PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Culture evolves

Andrew Whiten, Robert A. Hinde, Kevin N. Laland and Christopher B. Stringer

Phil. Trans. R. Soc. B 2011 **366**, 938-948
doi: 10.1098/rstb.2010.0372

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2011) **366**, 938–948
doi:10.1098/rstb.2010.0372

Introduction

Culture evolves

Andrew Whiten[1,*], Robert A. Hinde[2], Kevin N. Laland[3] and Christopher B. Stringer[4]

[1]*Centre for Social Learning and Cognitive Evolution, School of Psychology, St Andrews KY16 9JU, UK*
[2]*St John's College, Cambridge CB2 1TP, UK*
[3]*Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, St Andrews KY16 9TS, UK*
[4]*Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK*

Culture pervades human lives and has allowed our species to create niches all around the world and its oceans, in ways quite unlike any other primate. Indeed, our cultural nature appears so distinctive that it is often thought to separate humanity from the rest of nature and the Darwinian forces that shape it. A contrary view arises through the recent discoveries of a diverse range of disciplines, here brought together to illustrate the scope of a burgeoning field of cultural evolution and to facilitate cross-disciplinary fertilization. Each approach emphasizes important linkages between culture and evolutionary biology rather than quarantining one from the other. Recent studies reveal that processes important in cultural transmission are more widespread and significant across the animal kingdom than earlier recognized, with important implications for evolutionary theory. Recent archaeological discoveries have pushed back the origins of human culture to much more ancient times than traditionally thought. These developments suggest previously unidentified continuities between animal and human culture. A third new array of discoveries concerns the later diversification of human cultures, where the operations of Darwinian-like processes are identified, in part, through scientific methods borrowed from biology. Finally, surprising discoveries have been made about the imprint of cultural evolution in the predispositions of human minds for cultural transmission.

Keywords: culture; cultural evolution; traditions; social learning; human evolution; cognition

1. INTRODUCTION AND OVERVIEW

Culture, broadly conceived as all that individuals learn from others that endures to generate customs and traditions, shapes vast swathes of human lives. Cumulative cultural achievements, from technology to social institutions, have allowed our species to invade and exploit virtually every region of the planet. Accordingly, this special capacity for culture is often thought to represent a qualitative distinction between our species and the rest of nature, and our relative independence from the Darwinian forces that shape the natural world.

A different perspective has grown in a diverse range of disciplines that instead focus on the evolution of culture,[1] and thus address continuities as well as discontinuities. Here, we bring these different endeavours together to facilitate cross-fertilization among them and encourage the building of a more coherent science embracing the different strands of the evolution of culture. We have sought to include a breadth of studies that illustrate the importance, excitement and extensive scope of this rapidly expanding field. In introducing the papers, we allocate them to four main themes (parts 1–4), each of which has seen substantial and radical progress in recent years.

The first theme concerns the evolution of social learning, traditions and other culturally related phenomena, which have proved to be far more widespread across the animal kingdom than imagined a half-century ago, and more complex in their manifestations [1–8]. The pace of discovery in this area has accelerated markedly in this century [9–11]. A rich variety of underlying social learning processes, strategies and behavioural consequences has also been identified [12–17]. These discoveries are of considerable scientific importance from several perspectives. One is that the identification and understanding of this 'second inheritance system' [18–20], operating in addition to and in interaction with genetic inheritance, has far-reaching consequences for our broader understanding of evolutionary biology. A second is

* Author for correspondence (a.whiten@st-andrews.ac.uk).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2010.0372 or via http://rstb.royalsocietypublishing.org.

One contribution of 26 to a Discussion Meeting Issue 'Culture evolves'.

that the nature of human culture becomes less mysterious as allied manifestations are charted among non-human animals and early hominins, and inferences drawn about the evolutionary foundations of humanity's distinctive cultural faculties.

The sense of 'culture evolves' in this first part of the issue thus refers to the *emergence* and nature of cultural processes and capabilities in the animal kingdom. In the next two parts, which focus specifically on the hominin case, the sense of 'culture evolves' widens to embrace the evolution of culture and its products *per se*, because a distinctive hominin development is that culture has become cumulative, with progressive changes building on previous generations' achievements. Today, such accumulation is evident within our lifetimes, as exemplified by digital technology and genetic engineering. By contrast, evidence for cumulative achievements is both minimal and controversial among all the diverse manifestations of animal culture analysed in part 1.

Part 2 turns to the beginnings of hominin culture traced in the early records of stone tool manufacture, which now extend back to approximately 2.6 Ma [21], with recent evidence suggesting stone tool use for butchery as long as 3.4 Ma [22]. Given that metal blades generally replaced stones a mere few thousand years ago, lithic cultures must have pervaded millions of years of recent hominin evolution. Of course other, non-preserved elements of both material and non-material culture were likely coevolving in these times and before: but we are immensely fortunate that the ancient and rich lithic record is available. Hundreds of millennia of reliance on the cultural information required is likely to have profoundly shaped the evolving human mind. The four papers of part 2 [23–26] together assess the most important recent discoveries about how culture evolves through these Stone Ages.

Here, we highlight two significant sets of discoveries. The first concerns the understanding achieved by a combination of remarkable re-fitting ('retro-manufacture') of flakes knapped from cores 2 Ma, coupled with skilled reconstruction of knapping techniques [27] and the archaeological recovery of ancient artefacts. Such advances have revealed more sophisticated early technological skills than previously imagined as well as subtle markers of cumulative culture. The second set of discoveries, something of a scientific revolution, concerns the emergence of symbolic culture, classically identified with the era of European cave paintings, approximately 12–30 Ka. The latter, together with evidence such as burials, led to a long-standing hypothesis that this period represented an 'Upper Palaeolithic revolution' in culture [28]. However, over the last decade or so, an extensive body of much more ancient discoveries has revealed surprisingly rich cultural achievements, including such apparently aesthetic items as shell beads, dating back at least 100 Ka [26,29].

The surprising cultural achievements suggested by these latter developments provide a bridge to the third part of the issue [30–37], where papers address the later accelerating, tree-like growth of regional cultural diversity. Two major aspects of what has recently been achieved in such work deserve emphasis here. The first is the extent to which various well-established methodologies in the natural sciences have been applied to the subject of culture, traditionally tackled in disciplines such as cultural anthropology through more qualitative approaches. Scientific approaches to culture exemplified by systematic methodologies, quantification, hypothesis-testing, mathematical modelling, rigorous statistical evaluation, objectivity, inter-observer reliability and experimentation have become more prominent in recent years. The methodological aspirations embodied in this new work integrate it more closely with natural sciences approaches evident in parts 1 and 2, and raise optimism about the prospects for a more unified and broad-based 'science of culture' [19,38–40].[2]

