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Towards a unified science of cultural evolution

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Abstract: We suggest that human culture exhibits key Darwinian evolutionary properties, and argue that the structure of a science of cultural evolution should share fundamental features with the structure of the science of biological evolution. This latter claim is tested by outlining the methods and approaches employed by the principal sub-disciplines of evolutionary biology and assessing whether there is an existing or potential corresponding approach to the study of cultural evolution. Existing approaches within anthropology and archaeology demonstrate a good match with the macroevolutionary methods of systematics, paleobiology and biogeography, while mathematical models derived from population genetics have been successfully developed to study cultural microevolution. Much potential exists for experimental simulations and field studies of cultural microevolution, where there are opportunities to borrow further methods and hypotheses from biology. Potential also exists for the cultural equivalent of molecular genetics in 'social cognitive neuroscience', although many fundamental issues have yet to be resolved. It is argued that studying culture within a unifying evolutionary framework has the potential to integrate a number of separate disciplines within the social sciences.

Keywords: Cultural Anthropology; Cultural Evolution; Cultural Transmission; Culture; Evolution; Evolutionary Archaeology; Evolutionary Biology; Gene-Culture Coevolution; Memes; Social Learning.

1. Introduction

Parallels or analogies between biological and cultural evolution have been noted by a number of eminent figures from diverse fields of study (e.g. Darwin, 1871; Dawkins, 1976; Dennett, 1995; Dobzhansky, Ayala, Stebbins, & Valentine, 1977; Hull, 1982; Huxley, 1955; James, 1880; Medawar, 1982; Popper, 1979; Skinner, 1981), and in the last few years a burgeoning literature exploring this relationship has emerged (e.g. Aunger, 2002; Aunger, 2000b; Blackmore, 1999; Boyd & Richerson, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004; Mace & Holden, 2005; Mesoudi, Whiten, & Laland, 2004; Mufwene, 2001; Pagel & Mace, 2004; Plotkin, 2002; Richerson & Boyd, 2005; Runciman, 2005; Shennan, 2002; Wheeler, Ziman, & Boden, 2002; Ziman, 2000).

The implication of this growing body of theory is that culture exhibits key Darwinian evolutionary properties. If this is accepted, it follows that the same tools, methods and approaches that are used to study biological evolution may productively be applied to the study of human culture, and furthermore that the structure of a science of cultural evolution should broadly resemble the structure of evolutionary biology. In the present paper we attempt to make this comparison explicit, by examining the different approaches and methods used by evolutionary biologists and assessing whether there is an existing corresponding approach or method in the study of cultural evolution. Where such an existing correspondence is not found, we explore whether there is the potential to develop one. We also explore potential differences between biological and cultural evolution.

The purpose of this comparison is primarily to stimulate a more progressive and rigorous science of culture. While evolutionary biology has become enormously productive since Darwin's theory of evolution was formulated, the discipline that professes to be most directly engaged in the study of culture - cultural or social anthropology - has been much less demonstratively productive over the same time period, particularly in terms of establishing a secure body of data and theory that earns and deserves the attention of researchers working in sister disciplines. This is increasingly acknowledged by many of its own practitioners (e.g. Bennett, 1999; Bloch, 2000; Kuper, 1999). For example, in a recent review of the history of anthropology, Bennett (1999) states that “the cultural side of the discipline tends to smother its data with personal and arcane theorizing” (p. 951), while another anthropologist, Bloch (2000), states that cultural anthropology “with time, has become theoretically more and more vague, pretentious and epistemologically untenable” (p. 202).

Why has biology been so much more successful than anthropology and many related fields of social science over the past 150 years? We do not believe that biologists are on average more able than researchers who have traditionally studied culture, nor is biology significantly easier to study than culture. Rather, we suspect that two factors are of particular importance. First is the relative willingness of biologists to make simplifying assumptions and use what may be comparatively crude but workable methods, in order to make complex systems tractable and contribute to the steady accumulation of reliable knowledge that will ultimately form the basis of a sophisticated understanding of the phenomena in question. While many social scientists frequently object that human culture is too complex to be amenable to such simplifying assumptions and methods, the relative success of biologists in studying enormously complex biological systems render such objections open to question.

Second, and particularly relevant to this article, the theory of evolution encompasses and integrates a multitude of diverse sub-disciplines within biology, from behavioural ecology to paleobiology to genetics, with each sub-discipline stimulating and contributing to several others (see Mayr, 1982 for further details of this 'evolutionary synthesis'). The social sciences, in contrast, have no such general synthesising framework, and the greater part of disciplines such as cultural anthropology, archaeology, psychology, economics, sociology and history remain relatively insular and isolated, both from each other and from the biological and physical sciences. Adopting an evolutionary framework can potentially serve to highlight how these disciplines are, in fact, studying complementary aspects of the same problems, and emphasise how multiple and multidisciplinary approaches to these problems are not only possible but necessary for their full exposition. At present, many of the individual studies considered below are the result of independent developments at the fringes of separate fields of study. Placing these disparate studies side-by-side within a broader evolutionary framework, as is done here, will hopefully contribute towards creating a coherent unified movement and bring evolutionary analyses of cultural phenomena into the mainstream.

An evolutionary framework also brings with it a set of proven methods that have rich potential within the study of culture. We note below a number of cases in which methods developed within evolutionary biology have been adapted for use in the study of culture, such as phylogenetic analyses or population genetic models. As we shall see, several of these evolutionary methods have already contributed to significant advances over more traditional non-evolutionary methods.

The left hand side of Figure 1 illustrates the overall structure of evolutionary biology, as described by Futuyma (1998, pp. 12-14) in what is, perhaps, the most widely used undergraduate textbook in the field. The study of biological *macroevolution* deals with change at or above the species level, while biological *microevolution* concerns changes within populations of a single species. The former comprises systematics, paleobiology and biogeography, while the latter involves population genetics (theoretical, experimental and field-based), evolutionary ecology and molecular genetics. In Sections 2 and 3 we examine each of the sub-disciplines of evolutionary biology in turn, first outlining their general methods then briefly describing examples of recent studies to illustrate how those methods are applied and the kind of results they yield. This is followed in each case by a discussion of existing analogous or equivalent methods within the social sciences regarding human culture, again describing recent key studies. These cultural disciplines, and the way in which they map onto the structure of evolutionary biology, are illustrated on the right hand side of Figure 1.

While there may be no obvious precedent for two distinct fields to exhibit the same internal structure, the similarity of underlying processes (Mesoudi *et al.*, 2004) leads us to expect a correspondence. We believe that this mapping will (1) help make sense of actual developments in the study of cultural evolution; (2) suggest new research programmes and hypotheses; and (3) help identify the most promising research strategies.

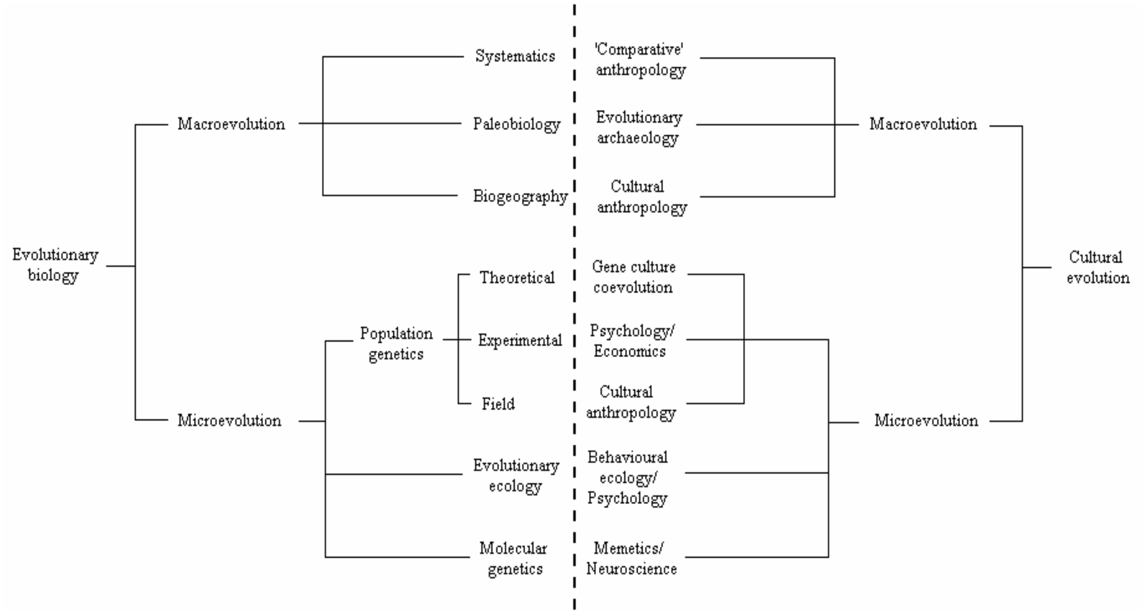

Figure 1 – Major subdivisions within evolutionary biology (left hand side; after Futuyma 1998) and corresponding disciplines currently or potentially employed in the study of cultural evolution (right hand side)

It is important first to define ‘culture’ explicitly and to specify the precise theory of cultural evolution that we are advocating. Following Richerson and Boyd (2005), we define *culture* as “information capable of affecting individuals’ behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission” (p. 5). ‘Information’ is employed as a broad term incorporating ideas, knowledge, beliefs, values, skills and attitudes. *Cultural evolution* is characterised as a Darwinian process comprising the selective retention of favourable culturally transmitted variants, as well as a variety of non-selective processes, such as drift (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). This contrasts with the progressive, unilinear theories of ‘cultural evolution’ (e.g. Tylor, 1871), in which human societies were seen as progressing through a fixed set of stages, from ‘savagery’ through ‘barbarism’ to ‘civilisation’. This erroneous view of evolution drew more from Spencer than Darwin, and such flawed evolutionary ideas persisted within anthropology until the mid-20th century (e.g. Steward, 1955; White, 1959). The development of a genuinely Darwinian theory of cultural evolution remained in its infancy (e.g. Campbell, 1960) until the pioneering works of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985). These researchers not only provided a rich theoretical groundwork for analysing culture in terms of modern evolutionary theory, but also developed rigorous mathematical treatments of cultural change inspired by population genetic models (see Richerson & Boyd, 2005 for an accessible account of this work).

