingly contrarian. Indeed, the rise and spread of the meme concept is itself one of the strongest arguments in its favour.

In his original (1976) presentation of these ideas Dawkins argued that memes literally evolve by a Darwinian process of variation and selective retention. Although gene evolution and meme evolution occur in different media and at different rates, he claimed, they are fundamentally the same process. In his later writings (1982) Dawkins retreated to a weaker position, claiming that meme evolution is merely analogous to organic evolution. In Chapter 8 Daniel Dennett offers a meme's eye explanation for Dawkins' retraction. Dennett suggests that social scientists had set up an aggressive set of filters to weed out memes that appear even remotely sociobiological in nature. To avoid knee-jerk dismissals of his theory, Dennett hypothesizes, Dawkins weakened his view – without good reason – to something that would appear more congenial to these reactionary critics. Regardless of whether this is an accurate portrayal of events, Dennett's defence of full-blooded meme theory warrants careful consideration.

There are two steps in Dennett's argument for the literal truth of meme evolution. First, he assumes that evolution occurs whenever a population of entities satisfies the three conditions for natural selection: heredity, variation and differential fitness. Another way to put this point is that natural selection is a 'substrate neutral' process, it occurs in any physical medium (computers, immune systems, brains, biological systems and so forth) provided that these three conditions are satisfied. The second premise states that memes satisfy these conditions. Memes are heritable insofar as they are passed on intact (more or less) from brain to brain. Memes vary from one another, both in their content and in the actions that they proscribe. Finally, memes affect the phenotype in ways that impact their fitness, where 'fitness' is understood in non-reproductive terms as a meme's tendency to be more or less popular or acceptable. Dennett's essay proceeds to defend this view using a range of examples. Of these, Dennett's discussion of the 'faith meme' is perhaps the most compelling. The faith meme is the idea that some beliefs should be held simply on authority (for example religious authority) or 'as a matter of faith' and can therefore not be subjected to rational scrutiny. Dennett argues that this is an extremely fit meme because it has effectively immunized itself against the influence of competing rationality memes.

A critic of memetics might argue that this theory is merely a relabelling of common-sense ideas. We are all familiar with the fact that some ideas become popular while others are lost to history. What additional insight does one gain by calling these ideas 'memes' and describing this process in quasi-Darwinian terms?

In responding to this challenge, Dennett argues that the meme's eye perspective has at least one explanatory advantage over competing common-sense accounts. He notes that a key feature of our common-sense framework is its normative character. Folk psychology holds that all things being equal, ideas that are true, beautiful or noble tend to be popular. Similarly, if an idea is false, ugly or immoral then, *ceteris paribus*, it should fade away. Hence the common-sense explanation for why a given idea spreads (or not) is that it possesses (or lacks) the relevant normative properties. The advantage of meme theory becomes apparent, Dennett argues, in cases where this common-sense framework breaks down. These are cases where a bad idea persists despite being recognized as such, or where a recognizably good idea fails to catch on. The claim here is not that these situations contradict the normative account of idea transmission (note the *ceteris paribus* clauses); Dennett's point is that our common-sense framework offers no theoretical explanation for why these oddball cases occur. By contrast, meme theory supposedly possesses the resources for dealing with these sorts of cases. Specifically, the thing that all adaptive memes have in common, regardless of whether they are considered good or bad, is 'a phenotypic effect that systematically tends to disable the selective forces arrayed against them' (p. 153). In other words, meme theory predicts that the most popular ideas are able to infiltrate our 'memetic immune system' (or 'meme filter'). Meanwhile, unpopular ideas are just those that the filter is tuned to identify and discard. The faith meme is allegedly an example of the former. A superior but poorly advertised technological gadget might qualify as an example of the latter.

How convincing is Dennett's defence of the explanatory virtues of memetics? One potential problem with his argument lies in the vague characterization of the selective forces influencing meme evolution. The fittest meme is one that is disposed to pass through the filters of our memetic immune system. But what exactly *is* this mechanism and what principles govern its operation? One standard (though often implicit) suggestion is that people are disposed



to favour memes that promote their reproductive fitness and to discard memes that threaten survival and reproduction. Harmful memes that nonetheless become popular are the ones that manage to slip through these filters.

But there are some serious problems with the view. Either the principle *promote genetic interest* is itself a type of meme (something we acquire through social transmission) or it is not. If this principle is encoded as a type of meme, then it is capable of spreading by horizontal transmission. If a tradition spreads horizontally, then its fitness is not constrained by how well it promotes reproductive fitness. Therefore, it remains a mystery why the memes influencing our memetic immune system would favour memes that promote reproductive fitness. On the other hand, if this rule is not encoded by memes, if they are in some sense genetically encoded, then the meme filter would be useless against rapidly evolving memes. In an evolutionary arms race memes will always out-compete genes – this is another consequence of their horizontal transmission. At this point meme theory runs the risk of losing its explanatory advantage over the common-sense (normative) account. If it turns out that the alleged meme filter does not promote genetic fitness as a rule, then what are the principles according to which it operates? It had better not be the case that this mechanism follows the rule: accept an idea if it is good, beautiful, noble and so forth and reject an idea if it is ugly, immoral or bad. Otherwise, any difference between the two theories is merely terminological.

Susan Blackmore tackles some of the more technical issues associated with meme theory in Chapter 9. Her primary goal in this essay is to identify the conditions that must be in place for meme evolution to get up and running. One of the requirements that she identifies is a special form of high fidelity learning called *true imitation*. True imitation, which is found in only a few species, including apes (Whiten *et al.*, Chapter 23), involves the acquisition of some distinctive skill by observing its performance. Blackmore explains that true imitation differs from other, more common forms of learning like *stimulus enhancement* in ways that are crucial to meme theory. Stimulus enhancement involves the acquisition of information about some salient feature of the environment, like a potential food source, by observing the behaviour of other organisms. But this form of learning does not include the transmission of a distinctive skill, such as a particular method for extracting the food. Although stimulus enhancement facilitates the transmission of useful information among organisms, Blackmore sees no theoretical benefit in characterizing this type of information exchange as a form of meme transmission. One way of interpreting Blackmore is that she reserves the term ‘meme’ for units of information that possess a recognizable structure which is largely preserved across transmission events. Insofar as stimulus enhancement involves the acquisition of ‘knowledge that’ without the transmission of ‘knowledge how’, this mode of learning is less structure-preserving than true imitation.

In contrast to Dennett and Blackmore, in Chapter 10 Mark Jeffreys takes it as his starting point that the meme concept is a mere metaphor: it attempts to explain the unknown (cultural evolution) in terms of the known (population genetics). The question for Jeffreys is to what extent does this metaphor offer scientific insight. One aspect of meme theory of which Jeffreys is particularly critical is the comparison between memes and parasites. For instance, in Chapter 8 Dennett claims that,

We might compare these airborne invaders of our eyes and ears [memes] to the parasites that enter our bodies by other routes. There are the beneficial parasites such as the bacteria in our digestive

systems without which we could not digest our food, the tolerable parasites, not worth the trouble of eliminating, such as all the normal denizens of our skin and scalps, and the pernicious invaders that are hard to eradicate such as fleas, lice and the AIDS virus. (p. 152)

Jeffreys raises several ontological objections to the meme-as-parasite metaphor. For one thing, it is impossible to draw a discrete boundary between the so-called meme parasite and its human host. This leaves memes ‘suspiciously disembodied’, he argues. However, the problem with this objection becomes apparent when we consider parallel cases in biology. The eukaryotic cell is thought to have originated out of a mutualistic relationship between two single celled prokaryotes. In the early days of this association it would have been easy to identify the boundaries between the cells that we now identify as mitochondria and their larger, engulfing symbionts. Millions of years later, the two are so closely integrated that their boundaries are much less well defined. Similarly, it might have been much easier to distinguish memes and their hosts during the early days of meme evolution. Perhaps in the early days of culture it was more obvious how certain minds were becoming ‘infected’ with these new memetic parasites. But as in the cellular case, after millennia of co-evolution the boundary between these two kinds of entity has become blurred.

A related epistemic objection to the parasite metaphor is that it sheds no light on the distinctive ways in which memes are replicated. Jeffreys points out that there is no mystery surrounding the replication of parasites, these microorganisms employ the same DNA-based copying mechanisms as their hosts. However, if memes exist, they are copied by mechanisms which are fundamentally unlike those which are involved in the replication of their brainy hosts. Comparing memes to parasites – or, indeed, simply labelling them as replicators and leaving it there – fails to identify meme replication as a serious theoretical problem. Jeffreys concludes that until the mechanisms of meme replication are identified, the meme metaphor will continue to raise more questions than it answers.