A second development we highlight is engagement with the parallels between biological and cultural evolution. Such parallels concerning language were recognized long ago by Darwin himself, initially in the *Origin* [41], and later in the *Descent* [42] where he remarked that 'We find in distinct languages striking homologies due to community of descent, and analogies due to a similar process of formation. The manner in which certain letters or sounds change when others change is very like correlated growth. We have in both cases the reduplication of parts, the effects of long-continued use, and so forth. The frequent presence of rudiments, both in languages and in species, is still more remarkable'. A more generalized recognition of such similarities was made famous in Dawkins' [43] concept of the 'meme', proposed as a cultural unit analogous to the gene. The application of the meme concept in serious research on culture has remained relatively minimal and much debated [44]. Here, however, Shennan [31] argues that the 'meme's eye view' offers a significant theoretical perspective that the field ought to embrace. Shennan also builds on the now extensive body of cultural evolution theory built in the last 30 years, largely stimulated through the foundational work of Cavalli-Sforza & Feldman [18] and Boyd & Richerson [19,45]. These authors have pioneered a rigorous science of culture that spans biology, psychology and anthropology, using methods adapted from evolutionary biology. Cultural evolution theory recognizes and exploits parallels between biological and cultural change, but tailors its mathematical models and methods to the specific and unique processes of culture. Further impetus has come from the application of phylogenetic methods to interpret aspects of human cultural variation, and reconstruct cultural histories [30,33,46].

Mesoudi *et al.* [47] pointed out that since Darwin set out his theory without the knowledge of genes, many questions about the extent to which cultural evolution exhibits Darwinian features can be addressed while skirting the 'meme debate'. Instead, Mesoudi *et al.* worked directly from the core concepts in the *Origin* [41] to explore the extent and manner in which cultural evolution, like biological evolution, encompasses (or if not, in what ways it differs interestingly from) Darwinian processes that include variation, competition, selection, inheritance, accumulation of modifications, adaptation,

geographical distribution, convergent evolution and changes of function. Further below, we return to how papers in part 3 address such matters.

A different perspective is provided in the four papers of part 4, which do not so much address cultural evolution itself, as how it has shaped minds to acquire complex cultural repertoires [48–51]. In principle, this is an issue relevant for the subjects of part 1, insofar as the young of any species that displays some degree of culture is expected to be subject to selection pressures shaping ontogenetic processes to facilitate cultural learning. However, we judged that the unique scale of cultural acquisitions in the human case justifies focusing part 4 on the cultural and socio-cognitive worlds of humans, with a particular focus on children.

Of course social learning, especially imitation, has long been studied in developmental psychology and continues to be so [17]. Two particularly relevant contemporary developments are addressed here. One concerns the capacity for selecting *what* to imitate; the other concerns the capacity for selecting *whom* to learn from.

With regard to the first capacity, recent ingenious studies have shown that already in infancy, novel actions of others are selectively copied in ways that show a sophisticated grasp of the logic of human action: infants were more likely to copy the rather bizarre action of switching on a light by touching it with one's head if the hands were free, than if they were bound up in a blanket (so the head had to be used), a phenomenon called 'rational imitation' [52]. Here, Csibra & Gergely [48] offer additional evidence that infants are sensitive to other's signals that certain actions are pedagically directed at them, and 'for' them. However, equally surprising have been demonstrations that young children can be prone to what has recently been called 'over-imitation', being apparently involuntarily motivated to copy certain intentional adult actions that are visibly ineffectual in gaining a desirable outcome [49]. On the face of it, these findings appear to be in direct opposition to those dubbed 'rational imitation', an intriguing contrast discussed further in part 4.

With regard to the second capacity, theoretical models of cultural learning have long suggested that the young might be biased to learn from some informants or models rather than others [18,19]. Two papers in part 4 provide convergent evidence for such selectivity (see also [37]). Hewlett *et al.* [50] provide the first detailed observational evidence for such learning biases among children growing up in hunter–gatherer communities, while Harris and Corriveau [51] use experimental procedures to demonstrate the early emergence and developmental time-course of such biases.

Such developmental studies remind us of the complexity of the processes that lie between biological propensities and culture, but this is true across all four themes. Hinde [53] emphasized the need to understand the diachronic and dialectical relations between a species' cultural propensities, behaviour, dyadic interactions, interpersonal relationships, environment and socio-cultural structures. This is perhaps most challenging in relation to the foci of parts 3 and 4.

We return to each of the four main themes further below and highlight contributions made to them in the constituent papers. First, however, we briefly address some important core definitions.

2. DEFINITIONS OF CORE CONCEPTS

The field covered by this issue has often been bedeviled by confusing variations in the definitions of several technical terms, from 'imitation' to 'culture' itself. Famously, Kroeber & Kluckhohn [54] listed 168 definitions of 'culture' in the literature extant at the time; more have arisen since. Here, we address three concepts we judge central to the present issue.

We begin with 'traditions', since this has been important in the work reviewed in part 1, and the basic concept appears less contentious than 'culture' itself. Fragaszy & Perry [55, p. xiii] offered an oft-cited but minimal definition of a tradition as 'a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning'. The minimum of two individuals required makes sense insofar as we might say 'my friend and I have developed a tradition of dining out on Mondays'. However, the concept of tradition becomes of more interest when an idea or behaviour pattern spreads by social learning across multiple individuals, to become a population-level phenomenon (with different populations potentially developing different traditions, although this is not necessary to define tradition *per se*). Thus, traditions may vary in number of practitioners, from two to many (elsewhere Fragaszy [56, p. 61]) refers to a tradition as 'a behavioural practice that is shared among members of a group'. 'Persists over time' in Fragaszy & Perry [55] may also seem regrettably elastic, yet this makes sense insofar as a continuum is possible, from mere fads and fashions (perhaps lasting only weeks or even much less) to those that pass down very many generations (well illustrated in the papers of part 2). No neat cut-off on this continuum will circumscribe traditions; rather, particularly robust evidence of traditions comes from those that are of long duration, or rely on multiple transmission events, whether between generations or within them.

The crucial component of 'social learning' embedded within the concept of tradition refers to learning from others, more formally defined by Heyes [57] as 'learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products'. The last part of this definition acknowledges that social learning may extend to learning from such things as objects made or used by others, or more generally the results of other's actions, such as the availability of part-processed foods (e.g. cracked shells or nuts). This overarching concept of social learning can be dissected into numerous alternative or constituent underlying processes, from the very elementary, such as stimulus enhancement, in which the learner's attention is simply drawn to some locus by the model's

actions, to more sophisticated ones such as the imitative learning of complex skills. These are classified and defined elsewhere in comprehensive recent taxonomies [14,15] and as they arise in papers in this issue. Such social learning is a necessary ingredient of, although not a sufficient criterion for, the existence of traditions as described above.