We also emphasise that the theory of cultural evolution is distinct from the field of *evolutionary psychology* (e.g. Barkow, Cosmides, & Tooby, 1992; Pinker, 1997), which deals with *biologically* evolved features of the human mind, shaped by genetic rather than cultural inheritance. Evolutionary psychology therefore more accurately belongs on the left hand side of Figure 1 (although it is not shown), and should be distinguished from the separate cultural inheritance system outlined on the right-hand side. Although some evolutionary psychologists tend to downplay the role of transmitted culture (e.g. Tooby & Cosmides, 1992, pp. 115-117), there is ample evidence that culture plays a powerful causal role in determining human behaviour and cognition (Richerson & Boyd, 2005; Tomasello, 1999). Of course, biologically evolved features of cognition do affect cultural processes in important ways, as emphasised by gene-culture co-evolutionists (e.g. Durham, 1992). This interaction is discussed further in Section 3.4.2.

To illustrate the Darwinian nature of a modern evolutionary theory of culture, and build an empirical case for such a theory, Mesoudi *et al.* (2004) explicitly compared the empirical evidence for biological evolution presented by Charles Darwin in *The Origin of Species* (1859) with present day evidence from the social sciences regarding human culture. In *The Origin*, Darwin presented meticulous evidence for *variation* in the characteristics of individuals within a species, for the *selection* (natural or artificial) of individuals possessing certain characteristics, and for the *inheritance* of those selected characteristics to the next generation. Mesoudi *et al.* (2004) collated equivalent evidence that culture similarly exhibits these key properties. For instance, there is evidence for considerable *variation* in terms of the diversity of cultural knowledge, beliefs and artifacts, as illustrated by the 4.7 million patents issued in the U.S. since 1790 (Basalla, 1988) and the 6800 languages spoken world-wide (Grimes, 2002). Cultural *selection* occurs as a result of competition for limited attention, memory and expression. For example, psychologists have demonstrated interference in the recall of similar (competing) words (Baddeley, 1990), while archaeologists have tracked increasing frequencies of one artifact and the corresponding decreasing frequencies of competing artifacts (O'Brien & Lyman, 2000). The *inheritance* of successful cultural traits has been demonstrated in numerous studies of the transmission of skills and beliefs in traditional societies (e.g. Cavalli Sforza, Feldman, Chen, & Dornbusch, 1982; Hewlett & Cavalli-Sforza, 1986) and studies of social learning in children (e.g. Bandura, 1977; Whiten *et al.*, 1996).

These three basic characteristics (variation, selection and inheritance) generate a number of other phenomena observed by Darwin in biological evolution and which are also evident in human culture (Mesoudi *et al.*, 2004). Cultural traits go *extinct* as a result of competition, as occurred for the gun in Japan (Perrin, 1979) and bone tools in Tasmania (Diamond, 1978). Basalla (1988) amassed extensive historical evidence for the gradual *accumulation of modifications* over time, such as Joseph Henry’s 1831 electric motor, which borrowed many features from the steam engine, or Eli Whitney’s 1793 cotton gin, which was based on a long line of Indian devices. Cultural traits can be said to *adapt* to their environment, as demonstrated by the work of human behavioural ecologists (Smith & Winterhalder, 1992). Evolutionary principles can account for the *geographical distribution* of cultural variation, such as the diffusion or descent of various traits in African societies (e.g. Hewlett, De Silvestri, & Guglielmino, 2002). Culture exhibits the *convergent evolution* of similar forms in unrelated lineages, such as the tendency for both teddy bears (Hinde & Barden, 1985) and cartoon characters (Gould, 1980) to become increasingly neotenous over time. Finally, cultural traits *change in function* or become *vestigial*, as documented by Basalla (1988) for numerous technological artifacts, such as the no longer functional QWERTY keyboard layout or Edison's gramophone, originally used for dictation. A more detailed account of the case for cultural evolution can be found in Mesoudi *et al.* (2004) and Richerson and Boyd (2005). Finally, Mesoudi *et al*. (2004) noted that, just as Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance, a theory of cultural evolution likewise does not necessarily have to rest on the existence of memes or particulate cultural transmission, a topical issue but one of great contention (Henrich & Boyd, 2002; Aunger, 2000b).

This last point highlights the fact that, while there are many fundamental similarities between biological and cultural change, the two processes are certainly not identical, and biological methods and models cannot and should not be unthinkingly applied to cultural phenomena without careful consideration of any potential differences (Plotkin, 2002). On the other hand, critics (e.g. Bloch, 2000; Gould, 1991; Pinker, 1997) commonly reject outright any evolutionary analysis of culture by appealing to putative differences which are frequently illusory or unfounded. In the following sections and in Section 4 we will assess the validity of each of these potential differences and their implications for a science of cultural evolution.

2. Macroevolution

This section sketches the principle approaches to macroevolution adopted by biologists, namely systematics, paleobiology and biogeography, and considers corresponding approaches in the study of cultural evolution.

2.1. Systematics

2.1.1. Biology. *Systematics* is the study of the diversity of organisms and of the relationships between them. Modern systematists adopt the principles of *cladistics*, which holds that these relationships should be based exclusively on *phylogeny*, or descent (Futuyma, 1998; Harvey & Pagel, 1991; Hennig, 1966). Hence modern systematists seek to reconstruct the evolutionary history of species based on similarities in their morphological, behavioural or genetic characters. (A biological *character* is defined as an inherited trait or feature, while a *character state* describes the form or value of that character. For example, 'blue' and 'brown' are character states of the character 'eye colour'.) This section only concerns the analytical techniques used to identify these relationships, rather than the methods used to obtain the geographical or archaeological data used in these analyses, which are discussed in the following sections.

Two species might share a character or character state either because they each inherited it from a common ancestor (*homology*) or because the character evolved independently in the two species' separate lineages (*analogy*). In order to eliminate the latter and determine phylogenetic relationships, systematists identify *shared derived characters*, i.e. traits that evolved only once in a pair of species' common ancestor, but are not observed in close relatives. Because shared derived characters are unique to species directly related by descent, they can be used to identify branching points in the phylogeny. The principle of parsimony (or some equivalent method) can then be used to construct a phylogenetic tree which requires the fewest number of these branching points, often using computer programs such as PAUP (Swofford, 1998) or MacClade (Maddison & Maddison, 1992).

For example, Burns, Hackett and Klein (2002) recently applied phylogenetic analyses to the morphological features of 88 species of Darwin's finches of the Galapagos Islands, finding that all descended from a common ancestor originating in the Caribbean, rather than South America as had commonly been thought. The evolutionary history of specific traits can also be studied using phylogenetic methods, such as Whiting, Bradler and Maxwell's (2003) finding that, while the common ancestor of all insects is thought to have possessed wings for flight, the common ancestor of the stick insects was wingless, and wings re-emerged in the stick insect lineage on a number of independent occasions.

Phylogenetic methods are also used to identify general patterns of evolution. For instance, Goodwin, Balshine-Earn and Reynolds (1998) found that 'mouthbrooding' behaviour in cichlid fish, in which eggs are incubated in the mouth of the parent, has evolved on 10-14 independent occasions from the ancestral state of guarding eggs in nests, illustrating convergent evolution. The association of mouthbrooding with reduced fecundity and larger eggs additionally illustrates the selective effects of one trait on others.

2.1.2. Culture. Just as biologists seek to reconstruct a species' evolutionary history using shared characters, anthropologists seek to reconstruct the history of groups of people based on cultural traits, such as language, tools, customs or beliefs. In doing so, anthropologists have faced the same problem as evolutionary biologists, that of distinguishing between homologous and analogous traits. Indeed, this was recognised within anthropology as long ago as 1889 by Francis Galton, which has led to it being referred to as 'Galton's problem'.

The fact that Galton's problem is virtually identical to the problem faced by biologists has recently led a number of anthropologists to adopt the same solutions. Mace and Pagel (1994) argued that the phylogenetic analyses used by systematists are superior to previous attempts to solve Galton's problem, such as Murdock's cross-cultural sample (Murdock & White, 1969) or the statistical removal of inherited traits (e.g. Dow, Burton, White, & Reitz, 1984), both of which involve the loss of important aspects of the data. Mace and Pagel (1994) treated cultural traits as equivalent to biological characters, with independent instances of cultural change occurring when a cultural trait is invented, acquired from another culture, changed or lost. Shared, derived characters can then be identified, and the parsimony-based computer programs developed by systematists can be used to reconstruct the most likely evolutionary history of those cultural traits of interest.

For example, Holden (2002) applied cladistic methods to linguistic data from 75 Bantu languages spoken in sub-Saharan Africa. Items of basic vocabulary whose meanings were common to all groups (e.g. 'man', 'woman') were taken as characters, and the different lexical forms used to represent these meanings were treated as character states. A shared character state was therefore one in which the same word form was used for the same meaning in both languages. Geographical and archaeological data were also obtained (see next sections). It was found that the linguistic data showed a good fit with the phylogenetic tree model, and that this tree correlated with geographical proximity and archaeological data suggesting that language was associated with the spread of farming across prehistoric Africa. A further study on the same populations (Holden & Mace, 2003) suggested that the acquisition of cattle led to a change from matrilineal to patrilineal inheritance of wealth.

Using similar methods, Gray and Jordan (2000) found that the distribution of 77 Austronesian languages was most consistent with a single common ancestral form in Taiwan which rapidly spread through the region, while Gray and Atkinson (2003) found evidence supporting the theory that the Indo-European language group was associated with the spread of agriculture from Anatolia around 8000-9500 years ago.