In Chapter 11 Scott Atran offers an external critique of the meme metaphor, arguing that so-called memes do not admit of sufficiently high fidelity replication to qualify as units of evolution. There is a fundamental disanalogy between the way that genes are replicated and the process by which ideas are transmitted, Atran argues. Whereas genes are replicated by a template copying process, ideas spread from one mind to another by a process of what Atran describes as ‘inferential reconstruction’. Atran emphasizes the fact that we do not have direct access to the contents of other people’s thoughts. Instead, our access is limited to their syntactically coded utterances, gestures and actions. Atran claims that these ‘external representations’ are typically poor reflections of the underlying ideas that generate them. Hence, interpreting another person’s speech or behaviour involves considerable amounts of inferential reconstruction on behalf of the interpreter. Following Dan Sperber (1996), Atran maintains that this reconstruction process has the potential to rapidly degrade the fidelity of a representation over successive transmission events. In support of this claim Atran cites several experiments where, as in the children’s Chinese whispers, a phrase or image being passed along a chain of individuals undergoes considerable distortion by the time it reaches the end of the line. This challenge to memetics (and to evolutionary accounts of culture in general) has come to be known as the diffusion problem: if the very act of transmission degrades the fidelity of cultural representations, then it appears that there is no stable cultural entity that is capable of undergoing cumulative cultural evolution.

This objection raises a paradox for anyone who views culture as a transmission process. It is a brute fact that many cultural traditions do not degrade in fidelity over time. So there must be some additional process that compensates for the potential loss of fidelity due to transmission error. The place where we should look for such compensatory mechanisms, Atran argues, is in the innate architecture of the human mind. Like most evolutionary psychologists, Atran views the mind as containing numerous ‘mental modules’ or programmes that have been shaped by natural selection acting on genes. These modules are thought to supply content to cultural representations, content that would otherwise be lost to transmission error if it were not innately supplied (see also Sperber and Hirschfeld, Chapter 19, for a detailed defence of this view). From this line of reasoning Atran concludes that the meme construct should be abandoned in favour of a psychologically-oriented account of cultural evolution. What is central to culture according to Atran are the genetically specified representations that are impervious to transmission error.

Even if one accepts Atran’s claims that cultural transmission degrades the fidelity of a representation and that mental modules compensate for this loss (both of which are questionable assumptions), it doesn’t follow that culture can be reduced to psychology in the way that Atran suggests. In fact, his own examples reveal that certain ideas are transmitted more faithfully than others. Surely there must be something about those high fidelity memes themselves that makes them more degradation resistant than their competitors. Arguing along similar lines, in Chapter 12 Kim Sterelny proposes that some memes are fairly transparent in the sense that their acquisition involves little inferential reconstruction. Certain forms of spear-making technology, for example, are relatively easy to reverse engineer by inspecting the finished product. Sterelny argues that in at least these sorts of cases high fidelity transmission does not require the existence of innate mental modules.

Sterelny offers two further replies to Atran’s brand of psychological reductionism. First, he points out that the psychological perspective overlooks co-evolutionary interactions between culture and genes. Our current learning biases did not appear intact prior to the emergence of culture; at least some of our psychological dispositions would have been beneficial only after high fidelity cultural transmission was in place. The psychological reductionist pays attention to only one side of this co-evolutionary process – the selection pressure that minds place on ideas – while ignoring the converse pressure that ideas have placed on minds. Second, Sterelny argues that at least in the case of some traditions, their attractiveness is independent of our particular psychological make-up. Of course, one requires some sort of mind to recognize the value of a good spear or the controlled use of fire. But the value of these items would be recognizable to a wide range of possible psychological beings. Thus, if individual memes have an inherent fitness value, one that supervenes on an indefinitely large range of possible psychological configurations, it follows that meme fitness is not reducible to particular human psychological dispositions.

One of the important insights that Sterelny brings to this discussion is that different models of cultural evolution are more or less suited to describing different kinds of cultural phenomena. The key factor in deciding which of the available models best captures the evolution of a particular cultural tradition depends on the level at which variation appears. Some traditions are embraced by an entire cultural group. Sterelny proposes that such community-wide belief systems are best understood in terms of niche construction theory (see Part IV) rather than meme theory. Dropping down a level, some traditions are passed on primarily from parent

to offspring with a certain amount of ‘leakage’ to non-kin. Dual inheritance models are, on Sterelny’s view, best suited for describing selection at this level (see Part IV and below). Finally, some cultural items vary primarily at the level of the individual idea. Only in these sorts of cases, Sterelny claims, does ‘the fitness of memes themselves play a crucial explanatory role’ (p. 249). Thus, Sterelny’s account of meme theory is fairly restrictive. In order to satisfy the conditions for a meme-style explanation a cultural item must both vary at the level of the idea (and not at the level of biological lineages or cultural groups) and be resistant to diffusion by transmission. Sterelny suggests that meme theory is therefore best suited to explaining the approximately 100,000 year period of human evolution when culture consisted largely of simple utilitarian skills and artefacts that satisfy these two conditions. It is important to note, however, that Sterelny does not accept the Sperber/Atran explanation for why less transparent cultural items are degradation resistant. He does not appeal to innate mental modules to avoid the diffusion problem. Instead, Sterelny’s alternative explanation for the accumulation of more complex cultural phenomena appeals to the idea of niche construction and social scaffolding. These ideas are discussed in the following section.

### **Dual Inheritance Theory and Niche Construction**

Dual inheritance theory has been aptly described as ‘a hybrid cross between memetics and evolutionary psychology, with a little mathematical rigour thrown into the pot’ (Laland and Brown, 2002, p. 242). Like memetics, this theory views culture as a system of ideational phenomena (beliefs, skills, norms and so on) that can be transmitted in relatively discrete chunks among unrelated individuals. Like evolutionary psychologists, dual inheritance theorists assume that genetically encoded psychological dispositions influence the direction of cultural change. However, dual inheritance theorists offer a much more dynamic picture of the ways that genes and culture interact compared with either of these alternative frameworks. A typical dual inheritance model explicitly identifies two or more versions of a gene (A and a) as well as two or more cultural variants (C and c) that are distributed at a certain frequency in the population (for example AC: Ac: aC: ac). Each gene/culture combination is assigned a fitness value that influences its frequency in the next generation (for example  $Ac > AC = aC < ac$ ). In addition, cultural variants can spread horizontally among members of the same population (for example a certain proportion of AC changes to Ac). Once the relevant parameters are set, the model is run over many generations. Such simulations enable researchers to identify the ways that different genetic and cultural traits potentially co-evolve. In one famous example, Feldman and Cavalli-Sforza (1989) developed a dual inheritance model to determine whether dairy farming could have co-evolved with the gene for lactase production. In this model the gene for lactase experiences a fitness boost when paired with the cultural tradition of dairy farming; otherwise it is not selectively favoured. Similarly, the tradition of dairy farming is most advantageous when paired with the gene that allows for the efficient absorption of lactose. This model reveals some unexpected results. The lactose/dairy complex does become rapidly established in the population, but only when dairy farming is highly heritable among related kin. This result is surprising in the sense that it would have been difficult to predict without a dynamic model that explicitly represents gene–culture interactions (Durham, 1991).

The lactose example is somewhat unusual, however, in that, to date, dual inheritance models are not usually so empirically grounded. Rarely do these models identify known genes. More

often the ‘genes’ identified by dual inheritance theorists are actually traits with a complicated genetic basis that potentially interact with cultural factors in a multitude of ways. So, dual inheritance models are highly idealized. However, their simplicity is both a virtue and a vice. As Robert Boyd and Peter Richerson explain in Chapter 13, ‘The goal of such models is to isolate the population level consequences of a limited set of processes by stripping away all of the confusing detail due to other processes’ (p. 265). By exploring the properties of an idealized model it is possible to identify the minimal conditions required for certain traits or traditions to evolve. Idealized models also allow for the identification of general evolutionary trends that would be less visible in a collection of more complicated (though more realistic) models. However, as we shall consider momentarily, the simplicity of these models can also make their application to real-world situations questionable.