The term 'culture' itself is more contentious. Some authors essentially equate 'culture' with 'tradition' as described above, a long-standing practice such that we regularly find in the literature such titles as 'the cultural transmission of bird song' [58] and 'cultural transmission of feeding behaviour in the black rat' [59], the latter referring to specific techniques for stripping pine cones, that pups were shown to 'inherit' from their mothers through social learning. Other authors, noting the gulf between such cases as birdsong dialects and pine-cone-stripping traditions on the one hand, and the richness of human cultures on the other hand, have required additional criteria for use of the term 'culture' in relation to animal traditions. For example, Galef [60] and Tomasello [61] were concerned that animal cases such as these might be too readily assumed to be homologous (sharing evolutionary ancestry) with human culture, when they might really be merely analogous (dependent on different forms of social learning, for example). These authors argued that the term 'culture' should be reserved for cases dependent on processes of social transmission known to be influential in the human case, such as imitation and teaching. Other authors suggest further criteria that pick out closer links to human culture, such as multiple traditions spanning different modes of behaviour, like technology and social customs [62] or accumulation over generations [63]. Clearly, nobody can legislate for a 'correct' definition (there can be no such thing) and variant usages are by now well-embedded in existing literatures. In these circumstances our policy is, first, to urge all authors writing in this issue to define their terms to clearly facilitate good scientific communication; and second to counsel readers to be alert to the variations in the wider literature noted above. In any case the interesting questions in relation to human culture are not so much about whether certain animals can or cannot be said to 'have culture' (evidently, non-human species described as cultural will not display all the components of *human* culture), but rather whether such animals display significant elements of culture that suggest a deeper understanding of the roles of such phenomena in the biological world, as well as the potential foundations they provided for the emergence of uniquely human culture. Social learning and traditions are widely seen as two such elements.

3. CULTURE EVOLVES IN THE ANIMAL KINGDOM

Studies of social learning, traditions and culture in non-human animals (henceforth 'animals') have blossomed in recent times, becoming one of the six major areas to populate the latest, gargantuan *Encyclopedia of Animal Behaviour* [64]. This would not have been the case a decade or two ago. The coming of age for this area of research means that a now vast literature cannot comprehensively be addressed by the eight papers that make up our part 1. We have instead invited contributions that emphasize what we see as two major classes of discovery in this area of research: first, that social learning and traditions exist widely across the animal kingdom, and second, that their significance pervades many—indeed arguably most—dimensions of some animals' lives. The first of these points is illustrated by papers reviewing recent findings spanning fish, birds, primates and other mammals [2–7], and the second by reference to the extensive range of phenomena incorporated into traditions described here, including foraging techniques, tool use, food types and sites, travel routes, predator recognition, social customs and mate choice.

The rise to prominence of this work has multiple sources. One appears to be that at least for long-lived species like primates and cetaceans, the discovery of major roles for cultural processes represents the fruition of decades of patient field studies at multiple different sites, allowing the documentation of putative regional cultural variations as well as the rise, spread and loss of traditions over time. Other factors include advances in methodologies that include long-term, systematic observational studies that minutely trace the ontogeny, rise, spread and in some cases demise of traditional behaviour patterns; cross-fostering and translocation experiments (recently elegantly achieved in birds by careful transfers of eggs and in fishes through the transfer of individuals and populations); diffusion experiments of varied kinds in which new behaviour patterns are seeded in one or two individuals, allowing quantification of subsequent spread across a community; and the development of formal theory (for instance, on social learning strategies), which has stimulated empirical research and led to testable predictions.

The importance and significance of this body of work can be appreciated from more than one perspective. For some authors this is an anthropocentric one. What do the discoveries described in part 1 suggest were the pre-hominin evolutionary foundations on which humans' distinctive cultural nature has been built? A primary answer to this question should in principle be provided by a series of comparative analyses, beginning with inferences about our last common ancestor with chimpanzees and then the other great apes, based on shared features of cultural transmission. This procedure can be repeated to make inferences about such increasingly distant ancestors as those shared in turn with other primates, mammals, vertebrates and perhaps beyond. The evidence remains too patchy to underwrite any such comprehensive analyses to be pursued with confidence as yet—unlike, say, anatomy where it was feasible to establish phylogenies long ago. Here, Whiten [6] offers an initial attempt at the task for the most-recent great ape phylogeny, but even here, data for bonobos and gorillas remain minimal when compared with those available for common chimpanzees and orangutans.

Such analyses aspire to establish homologies between different taxa in the cultural phenomena

they display, the critical inferences being about similarity through descent from common ancestors. But striking similarities can also arise through convergent evolution. This means that studies of species only distantly related to ourselves can nevertheless cast light on fundamental principles that illuminate aspects of human culture and are often of considerable interest in their own right. An example concerns 'teaching', defined in functional terms (rather than the intentional terms more familiar to us in the human case), as actions costly to a teacher yet beneficial to a pupil in such consequences as enhanced levels of skill, and here identified in meerkats by elegant field experiments [4], but observed in diverse avian and other taxa too. Another example concerns the functional rules that animals and human children deploy when they engage in social learning. Articles in several parts of this issue (e.g. [2,5,6,25,37,50,51]) describe experimental evidence that rules such as 'conform to the majority behaviour', 'copy the most successful individual' and 'learn from familiar individuals' are used by a range of distantly related animals, as well as humans, although differing underlying processes may be involved.

Illuminating the roots of human culture, however, is far from the only reason for current interest in animal culture. Understanding cultural transmission in animals carries much more general significance because it constitutes a second inheritance system [18–20] that has emerged on the back of the antecedent genetic inheritance, with which it may interact in turn. Coupled with a capacity for innovation, this provides a means for adjustment and accommodation to local conditions on a much more rapid timescale than its genetically based equivalents. Such changes may occur with respect to an animal's environment in ways paralleling biological adaptation, examples of which are provided here in relation to such activities as foraging and predator avoidance [2–6]. In addition, an existing culture may itself become part of the selective regime, an instance of niche construction [65]. Social conventions illustrate this point well, as in those described for capuchin monkeys by Perry [5]. Once certain social conventions exist, whether they be the supposed bond-testing 'games' of capuchins, or local human languages, cultural transmission becomes the key to interacting successfully with others in such communities. In humans, cultural niche construction reaches its zenith, with recent genetic data suggesting that cultural practices extensively modified the biological selection acting on our species [66,67]. The articles by van Schaik & Burkart [7] and Reader *et al.* [8] provide other, non-human examples, in which social learning is thought to have driven brain evolution and favoured a suite of other cognitive capabilities in the process.

Further parallels with biological evolution are provided by the potential of cultural processes to generate variations in behaviour over time and in space (regional traditions). As noted above, culture can provide faster adaptation than is possible through genetic change. Moreover, learning from others can allow the learner to reap the benefits of much prior filtering by others of what is locally adaptive [68]. Such benefits are highlighted in several papers in part 1 (e.g. [2–7]) as well as elsewhere [36]. However, over-reliance on what others in one's community do carries the danger of maladaptive behaviour when environments change, a point powerfully made in the influential cultural modelling work of Boyd & Richerson [19,69]. This and the animal social foraging literature [70] have emphasized the frequency-dependent quality of social learning. Social learning can be viewed as 'information parasitism' and accordingly, some balance of social learning (information 'scrounging') and asocial learning ('information producing') is expected in a population (but see Rendell *et al.* [35], for a counter perspective). This and other theoretical reasons for why social learning might not be expected to be as common in nature as some of the above considerations might predict are set out by Rieucau & Giraldeau [1] in the opening paper of part 1.