The recognition that cultural traits may be directly acquired from other cultures, i.e. transmitted horizontally (within a generation), raises possible objections (e.g. Gould, 1991; Moore, 1994) to the use of these biological methods, which were originally developed to deal only with vertical (parent-to-offspring) transmission and hence might be unsuitable for studying some cultural evolution. However, as noted by Mesoudi *et al.* (2004), any putative dichotomy contrasting a 'divergent, branching biological evolution' with a 'convergent, cross-fertilising cultural evolution' is a distortion of both biology and culture. Significant cross-lineage transfer occurs in biological evolution, especially for microbes (Doolittle, 1999; Rivera & Lake, 2004) and plants (Abbott, James, Milne, & Gillies, 2003), while the convergent nature of culture is an empirically testable hypothesis rather than a statement of fact. Tackling the issue systematically and quantitatively, Tehrani and Collard (2002) found a greater role for branching 'phylogenesis' than convergent 'ethnogenesis' in Turkmen textile patterns, while Collard, Shennan and Tehrani (2005) have found that the best available cultural datasets show just as good fit with a branching phylogenetic model as do biological datasets. In the short term, there are likely to be plenty of datasets for which these methods may be useful, while ultimately, it may be mutually beneficial for biological and cultural evolutionists to develop mathematical techniques that incorporate both horizontal transfer and vertical descent.

Another potential objection to the use of cladistic methods in anthropology is the difficulty of identifying distinct 'characters' in cultural artifacts (see also criticisms of memetics in Section 3.5.2.). The identification of characters in culture is undoubtedly difficult (O'Brien & Lyman, 2003, p.143), but it is important to acknowledge that it is also difficult for biological characters, and this difficulty has not prevented biologists from producing valuable work using the character concept (Wagner, 2000).

2.1.3. Conclusions. Treating cultural traits as equivalent to biological characters allows anthropologists to apply the same rigorous phylogenetic methods to cultural data as used by evolutionary biologists. This is because anthropologists and biologists share the same crucial goals: to reconstruct the history of certain traits and to identify general patterns of change. A number of studies applying phylogenetic methods to cultural data demonstrate that such methods can be successfully used to achieve these goals, for example in determining whether a group of traits are related by descent, whether their spread was associated with other traits, or whether they generated selection for other traits.

2.2. Paleobiology

2.2.1. Biology. The aim of paleobiology is to use the fossil record to identify prehistoric species and reconstruct their evolutionary history (Futuyma, 1998; Simpson, 1944), consequently helping to explain the present diversity and distribution of living species. The principle methods involve the collection of fossils and analysis of their features, with age and environment reconstructed based on these features and the characteristics of the surrounding rocks. Analysis of these data often involves the use of the phylogenetic methods described above in order to distinguish between homologous and analogous traits. The fossil record is a much more direct (albeit incomplete) source of evidence about the evolutionary past than the distribution of existing species, and additionally allows paleobiologists to provide an absolute time scale for evolutionary events using radio-decay dating techniques.

For example, Zhou, Barrett and Hilton (2003) describe exceptionally well-preserved fossils from north-eastern China from the Early Cretaceous period, the forms of which support the theories that birds are direct descendants of the dinosaurs, that feathers evolved before flight, and that there was rapid adaptive radiation of bird ancestors. Seiffert, Simons and Attia's (2003) phylogenetic analysis of strepsirrhine primate fossils, meanwhile, suggests that the group is much older than was previously thought and has an Afro-Arabian origin. These studies, and countless others, show that fossil evidence can be used to date evolutionary events, support hypotheses concerning the origin of traits, and reveal general evolutionary patterns such as adaptive radiation.

2.2.2. Culture. In general, archaeologists have similar goals to paleobiologists – to identify prehistoric artifacts, to reconstruct lineages of these artifacts and of the people associated with them, and to reveal the evolutionary relationships between these lineages. The basic methodology – extracting specimens from the ground – is also similar. It is only recently, however, that some archaeologists have begun to adopt explicitly evolutionary models and tools (for overviews see O'Brien & Lyman, 2002; Shennan, 2002). The key assumption underlying both paleobiology and archaeology is that similar forms which vary through time are causally connected by inheritance (which O'Brien & Lyman, 2000 term the assumption of 'heritable continuity'). Such sequences of causally connected forms constitute evolutionary lineages. Simpson (1961) proposed that evolutionary lineages should be used as a means of defining a species, rather than requiring reproductive isolation (Mayr, 1963), and this 'evolutionary species' concept is increasingly being used in evolutionary biology (Wiens, 2004). The same lineage-based species concept has been suggested by Hull (1982) for culture, and extended by O'Brien and Lyman (2000) specifically for prehistoric artifacts.

O'Brien and Lyman (2000) have argued that evolutionary lineages can be reconstructed using the method of *seriation*, in which a collection of artifacts is ordered according to their similarity: the more features two artifacts share, the closer they are in the order; the fewer they share, the further apart they are placed. Where such orderings exhibit gradual, overlapping change, it can be assumed that the seriation represents an evolutionary lineage causally connected by cultural transmission.

Early archaeologists used the method of seriation to identify lineages of coins (Evans, 1850), stone tools (Pitt-Rivers, 1875) and Egyptian pottery (Petrie, 1899). The method fell out of favour, however, in the mid-20th century, which O'Brien and Lyman (2000) attribute to the increased popularity of an essentialist stance in archaeology, in which types are perceived to have distinct 'essences' and change only occurs when one type suddenly transforms into another. This contrasts with evolutionary 'population thinking' (Mayr, 1982) which recognises naturally occurring variation within populations, rather than focusing on typological essences. O'Brien and Lyman (2000) have consequently made efforts to reintroduce seriation into archaeology as a method of studying evolutionary change in artifacts. This is demonstrated by their analysis of projectile points from south-western U.S.A., which they show to exhibit continuous, gradually changing variation rather than a small number of distinct types. O'Brien and Lyman (2000) argue that forcing artifacts into distinct categories often distorts their true phylogenetic relationships.

The method of seriation is nonetheless vulnerable to the same problem as similar methods in paleobiology: distinguishing between homologies and analogies. Hence O'Brien, Darwent and Lyman (2001) and O'Brien and Lyman (2003) have argued that it is also necessary to adopt the cladistic methods described above to reconstruct evolutionary lineages accurately. For example, O'Brien *et al.* (2001) and O'Brien and Lyman (2003) carried out a phylogenetic analysis of 621 Paleoindian projectile points from south-eastern United States (see Figure 2), while Tehrani and Collard (2002) used similar methods to reconstruct the history of Turkmen textile patterns.

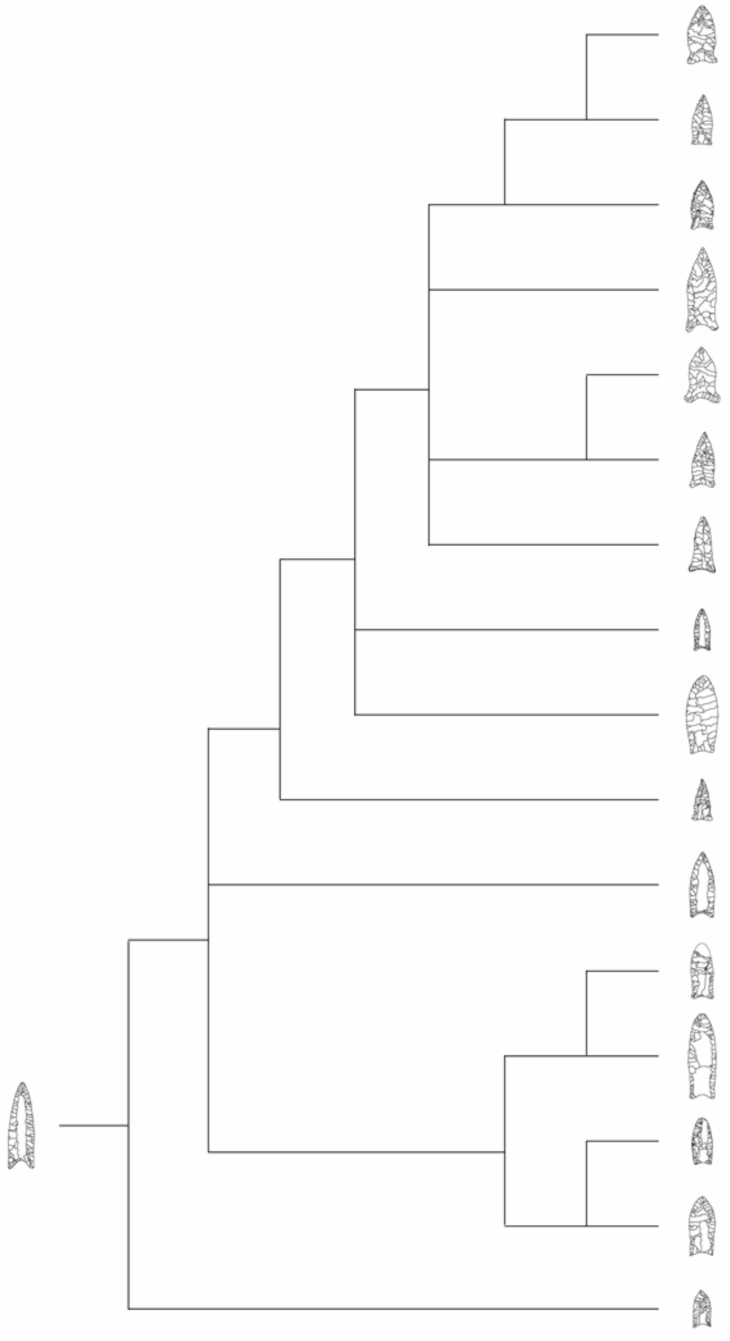

Figure 2 – A phylogenetic tree of 17 projectile points from south-eastern United States, from O'Brien and Lyman (2003), illustrating divergence from a single common ancestor.

Other evolutionary archaeologists have adapted neutral drift models from evolutionary biology (e.g. Crow & Kimura, 1970) to account for 'stylistic variation' in artifacts. For example, Neiman (1995) demonstrated that changes in decorative styles of Illinois Woodland ceramics can be predicted by a model incorporating the selectively neutral but opposing forces of drift and innovation. Bentley and Shennan (2003) found that the frequencies of West German pottery decorations over 400 years can be predicted by a similar model of unbiased cultural transmission, with some anti-conformist bias in later periods.