Presentations of dual inheritance models tend to be fairly mathematically laborious and do not always make for engaging reading. However, Boyd and Richerson’s model of the evolution of ethnic markers is an exception to this trend. Ethnic markers are behaviours that signal an individual’s affiliation with a particular cultural group. Often these behaviours are arbitrary, like the lilt in one’s speech or a particular form of dress. Although they are found in every known culture, ethnic markers serve no obvious function and thereby pose something of an evolutionary puzzle. Boyd and Richerson’s model offers an interesting ‘how possibly’ explanation for the evolution of ethnic markers. In their model, they imagine a population of individuals who must select a particular subsistence strategy (farming or herding) by observing how well each strategy is panning out for others. The environment is variable, so that in some generations herders do better than farmers and in other generations the opposite is true. The adaptive problem faced by each generation is which strategy is currently the best one going. However, as Boyd and Richerson note, in reality it is not always reliable simply to adopt whichever strategy seems to be working for one’s neighbours. Sometimes there are unknown interaction effects between the behaviour of interest and other practices that one adopts. For example, in some environments it is likely that becoming a successful herder requires cultivating a hair-trigger propensity for violence, a disposition that wards off potential cattle rustlers (Nisbett and Cohen, 1996). When such interaction effects are present it is not good enough simply to adopt the strategy that is most successful. One must also adopt the strategy that is benefiting others whom one most closely resembles. Ethnic markers conceivably provide an index of the degree of cultural similarity between oneself and a potential demonstrator. So, by copying individuals who share the same markers and are at the same time relatively successful one maximizes his or her fitness. An interesting feature of this model is that ethnic markers tend to become more pronounced over time. This suggests that ethnic markers, though in one sense arbitrary, have an important adaptive function in allowing a population adaptively to track fitness peaks in a changing environment.

Through the use of such minimalist models, dual inheritance theorists have identified several important generalizations about the nature of gene-culture co-evolution. For instance, Cavalli-Sforza and Feldman (1981) demonstrate how different types of horizontal transmission (many-to-one or one-to-many) can have a dramatic impact on the rate at which cultural traditions evolve. Another important result identified by Boyd and Richerson (1982, 1985) is that certain forms of intragroup horizontal transmission allow for group-level selection. Although lacking in empirical support, these models provide vivid depictions of the ways genes and culture can (and cannot) co-evolve.



An important criticism of dual inheritance models is that they sometimes make questionable assumptions about human psychology (Atran, Chapter 11; Sterelny, Chapter 12). Take Boyd and Richerson's assumption that humans sample widely from the pool of available demonstrators, mimicking those who are both similar and successful. How realistic is this picture? One might argue that people rarely get the opportunity to sample from a range of cultural parents as opposed to having particular traditions foisted upon them. For that matter, the choice about which subsistence strategy to adopt is rarely such a simple two-factor decision. One of the potential dangers of using such idealized models is that the evolutionary impact of more complex (and arguably more realistic) decision rules are left unexplored.

A related criticism of dual inheritance models draws on the diffusion problem raised by Atran (Chapter 11) in his objection to meme theory. Recall that this criticism states that since the fidelity of a given tradition degrades as a result of social learning there is no stable cultural entity capable of undergoing cumulative evolution. Dual inheritance models typically help themselves to the assumption that cultural variants are, in fact, transmitted with high fidelity. This is another, potentially even more troubling respect in which these models are psychologically unrealistic. The diffusion problem, if it is real, threatens dual inheritance models just as much as it does memetics.

In response to this worry, Joseph Henrich and Robert Boyd (Chapter 14) developed a model that aims to show how cumulative evolution can occur *at the population level* despite low fidelity transmission among individual demonstrators and learners. In their model they imagine that individuals are endowed with a 'conformist bias' that encourages them to adopt the behaviour that is most prevalent in the community. Even when social learning is highly error prone, they demonstrate, this conformist bias operating in conjunction with strong individual-level selection allows the tradition to persist in a population. A similar result can be obtained by relaxing the degree of selection pressure and introducing a second 'prestige bias' that leads individuals to copy the most successful individuals in the group. Again, even at low levels of fidelity, conformist and prestige biases compensate for the diffusion problem and allow for cumulative cultural evolution at the population level.

In Chapter 15 Sterelny objects to this response to the diffusion problem on the grounds that Henrich and Boyd's model is psychologically unrealistic. In particular, Sterelny questions whether it is typically possible to estimate the long-run success of a demonstrator by observing his or her behaviour (a challenge directed primarily at the prestige bias). Many traditions are relatively opaque, Sterelny notes, in the sense that they do not wear their reproductive consequences on their sleeves. This is especially the case for traditions that have delayed developmental consequences, such as the influence of certain parenting strategies on offspring's moral and emotional development (Linqvist, 2007).

This view about the failure of dual inheritance models to explain cumulative evolutionary change raises a paradox similar to the one encountered in the case of memetics. On the one hand, we know that cumulative cultural evolution does occur. On the other hand, models of this process require unrealistic assumptions about the nature of human psychology and/or the strength of selection. Sterelny, for one, is unwilling to accept the evolutionary psychologist's solution to this problem. That is, he doesn't think that there are innately specified modules that compensate for the loss of information by social transmission. Instead, Sterelny suggests that humans have evolved a cultural solution of 'scaffolding' the transmission of cultural materials. Practices like the explicit teaching of hunting and tool-making or the telling of

stories and fables effectively reinforce certain traditions in the minds of social learners, thereby compensating for the potential loss of information by transmission error.

From an evolutionary perspective, Sterelny views social scaffolding practices as a special case of niche construction, a process whereby groups of organisms modify features of their environment in ways that benefit them as a collective. Niche construction theory is the fourth and final member in the family of recent approaches to cultural evolution being explored in this volume. This approach is sometimes described as turning the standard model of adaptation on its head. According to the standard model, the environment is regarded as a sort of filter that selects among organism-produced variation. When the environment changes new variants are selected, and so the process continues. Niche construction theory suggests an alternative way of coping with environmental change. Instead of adapting to environmental pressures, some populations modify their environments in ways that make certain adaptive changes unnecessary. Prototypical examples of niche construction often draw upon non-human examples of epigenetically inherited traits, such as the large mound-dwellings that termites create to protect the colony against temperature fluctuations. Each generation of termites expands upon its mound-dwelling and then passes the modified product on to future generations. Through this process of cumulative niche construction, successive generations of termites are able to build up a highly adaptive structure that relieves them from certain selection pressures. Of course, the adoption of a mound-dwelling lifestyle is bound to come with its own set of adaptive challenges. However, in some cases the fitness landscape created by a modified environment is easier for a population to climb than one that has not been altered. Adapting to fluctuating desert temperatures would arguably involve more radical physical and behavioural changes than the ones required for mound construction and habitation.

Niche construction theorists see a direct parallel between these sorts of examples and what humans do when they construct certain social institutions. In some cases a social institution will take on an evolutionary momentum of its own, imposing selection pressure on both genes and other culturally transmitted traditions. This process is particularly salient in cases where a social institution is perpetuated by the community as a whole. For example, a system of legal or moral norms perpetuated by an entire community can serve as a background against which particular gene-culture combinations are more or less successful. In such cases selection potentially acts at three levels. First, there is potentially variation and selection at the level of the entire community or social group, for example if some legal and moral norms make the collective more competitive than its rivals. Second, there is potentially variation and selection among cultural traditions within the community in their tendency to be more or less successful under the prevailing legal or moral system. Finally, both the community-wide social system and the individually varying cultural traditions potentially impose selection pressure on particular genes. A characteristic of niche construction theories is that they allow for variation and selection at these three levels.

In their defence of this perspective, in Chapter 16 Kevin Laland, John Odling-Smee and Marcus Feldman argue that niche construction theory is an essential complement to dual inheritance models. In one of their more illustrative examples, these authors describe the case of the Kwa-speaking yam cultivators of West Africa whose rainforest clearings led to the creation of breeding pools for mosquitoes. This environmental modification led to an increase in malaria and, in turn, selection for the sickle-cell allele that enhances malaria resistance. These authors argue that ‘the causal chain is so long that simply plotting the cultural trait of

yam cultivation against the frequency of the sickle-cell allele would be insufficient to yield a clear relationship between the cultural trait and allele frequencies' (p. 341). In this case it is necessary to identify three distinct systems that are capable of varying independently of one another: the cultural tradition of yam cultivation, the external environment in which mosquito pools form and the alleles for sickle-cell anaemia. As in the termite example, a modified feature of the physical landscape both enables the Kwa to adapt to their broader environment and serves as a selective niche to which they must genetically adapt.