4. CUMULATIVE CULTURE EVOLVES IN ANCIENT HOMININS

A panoramic view across the 2.6 Myr record of hominin stone tool-making reveals the beginnings of a capacity for cumulative cultural progress, which was ultimately to transform *Homo sapiens* into the richly cultural species we are today. This became particularly clear as the Oldowan phase of relatively elementary stone flaking was surpassed after about 1.6 Myr by the Acheulian phase, characterized by artefacts with consistent shapes that were the clearly intended endpoints of a more sophisticated knapping process. Notable was a double bilateral symmetry appearing as a rough pear shape from one perspective, much thinned by skilled flaking, to 'flatten' it from the orthogonal perspective [23–25]. However, the potential cultural accumulation inferred appears to span at least two hominin genera, so the cumulative cultural capability of each genus requires untangling. The evidence for cultural borrowing across hominin species, such as the Chatelperronian and other transitional technologies, implies that gain of cumulative knowledge could plausibly have occurred across different lineages.

Our understanding of the cumulative cultural achievements of the Stone Age has been transformed over the last dozen years or so by the integrated exploitation of a diverse range of evidential sources, often depending on extremely careful, painstaking and effortful work. These sources include (i) the primary one of archaeology, which in this period has established much earlier dates than known before, both for the emergence of lithic tool-making and for skilled knapping; (ii) inferences drawn by highly skilled re-creation by scientists of knapping techniques that produce the kinds of artefacts recovered; (iii) linked observations of knapping and other techniques used by peoples such as the Irian Jaya, who preserved a complex lithic tool culture; and (iv) the careful refitting of recovered sets of flakes to their cores, allowing the retro-construction of the knapping sequences used by their makers [23–25,71]. Here, Stout [25] builds on these combined sources to generate a systematic analysis of the complexity of manufacturing techniques, tentatively concluding from this that through

the whole Stone Age (extending beyond the Acheulian to later, more sophisticated achievements such as the Levallois), there has been an approximately exponential increase in quantifiable complexity of techniques.

Intriguingly, such progress appears remarkably lacking in the Oldowan. The above-listed sources of evidence applied to the oldest known Oldowan artefacts show their manufacture to have relied on a good appreciation of fracture processes in stone-working, which exceeded that apparent in the efforts of great apes who have knapped sharp flakes in recent experimental contexts [21]. Over the next approximately 1 Myr, Oldowan artefacts showed little if any progress beyond this—indeed, later ones often appear less sophisticated [23,25].

However, Oldowan knapping itself may plausibly have represented a cumulative step built on the prior use of stone tools for butchery, which recent evidence dates back to about 3.4 Ma [22]. We note that this latter date takes our perspective back more clearly than does the 2.6 Myr figure, to pre-*Homo* times, when there was as yet no discernable rise in brain size beyond that of a great ape. Indeed, the Oldowan and pre-Oldowan record now stretches back half way to the time of our inferred common ancestor with chimpanzees. This, combined with our rich knowledge of varied chimpanzee percussive wooden-tool-use, and the use of unmodified stone tools to crack nuts on anvils, suggests a step-wise, cumulative transition from such a repertoire in our common ancestor to pre-Oldowan and then Oldowan achievements [72].

By contrast with the Oldowan, technological progress within the Acheulian is better documented [24,25], but its pace was still inordinately slow when compared with recent rates of cumulative cultural change. For example, Goren-Inbar's [24] studies of a rich archaeological assemblage spanning 800–700 Ka reveals 'a cultural continuum over at least 50 000 years' marked by essentially similar artefact characteristics. Such an age of cultural stability is scarcely imaginable from the perspective of our recent and current rates of cultural turnover. Indeed, the whole million-year-long Acheulian period has frequently been seen as reflecting such stasis. Recent studies summarized here [24,25] take issue with this, demonstrating increasingly rich variations, and ever-earlier signatures of sophisticated manufacturing processes from some of the earliest Acheulian assemblages. Similarly, even the Oldowan, despite the lack of clear 'progress' within it, should not be regarded as monolithic; it incorporated geographical and temporal patterning in variants described in this section [23,25].

Inferences about cultural transmission processes at these times are naturally limited. Cautious inferences are made here through a combination of direct observational evidence from the present-day stone knapping cultures and inferences drawn from scientists' own experiences in learning different grades of knapping techniques [23–25]. Of course, present-day knappers have brains much larger than the hominins who knapped in the early Acheulian period. Nevertheless, Goren-Inbar [24] is led to conclude that given the intimate and far-reaching roles of linguistic interchange described in cultural transmission among the present-day knapping peoples, the complex techniques implicated in her 700–800 Ka artefacts also imply the necessity of significant linguistic pedagogical support. This may be an area where some of the experimental techniques developed to study cultural transmission in animals could usefully be brought to bear on the processes of social learning necessary for different grades of stone working. At the time of writing, more than one such exploratory effort is underway.

As we move beyond the Acheulian to survey the most recent quarter-million years or so, we again note dramatic reappraisals of our picture of cultural evolution, this time driven mainly by the sheer weight of increasingly early and diverse archaeological discoveries, including blade and microlithic technology, bone tools, various kinds of artwork and decorations, like beads and pigments, as well as refined tools like spear points and awls [26]. This has transformed the picture from one of a cultural 'symbolic' revolution around 30 Ka to a longer, drawn-out history extending back long before 100 Ka and taking the form of a bush, with multiple growth points and extinctions, governed by factors including ecology and population structures, of the kind familiar in biological evolution [26,73]. The evidence again suggests cross-species cultural transmission.

5. HUMAN CULTURE EVOLVES AND DIVERSIFIES: HOW DARWINIAN IS CULTURAL EVOLUTION?

The last paper of part 2 provides a natural bridge to the eight papers that make up part 3. These are largely organized around two related themes: first, the spread and diversification of human cultures, and second, the question of how the underlying processes reflect, extend or differ from the Darwinian principles already familiar in the case of biological evolution.

The first two of these papers offer broad overviews. In their different ways these provide an overarching context for the papers that follow, as well as linking to the earlier sections. Shennan [31] provides a concise overview of key principles in biologically inspired approaches to cultural evolution, summarizing fundamental theoretical foundations [18,19] and going on to illustrate the recent growth in empirical work that engages with cultural evolutionary theory. As Shennan shows, the scope of this body of work now ranges from Acheulian artefacts to more recent examples that include such diverse cases as hunter–gatherer projectile points, pottery designs, iron-smelting and baby names. Shennan defends the 'memes-eye view' of such cases, which focuses on the principles governing the evolution of cultural attributes themselves, as theoretically important in the way it complements person-centred analyses, as well as being pragmatic given the raw data typically available in archaeology and often in other disciplines.

Foley & Mirazón Lahr [32] review also takes a broad perspective but a different, complementary one. They offer an overview of cultural evolution in *Homo sapiens*, from approximately 200 000 years ago to the present, analysed in terms of five successive phases which thus overlap and link with the studies

of part 2. Each of the last four phases, from around 120 Ka on, is marked by accelerating cultural achievements (echoing the analysis of Stout [25] referring to even earlier times) and greater diversity. Phase 3 is also intertwined with migration out of Africa and the later phases with the spread of populations, which diversified both biologically and culturally as they spread and settled around the world.