As well as prehistoric artifacts, past cultures - unlike past species - have often left detailed written records or direct historical evidence of their knowledge, skills and technology. For example, Hinde and Barden (1985) found that the facial dimensions of teddy bears became increasingly baby-like over an 80 year period, which they attributed to a biologically evolved human preference for baby-like faces. Basalla (1988), meanwhile, collected numerous examples of technological change, which exemplify the gradual modification of preceding technology (see also Petroski, 1994; Ziman, 2000). For example, while Eli Whitney’s cotton gin is commonly described as unprecedented, it was in fact based on existing mechanical cotton gins used to extract other varieties of cotton seed, which were in turn derived from previous Indian gins and before that an older still sugar cane press (Basalla, 1988, pp. 32-33). Such gradual, cumulative change suggests the presence of evolutionary lineages of artifacts linked by cultural transmission.

Methods developed within evolutionary biology can also be applied to relatively recent historical data. Howe *et al.* (2001) describe how different manuscript versions of the same text can be used to reconstruct the evolution of that text. This was demonstrated by Barbrook *et al.* (1998), who used cladistic methods to reconstruct the historical relationships between 58 different manuscripts of Chaucer’s ‘The Canterbury Tales’, improving on previous non-phylogenetic reconstructions. Bentley, Hahn and Shennan (2004), meanwhile, found that the frequencies of first names and patent applications in 20th century U.S.A. both conform to a simple model of random copying originally developed in evolutionary biology (Crow & Kimura, 1970). This neutral model represents a useful null hypothesis describing the case where no selection is operating.

2.2.3. Conclusions. Archaeologists face essentially the same task as paleobiologists – to identify earlier forms of the phenomena of interest (often now extinct or superseded) and reconstruct their history. It is therefore not surprising that the tools and approaches used by paleobiologists have been successfully imported into archaeology. Adopting evolutionary ‘population thinking’ (O'Brien & Lyman, 2000), using the methods of cladistics (Mace & Holden, 2005), and importing models of selection or drift (Neiman, 1995) can produce a more accurate understanding of the past than traditional archaeological methods. Historical records of cultural artifacts will often be more complete and accurate than the fossil record, offering a potentially important role for historians in the study of cultural evolution.

2.3. Biogeography

2.3.1. Biology. Biogeography is the study of how biological, ecological, geographical and historical factors determine the spatial distribution of organisms (Brown & Lomolino, 1998; Futuyma, 1998). Members of a population may adapt to their new environments when they disperse, or populations may be divided by physical barriers and evolve distinctively. Islands are often of particular interest to biogeographers (e.g. MacArthur & Wilson, 1967) because of their isolation from other terrestrial ecosystems. Long-term geographical factors such as climate change or tectonic plate movement can affect organisms’ spatial distribution, as well as shorter-term ecological factors such as competitors or pathogens. Fossil evidence and phylogenetic analyses are used to infer the past distribution of organisms, which can help to explain their present distribution, and which has led biogeography to become intimately linked with both paleobiology and systematics.

The methods of biogeography can be classed as either descriptive or analytical. Descriptive methods consist of documenting the present distribution of organisms in space, along with their ecology and physical environment. Once these data have been gathered, analytical models, including the cladistic techniques described above, can be constructed and tested to try to explain this distribution.

For example, Stephens and Wiens (2004) sought to explain the geographical distribution of emydid turtles in eastern North America, which exhibit two broad patterns of community structure. Phylogenetic analyses of morphological and molecular data combined with details of habitat and diet revealed that the differences between the two groups are predominantly due to ‘phylogenetic conservatism’ (i.e. descent from two distinct evolutionary lineages), although the dispersal of several species from one group to the other has reduced these differences.

Roca *et al.* (2004) used fossil data to explain the distribution of an island species. Phylogenetic analyses of genetic and fossil evidence suggest that around 76 million years ago the solenodons - small, burrowing insectivores from the West Indies - diverged from other insectivores rather than from the tenrecs or the rodents. This date coincides with the separation of the islands from mainland North America due to tectonic movement and/or rising sea levels, supporting the hypothesis of divergence due to geographical separation.

2.3.2. Culture. The geographical distribution of cultural traits is shaped, at least in part, by similar factors to those affecting the distribution of organisms. Just as the past dispersal of organisms can help to explain the present distribution due to biological inheritance, cultural traits can also persist through time due to trans-generational cultural transmission. While organisms can disperse to new environments, cultural traits can spread by the movement of culture-bearing people or the diffusion of ideas and technology among non-kin. Cultural traits may also arise as adaptations to local ecological conditions.

The field of social science most equivalent to biogeography is again anthropology. One of the main goals of cultural anthropology has been to document and map the worldwide distribution of cultural traits, resembling the descriptive methods of biogeography. This has resulted in databases such as Murdock’s Ethnographic Atlas (Murdock, 1967), the Human Relations Area Files (Murdock *et al.*, 1987) and, for languages, the Ethnologue (Grimes, 2002).

More recently, evolutionarily-informed analytical models have been developed to attempt to account for the distributions of cultural traits captured by these databases. The field of human behavioural ecology (see Section 3.4.2) operates, with some success, on the premise of a correspondence between cultural and ecological variation (Smith & Winterhalder, 1992). Other researchers have endeavoured to distinguish ecological from ‘inherited tradition’ explanations. Guglielmino *et al.* (1995), for example, used the Ethnographic Atlas to analyse the distribution of 47 cultural traits in 277 African societies. Most of the traits, particularly family and kinship traits, correlated with linguistic group, suggesting vertical transmission. A minority of traits were distributed according to geographical proximity, consistent with horizontal diffusion between groups, while the distribution of none of the traits could be explained by ecology alone.

Similarly, Hewlett, de Silvestri and Guglielmino (2002) combined data from the Ethnographic Atlas and the Ethnologue with newly emerging genetic data to study the distribution of cultural traits in 36 African populations. Twenty of these traits were distributed according to language and/or genes, suggesting vertical cultural transmission, twelve traits correlated with geographical proximity, suggesting diffusion, and four followed ecology, suggesting independent adaptation to local conditions.

A further parallel with biogeography lies in the use of cladistic methods to help explain the present distribution of cultural traits, which we have already seen, for example, for African and Austronesian languages (Gray & Jordan, 2000; Holden, 2002). Yet another parallel lies in the value of physical barriers in studying the spatial distribution of culture. For example, Cavalli-Sforza and Wang (1986) applied a ‘stepping-stone’ model, developed within biology to study genetic distributions, to linguistic data from 17 Micronesian islands, finding that the degree to which languages shared words declined with the negative exponential of the distance between those islands, just as has been found for biological traits.

Another example of the use of islands to study cultural evolution involves the case of the prehistoric inhabitants of Tasmania, whose cultural repertoire significantly decreased in size and complexity since their isolation from mainland Australia (Diamond, 1978; McGrew, 1987). Henrich (2004) developed a model showing that the reduction in population size caused by this physical separation was sufficient to cause the breakdown and loss of relatively complex cumulative skills and tools, due to the paucity of models from whom to learn such skills. Henrich’s (2004) analysis demonstrates the interactive effects of demography and geography on the distribution of cultural traits.

2.3.3. Conclusions. There is a clear parallel in the aims, methods and findings of biogeography and anthropology. Both disciplines aim to explain the spatial distribution of traits, and do this descriptively by documenting spatial variation in forms, and analytically by developing theoretical models to account for patterns in this variation. While the descriptive stage has been carried out by anthropologists for decades independently of a Darwinian model of cultural evolution, analytical models have benefited from biological tools such as the methods of cladistics and population-genetic and fitness-maximisation models. Similar factors have moreover been found to influence the distribution of biological and cultural traits, such as transmission dynamics (e.g. vertical/descent or horizontal/diffusion), geographical phenomena (e.g. physical barriers) and ecological factors.

However, we see potential here for the science of cultural evolution to become more predictive, along the lines of evolutionary biology, by specifying *a priori* which traits should follow these different evolutionary dynamics and under which conditions. For example, Boyd and Richerson (1985) predict that cultural traits which constitute adaptations to relatively rapidly changing environmental conditions should be transmitted horizontally, whereas cultural traits that constitute adaptations to environmental conditions that are stable across biological generations (although not stable enough to have become genetically specified) should show evidence of conservative vertical transmission. Further predictions are given in Section 3.3.

2.4. Macroevolution: General conclusions

The evidence concerning macroevolutionary patterns reveals a broad fit between the methods and approaches of evolutionary biology and those of the social sciences. This is primarily because a number of anthropologists and archaeologists are already importing biological methods and models into their fields, with considerable success. Phylogenetic methods have been used by anthropologists to explain the spatial distribution of various cultural traits, and by evolutionary archaeologists to reconstruct evolutionary lineages of material artifacts. As this suggests, there is already considerable cross-fertilisation of ideas and methods in these disciplines, which we argue is a key benefit of adopting a unified evolutionary framework.

We have also seen cases where the evolutionary methods have proved significantly more effective than traditional non-evolutionary methods, such as the adoption of evolutionary ‘population thinking’ in archaeology, or the cladistic solution to Galton’s problem.

3. Microevolution

One of the central principles of the evolutionary synthesis of the 1930s was that large-scale macroevolutionary patterns of change are the result of small-scale microevolutionary changes in gene frequencies within populations (Mayr, 1982). A complete theory of cultural evolution would therefore require studies of small-scale changes in populations of cultural traits. The following sections outline the approaches to microevolution developed by evolutionary biologists – population genetics (theoretical, experimental and field), evolutionary ecology and molecular genetics – along with corresponding methods in the study of cultural evolution.

3.1. Theoretical population genetics

3.1.1. Biology. Significant advances were made in the study of biological evolution before its molecular basis was understood, in no small part through the use of simplified mathematical models, pioneered by Fisher (1930), Wright (1931) and Haldane (1932). In the simplest models, sexually reproducing individuals in a large (‘infinite-sized’) population each contribute to an aggregate gene-pool. Under the assumptions of random mating, and with no migration, selection or mutation, allele frequencies will remain constant over successive generations (the Hardy-Weinberg principle). Deviations from this simple case can be incorporated into population genetic models, such as mutation, non-random (e.g. assortative) mating, or the impact of processes such as natural selection or random genetic drift. Overall allele or genotype frequencies in successive generations can be tracked mathematically to simulate the process of evolution, often to find out whether a particular genetic trait can invade and spread through a population and, if so, to explore the possible evolutionary consequences of this invasion.