Up to this point it has been argued that dual inheritance theory offers several advantages over alternative theories of cultural evolution. Unlike memetics, dual inheritance models explicitly represent the co-evolutionary dynamics between particular traditions and alleles. Another advantage of dual inheritance models is that they abstract away from the details of particular evolutionary scenarios and strive for a general account of how certain types of traditions evolve. We have seen that in order to explain cumulative cultural evolution these simple models rely on some questionable psychological assumptions. Niche construction theory potentially provides a more detailed framework for understanding how cultural transmission works. Instead of being a 'leaky' or error-prone learning process, cultural transmission potentially involves the active 'scaffolding' of traditions in naive social learners. This suggestion differs markedly from the alternative, evolutionary psychological hypothesis that genetically specified modules explain the fidelity of cultural representations. To decide between these alternatives the natural place to look is the psychological evidence. The emergence of dual inheritance models has sparked renewed interest in the mechanisms involved in social learning and transmission. It is to this subject that we now turn.

### **Psychological Mechanisms**

Cultural evolution theorists have historically employed a 'top-down' approach in their classification of psychological mechanisms. They begin by asking, what are the conditions that culture must satisfy in order to evolve by natural selection? This leads to the identification of a handful of functional role categories: there must be some source of novel variation, a process by which variants are preserved and another process that selects among them. Only then do cultural evolutionists begin to search for psychological mechanisms to fill those roles. For example, innovation and creativity are posited as novelty generators. Imitation learning is characterized as a mechanism for high fidelity transmission. And various preferences and psychological biases are posited as selective filters. There are both advantages and drawbacks to this top-down approach (some of these were discussed earlier in the context of dual inheritance models). One benefit is that theorists are able to abstract away from irrelevant psychological details about how mental processes are realized at the cognitive or neurological level. From an evolutionary perspective it doesn't matter how neurons store cultural information as much as that they do. Another advantage is that the top-down approach can identify functional similarities in mechanisms that appear distinct at lower levels of description. Although trial and error learning appears to have little in common with drawing inferences about another person's thoughts, both of these mechanisms fall under the same functional category of fidelity degrading processes. A third advantage of the top-down approach is that it can suggest novel hypotheses about how psychological mechanisms work. This is exemplified in an interesting



essay by Joseph Henrich and Francisco Gil-White (Chapter 18) on the evolution of prestige, which is described in more detail below.

It is also important to note the potential drawbacks of the top-down approach. One problem is that this strategy tends to generate an overly simplified picture of the mind. The emphasis often placed on identifying the *minimal* conditions for cultural evolution leads inevitably to an impoverished psychological taxonomy. The top-down approach often ignores the possible ways that other, unidentified mental processes might impact the direction of cultural change. A second challenge for top-down theorists lies in the potential mismatch between functional roles and psychological mechanisms. Sometimes it is questionable whether a given psychological mechanism is capable of performing the functions being assigned to it. For instance, imitation learning is typically identified as the mechanism responsible for transmitting all sorts of cultural information. However, in Chapter 19 Dan Sperber and Lawrence Hirschfeld argue that imitation learning, as it is commonly understood by psychologists, involves the copying of overt skills and behaviours. Since many cultural representations are not associated with a particular behaviour or skill, imitation learning cannot be the primary mechanism involved in cultural transmission (cf. Heyes, 1993). In order to overcome these two obstacles it is often necessary for cultural evolutionists to supplement their psychological taxonomy with findings from empirical psychology, and this sometimes requires making significant revisions to existing evolutionary models.

Henrich and Gil-White's analysis of prestige is a success story for the top-down approach. These authors distinguish prestige from dominance along the following lines. Whereas dominance is a form of social status acquired by exerting force over subordinates, prestige is a form of status bestowed on certain individuals because they possess some valued skill or knowledge. Henrich and Gil-White argue that prestige recognition is a relatively recent adaptation in humans. Once humans became capable of passing on acquired knowledge, a sort of informational economy was born. Every generation a cohort of naive social learners must decide whom among the available cultural role-models to emulate and learn from. Individuals who copy the most knowledgeable or skilled demonstrators enjoy a fitness advantage. However, it is not always obvious, especially over short exposure periods, which of the available demonstrators possesses the most adaptive skill set. Henrich and Gil-White propose that prestige recognition evolved as a way to minimize this discrimination cost. If the amount of prestige a person receives is an honest signal of his or her long-term success, then one can acquire the most adaptive skills by copying the most prestigious demonstrators. In turn, they argue that it is in an individual demonstrator's interest to acquire as many followers as possible. Thus, prestigious individuals are in competition with one another for followers and are therefore predicted to engage in various sorts of non-threatening behaviours that make them seem more attractive. This hypothesis predicts that prestige will be associated with a very different suite of psychological features from dominance. Maintaining dominance involves striking fear into subordinates and it is therefore associated with aggression and submission. Earning prestige, which involves winning the esteem of followers, is associated with non-threatening gestures like self-deprecation and submission. Henrich and Gil-White provide considerable psychological support for their thesis that these two distinct processes are served by different psychological mechanisms. This case illustrates how reasoning about the functional requirements for the transmission of culture can generate novel top-down predictions about the structure of psychological mechanisms.

It is relatively rare, however, that insights from cultural evolution theory lead to this sort of refinement of existing psychological categories. A more common criticism of these theories is that their list of psychological mechanisms is impoverished in respects that are relevant to cultural evolution. For example, one of the more salient features of human psychology is our capacity for rational deliberation. As Dennett noted in his discussion of memetics (Chapter 8), there is an apparent tension between our common-sense normative account of why some ideas are more popular than others (because they are true or more virtuous) and evolutionary accounts that appeal to differential fitness among memes. Dennett argued that the evolutionary approach has certain explanatory advantages over the normative framework. He claims that only evolutionary models explain why some ideas remain popular despite violating our standards for rational acceptability. By contrast, in Chapter 17 Christopher Boehm argues that an adequate theory of cultural change cannot be entirely free of normative considerations. Boehm identifies a process he calls ‘rational pre-selection’ that guides decision-making not only in humans, but allegedly in other primates as well. In troops of *Hamadryas* baboons, Boehm explains, individual group members engage in a sort of voting process about where to search for food. The votes of older more experienced group members carry more weight than those of novices, but eventually the group moves in the direction decided upon by a complex group decision-making process. Boehm argues that even this relatively simple democratic process involves a form of rational pre-selection that cannot be explained in terms of ‘blind’ variation and selective retention. This is perhaps true if one takes the analogy to *blind* genetic variation as a critical feature of cultural evolution models: humans and probably many other creatures often ‘look before they leap’. However, in the baboon case one need not appeal to a normative notion of rationality or justice to explain their collective decision-making behaviour. Some individuals have displayed an aptitude for finding water and food and others know to rely on them as a guide. Cultural evolution models easily explain the evolution of this behaviour in terms of the selection of certain social traditions at the level of the troop. Granted, this theory lacks the resources for explaining the social interactions among group members as they unfold moment by moment. But such proximate level explanations are not in conflict with the ultimate level explanations that cultural evolution models offer.

In the case of rational pre-selection in humans, however, Boehm could potentially make a stronger case. He argues that humans routinely evaluate alternative courses of action before putting any one of them into action. What is interesting about this process is not so much that it involves a form of pre-selection, but rather that it is *rational* (that is, governed by norms of rationality). For example, it is generally thought that beliefs should be subject to critical scrutiny when possible and that those lacking an evidential basis should be discarded. Such standards for what counts as a rational or justified belief do not involve an estimation of its evolutionary consequences. This is the main respect in which human deliberation appears to differ from what baboons are doing. Nor is it clear that our standards of rationality can be explained as the product of cumulative selection on cultural variants. At the memetic level, cultural variants are expected to spread only insofar as they are capable of replicating and spreading more efficiently than competitors – nothing about this process guarantees that memes promoting rational deliberation will be favoured. Nor is selection at the level of cultural lineages or groups likely to favour rationality norms. Religious belief systems that explicitly denounce the need for evidence or rational scrutiny are favoured by cultural group selection when they promote intergroup cooperation and organize the punishment of ‘free

riders' (Wilson, 2002). Arguably, these ends can be achieved more readily by an irrational belief system than by a rational one. Thus, the prevalence of norms for rationality in human societies remains a potential mystery for cultural evolution theories. Until these theories can make clear the link between rationality norms and fitness at some level of cultural or biological organization, rational pre-selection will have to be regarded as a non-evolutionary process capable of directing the course of cultural change.