A recurrent theme in these two papers, others in this issue [26,36] and elsewhere [73] concerns the ways in which these processes have been shaped, sometimes very severely, by interactions between demographic and environmental factors. Some of the principles revealed here echo biology, such as the relationships between diversity (both biological and cultural) and such basic factors as latitude, temperature and rainfall [32]. Such analyses have offered compelling explanations for the apparently sporadic growth and fading of early cultural developments in Africa in the period up to about 50 Ka, after which more continuity is observed [26,31,32,73].

An intimate linkage between demographic factors and culture, in the form of language evolution, is also demonstrated by Gray [33] in cases such as the spreading of peoples and languages eastwards across the island communities of the Pacific in more recent times. This work provides an excellent example of the application of numerical phylogenetic methods, borrowed and modified from biological contexts, to reconstruct cultural phylogenies. These methods have been much elaborated over the last decade and applied to increasingly wider cultural forms, from languages to artefacts [46,74,75]. In this issue, these methods are extended for the first time to socio-political evolution [30]. A remarkable linkage between culture and biology is graphically illustrated by the convergence between the picture of the peopling of the Pacific islands based on language phylogenies [33], and that derived from the analysis of gut flora [76]. In the case of socio-political phylogenies, Currie & Mace [30] address long-standing evolutionary theories in anthropology that are numerically tested here for the first time and as a result, supported in a new and objective fashion.

A different, but equally weighty numerical analysis is offered for another aspect of language evolution by Calude & Pagel [34]. In the evolution of lexicons, some classes of word meanings are replaced by new word-forms relatively rapidly, while others have lives up to a hundredfold longer. Calude & Pagel identify fundamental principles concerning the frequency of usage and parts of speech that explain much of this evolutionary variance across a broad world sample of languages. The parallels with biological, Darwinian evolution are, once again, striking [77].

As Shennan [31] (following [18]) notes, cultural change can occur through 'cultural selection' (for example, people select the most efficient axes) and/or 'natural selection' in the conventional sense (the reproductive success of the best axe makers promotes the evolution of those axes). In addition, the forms that culture evolves into provide an array of selection pressures on the biological sphere, instances of which are the subject of diverse papers here including van Schaik & Burkart [7] and those of part 4. One of the most fundamental forms of selection is likely to be upon capacities and strategies for social learning themselves. Rendell *et al.* [68] have taken a novel approach to this by organizing a computer-based tournament involving Darwinian competition among over 100 different learning strategies submitted. Strategies that fared most successfully in mastering the exploitation of an initially unknown environment were found to rely strongly on social learning. Here, Rendell *et al.* [35], extend this work to examine the wider implications of different learning strategies for cultural evolution. Drawing a distinction between effects on individuals' knowledge versus the behaviour they express, Rendell *et al.* discover intriguing differences in the effects of a heavy reliance on cultural transmission on these two factors, which together confer adaptive plasticity in relation to environmental change.

The theme of the adaptive nature of culture continues in the work of Collard *et al.* [36], who focus on the relationship between the complexity of material culture and the degree of risk involved in the local foraging niche. Here again we see an application of quantification to complex material, in this case the sophistication of the local hunting and gathering implements employed, which in some ways parallels and complements Stout's [25] numerical analysis of the complexity of stone tools. In the case study presented, Collard *et al.*'s data do not support the hypothesis tested, but this illustrates an important consequence of the numerical and objective approaches encouraged in this issue: that clarity is achieved whether the hypothesis chosen for examination is supported or not. Negative but reliable findings are as important in constructing a robust science of culture as are positive ones. In this case, they lead to new hypotheses about the distinct roles that different causes of cultural diversity play at different spatial scales.

Henrich & Broesch [37] provide a complementary analysis of cultural adaptation, building on the extensive foundations provided by the modelling literature discussed by Shennan [31], to which Henrich has made extensive contributions (e.g. [78]). Here, hypotheses derived from the theoretical literature concerning biases such as selective learning from high-prestige models are empirically tested, and supported. The data suggest a two-phase model of cultural learning, in which young children first learn from their primary attachment figures, then later become more selective in learning from the best available models. This analysis links directly with the studies of Harris & Corriveau in part 4, which experimentally demonstrate an ontogenetic shift of this kind, in which children become progressively skilled at discriminating the most useful sources of adaptive information.

6. THE EVOLUTION OF CULTURAL MINDS

The extent and rate of cultural acquisition that a child's brain must handle is vast, and natural selection, in the course of tripling brain size over the period discussed in part 2, can be expected to have moulded the

developmental processes profoundly to facilitate this. A similar principle is suggested in the 'cultural intelligence hypothesis' applied to the great ape case by van Schaik & Burkart [7], but the nature of human culture predicts a yet more profound scale of ontogenetic adaptation.

Since humans turned to agriculture a mere 10–12 Kyr ago, the long hunter–gatherer way of life that preceded this is likely to have provided the context for major aspects of this developmental adaptation. With reference to a range of sources of evidence from butchery millions of years ago [22] to javelin-like spears 400 Kyr old [79], some level of hunting–gathering has been inferred to have characterized our genus from its inception. Study of the present-day hunting–gathering people has thus been seen as a valuable route to insights into the behavioural details corresponding to hunting and gathering niches. However, the corpus of studies of hunter–gatherer childhood [80], and in particular the study of children's acquisition of hunter–gatherer culture, has remained minuscule within developmental psychology, despite the above rationale for its great theoretical importance. Writers on cultural evolution have in recent years commented on a (largely anecdotal) literature suggesting that, contrary to claims that teaching makes human culture distinctive, teaching plays only a minimal role in hunter–gatherer culture, by comparison with observational learning. Two papers in this section offer conceptual and empirical analysis of this issue. Csibra & Gergely [48] provide evidence that infants are sensitive to often subtle cues ('natural pedagogy' in the authors' terminology) that an adult's actions are performed 'for them' to learn from. Hewlett *et al.* [50] directly address the role of teaching in hunter–gatherer childhood with some of the first objective and numerical studies of its occurrence. Consistent with the proposal that pedagogy is natural and universal in humans [48], they find that deliberate teaching does occur, especially in the context of caregiver-to-child transmission.

Lyons *et al.* [49] present new data on the recently discovered phenomenon of 'over-imitation', in which young children copy actions of others despite those actions being visibly ineffectual. The authors present evidence that children are remarkably inflexible in learning to act otherwise. However, consistent with the proposal that they are receptive to deliberate demonstration, children do not reproduce a model's accidental or unintended actions. Such receptivity to deliberate demonstration is likely to facilitate children's adoption of 'opaque' procedures whose causal workings may be difficult for them to fully discern. Nevertheless, the final paper by Harris & Corriveau [51] emphasizes that even if children are sometimes hyper-receptive with respect to what they learn, they are selective about whom they learn from. Their findings support other papers in the volume in proposing that children have several biases in their selection of models and informants [37,50]. Such biases are likely to promote vertical learning from familiar and reliable caregivers as well as oblique and horizontal efficient learning from other members of the local culture.