For example, McKone and Halpern (2003) developed a population genetic model of androgenesis, a rare phenomenon seen in freshwater clams, Saharan cypress trees and stick insects, where the offspring acquire nuclear DNA from the male parent only. The model predicted that mutations causing androgenesis will often spread rapidly to fixation in an initially nonandrogenetic population, and in some cases cause extinction of that population due to the loss of females, perhaps explaining its rarity.

3.1.2. Culture. Models of *cultural evolution* and *gene-culture co-evolution* adopt essentially the same methods as above. The latter (sometimes also referred to as *dual-inheritance theory*) assimilate cultural inheritance into population genetic models, developing mathematical models that incorporate both biological and cultural evolution simultaneously and interactively, while ‘cultural evolution’ models are formulated exclusively at this cultural level (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976; Laland, Kumm, & Feldman, 1995). These models exploit parallels in the demographic consequences of biological and cultural change with, for instance, differential adoption and innovation in culture modelled as equivalent to natural selection and mutation within biology, and with other processes such as drift, migration and assortative mating operating equivalently in both cases.

In gene-culture coevolution models, each individual is often described in terms of a combination of genetic and cultural traits, or their ‘phenogenotype’. This requires that transmission rules for both genes and culture must be considered, with selection on genes affecting the adoption of cultural traits and vice versa. As well as adopting the same general methods and principles as population genetics, in many cases gene-culture coevolution researchers have adapted specific established population genetic models to render them suitable to features of culture that are not directly analogous to their biological counterpart.

Researchers in these fields recognise that cultural transmission can be very different to biological transmission. While the latter is primarily vertical, Cavalli-Sforza and Feldman (1981) have modelled the consequences of horizontal and oblique (from unrelated members of the parental generation) cultural transmission. Boyd and Richerson (1985) and Henrich and Boyd (1998) have demonstrated mathematically that a ‘conformist’ cultural bias, in which individuals are predisposed to adopt the most popular cultural trait in a group, can evolve in a wide variety of environmental conditions and leads to stable differences between cultural groups, potentially leading to cultural group selection (Boyd & Richerson, 1985). Other models consider a variety of other forms of transmission biases (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Feldman & Cavalli-Sforza, 1976). Importantly, many of these biases are unique to cultural transmission and will generate evolutionary dynamics with no obvious parallel in biology. Such differences do not, however, invalidate an evolutionary analysis of culture.

Models have also been developed for specific cases of gene-culture coevolution. For example, Feldman and Cavalli-Sforza (1989) modelled the coevolution of genes for lactose absorption and the cultural trait of dairy farming, finding that the allele for lactose absorption will spread provided there is a high probability that the offspring of dairy farmers themselves become dairy farmers, but not otherwise, even with a significant viability advantage. Another case study examined the evolution of handedness (Laland, Kumm, Vanhorn, & Feldman, 1995), proposing a model that gave a better fit to patterns of handedness in families and among twins than leading purely genetic models.

As well as population genetic methods, biological models of neutral genetic drift (Crow & Kimura, 1970) have been adapted to study the evolution of cultural traits such as names and patents (Bentley *et al.*, 2004), demonstrating that the distribution of such traits can be accounted for by chance events. Boyd and Richerson (1985), meanwhile, have developed a model of runaway cultural selection similar to runaway sexual selection, which they argue can account for a range of cultural traits, from oversized yams in Ponapae to extensive tattooing in Polynesia (paralleling elaborate sexually selected biological traits such as the peacock’s tail).

Mathematical models such as these are often treated with suspicion and even hostility by some social scientists, who consider them to be oversimplifications of reality (see Laland, Kumm, & Feldman, 1995 and associated comments). The alternatives to gene-culture coevolution analyses, however, are usually either analysis at a single (purely genetic or purely cultural) level or vague verbal accounts of ‘complex interactions’, neither of which we believe to be productive. Gene-culture analyses have repeatedly revealed circumstances under which the interactions between genetic and cultural processes lead populations to different equilibria than those predicted by single-level models, or anticipated in verbal accounts (Laland, Kumm, & Feldman, 1995), as illustrated by the aforementioned examples of dairy farming and handedness.

Interestingly, fifty years ago the same reservations about simplifying assumptions were voiced about the use of population genetic models in biology by the prominent evolutionary biologist Ernst Mayr (1963). He argued that using such models was akin to treating genetics as pulling coloured beans from a bag (coining the phrase ‘beanbag genetics’), ignoring complex physiological and developmental processes that lead to interactions between genes. In his classic article “A defense of beanbag genetics”, J.B.S. Haldane (1964) countered that the simplification of reality embodied in these models is the very reason for their usefulness. Such simplification can significantly aid our understanding of processes that are too complex to be considered through verbal arguments alone, because mathematical models force their authors to explicitly and exactly specify all of their assumptions, to focus on major factors, and to generate logically sound conclusions. Indeed, such conclusions are often counterintuitive to human minds relying solely on informal verbal reasoning. Haldane (1964) provided several examples where empirical facts follow the predictions of population genetic models in spite of their simplifying assumptions, and noted that models can often highlight the kind of data that need to be collected to evaluate a particular theory.

Ultimately, Haldane (1964) won the argument and population genetic modelling is now an established and invaluable tool in evolutionary biology (Crow, 2001). We can only echo Haldane’s (1964) defence and argue that the same arguments apply to the use of similar mathematical models in the social sciences (see also Laland, 1993; Laland, Kumm, & Feldman, 1995; Mace & Pagel, 1994; Pagel & Mace, 2004).

3.1.3. Conclusions. A number of researchers have imported the methods of theoretical population genetics to study the coevolution of genes and culture, and the dynamics of cultural change over time. These methods have provided a rigorous analysis of many cultural evolutionary processes and case studies. The differences between biological and cultural inheritance are not ignored and do not invalidate such models, while many of the criticisms of the use of such analytical models in the social sciences have been addressed in a parallel debate within evolutionary biology.

3.2. Experimental population genetics

3.2.1. Biology. As well as using the theoretical models described above, population geneticists have studied microevolutionary processes experimentally by breeding multiple generations of study organisms in the laboratory, in order to simulate evolution under controlled conditions. Laboratory-based experiments have been used to estimate the rate and effect of mutation, detect adaptation to experimentally induced environmental conditions (e.g. different temperatures), and measure responses to the artificial selection of single or multiple traits (Futuyma, 1998; Hartl & Clark, 1997).

In a typical artificial selection experiment, a population of a species, such as *E. coli* or *Drosophila,* is measured for some desired trait (e.g. temperature resistance). In each generation only a subset of the population is allowed to reproduce, with the reproducing individuals chosen according to the desired trait (e.g. those most resistant to high temperatures). After a number of generations the population is again tested for the trait to estimate the response to this selection regime.

For example, Torres-Vila *et al.* (2002) employed a laboratory-based artificial selection paradigm to investigate the genetic basis of polyandry (females mating with more than one male) in a normally non-polyandrous species of moth. Initially 150 pairs of moths were allowed to mate freely, and all of the fertilised females were assessed for their tendency to solicit further matings. In five subsequent generations only females displaying polyandrous behaviour were allowed to mate, resulting in a significant increase in the frequency of polyandry and indicating the successful artificial selection of this trait.

Natural selection can be simulated by manipulating environmental conditions and allowing the population members to compete naturally amongst themselves, with those individuals best suited to the imposed conditions out-breeding less suited individuals. After a number of generations the population is tested for adaptation to the imposed conditions. Kennington *et al.* (2003), for example, experimentally simulated the natural selection of body size in *Drosophila* in response to humidity. Separate populations were maintained at either high or low humidity and were allowed to breed freely. After 20 weeks (5-10 generations) it was found that the low humidity lines were significantly smaller than the high humidity lines, which Kennington *et al.* (2003) argued occurred because large flies have a low surface area relative to weight, lose less water and so are better adapted to low humidity. This experimental result also helps to explain the geographical distribution of *Drosophila* in the wild, with large body sizes found at high latitudes with low humidity.

3.2.2. Culture. One parallel with this work lies in laboratory based psychological experiments simulating cultural transmission. Where population genetic experiments simulate biological evolution by studying the transmission of genetic information from generation to generation through the reproduction of individuals, psychological experiments can potentially simulate cultural evolution by studying the transmission of cultural information (e.g. texts or behavioural rules) from one individual to another through social learning.

One method for simulating cultural evolution was developed by Gerard, Kluckhohn and Rapoport (1956) and Jacobs and Campbell (1961). A norm or bias is established in a group of participants, usually by using confederates, and one by one these participants are replaced with new, untrained participants. The degree to which the norm or bias remains in the group after all of the original group members have been replaced represents a measure of its transmission to the new members.

For example, Baum *et al.* (2004) studied the transmission of traditions using a task in which participants received financial rewards for solving anagrams. Groups of individuals could choose to solve an anagram printed on either red or blue card: the red anagrams gave a small immediate payment, while the blue anagrams gave a larger payoff but were followed by a ‘time-out’ during which no anagrams could be solved. By manipulating the length of this time-out, the experimenters were able to determine which of the two anagrams gave the highest overall payoff (i.e. where the blue time-out was short, blue was optimal, and where the blue time-out was long, red was optimal). Every 12 minutes one member of the group was replaced with a new participant. It was found that traditions of the optimal choice emerged under each experimental condition, with existing group members instructing new members in this optimal tradition by transmitting information about payoffs and timeouts, or through coercion.

Key similarities exist between this study and the experimental simulations of natural selection described above. In Kennington *et al.*’s (2003) study with *Drosophila*, where the experimentally determined conditions of low humidity favoured small body size, smaller individuals out-reproduced larger individuals. Hence genetic information determining ‘small body size’ was more likely to be transmitted to the next generation through biological reproduction, and the average body size of the population became gradually smaller. In Baum *et al.*’s (2004) study, where the experimentally determined conditions favoured red anagrams (when the blue time-out was relatively long), choosing red anagrams gave a larger payoff to the participants. Hence the behavioural rule ‘choose red’ was more likely to be transmitted to the new participants through cultural transmission, and the overall frequency of choosing red gradually increased.

Baum *et al.*'s (2004) method could easily be adapted to study the cultural evolution of attitudes or beliefs. Groups of participants could be asked to discuss a contentious issue, then every generation the participant with the most extreme opinion in a certain direction removed and replaced with a random participant. After a number of generations the group should hold more extreme views (in the opposite direction to those of the removed participants) than average members of the larger population.