Following Atran's objection to memetics, in Chapter 19 Sperber and Hirschfeld argue that the mechanisms for cultural transmission identified by most cultural evolution theorists couldn't possibly support high fidelity transmission and cumulative cultural evolution. Imitation learning, they argue, is ineffective when it comes to transmitting concepts or beliefs that are not explicitly manifested in a sequence of behaviours. The transmission of abstract concepts and beliefs therefore requires inferential reconstruction. And this process must in turn be constrained, they claim, by domain-specific cognitive modules that are largely genetically acquired. The fact that different cultures display surprising similarities in their beliefs about the supernatural and in their 'folk biological' categorization systems is cited as further evidence of a shared psychological architecture.

One objection to Sperber and Hirschfeld's argument is that they overstate their conclusion. Many kinds of cultural phenomena (like tools and hunting techniques) could conceivably be transmitted by imitation learning alone. Therefore not all forms of cumulative cultural evolution require that imitation learning be supplemented by buffering mechanisms. Another reply to Sperber and Hirschfeld resists the inference that buffering mechanisms must be innate. Humans engage in various sorts of behaviours that 'scaffold' the acquisition of cultural information in social learners. These social scaffolding behaviours, such as the explicit teaching of an idea or the repetition of a skill until the learner has 'got it', could easily correct for potential loss of fidelity due to imitation. Moreover, many of these traditions could be transmitted socially and would not require the genetic evolution of a domain-specific cognitive architecture.

In Chapter 20 Laureano Castro and Miguel Toro identify another social scaffolding mechanism that can augment imitation learning: parental approval and disapproval of an offspring's beliefs and actions. Approval serves as a form of positive reinforcement without requiring that the offspring directly see the adaptive benefits of a belief or action. Likewise, disapproval allows the offspring to acquire information about the adaptive value of a behaviour that he or she is self-discovering without having to experience its negative implications at first hand. A further function of parental approval and disapproval is that these behaviours communicate to a social learner whether they have adequately mastered a particular skill or idea, thereby enhancing the fidelity of imitation learning. Castro and Toro note that there is no evidence of parental approval or disapproval in any other primate besides us. This supports the claim that approval mechanisms are one of the important components in our unique capacity for cumulative cultural evolution. Although they do not discuss the developmental origin of approval mechanisms, it is conceivable that these are transmitted at least in part by non-genetic means. Once such mechanisms are in place they could potentially scaffold the development of beliefs about the supernatural, folk biological categories and other bodies of adaptive knowledge.

The essays in Part V identify an interesting new direction for theories of cultural evolution. Traditionally these theories have operated with a minimalist account of the mechanisms

involved in social transmission. Decisions about whom to imitate were seen as an individually guided process much like trial and error learning, where the agent samples and evaluates the available models. Imitation itself was often taken for granted as a high fidelity process requiring little social enhancement. Questions about the plausibility of these assumptions led to a more elaborate picture where models play an active role in guiding the acquisition of cultural information. Future directions for this theory will explore why such social scaffolding mechanisms evolved exclusively in humans and what sort of genetic adaptations contributed to their evolution.

### **Culture in Non-human Animals**

Until recently, the suggestion that culture might be found in other species would have been scoffed at by most scientists. Culture has historically been regarded as one of those sacrosanct traits, like tool use (Allen, 1997), language (Deacon, 1997) and moral reasoning (Joyce, 2006), that distinguish humans from other animals. This view was challenged in the 1960s by Jane Goodall and fellow primatologists who reported field observations of population-specific behaviours that appeared to be socially acquired (Goodall, 1968, 1973). Another example, potato-washing in Japanese macaques, has become one of the most glorified cases of primate culture (our own species notwithstanding). Primatologists were present when Imo, a young female macaque, first hit upon this strategy of removing soil from her food and they carefully documented the spread of this behaviour to her fellow troop members. In reporting this event, Masao Kawai (1965) was careful to describe potato-washing as a *pre-cultural* behaviour. However, this and other animal traditions are now commonly described as instances of animal culture, full stop. This choice of wording would be less controversial if 'culture' had an accepted theoretical definition against which such claims could be evaluated. But as many of the essays in this volume note, there is little agreement about what the defining features of culture are. The debate over how to label animal traditions is therefore more than just a semantic one. At issue is the question of whether human and animal cultures, though obviously different in certain respects, can be explained in terms of the same Darwinian principles.

Theorists who view animal traditions as continuous with human culture tend to emphasize their similarities: both are acquired by observational learning, both can involve arbitrary or non-functional behaviours, both forms of culture are capable of descent with modification and local adaptation. However, critics who argue for a difference in kind note that animal traditions are fairly piecemeal in character, usually involving a patchwork of context-specific behaviours like nut-cracking and termite-fishing rather than an integrated suite of practices. A second difference is that (arguably) only human cultural representations are symbolic (Deacon, 1997), which seems an important factor in explaining their spread and development. Another critical difference is that human cultures have elements which are explicitly taught while, as far as anyone knows, all animal traditions are gleaned exclusively by observation (Sapolsky, Chapter 21). This fact has been used to explain another distinguishing feature: even the simplest forms of human culture are much richer than any animal tradition. Regardless of whether one is talking about tool-making in ravens, song evolution in finches or termite-fishing in chimps, the potential for complexity and cumulative evolution appears quite limited. So there must

be something distinctive about the human mind that explains the informational complexity of human culture. The four essays in Part VI address these and other related issues.

Robert Sapolsky, in Chapter 21, challenges one of the purported differences between human and animal cultures, arguing that in some species culture is not as piecemeal as most researchers assume. Sapolsky acknowledges that many reported cases of animal culture involve isolated behaviours that occur in circumscribed contexts. However, he goes on to identify a less frequently described form of 'social culture' that affects a broad range of different social interactions. The best documented example of social culture involves a particular troop of baboons that experienced a sudden loss of adult males due to disease. This event caused a sea change in the troop's social milieu. Interactions went from being highly aggressive and stressful to relaxed and welcoming. The key feature of this example is that the adoption of a relaxed cultural style permeated a range of different behaviours including grooming rates, number of aggressive encounters and individuals' willingness to accept new troop members. Not only does this example challenge the assumption that animal culture is piecemeal, it also suggests that animal social cognition is more flexible than many authors have assumed. On the traditional view animal social cognition is regarded as highly domain-specific. For example, the way that an animal responds to a dominance threat is thought to be unrelated to its parenting style or grooming behaviour. Likewise, humans are sometimes considered unique in their capacity for cross-domain reasoning (Sterelny, 2003). However, if Sapolsky is correct about the nature of social culture in baboons, these organisms are cognitively more flexible than has been traditionally assumed.

Like the potato-washing example, Sapolsky's observations of social culture in baboons involved careful fieldwork spanning several years. Students of animal culture do not always have the time and resources for this kind of detailed analysis. Thus, in recent years there has been an effort to develop more efficient strategies for documenting animal culture. One of the most influential techniques was pioneered by Andrew Whiten and his colleagues (1999) who claim to identify a range of cultural differences among chimpanzee populations. These researchers drew upon existing behavioural reports from seven distinct field locations. Their analysis revealed 42 categories of behaviour that varied among the different research sites. In the next stage of their analysis Whiten *et al.* excluded any behaviour that could be explained as an adaptation to the local environment. Once these ecologically meaningful behaviours are discounted, 39 behavioural differences remain. The majority of these differences involve foraging or feeding. For example, some chimpanzee use stones to pound nuts, others do not use any form of anvil but instead employ a stick to probe ant mounds and so on. Whiten *et al.* argue that these behaviours cannot be attributed to genetic differences among the populations. Nor, they argue, are these behaviours likely to have been acquired by individual (non-social) learning. On these grounds Whiten *et al.* infer that chimpanzee groups possess at least 39 distinct cultural traditions.