7. OMISSIONS

A major goal of this issue is to indicate the current breadth and scope of contemporary scientific approaches to the evolution of social learning, traditions and culture. However, the field has become very large and some regrettably substantial omissions are inevitable. Here we can do no more than acknowledge some of these and indicate some entry points to the larger literature. We note some complementary collected works and recent books on our topic [81–88].

In relation to part 1, we must recognize inevitable gaps in our coverage both taxonomically, for example concerning cetaceans [89] and invertebrates [90], and in relation to the range of behaviour patterns concerned, such as vocal traditions [91].

We have not included papers in the cultural evolution modelling tradition of Cavalli-Sforza & Feldman [18] and Boyd & Richerson [19], although several papers in this issue (e.g. [2,31,35,37,51]) draw on this tradition. Moreover, we have opted to focus here on culture *per se*, at the cost of neglecting the larger subject of gene–culture coevolution. Recent reviews of this work draw on progress in genomics [66,67]. More generally, mathematical modelling has also not been given great prominence in this issue, in favour of a relentless focus on heavily empirical studies. The powerful and indeed foundational role of modelling and associated theory [18,19] is nevertheless acknowledged, and it continues with vigour [92].

In relation to part 3, we must acknowledge that the cultures that have evolved around the world, even through just the most recent few millennia, are so rich as to defy any comprehensive treatment. They are the subjects of vast literatures in archaeology, anthropology, history and kindred disciplines. However, systematic and evolutionary approaches to the associated databases of the kinds explored in this issue remain relatively few. We have striven to illustrate some of the most interesting ways in which this state of affairs is changing.

The final, developmental part in the issue has its own omissions. Perhaps, the most obvious is the study of language acquisition, which represents a substantial instance of cultural transmission, and about which a deep understanding has been achieved through decades of study [93]. Other relevant literatures include those dealing with comparative studies of children and non-human species (typically apes) [94] and cross-cultural developmental psychology [95].

8. CONCLUDING REMARKS

We shall not attempt to reprise again here the overview of this issue we have offered above. We believe the contents of the issue offer a uniquely broad 'map' of many of the leading edges of current research addressing different aspects of the evolution of culture, particularly from the overtly scientific approaches we have favoured. In relation to this latter aspect of our endeavours, the array of both novel and well-tested, reliable methodologies included here are no less important to report than the resulting discoveries, exciting as so many of these are, for we think these methodologies are here shown to hold much promise for further revealing how and why culture evolves.

The authors of this Introduction wish to thank all those authors of papers in the issue who commented on our earlier drafts, particularly James Broesch, Gergely Csibra, Tom Currie, Paul Harris, Barry Hewlett, Tore Slagsvold and Dietrich Stout.

ENDNOTES

[1]Although the study of the evolution of culture has seen remarkable recent progress of the kind that underwrites this issue, it is important to recognize that the topic has a long history, largely associated with post-Darwinian cultural anthropology (e.g. [96,97]: but see also [98]). A brief overview and selected bibliography of this work is offered in the electronic supplementary material. A more extended, complementary bibliography spanning 114 articles is in the electronic supplementary material provided by Currie & Mace [30].

[2]Likewise, the creation of a 'science of culture' was an aspiration of many cultural anthropologists in the early twentieth century, including those concerned with the evolution of culture [99,100], although such writings were typically discursive and theoretical, incorporating little empirical material (see electronic supplementary material).

REFERENCES

1 Rieucau, G. & Giraldeau, L.-A. 2011 Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Phil. Trans. R. Soc. B* **366**, 949–957. (doi:10.1098/rstb.2010.0325)

2 Laland, K. N., Atton, N. & Webster, M. M. 2011 From fish to fashion: experimental and theoretical insights into the evolution of culture. *Phil. Trans. R. Soc. B* **366**, 958–968. (doi:10.1098/rstb.2010.0328)

3 Slagsvold, T. & Wiebe, K. L. 2011 Social learning in birds and its role in shaping a foraging niche. *Phil. Trans. R. Soc. B* **366**, 969–977. (doi:10.1098/rstb.2010.0343)

4 Thornton, A. & Clutton-Brock, T. 2011 Social learning and the development of individual and group behaviour in mammal societies. *Phil. Trans. R. Soc. B* **366**, 978–987. (doi:10.1098/rstb.2010.0312)

5 Perry, S. 2011 Social traditions and social learning in capuchin monkeys (*Cebus*). *Phil. Trans. R. Soc. B* **366**, 988–996. (doi:10.1098/rstb.2010.0317)

6 Whiten, A. 2011 The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* **366**, 997–1007. (doi:10.1098/rstb.2010.0334)

7 van Schaik, C. P. & Burkart, J. M. 2011 Social learning and evolution: the cultural intelligence hypothesis. *Phil. Trans. R. Soc. B* **366**, 1008–1016. (doi:10.1098/rstb.2010.0304)

8 Reader, S. M., Hager, Y. & Laland, K. N. 2011 The evolution of primate general and cultural intelligence. *Phil. Trans. R. Soc. B* **366**, 1017–1027. (doi:10.1098/rstb.2010.0342)

9 Laland, K. N. & Galef, B. G. (eds) 2009 *The question of animal culture.* Cambridge, MA: Harvard University Press.

10 Price, E. E., Caldwell, C. A. & Whiten, A. 2010 Comparative cultural cognition. *Wiley Interdiscip. Rev. Cogn. Sci.* **1**, 23–31. (doi:10.1002/wcs.014)

11 Kendal, R. L., Galef, B. G. & van Schaik, C. P. (eds) 2010 Capturing social learning in natural contexts: methodological insights and implications for culture. *Learn. Behav.* (special issue) **38**, 187–336.

12 Galef Jr, B. G. & Heyes, C. M. (eds) 2004 Social learning and imitation. *Learn. Behav.* (special issue) **32**, 1–144.

13 Laland, K. N. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14.

14 Whiten, A., Horner, V., Litchfield, C. & Marshall-Pescini, S. 2004 How do apes ape? *Learn. Behav.* **32**, 36–52.

15 Hoppitt, W. & Laland, K. N. 2008 Social processes influencing learning in animals: a review of the evidence. *Adv. Study Behav.* **38**, 105–165. (doi:10.1016/S0065-3454(08)00003-X)

16 Thornton, A. & Raihani, N. J. 2008 The evolution of teaching. *Anim. Behav.* **75**, 1823–1836. (doi:10.1016/j.anbehav.2007.12.014)

17 Heyes, C. M., Huber, L., Gergley, G. & Brass, M. (eds) 2009 Evolution, development and intentional control of imitation (whole issue). *Phil. Trans. R. Soc. B* **364**, 2291–2443. (doi:10.1098/rstb.2009.0049)

18 Cavalli-Sforza, L. L. & Feldman, M. W. 1981 *Cultural transmission and evolution*. Princeton, NJ: Princeton University Press.

19 Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process.* Chicago, IL: Chicago University Press.