Experimental economists have also recently begun to study the transmission of behavioural traditions that emerge when chains of successive participants play economic games. For example, Schotter and Sopher (2003) had successive pairs of participants play a game in which two players chose one of two options without communicating. If they chose different options, neither got any payoff, encouraging coordination. If both chose the first option then the first player benefited more than the second, while if both chose the second option the second player benefited more, creating conflict. Transmission was effected by allowing each player to view the behavioural history of all previous players and/or to receive explicit advice from the preceding player in the chain. It was found that stable conventions emerged in which both players consistently chose one option, and that these conventions were mainly due to explicit advice rather than behavioural history.

A similar methodology exists within experimental psychology. The *transmission chain method*, as developed by Bartlett (1932), involves a text or picture being passed along a linear chain of participants. The first participant in such a chain reads or views the stimulus material and later recalls it. The resultant recall is then given to the next participant in the chain to recall, the result of which is given to the third, and so on along the chain. Studying how the material changes as it is transmitted, and comparing the degradation rates of different types of material, can reveal specific biases in cultural transmission.

Mesoudi and Whiten (2004) used this method to study the cultural transmission of event knowledge. Everyday events, such as going to a restaurant, are thought to be represented in memory hierarchically, in which a global high-level proposition (e.g. 'go to restaurant') can be subdivided into lower-level propositions (e.g. 'sit down', 'order', 'eat', 'pay'), each of which can be sub-divided further (e.g. 'look at menu', 'select food', 'call waiter'). Mesoudi and Whiten (2004) found that when descriptions of such events expressed entirely at a low hierarchical level were passed along multiple chains of participants, they were spontaneously transformed into higher hierarchical levels.

Linear transmission chain studies such as those of Schotter and Sopher (2003) and Mesoudi and Whiten (2004) bear less similarity to the experimental paradigms of population genetics. Nevertheless, Schotter and Sopher's (2003) study provides important data on the mode of cultural transmission (explicit advice versus behavioural history), data which might be needed as a preliminary to more advanced experimental manipulations. Studies such as Bartlett (1932) and Mesoudi and Whiten (2004), while not imposing a selection regime on the transmission of cultural traits, are in a sense simulating selection 'in the wild' (see Section 3.3.2), as cultural information is being shaped by the minds of the participants it passes through. In Mesoudi and Whiten (2004), the implicit hierarchical structure of memory causes the selection of event knowledge at high hierarchical levels; hence, there is selection due to evolved or implicit features of human cognition. A design more explicitly along the lines of a natural selection population genetic experiment might involve exposing different chains of people to different experimental conditions, or having each chain composed of different types of people with alternative pre-existing knowledge.

Finally, as well as simply detecting the *presence* of directional selection, population geneticists may obtain quantitative estimates of the *strength* of selection. Cultural transmission experiments would benefit from the development of similar measures, and once again there are opportunities to borrow usefully from biology. Stabilising selection might also be studied in this manner, by testing whether certain beliefs or ideas are converged upon following an experimentally induced deviation (see Section 3.3).

3.2.3. Conclusions. Although laboratory based experiments are an established approach to the study of biological evolution, relatively little experimental work exists in psychology or economics that has studied the dynamics of cultural transmission. Such studies are essential for a full understanding of cultural evolution. Psychological studies of cultural transmission would benefit from explicitly drawing on the methods of experimental population genetics, both in the design of experiments and in the analysis of data.

3.3. Population genetics – field studies

3.3.1. Biology. The third approach within population genetics is the study of evolution in naturally occurring populations. Observational studies or field experiments can give estimates of the heritability of traits by measuring parent-offspring correlations, and measures of mortality and reproductive success can be used to estimate the mode and strength of selection on those traits (Endler, 1986; Futuyma, 1998).

The *mode* of selection (Endler, 1986; Simpson, 1944) refers to whether selection is *directional* (i.e. individuals at one end of a distribution are favoured, causing a change in the mean trait value), *stabilising* (i.e. intermediate individuals are more successful than those at the extremes, decreasing variation in the trait) or *disruptive* (i.e. extreme individuals do better, increasing variation in the trait).

The *strength* of selection is commonly represented by the *selection gradient*, a multiple regression-based measure of the relationship between relative fitness and variation (Arnold & Wade, 1984; Lande & Arnold, 1983). Selection gradients have become a common currency within evolutionary biology for estimating the strength and mode of selection, and for making comparisons between populations (e.g. Endler, 1986; Hoekstra *et al.*, 2001; Kingsolver *et al.*, 2001). The actual methods used to obtain these measures are varied. Endler (1986) lists ten common methods for detecting natural selection in the wild, and the corresponding results that would suggest its operation, as summarised in Table 1.

Table 1 – Methods for the detection of natural selection in the wild and results that would suggest the presence of selection as given by Endler (1986: chapter 3 esp. Table 3.1).

	Method	**Result indicative of selection**
1	Exploring the relationship between a trait and an environmental factor (source of selection)	Correlation between the trait and an independent environmental (selective) factor
2	Comparing closely related species living in the same region	Homologous traits affected in same manner, e.g. divergence in similar traits due to competition (character displacement)
3	Comparing unrelated species living in similar habitats	Similarities in analogous traits due to convergent evolution
4	Comparing gene frequencies with those predicted by a null (no selection) model	Deviation of gene or genotype frequencies, number of alleles, or disequilibrium, from the null model
5	Long-term study of trait distribution	Long-term stability or regular directional change in the trait
6	Perturbation of natural populations	The trait diverges from the new post-perturbation mean
7	Long-term study of demography (e.g. survivorship, fecundity)	Particular demographic patterns are associated with particular trait values over time
8	Comparing the trait distribution of different age-classes or life-history stages	Differences in trait frequency distributions between age classes
9	Using knowledge of fitness, genetics, physiology etc. to predict short-term change in a trait	Predictions confirmed
10	Using fitness-maximisation models to predict an observed trait frequency or distribution at equilibrium	Predictions confirmed

There are literally hundreds of examples of natural selection being demonstrated in natural populations of organisms by the above methods (Endler, 1986). Recent examples include Donley *et al.*'s (2004) analysis of similar morphological and biomechanical specialisations in lamnid sharks and tuna, such as a 'thunniform' body shape, in both cases caused by selection for fast movement through water. This convergent evolution (Endler's 3rd method) has occurred independently during the 400 million years since the two groups diverged from a common ancestor. Marko (2005), meanwhile, found evidence for character displacement (Endler's 2nd method) in two closely related species of rocky-shore gastropods. Significant differences in shell shape were observed only where the two species overlapped, caused by divergent selection as a result of competition.

3.3.2. Culture. Cultural traits have similarly been studied in natural human populations, although mostly not within an explicit evolutionary framework and hence without the formalised hypotheses, methods and measures of selection employed within evolutionary biology as seen above. We will briefly discuss three relevant research traditions - anthropological field studies, rumour research, and the diffusion of innovations - before outlining how more formal, theoretically-driven methods developed within biology might be applied to cultural data.

First, anthropological field studies have examined the acquisition of cultural knowledge in traditional societies. Members of a community are typically interviewed to find out from whom they acquired their knowledge or skills. For example, Hewlett and Cavalli-Sforza (1986) interviewed members of the Aka of central Africa, finding that the majority (80.7%)

of practical skills were said to be acquired from parents, 5.2% from other family members and 12.3% to unrelated individuals. Similarly, Aunger (2000a) found that food taboos are acquired predominantly from biological parents in a horticultural society from the Democratic Republic of Congo, with a subsequent less influential phase of learning from non-kin.

Second, the field of social psychology devoted to rumour research (Rosnow, 1980, 1991) has generated a number of field studies examining the transmission of rumours through naturally occurring populations. A rumour is defined as a belief passed from person to person without secure standards of evidence being present (Allport & Postman, 1947, p. ix). Studies have used questionnaires to track either naturally occurring or experimentally introduced rumours through a small population. Jaeger, Anthony and Rosnow (1980), for example, used confederates to plant a rumour in a college that some students had been caught smoking marijuana during final exams, obtaining details of transmission using questionnaires. Bordia and Rosnow (1998) have more recently studied the transmission of a rumour through an internet community, with the electronic record of communications allowing the longitudinal study of all stages of transmission, rather than relying on retrospective accounts.

Finally, research in sociology on the diffusion of innovations (Rogers, 1995) examines how new ideas and technologies are transmitted through naturally occurring populations. Typically, questionnaires or interviews are employed to assess the past and present use of the innovation by the respondent, and used to compile a picture of diffusion through the population. Classic studies have examined the diffusion of new types of seed amongst farmers (Ryan & Gross, 1943) and antibiotic amongst doctors (Coleman, Katz, & Menzel, 1966). A recurring finding from over 3000 diffusion studies is an *S*-shaped cumulative adoption curve (Rogers, 1995), which indicates a slow initial uptake, followed by a rapid increase in adoption, and finally another slow period as the population reaches saturation (similar sigmoidal dynamics characterise the diffusion of alleles).

Many of these diffusion studies, however, can be criticised for not clearly identifying *a priori* the putative selection pressure responsible for the diffusion, and then testing this prediction in natural populations, as is commonly done in evolutionary biology (Endler's method 1). Instead, diffusion of innovations research has produced a list of *a posteriori* and somewhat vague qualities that supposedly explain diffusion rates, such as 'trialability' or 'complexity' (Rogers, 1995). One recent study that *did* specify *a priori* a hypothesised selection pressure is Bangerter and Heath's (2004) study of the 'Mozart effect', the idea that exposure to classical music enhances intelligence, especially during childhood. While having very weak scientific support, this idea has gained wide currency in the U.S. mass media, which Bangerter and Heath (2004) hypothesised was because it offers a cheap and easy way of supposedly enhancing one's child's development. This hypothesis predicts that the Mozart effect should be more prevalent in the mass media of states where there is poor academic performance and low spending on education, which Bangerter and Heath (2004) showed to be the case.