This study has inspired several similar investigations that have identified cultural traditions in monkeys, orang-utans, whales and dolphins (Laland and Janik, Chapter 22). In each case the same methodology is employed: any population-specific behaviours that are not ecologically meaningful and which cannot be attributed to genetic differences are identified as cultural. However, in Chapter 22 Kevin Laland and Vincent Janik identify several flaws in this methodology. These studies do not carefully explore the role that genetic differences might play in contributing to behavioural differences. Nor are the researchers who conduct



these studies sufficiently familiar with local ecological conditions to rule out adaptation as an alternative explanation. More fundamentally, however, Laland and Janik object that this methodology rests on a pair of faulty assumptions. First, it is assumed that a trait is cultural only if it is not ecologically meaningful. The problem is that cultural traits can themselves evolve by natural selection and thereby promote ecologically meaningful behaviour. Second, Whiten *et al.*'s methodology fallaciously assumes that behaviours are either culturally or genetically specified. In fact, no 'cultural' trait lacks a genetic basis; and many 'genetic' traits are modified by culture. Dual inheritance theory offers a particularly vivid illustration of how both cultural and genetic factors contribute to the development of certain behaviours (see Part IV). As a way of transcending these problematic assumptions, Laland and Janik offer several alternative methods for identifying culture in animals.

In Chapter 23, 'How Do Apes Ape?', Andrew Whiten and his colleagues explore the psychological dimension of chimpanzee culture. The verb 'to ape' was introduced into the animal culture literature by Michael Tomasello (1996) as something of a technical term. Tomasello defined 'aping' as a kind of imitation learning where the observer adopts a specific action from a demonstrator. Learning to fish for termites with a stick is not necessarily aping, on this view, unless the observer adopts the exact sequence of bodily movements from the demonstrator. Tomasello argued that according to the evidence that was available at the time, apes cannot ape. Instead, apes were thought to be capable of mere 'emulation learning', a form of stimulus enhancement where the observer learns something about the environment (for example that sticks can be used as tools) without acquiring a specific skill. However, as Whiten *et al.* note, a considerable amount of research on apes' capacity for social learning has transpired since the publication of Tomasello's essay. It is now recognized that apes can ape, the question is how or, more specifically, what learning strategies do apes employ when learning by observation?

Based on their review of the recent evidence, Whiten *et al.* conclude that the distinction between imitation learning (or aping) and emulation learning is too coarse-grained. Apes are capable of a variety of different forms of observational learning that fall between these two extremes. For instance, chimps are capable of 'goal emulation' where they acquire the objective of a demonstrator (for example to acquire food from inside a container) without mimicking exactly the demonstrator's movements. Whiten *et al.* distinguish goal emulation from the less cognitively sophisticated task of 'results emulation', where the observer learns about a certain result from a demonstrator (for example that some containers hold food) without recognizing that the observer was striving to achieve some goal (for example looking for food). Apes also engage in 'object movement re-enactment' which involves copying the form of a caused object movement (for example swinging a hammer), though not necessarily by adopting the exact same movements as the demonstrator. Generally speaking, Whiten *et al.* note that apes tend to be more focused on the objects that a demonstrator is manipulating, and the results of those manipulations, than they are on the exact behaviours or strategies demonstrators employ. If an observer acquires a goal from a demonstrator, but is unsuccessful in using his or her own strategy for achieving that goal, then the demonstrator might refocus attention on the way in which the demonstrator executed that end. This would be a case of frustrated goal emulation leading to full blown aping. However, as Whiten *et al.* note, apes will resort to strict imitation only when their own attempts to achieve some goal have been unsuccessful. So, apes employ a collection of social learning strategies. Sometimes they learn that a particular object

has the potential to be useful (for example as a general purpose hammer) without associating that object with a specific goal. At other times an ape will acquire a goal from a demonstrator, but insist on employing its own strategy for realizing that end. If, however, that strategy isn't working an observer will sometimes consult the demonstrator's exact movements and try to ape his or her actions exactly. There is some evidence that humans are less flexible in their social learning strategies. More often, a child will adopt the exact actions of a demonstrator (they will ape) without first striking out on their own. A simple way of viewing the differences is that children are more intent, at least initially, on copying what the demonstrator is doing than they are on deciphering the reason for doing it. It seems likely that this emphasis on behavioural process is a key ingredient in explaining the richness of human culture.

However, the finding that chimpanzees are capable of imitative learning (aping) poses a puzzle for theories of cultural evolution. If chimps are capable of aping, then why is chimpanzee culture significantly less complex than human culture? The traditional explanation (Tomasello, 1996) appealed to chimps' inability to ape as the reason for why useful behaviours, when they arise, are usually not preserved over successive generations. However, Whiten *et al.*'s analysis suggests that chimp culture should be more complex than it is. Suppose that some chimp has hit upon a particular strategy for building shelters that requires following a particular sequence of steps. Others might initially attempt to construct this shelter using a strategy of their own. But after several unsuccessful attempts, one would expect those observers to consult the demonstrator a second time, paying closer attention to her techniques. Thus, one might expect to find at least some complex cultural artefacts – shelters, perhaps weaponry – given that apes have the capacity to ape (albeit a somewhat reluctant one).

In Chapter 24 Tomasello identifies several additional features of the human psyche, besides the capacity for imitation, that potentially explain why human culture is so distinctive. One of these is our capacity for language. As evolutionary biologists John Maynard-Smith and Eors Szathmari (1997) have suggested, the emergence of language might have constituted a 'major transition' in human evolution because it provides an efficient means for encoding vast amounts of information. Perhaps there is simply an upper limit to how cognitively complex a non-linguistic culture can become. However, this cannot be the whole explanation for why human culture is so different from what we find in other primates. First, it is implausible that any tool more complex than a stick or anvil requires language to facilitate its social transmission. Even without language, chimp culture could become a lot more complex than it is. Second, this explanation merely pushes the question back a level. If language is the necessary ingredient for complex culture, then what sorts of psychological abilities had to be in place before it could evolve?

Tomasello also mentions our capacity for joint attention as a key ingredient for human culture. From a very early age, an infant's attention is drawn to the objects that she sees her caregivers attending to. Thus, from the beginning a child's environment is interpreted through the eyes of her caregiver. Tomasello sees this capacity as being closely related to humans' tendency to identify others as intentional agents (agents with beliefs and goals). So, perhaps it is our ability to read the intentions of others, to see that they have beliefs and goals, that explains our absorbency as cultural sponges.

But this can't be the whole story, either. Chimps are also capable of joint attention, especially at a young age. And as Whiten *et al.* note, chimps seem quite adept at identifying and emulating the goals of their fellow troop members.

Perhaps, then, the reason why humans are so culturally distinct lies not in a difference in kind but rather in a difference in degree. Like chimps, humans are capable of imitation. However, we imitate more readily and are less likely to try a new strategy when we've seen one that works. Also like chimps, humans are capable of joint attention and of reading others' intentions. However, in humans these capacities are exaggerated to the level of an obsession. As infants we are fixated on what our caregivers are attending to. As adults, we continue to interpret the world in terms of beliefs and desires even when none exist. Hence, the rudiments for complex culture appear to be present in other species, only in humans they are exaggerated. If this view is correct, one can imagine that it would be fairly easy to transform chimpanzees into a robustly cultural species. Only a few slight modifications would be required. Just turn up their interest in the thoughts and aims of others, have them engage in joint attention from an early age and make them more conformist in their imitative proclivities. After a few thousand generations of cultural evolution these primates will potentially have evolved a complex culture rivalling what one finds in humans.