20 Whiten, A. 2005 The second inheritance system of chimpanzees and humans. *Nature* **437**, 52–55. (doi:10.1038/nature04023)

21 Toth, N. & Schick, K. (eds) 2006 *The Oldowan: case studies into the earliest stone age*. Gosport, IN: Stone Age Institute Press.

22 McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R. & Bearat, H. A. 2010 Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**, 857–860. (doi:10.1038/nature09248)

23 de al Torre, I. 2011 The origins of stone tool technology in Africa: a historical perspective. *Phil. Trans. R. Soc. B* **366**, 1028–1037. (doi:10.1098/rstb.2010.0350)

24 Goren-Inbar, N. 2011 Culture and cognition in the Acheulian industry: a case study from Gesher Benot Ya'aqov. *Phil. Trans. R. Soc. B* **366**, 1038–1049. (doi:10.1098/rstb.2010.0365)

25 Stout, D. 2011 Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* **366**, 1050–1059. (doi:10.1098/rstb.2010.0369)

26 d'Errico, F. & Stringer, C. B. 2011 Evolution, revolution or saltation scenario for the emergence of modern cultures? *Phil. Trans. R. Soc. B* **366**, 1060–1069. (doi:10.1098/rstb.2010.0340)

27 Roux, V. & Bril, B. (eds) 2005 *Stone knapping: the necessary conditions for a uniquely hominin behaviour.* Cambridge, UK: McDonald Institute Monographs.

28 Mellars, P. & Stringer, C. 1989 *The human revolution: behavioural and biological perspectives on the orgins of modern humans.* Edinburgh, UK: Edinburgh University Press.

29 McBrearty, S. & Brooks, A. 2000 The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563. (doi:10.1006/jhev.2000.0435)

30 Currie, T. E. & Mace, R. 2011 Mode and tempo in the evolution of socio-political organization: reconciling 'Darwinian' and 'Spencerian' evolutionary approaches in anthropology. *Phil. Trans. R. Soc. B* **366**, 1108–1117. (doi:10.1098/rstb.2010.0318)

31 Shennan, S. 2011 Descent with modification and the archaeological record. *Phil. Trans. R. Soc. B* **366**, 1070–1079. (doi:10.1098/rstb.2010.0380)

32 Foley, R. A. & Mirazón Lahr, M. 2011 The evolution of the diversity of cultures. *Phil. Trans. R. Soc. B* **366**, 1080–1089. (doi:10.1098/rstb.2010.0370)

33 Gray, R. D., Atkinson, Q. D. & Greenhill, S. J. 2011 Language evolution and human history: what a difference a date makes. *Phil. Trans. R. Soc. B* **366**, 1090–1100. (doi:10.1098/rstb.2010.0378)

34 Calude, A. S. & Pagel, M. 2011 How do we use language? Shared patterns in the frequency of word

use across seventeen world languages. *Phil. Trans. R. Soc. B* **366**, 1101–1107. (doi:10.1098/rstb.2010.0315)
35 Rendell, L., Boyd, R., Enquist, M., Feldman, M. W., Fogarty, L. & Laland, K. N. 2011 How copying affects the amount, evenness and persistence of cultural knowledge: insights from the social learning strategies tournament. *Phil. Trans. R. Soc. B* **366**, 1118–1128. (doi:10.1098/rstb.2010.0376)
36 Collard, M., Buchanan, B., Morin, J. & Costopoulos, A. 2011 What drives the evolution of hunter–gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. *Phil. Trans. R. Soc. B* **366**, 1129–1138. (doi:10.1098/rstb.2010.0366)
37 Henrich, J. & Broesch, J. 2011 On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Phil. Trans. R. Soc. B* **366**, 1139–1148. (doi:10.1098/rstb.2010.0323)
38 Durham, W. H. 1990 *Coevolution: genes, culture and human diversity*. Stanford, CA: Stanford University Press.
39 Cronk, L. 1999 *That complex whole: culture and the evolution of human behaviour*. Bolder, CO: Westview Press.
40 Mesoudi, A., Whiten, A. & Laland, K. N. 2006 Towards a unified science of cultural evolution. *Behav. Brain Sci.* **29**, 329–383. (doi:10.1017/S0140525X 06009083)
41 Darwin, C. 1859 *The origin of species*. London, UK: Murray.
42 Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: Murray.
43 Dawkins, R. 1976 *The selfish gene*. Oxford, UK: Oxford University Press.
44 Aunger, R. (ed.) 2000 *Darwinizing culture: the status of memetics as a science*. Oxford, UK: Oxford University Press.
45 Richerson, P. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: Chicago University Press.
46 Mace, R., Holden, C. J. & Shennan, S. (eds) 2005 *The evolution of cultural diversity: a phylogenetic approach*. London, UK: UCL Press.
47 Mesoudi, A., Whiten, A. & Laland, K. N. 2004 Is human cultural evolution Darwinian? *Evolution* **58**, 1–11. (doi:10.1111/j.0014-3820.2004.tb01568.x)
48 Csibra, G. & Gergely, G. 2011 Natural pedagogy as evolutionary adaptation. *Phil. Trans. R. Soc. B* **366**, 1149–1157. (doi:10.1098/rstb.2010.0319)
49 Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M. & Keil, F. C. 2011 The scope and limits of overimitation in the transmission of artefact culture. *Phil. Trans. R. Soc. B* **366**, 1158–1167. (doi:10.1098/rstb.2010.0335)
50 Hewlett, B. S., Fouts, H. N., Boyette, A. H. & Hewlett, B. L. 2011 Social learning among Congo Basin hunter–gatherers. *Phil. Trans. R. Soc. B* **366**, 1168–1178. (doi:10.1098/rstb.2010.0373)
51 Harris, P. L. & Corriveau, K. H. 2011 Young children's selective trust in informants. *Phil. Trans. R. Soc. B* **366**, 1179–1187. (doi:10.1098/rstb.2010.0321)
52 Gergely, G., Bekkering, H. & Király, I. 2002 Rational imitation in preverbal infants. *Nature* **415**, 755. (doi:10.1038/415755a)
53 Hinde, R. A. 1987 *Individuals, relationships and culture: links between ethology and the social sciences*. Cambridge, UK: Cambridge University Press.
54 Kroeber, A. L. & Kluckhohn, C. 1952 Culture: a critical review of concepts and definitions. *Pap. Peabody Museum Am. Archaeol. Ethnol.* **47**, 41–72.
55 Fragaszy, D. M. & Perry, S. (eds) 2003 *The biology of traditions: models and evidence*. Cambridge, UK: Cambridge University Press.
56 Fragaszy, D. M. 2003 Making space for traditions. *Evol. Anthropol.* **12**, 61–70. (doi:10.1002/evan.10104)
57 Heyes, C. M. 1994 Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**, 207–231. (doi:10.1111/j.1469-185X.1994.tb01506.x)
58 Slater, P. J. B. 1986 The cultural transmission of bird song. *Trends Ecol. Evol.* **1**, 94–97. (doi:10.1016/0169-5347(86)90032-7)
59 Terkel, J. 1995 Cultural transmission in the black rat: pine-cone feeding. *Adv. Study Behav.* **24**, 119–154. (doi:10.1016/S0065-3454(08)60393-9)
60 Galef, B. G. 1992 The question of animal culture. *Hum. Nat.* **3**, 157–178. (doi:10.1007/BF02692251)
61 Tomasello, M. 1994 The question of chimpanzee culture. In *Chimpanzee cultures* (eds R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. Heltne), pp. 301–317. Cambridge, MA: Harvard University Press.
62 Whiten, A. & van Schaik, C. P. 2007 The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603–620. (doi:10.1098/rstb.2006.1998)
63 Levinson, S. C. & Jaisson, P. (eds) 2006 *Evolution and culture*. Cambridge, MA: MIT Press.
64 Breed, M. D. & Moore, J. (eds) 2010 *Encyclopedia of animal behaviour*. Oxford, UK: Academic Press.
65 Laland, K. N., Odling-Smee, J. & Feldman, M. W. 2000 Niche construction, biological evolution and cultural change. *Behav. Brain Sci.* **23**, 131–175. (doi:10.1017/S0140525X00002417)
66 Laland, K. N., Odling-Smee, F. J. & Myles, S. 2010 How culture has shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**, 137–148. (doi:10.1038/nrg2734)
67 Richerson, P., Boyd, R. & Henrich, J. 2010 Gene-culture coevolution in the age of genomics. *Proc. Natl Acad. Sci. USA* **107**, 8985–8992. (doi:10.1073/pnas.0914631107)
68 Rendell, L. *et al.* 2010 Why copy others? Insights from the social learning strategies tournament. *Science* **328**, 208–213. (doi:10.1126/science.1184719)
69 Boyd, R. & Richerson, P. 1996 Why culture is common but cultural evolution is rare. *Proc. Brit. Acad.* **88**, 73–93.
70 Giraldeau, A. & Caraco, T. 2000 *Social foraging theory*. Princeton, NJ: Princeton University Press.
71 Stout, D. 2006 The social and cultural context of stone-knapping skill acquisition. In *Stone knapping: the necessary conditions for a uniquely hominin behaviour* (eds V. Roux & B. Bril). Cambridge, UK: McDonald Institute Monographs.
72 Whiten, A., Schick, K. & Toth, N. 2009 The evolution and cultural transmission of percussive technology: integrating evidence from paleoanthropology and primatology. *J. Hum. Evol.* **57**, 420–435. (doi:10.1016/j.jhevol.2008.12.010)
73 Powell, A., Shennan, S. J. & Thomas, M. G. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301. (doi:10.1126/science.1170165)
74 Lipo, C. P., O'Brien, M. J., Collard, M. & Shennan, S. J. (eds) 2006 *Mapping our ancestors: phylogenetic approaches in anthropology and prehistory*. New Brunswick, NJ: Aldine Transaction.
75 Forster, P. & Renfrew, C. (eds) 2006 *Phylogenetic methods and the prehistory of languages*. Cambridge, UK: McDonald Institute.
76 Renfrew, G. 2009 Where bacteria and languages concur. *Science* **323**, 467–468. (doi:10.1126/science.1168953)
77 Pagel, M. 2009 Human language as a culturally transmitted replicator. *Nature Rev. Gen.* **10**, 405–415.