3.3.3. Conclusions. There are some weak similarities between the methods used by evolutionary biologists to study evolution in naturally occurring populations of organisms and those which have been used to study cultural change 'in the wild'. Rumours and innovations are studied as they colonise novel environments, while anthropological studies provide estimates of heritability. The shorter time scale of some cultural evolution and the ability of people to report its means of transmission suggest that cultural evolution might be easier to detect than biological evolution (although such verbal reports would need to be supplemented with observational data).

The study of cultural evolution, however, is distinctly lacking in formal tests for cultural selection, as opposed to other forms of cultural change such as drift. Laland and Brown (2002) have argued that each one of Endler's (1986) methods for detecting natural selection in the wild (Table 1) can be adapted to study the selection of naturally occurring cultural traits. As mentioned above, sociological studies have successfully tracked changes in the frequencies of various traits following their natural or artificial introduction into a novel environment. The next step would be to demonstrate that these changes in frequency are the result of *selection*, for example by comparing the frequency of a newly introduced idea with the frequency of the idea in the parent population from which it diffused, predicting directional change. An alternative approach would be to test whether stabilising selection was operating on the character prior to the perturbation by investigating whether it returns to the original equilibrium, as predicted. We also encourage more studies like Bangerter and Heath (2004), which identify *a priori* a putative selection pressure - anxiety over child development - responsible for the spread of a cultural trait, and successfully predict the distribution of the trait from that selection pressure.

Another method is to investigate cultural character displacement, where two competing cultural lineages in the same region diverge in order to reduce direct competition (Laland & Brown, 2002). We might, for example, predict that the religious beliefs of people who live side-by-side with people of different, opposing beliefs (e.g. Muslims and Jews in the West Bank, or Catholics and Protestants in Northern Ireland) will be more divergent and extreme than the beliefs of people not in immediate contact with competing beliefs (e.g. Muslims in neighbouring Islamic countries such as Syria and Jews in Jewish-only regions of Israel, or Catholics in the Republic of Ireland and Protestants in mainland Britain).

Convergent cultural evolution, meanwhile, might be detected where cultural lineages from distant yet similar environments have evolved similar features. History is likely to be littered with examples of similar, independently evolved solutions to common problems, such as the independent evolution of writing by the Sumerians around 3000 B.C., the Chinese around 1300 B.C. and the Mexican Indians around 600 B.C., all in response to a need for stocktaking (Diamond, 1998).

Studies of cultural evolution could also adapt the measures of selection strength developed by biologists, such as the selection gradient. Quantitative measures of the rate of microevolution, like the darwin or the haldane (Hendry & Kinnison, 1999), might also be adapted to the cultural case. There is much opportunity here for the fertile transfer of good ideas from biology to the social sciences, with many of the methods currently being used by evolutionary biologists to investigate natural selection in the wild yet to be tried by researchers studying culture.

3.4. Evolutionary ecology

3.4.1. Biology. Ecology is the study of interactions between organisms and their environments (Begon, Harper, & Townsend, 1996). Evolutionary ecology focuses on the evolutionary processes by which organisms have become *adapted* to their environments (Cockburn, 1991; Futuyma, 1998). Such environmental features can be *abiotic*, such as temperature or rainfall, or *biotic*, such as food sources, predators, parasites, competitors or helpers, of both the same and different species. Ecologists have adopted a range of methods to study these processes, including field studies, natural and laboratory experiments and mathematical models. There is therefore a great deal of overlap with biogeography and population genetics.

For example, Korpimäki *et al.* (2002) set out to determine whether predation was responsible for the 3-5 year cycles in population densities of voles in northern Europe. By experimentally reducing numbers of the voles' predators, Korpimäki *et al.* (2002) were able to show a corresponding increase in the population density of voles compared to non-manipulated vole populations. This response was supported by a demographically-based population model which predicted that reduced predation produces a shift from 3-5 year cycles of vole population density to 1-year cycles.

3.4.2. Culture. Cultural traits can also be said to interact with, and adapt to, their environment. The environment in this case can be divided into three categories, two of which roughly correspond to the abiotic and biotic features that affect organisms. Hence cultural traits may adapt to *physical features of the environment* such as temperature or rainfall. Cultural traits may also compete with, and adapt to, *other cultural knowledge*, equivalent to the biotic environment. Finally, cultural traits may adapt to *biologically evolved or implicit features of human cognition*. This has no exact equivalent in the biological world, although perhaps there is a loose parallel in genetic or developmental constraints on adaptation, or in the coevolution of symbionts and hosts (Dennett, 2001, 2002).

As their names suggest, cultural ecologists (e.g. Steward, 1955) and human behavioural ecologists (e.g. Smith & Winterhalder, 1992) have studied the adaptation of cultural traits to the physical and social environment. We will discuss here the rigorous and explicitly Darwinian field of human behavioural ecology, which is directly equivalent to (and indeed emerged from) behavioural ecology within biology, usually using the same theoretical tools and models, such as optimal foraging theory (Stephens & Krebs, 1986). Although human behavioural ecologists often choose to downplay transmitted cultural processes, such work is valuable within a cultural evolutionary framework in specifying the microevolutionary process of cultural adaptation, and the adaptive cultural characters that may be transmitted to subsequent generations.

The practical methods of human behavioural ecology, like those of anthropology in general, involve observing and recording behaviour in natural environments, typically in small communities within traditional societies. Unlike conventional anthropology, however, these observations are guided by the predictions of formal mathematical models. This fieldwork, as well as the theoretical models it is designed to test, resemble the methods of evolutionary ecology. An example is the occurrence in Tibet of polyandry which has been shown to be functionally adaptive under the particularly harsh environmental conditions of the region (Crook & Crook, 1988).

As well as adapting to the physical environment, cultural traits may also adapt to other pre-existing cultural information. The study of this form of adaptation would incorporate competition between cultural traits, for which ecological concepts such as exploitation or interference might be useful. Mufwene (2001) has recently proposed a detailed ecological theory of language evolution along these lines.

Finally, because cultural traits predominantly rely on human minds for their storage and transmission, there is the possibility of adaptation to biologically evolved or developmentally acquired cognitive features of those minds. Hence transmission experiments and field studies can draw on findings from cognitive and developmental psychology concerning implicit memory structures, such as Mesoudi and Whiten's (2004) demonstration that the hierarchical structure of memory shapes the cultural transmission of event knowledge. Evolutionary psychology (e.g. Barkow *et al.*, 1992) also provides a rich theoretical and empirical body of research on biologically evolved features of human cognition that might be predicted to bias cultural transmission in particular directions. Sperber and Hirschfeld (2004) similarly argue that the diversity of some cultural traits, such as religious beliefs or classifications of animals and plants, are the result of adaptation to biologically evolved domain-specific cognitive capacities (e.g. folk-biology: Atran, 1998). There is also evidence that biomechanical properties of the human vocal apparatus significantly constrain the form of words (MacNeilage & Davis, 2000). The infant vocal tract, for example, favours simple consonant-vowel alternations such as ‘dada’ and ‘mama’ (MacNeilage & Davis, 2000), which may explain why such word forms are used in many languages to denote parents.

Of course, cultural knowledge does not exist solely in human brains, and does not exclusively rely on face to face communication for transmission. It may also be fruitful to study the adaptation of cultural traits to alternative transmission media such as printed documents or the internet, and to examine whether such media are merely direct extensions of cognitive capacities or whether they generate their own novel transmission constraints (see Donald, 1991).

3.4.3. Conclusions. Cultural traits may adapt to the physical environment, to other cultural knowledge, or to biologically evolved or implicit features of human cognition. While behavioural and cultural ecologists have produced a large body of work relating ecological factors to cultural beliefs, knowledge and skills, there is much less work on adaptation to the latter two ‘cultural environments’. Anthropological field work and psychological experiments are needed which measure features of these environments (pre-existing cultural knowledge and biologically evolved or implicit aspects of cognition) and make testable predictions regarding corresponding features of culture.

3.5. Molecular Genetics

3.5.1. Biology. One of the major achievements of 20th century biology was the discovery that sequences of DNA comprise the major part of the molecular basis of biological inheritance. Considerable progress has been made in biology as a result of this knowledge. The fields of molecular biology and genetics involve the study of the structure of DNA, RNA and proteins and the processes involved in their inheritance and expression (Futuyma, 1998; Watson *et al.*, 1987).

Molecular genetics has a number of specific uses in evolutionary biology (Futuyma, 1998). As mentioned above, molecular markers can be used to reconstruct and date phylogenetic relationships, as well as provide information on genetic variation, population structure and gene flow. Molecular techniques can also be used to investigate the functions of specific genes in the development of biochemical, morphological or behavioural phenotypic features.

3.5.2. Culture. One approach to culture that is explicitly analogous to genetics is *memetics*. In order to illustrate the universality and substrate-neutrality of his replicator-centred theory of evolution, Dawkins (1976) coined the term *meme* to describe a cultural replicator, or a unit of cultural transmission. Memetics has been developed further by Hull (1982), Dennett (1995), Blackmore (1999) and Aunger (2002; 2000b), amongst others. A common assumption of memetics is that cultural knowledge is stored in brains as discrete packages of semantic information, comparable to how biological information is stored as genes. Once expressed in behaviour or artifacts, these packages of learned information can be replicated in the heads of other individuals through social learning.

The recently burgeoning literature promoting memetics has attracted a number of criticisms (Laland & Brown, 2002). Some of these, such as the need to accommodate the merging of lineages, apply equally to a general theory of cultural evolution and have been discussed elsewhere in this paper. Specific to memetics is the criticism that culture cannot be divided into discrete units with clearly specified boundaries (Bloch, 2000; Midgley, 2000).

However, the same putative ‘criticism’ could equally be levelled at modern concepts of the gene (Laland & Brown, 2002). As documented by Portin (1993, 2002), the concept of the gene has undergone significant changes over the last 150 years. The classical view, held from Mendel (1866) until the 1930s, saw the gene as an indivisible unit of transmission, recombination, mutation and function. That is, a gene is a unit of information that is transmitted whole, within which no recombination occurs, which mutates independently from other genes, and which produces a single molecular product (as captured by James Watson’s famous canon “DNA makes RNA makes protein”). This simple and dated gene concept seems to be the view of the gene held by many social anthropologists who are critical of memetics.