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# Name Index

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- Abramovitch, R. 411, 413–14  
Adamson, L.B. 468  
Aiello, L.C. 344  
Akhtar, N. 484  
Akins, C.K. 469  
Albers, Patricia 118  
Alexander, Richard D. 65  
Allen, Barry xxxvi  
Allen, J.A. 345  
Althusser, Louis 69  
Altmann, N. 362  
Altmann, S.A. 362  
Ammerman, A. 117  
Aristotle, 455  
Atkinson, Q.D. 133–4, 135, 140  
Atran, Scot xii, xxvi, xxvii, xxviii, xxx, xxxv, 207–37, 248, 249–50, 256, 280–1, 282, 290, 296, 298–9, 302, 310–11, 312, 421  
Augustine, Saint 205  
Aunger, Robert 192, 193, 197  
Avital, E. 247
- Baldwin, J.M. 177, 179, 455  
Ball, J.A. 168  
Bard, K.A. 465, 468  
Barkow, Jerome H. xii, 46, 52, 80, 396, 401  
Baron, R. 293  
Barth, Frederik 264, 274, 366–7, 369, 379  
Basalla, George 197  
Bates, J.V. 411  
Bateson, G. 406  
Bauer, G.P. 411  
Baum, W.B. 433  
Beck, B.B. 26  
Beethoven, Ludwig van 150, 199  
Bell, P.A. 293  
Bellwood, P. 133  
Bennett, John W. 382  
Bentley, G. 94  
Benzon, W. 166  
Bergmann, Carl 345  
Bering, J.M. 469
- Bernardi, Bernardo 80  
Betzig, L.L. 52, 201  
Bickman, L. 407  
Binford, Lewis 113, 373  
Bjorklund, D.F. 469, 471  
Black-Michaud J. 369  
Blackmore, Susan xxv, 159–89, 197, 198, 199, 205, 211, 213, 225  
Bloomfield, Leonard 115  
Blute, M. 42  
Boas, Franz 63, 115, 123  
Boehm, Christopher xxxiv, 357–88  
Bond, R. 293  
Bonner, J.T. 26  
Borges J.L. 425  
Bourke, Robert 305  
Bowen, John R. 99–100  
Boyd, Robert xxx, xvi, xvii, xxix, xxx, 46, 47, 49, 51, 78, 81–2, 84, 138, 163, 170, 244, 247, 263–77, 279–304, 305–6, 308–9, 310, 312–19, 324, 325, 327–8, 347, 348, 399, 402, 421, 429, 430, 431–2  
Boyer, P. 256, 280, 282, 290, 299, 302, 310, 312, 421, 425  
Brahms, Johannes 150  
Braidwood, Robert J. 373  
Bray, Warwick 366  
Brockway, Raewyn 322  
Brodie, Richard 166, 168, 194  
Brody, G.H. 408  
Brown, Gillian. xii, xiii, xxviii  
Bryant, D. 138  
Buckley, Walter 370–1, 380  
Burke, M.A. 285  
Byrne, J.M.E. 468  
Byrne, R.W. 172, 467, 468, 469–70, 472
- Caesar, Julius 119  
Calder, N. 28  
Call, J. 462, 465, 466  
Calvin, William 196, 197  
Campbell, B.G. 372  
Campbell, Donald T. 364

- Campbell, J.D. 293  
 Campbell, K. 94  
 Carpenter, M. 466, 484  
 Castro, L. 321, xxxv, 429–34  
 Cavalli-Sforza, Luigi L. xiv, xv, xvi, xvii, xviii, xix, xx, xxviii, xxix, 25–35, 39, 46, 47, 48–9, 81, 94, 95, 102, 109, 110, 162, 168, 348, 429  
 Charman, T. 466  
 Cheney, D.L. 432  
 Childe, V.G. 40  
 Cloak, F.T. xiii, xiv, xv, xvi, 3–24, 164, 166  
 Cohen, Dov xxix  
 Cohen, Ronald 365  
 Coleman, J.S. 405  
 Collard, M. 137  
 Corp, N. 468  
 Cosmides, Leda xii, 65  
 Count, Earl W. 374  
 Cronin, H. 174  
 Custance, D.M. 464, 465, 469, 471  
  
 Daly, Martin 83  
 Darwin, Charles xi, xix, 20, 37–9, 46, 51, 62, 69, 70, 72–3, 78, 92, 111, 132, 160, 174, 192, 198, 199, 205, 248, 383  
 Das Gupta, Biman Kumar 100–1  
 Dawkins, Richard xiii, xv, xvi, xxii, xxiii, 81, 149, 150, 151–2, 155–6, 159, 161, 162, 164, 165, 167, 182, 184, 191, 193, 194, 197, 199, 207, 209, 211, 212–3, 214, 225, 241, 246, 248, 253, 301, 307, 339  
 Deacon, T. xxxvi, 163, 175  
 Delius, J. 165, 166  
 Dennett, Daniel C. xxiii, xxiv, xxv, xxxiv, 149–57, 160, 162, 165, 166, 167, 179, 191, 192–4, 199, 205, 213  
 Dentan, R.K. 394  
 Descartes, René 194  
 Deutsch, Karl W. 370  
 Dewaal, F.B.M. 457  
 Diamond, J. 133  
 Dollard, J. 407  
 Donald, M. 175  
 Dow, Malcolm M. xx  
 Driver, Harold E. 103  
 Durham, William H. xiv, xvii, xviii, xxviii, 37–60, 84, 112, 162, 165, 167, 168, 343  
 Dylan, Bob 150  
  
 Edgerton, R.B. 366  
 Eibl-Eibesfeldt, I. 15  
 Eggan, Fred 100, 101, 381  
 Einstein, Albert 391  
 Eldredge, N. 139  
 Ember, Melvin 101  
 Ensminger, J. 368  
  
 Fairey, P.J. 293  
 Faith, D.P. 138  
 Feldman, M. xxviii, xxix, xxxi, 31, 46, 47, 48–9, 81, 162, 168, 322, 335–54, 429  
 Firth, Raymond 378  
 Fisher, R.A. 30, 265  
 Fjellman, S. 358, 367  
 Flannery, Kent V. 364  
 Fodor, Jerry 422  
 Fortunato, L. 136  
 Fracchia, Joseph xiv, xviii, 61–87, 132  
 Fragaszy, D. 468  
 Franklin, Benjamin 141  
 Fredman, T. 464  
 Fried, Morton H. 364  
 Furet, François 67  
  
 Gabora, L. 166, 168  
 Galef, B.G. 430  
 Gallese, V. 176  
 Galton, Francis xix, 91–2, 94, 101, 136  
 Gentner, Dedre 192  
 Gil-White, F. xxxiii, 295, 318, 323, 329, 389–420  
 Gobineau, Arthur de 119  
 Godfrey-Smith, P. 142  
 Goldberg, T. 94  
 Goldman, A. 176  
 Goldman, I. 404, 408  
 Goldschmidt, Walter 366, 369, 382  
 Gomez, J.C. 465  
 Goodall, J. xxxvi, 483  
 Goodman, Nelson 226  
 Gould, Richard 113  
 Gould, Stephen Jay 136, 142, 192, 195–6, 201, 214, 307  
 Grant, G. 165, 166  
 Gray, Russell D. xx, xxi, xxii, 131–46  
 Green, R. 135–6, 141, 143  
 Greenhill, Simon J. xx, 131–46  
 Griffiths, Paul E. xvi  
 Gross, A.M. 407  
 Guglielmino, C.R. 349

- Gulliver, P. 367
- Haas, Mary 109
- Haeckel, Ernst 11
- Haiman, F.S. 409
- Haldane, J.B.S. 265
- Ham, R. 171, 463, 481
- Hamilton, W.D. 211, 265, 346
- Harris, M. 17
- Harris, P.L. 463, 467–8
- Hartigan, Richard Shelly 65
- Harvey, P. 99
- Hass, H. 15
- Hatch, E. 414
- Hawkes, K. 406
- Hawking, Stephen 391, 395
- Haydn, Joseph 150
- Hayes, C. 462
- Hayes, K.J. 462
- Henrich, Joseph xxx, xxxiii, 248, 279–304, 305, 313–4, 318, 323, 324, 327, 389–420, 430
- Herskovits, Melville J. 366
- Heyes, C.M. xxxiii, 171, 430, 466
- Hirata, S. 472
- Hirschfeld, Lawrence A. xii, xxvii, xxxiii, xxxv, 421–7
- Hobbes, Thomas 67, 75
- Hodder, Ian 117
- Hold, B.C.L. 411–14
- Holden, C.J. xxi, 135
- Holmberg, A.R. 404
- Holtgraves, T. 410
- Holy, L. 91
- Hooten, Earnst A. 111
- Horner, Victoria 461–77
- Howard, A. 367, 369, 378, 379
- Huang, C.T. 466
- Hull, David 144, 161, 210
- Hume, David 149, 226
- Ingold, T. 40, 46
- Insko, C.A. 293
- Irons, W. 46, 52
- Jablunka, E. 247
- Janik, Vincent M. xxxvii, xxxviii, 455–60
- Jantz, Richard 117
- Jasienska, G. 94
- Jeffreys, Mark xxv, xxvi, 191–206
- Johnson, A.W. 321, 366, 378
- Johnson, T.C. 407
- Jones, Blurton 15
- Jones, C.G. 337
- Joyce, Richard xxxvi
- Kant, Immanuel 69
- Kaufman, Terrence xx, xxi, 115, 122
- Kawai, Masao xxxvi
- Kelly, R.L. 405
- Kelman, H.C. 410
- Key, Patrick 117
- Khaldun, Ibn 75
- Kirch, P. 135–6, 141, 143
- Knauft, B.M. 264
- Konner, Melvin 78
- Kroeber, A.L. 40, 41, 103
- Kroll, Y. 408
- Kruger, A.C. 170, 467, 471, 481
- Krützen, M. 457–8
- Kummer, Hans 361–3 *passim*, 370, 372, 483
- Labov, W. 410
- Lack, D. 218
- Laland, Kevin N. xii, xiii, xxviii, xxxi, xxxvii, xxxviii, 168, 322, 335–54, 430, 455–60
- Lamarck, Jean-Baptiste 73, 111
- Lamb, Sydney 114
- Laplace, Pierre-Simon 69
- Lester, L. 138
- Levy, H. 408
- Lewontin, R.C. xiv, xviii, 61–87, 132, 239, 307, 322, 336
- Liebenberg, L. 405
- Linguist, Stefan xxx
- Linton, R. 40, 41, 381
- Litchfield, Carla A. 461–77
- Lloyd-Morgan, C.L. 473
- Locke, John 149
- Lord, Albert B. 377
- Lumsden, C.J. 46, 47, 50, 84, 162
- Lynch, Aaron 165, 194, 199
- McCarthy, John 154
- Mace, Ruth xix, xx, xxi, 91–106, 135
- McElreath, Richard 305, 430
- McGrew, W.C. 455
- McMahon, A. 140
- McMahon, R. 140
- Maddison D.R. 95
- Maddison, W.P. 95, 99