78 Henrich, J. & McElreath, R. 2007 Dual inheritance theory: the evolution of human cultural capacities and cultural evolution. In *Oxford handbook of evolutionary psychology* (eds R. I. M. Dunbar & L. Barrett), pp. 555–570. Oxford, UK: Oxford University Press.
79 Thieme, H. 1997 Lower Palaeolithic hunting spears from Germany. *Nature* **385**, 807–810. (doi:10.1038/385807a0)
80 Hewlett, B. S. & Lamb, M. E.(eds) 2005 *Hunter–gatherer childhoods: evolutionary, developmental and cultural perspectives*. London, UK: Aldine Transaction.
81 Wheeler, M., Ziman, J. & Boden, M. A. (eds) 2002 *The evolution of cultural entities*. Oxford, UK: Oxford University Press.
82 Carneiro, R. L. 2003 *Evolutionism in cultural anthropology: a critical history.* Boulder, CO: Westview Press.
83 Smith, K., Kalish, M. L., Griffiths, T. L. & Lewandowsky, S. 2008 Cultural transmission and the evolution of human behaviour. *Phil. Trans. R Soc. B* **363**, 3469–3476. (doi:10.1098/rstb.2008.0147)
84 Shennan, S. (ed.) 2009 *Pattern and process in cultural evolution*. London, UK: University of California Press.
85 Linquist, S. (ed.) 2010 *The evolution of culture*. Farnham, UK: Ashgate Publishing.
86 Blute, M. 2010 *Darwinian sociocultural evolution: solutions to dilemmas in cultural and social theory.* Cambridge, UK: Cambridge University Press.
87 Runciman, G. 2010 *The theory of cultural and social selection.* Cambridge, UK: Cambridge University Press.
88 Mesoudi, A. 2011 *Cultural evolution: how Darwinian evolutionary theory can explain human culture and synthesize the social sciences*. Chicago, IL: University of Chicago Press.
89 Rendell, L. & Whitehead, H. 2001 Cultures in whales and dolphins. *Behav. Brain Sci.* **24**, 309–324. (doi:10.1017/S0140525X0100396X)
90 Leadbeater, E. & Chittka, L. 2007 Social learning in insects—from miniature brains to consensus building. *Curr. Biol.* **17**, R703–R713. (doi:10.1016/j.cub.2007.06.012)
91 Janik, V. M. & Slater, P. J. B. 2003 Traditions in mammalian and avian vocal communication. In *The biology of traditions: models and evidence* (eds D. M. Fragaszy & S. Perry), pp. 213–235. Cambridge, UK: Cambridge University Press.
92 Enquist, M., Eriksson, K. & Ghirlanda, S. 2007 Critical social learning: a solution to Rogers's paradox of nonadaptive culture. *Am. Anthropol.* **109**, 727–734. (doi:10.1525/aa.2007.109.4.727)
93 Tomasello, M. & Bates, E. (eds) 2001 *Language development: the essential readings*. Oxford, UK: Blackwell.
94 Tomasello, M., Carpenter, C., Behne, T. & Moll, H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–691. (doi:10.1017/S0140525X05000129)
95 Rogoff, B. 2003 *The cultural nature of human development.* Oxford, UK: Oxford University Press.
96 White, L. A. 1959 *The evolution of culture*. New York, NY: McGraw-Hill.
97 Sahlins, M. D. & Service, E. R. (eds) 1960 *Evolution and culture*. Ann Arbor, MI: University of Michigan Press.
98 Pitt-Rivers, A. L.-F. 1906 *The evolution of culture and other essays*. Oxford, UK: Clarendon Press.
99 Murdock, G. P. 1932 The science of culture. *Am. Anthropol.* **34**, 200–215. (doi:10.1525/aa.1932.34.2.02a00020)
100 White, L. A. 1949 *The science of culture*. New York, NY: Grove Press.