- Malinowski, Bronislaw 364, 369, 379, 380  
 Marchetti, C. 32  
 Marck, J. 135  
 Margulis, Lynn 196  
 Markov, Andrey 99  
 Marshak, Alexander 372, 373  
 Marshall–Pescini, Sarah 461–77  
 Masters, M.A. 411  
 Matsuzawa, T. 467, 469  
 Maxwell, R.J. 406  
 Maynard-Smith, John xxix  
 Mayr, E. 20, 359  
 Medina, A. 321  
 Meggitt, Mervyn J. 368, 369, 379  
 Meltzoff, A.N. 171, 466, 484  
 Mendel, Gregor 7  
 Menozzi, P. 101  
 Merrill, Robert S. 367, 369, 377–8, 382  
 Mesoudi, Alex. xii  
 Miklosi, A. 466  
 Mill, John Stuart 64  
 Miller, G.F. 181  
 Miller, N.E. 407  
 Miller, Stanley 198  
 Mithen, Stephen 250  
 Moore, B.R. 176  
 Moore, John H. xx, xxi, 107–30  
 Morgan, C.L. 455  
 Morgan, Lewis Henry 62, 73  
 Morimura, N. 472  
 Moulton, V. 138  
 Mozart, Wolfgang Amadeus 150  
 Murdock, G.P. xix, 40, 91, 92, 94, 141  
 Myowa-Yamakoshi, M. 467, 469
- Nagell, K. 465, 484  
 Nakicenovic, N. 32  
 Nei, M. 102  
 Nicklas, Dale 120  
 Nisbett, Richard E. xxix  
 Nunn, C.L. 141
- Odling-Smee, J. xxxi, 168, 322, 335–54  
 Offerman, T. 408  
 Olguin, R.S. 465  
 Onoge, Omafume 381  
 Orr, H. Allen 192  
 Ortiz, S. 367, 368, 369, 378, 379  
 Ostrom, Elinor 326  
 Otterbein, Keith F. 101–2
- Owen, Roger 118  
 Ozouf, Mona 67
- Pagel, Mark xix, xx, 91–106, 134–5, 143  
 Parker, Charlie 150  
 Phares, J.E. 409  
 Piazza, A. 102  
 Pinker, Steven 195–6, 200–1  
 Plato, 153, 225  
 Plotkin, Henry 165, 195, 197  
 Povinelli, D. 254  
 Pugh, G.E. 50
- Radcliffe-Brown, Alfred 101  
 Radin, Paul 379  
 Ragan, P. 469  
 Rappaport, Roy A. 366, 378  
 Ratner, H.H. 170, 467  
 Reader, S.M. 430  
 Rendell, L. 457  
 Renfrew, Colin 109, 110, 117, 133  
 Reynolds, Vernon 365–6, 382  
 Richerson, Peter J. xvi, xvii, xxix, xxx, 46, 47, 49, 51, 78, 81–2, 84, 163, 170, 244, 247, 263–77, 293, 305–6, 308–9, 310, 312–19, 324, 325, 327–8, 347, 348, 360, 399, 402, 421, 429, 430, 431–2
- Ridley, M. 92, 99, 102  
 Ritchie, E. 409  
 Robertson, D.S. 339  
 Rogers, A.R. 429  
 Rogers, E.M. 410  
 Rosenbaum, M.E. 408, 409  
 Rosenberg, Alexander 64, 84  
 Ross, Robert M. xx, 131–46  
 Rouse, Irving 110, 117  
 Rowe, John H. 117  
 Roychoudhury, A.K. 102  
 Ruhlen, M. 41, 95  
 Russell, C.L. 468  
 Russen, A.E. 172, 470, 472  
 Ryckman, R.M. 409
- Sahlins, Marshall 73–4, 264  
 Sanderson, M.J. 134  
 Sapolsky, Robert M. xxxvi, xxxvii, 437–53  
 Saussure, Ferdinand D. 80  
 Savage-Rumbaugh, S. 471, 481  
 Schlottmann, R.S. 411  
 Schweizer, Thomas 103



- Service, Elman R. 364  
 Seyfarth, R.M. 432  
 Sharrock, Susan R. 118  
 Shennan, S. 324  
 Silverman, P. 406  
 Simmons, L.W. 405–6  
 Simon, H. 433  
 Smith, John Maynard 265, 293  
 Smith, P.B. 293  
 Snow, C.P. 61–2 *passim*, 68  
 Sober, E. 347  
 Socall, D. 410  
 Sokal, Robert R. 109  
 Sonnemans, J. 408  
 Spencer, Herbert xiii, 62, 73  
 Spencer, M. 140  
 Sperber, Dan xii, xxvi, xxvii, xxxiii, xxxv, 195–6,  
 201, 213, 229, 248, 249–50, 254, 256,  
 280–1, 282–3, 290, 296, 298–9, 302,  
 310–11, 312, 313, 421–7  
 Srull, T. 410  
 Stearman, A.M. 404  
 Sterelny, Kim xvi, xxvii, xxviii, xx, xxxi, xxxvii,  
 133, 141, 239–59, 305–33  
 Steward, Julian 100, 366  
 Stoinski, T.S. 465, 472  
 Stoneman, Z. 408  
 Stuart-Fox, Martin 80, 83  
 Sullivan, Arthur Sir 154  
 Sutton, Douglas G. xix  
 Swadesh, M. 133  
 Swift, 199  
 Szathmary, Eros xxix  
 Tannenbaum, P.H. 409  
 Teixidor, P. 465  
 Tëmkin, I. 139  
 Thomason, Sarah G. xx, xxi, 115, 122  
 Thorndike, E.L. 171  
 Thornhill, Nancy 201  
 Tinbergen, N. 4  
 Tomasello, M. xxxviii, xxxix, 170, 429, 462, 463,  
 465–7, 471, 479–90  
 Tooby, John xii, 65  
 Toro, Miguel A. xxxv, 321, 429–34  
 Tucker, I.F. 408, 409  
 Twain, Mark 141  
 Tylor, Edward Burnett 73  
 Ungar, S. 407  
 Van Schaik, C.P. 455–6, 457, 461  
 Visalberghi, E. 468  
 Voland, Eckart 103–4  
 Vrba, E.S. 345  
 Waddington, H.C. 433  
 Wallace, Alfred R. 174, 455  
 Wang, W.S.Y. 28  
 Want, S.C. 463, 467–8  
 Ward, R.H. 116  
 Wedel, Waldo R. 117  
 Wheeler, P. 344  
 White, D.R. xix, 92  
 White, Leslie 66, 67, 364  
 White, Lewis 63  
 Whitehead, H. 457  
 Whiten, Andrew xii, xxv, xxxvii, xxxviii, xxxix,  
 xl, 171, 173, 455, 457, 461–77, 481  
 Wilkins, J.S. 165, 167  
 Willey, Gordan 117  
 Williams, G.C. xv, xxii, xxiii 165, 174, 211  
 Wills, William 305  
 Wilson, Allan 344  
 Wilson, D.S. xxxv, 347  
 Wilson, E.O. 46, 47, 50, 63, 76, 78, 80, 84, 162  
 Wimsatt, W.C. 307  
 Wood, D. 466–7  
 Wood, J. 94  
 Wright, S. 265  
 Young, H.P. 285  
 Zahavi, A. 253  
 Zentall, T.R. 469