Advances in genetics since the 1930s, however, have shown this unitary gene concept to be inadequate and overly restrictive. Further reconceptualisation began in the 1970s following the discoveries of such phenomena as *overlapping genes*, where the same stretch of DNA codes for more than one protein; *movable genes*, DNA sequences that move around the genome; and *nested genes*, which reside inside other genes. Such revised conceptions have continued in the wake of modern discoveries, such as alternative splicing, nuclear and messenger RNA editing, cellular protein modification and genomic imprinting.

In alternative splicing, for example, one of several alternative versions of an exon is transcribed into a coding segment. Depending on which one is chosen, different proteins can be produced from the same gene. Exons can even be spliced in from other genes, and in some cases it produces not just one or two variants but hundreds or even thousands. Alternative splicing is not a rare or occasional event, and seems to occur in approximately half of all human genes (Modrek & Lee, 2002). Gone is the notion of ‘one gene - one protein’. In fact, genes seem much more like ideas - information that can be expressed in a multitude of different ways.

The modern concept of the gene is hence characterised as abstract, general and open, with fuzzy boundaries that change depending on the context in which the term is used (Portin, 1993, 2002). Indeed, there are now multiple, mutually incompatible gene concepts prevalent within biology (Stotz & Griffiths, 2004). So while the critics of memetics are probably correct in pointing out the vaguely and flexibly specified nature of the meme concept, exactly the same problem applies to the gene concept, which undoubtedly has been of enormous value in the study of biological evolution. The crucial point here is that both empirical and theoretical traditions within population biology have thrived in spite of this biological complexity, by using simple, discrete gene concepts.

However, there is still a gap between the detailed understanding of the cellular and molecular bases of genetic inheritance and the somewhat informal ideas of memetics. A more detailed picture of the mechanisms of cultural transmission requires an understanding of how the brain processes relevant information. Here, the most obvious analogy might be between molecular genetics and the molecular and cellular bases of learning and memory. However, such learning can be usefully studied at levels other than the molecular, ranging from purely cognitive analyses which say little directly about underlying neural bases, to studies that explicitly focus on supra-cellular aspects of how imitative and related processes are executed in the brain, studied through methods such as *f*MRi. These considerations suggest that because the storage and transmission of culturally transmitted information is so physically different to the genetic, it is here that scientists studying cultural transmission will need to venture further beyond the analogies between cultural and biological evolution that we have focused on so far. Already, one can perceive the beginnings of what has been called a ‘social cognitive neuroscience’ that aims to integrate all the required levels of analysis. Three of these levels - the neural, the whole brain and the cognitive - are outlined here.

First, at the *neural* level, the social learning community (see Hurley & Chater, 2005) has hailed as highly significant the discovery of ‘mirror neurons’ in the prefrontal cortex of monkeys, which activate both when the monkey observes a specific goal-directed hand action, such as grasping an object, and also when the monkey performs that same action (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). This match between observation and execution of motor actions has led some researchers to suggest that the mirror neuron system forms the basis for *imitation* (Melzhoff & Decety, 2003; Rizzolatti *et al.*, 2002; Williams *et al.*, 2001), which is one possible cultural transmission mechanism, and *theory of mind* (Gallese & Goldman, 1998), which has also been argued to be important in human cultural transmission (Tomasello, 1999; Tomasello, Kruger, & Ratner, 1993).

However, it has long been argued that rather than single memories or functions being determined by single neurons, memory is more likely to be determined by patterns of activation within neural circuits and the resulting connection strengths between neurons (Hebb, 1949). Phenomena such as long-term potentiation (Bliss & Lomo, 1973) and long-term depression (Dunwiddie & Lynch, 1978), as well as a multitude of pre- and post-synaptic changes in neural tissue, offer potential electrophysiological and biochemical mechanisms underpinning certain long-term memories (see Keysers & Perrett, 2004 for a Hebbian-based model of social cognition). These views of memory, in which single neurons are implicated in a range of functions and functions are determined by more than one neuron, resemble the complexity found in the genetic system discussed above, where one gene has a potentially wide range of functions and expressions.

Aunger (2002) has recently attempted to integrate memetics with neuroscience, arguing that a robust conceptualisation of the ‘meme’ must specify its material basis in the brain. Aunger (2002) proposes that memes should be seen as electrochemical states of multiple neurons, and offers a definition of a ‘neuromeme’ as “a configuration in one node of a neuronal network that is able to induce the replication of its state in other nodes” (p. 197). As acknowledged by Aunger (2002), however, any attempt to provide a more detailed description and theory of a neuromeme is severely limited by the current lack of understanding within neuroscience concerning the precise neural and molecular basis of how learned information is stored in the brain. One problem specific to the present discussion is that rat and monkey models may be limited in their relevance to studying culturally acquired information given these species’ limited capacity for culture, while invasive single neuron recordings are not performed on humans and other great apes.

Notwithstanding these complications, there is evidence from cognitive neuropsychology that cultural knowledge is often chunked and aggregated into higher order knowledge structures that may be separable (Plotkin, 2002). For instance, there are several reports of category-specific naming impairments of human patients with brain damage, who have been found to recognise and correctly name all items except those in a specific category, such as fruit and vegetables or country names (Crosson *et al.*, 1997). Such studies suggest that at least some learned knowledge stored in human brains is organised into separable semantic categories. There is also recent evidence that single neurons in the human medial temporal lobe respond to the higher order abstract representation of a specific person or building (Quiroga *et al.*, 2005).

Second, the charting of imitation and related processes at the *whole brain* level has focused principally on humans, including the study of neurological cases such as apraxia and its associated imitation deficits (Goldenberg & Hermsdorfer, 2002) and *f*MRi studies of imitation in normal (Iacoboni *et al.*, 2001; Rumiati *et al.*, 2004) and other groups, such as autistic individuals who experience difficulties in imitation (Avikainen, Kulomaki, & Hari, 1999).

If neuronal studies have been largely restricted to monkeys, and whole brain studies to adult humans, it is research at the *cognitive level* regarding social learning in great apes and, more recently, human children that has generated the richest current taxonomies of cultural learning, delineating such processes as program-level imitation, emulation and affordance learning (Byrne & Russon, 1998; Tomasello *et al.*, 1993; Want & Harris, 2002; Whiten & Ham, 1992; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Cognitive models that seek to explain how these operate have begun to proliferate, but remain few and quite crude in comparison to our understanding of genetic transmission mechanisms; they include Meltzoff and Moore's (1997) Active Intermodal Matching (AIM), Heyes' (2005) Associative Sequence Learning (ASL) and Byrne's (1999) String Parsing models. Interestingly, all of these models appeal to a foundation of mirror-neuron function, leading Whiten (2005a) to question whether they really solve, or instead merely assume solved, the essential 'correspondence problem' (Nehaniv & Dautenhahn, 2002) of mapping between equivalent actions in a model and a cultural learner. Others have explicitly tackled this problem in offering neural network models proposed to be capable of learning the appropriate correspondences (Keysers & Perrett, 2004; Laland & Bateson, 2001). Keysers and Perrett (2004) review data consistent with their hypothesis that in monkeys this is achieved by circuits linking premotor area F5, inferior parietal cortex PF/PFG and the superior temporal sulcus, and by the homologues of these areas in humans.

3.5.3. Conclusions. While genetic information is represented in sequences of DNA molecules, cultural information is represented primarily in the brain. Viewing culture as comprised of discrete units of information, or memes, can potentially make a complex system theoretically and empirically tractable, in the same way as the gene concept advanced biologists' understanding of biological evolution. Although memes can be characterised as vague entities with flexible and fuzzy boundaries, so can the modern concept of the gene. It should be remembered that there was at least 50 years of productive investigation into biological microevolution before the molecular basis of genetic inheritance was determined, and even now it is only partly understood.

A deeper understanding of the neural and molecular basis of culturally acquired information must rely on technological advances in, for example, neuroimaging techniques. However, we should also reserve the possibility that the same cultural information is specified by different neural substrates in different brains, severely limiting such methods for studying cultural transmission. In this case there may be no cultural equivalent to molecular biology, although models and methods examining cultural transmission at the behavioural and cognitive levels can still provide important insights.

Another possibility is that such methods will reveal that certain aspects of cultural transmission are *not* particulate, and are better characterised in terms of a blending process. Even in this case, however, evolutionary models are still applicable (Henrich & Boyd, 2002). Indeed, Darwin formulated his theory of evolution with little understanding of genes or Mendelian inheritance.

Delineation of the neural basis of cultural information will also bear on another oft-cited putative dis-analogy between biological and cultural evolution, that there is no clear equivalent to the genotype-phenotype (or replicator-interactor) distinction in culture. Loosely, we can speak of culturally acquired semantic information stored in brains as replicators and the expression of that information in behaviour or artifacts as their interactors. However, without further advances in memetics and neuroscience such a division is somewhat speculative. It may prove that forcing cultural inheritance too tightly into the biological model is in this case unproductive (Aunger (2002), for example, has developed an alternative model of cultural transmission based on signal theory).

The delineation of the genotype-phenotype distinction will also bear on whether cultural inheritance can be described as ‘Darwinian’ or ‘Lamarckian’, the former maintaining Weismann’s barrier between replicator and interactor, and the latter involving the inheritance of acquired phenotypic variation. Ultimately, we do not think that researchers should get too distracted by whether strict analogies to the replicator-interactor distinction can be drawn or whether cultural inheritance is Darwinian or Lamarckian, especially when the necessary neuropsychological evidence is lacking. Many of the methods described elsewhere in this article can be pursued despite a poor understanding of cultural transmission at the neural level.

3.6. Microevolution: General conclusions

The comparison between biological and cultural microevolution has produced mixed results. First, a well-developed body of theory exists which has drawn on the mathematical population genetic models within biology to provide a rigorous and successful analysis of cultural evolution. This is predominantly the work of gene-culture coevolution, although neutral models of genetic drift have recently also been successfully applied to cultural traits.

Second, experimental and field studies of cultural microevolution typically lack the rigour of equivalent studies within experimental and field population genetics. Explicit tests for selection, such as the artificial selection paradigm or Endler’s (1986) various tests for selection in natural populations, and quantitative measures of the strength of that selection, such as selection gradients, have not yet been employed. A number of opportunities exist for psychologists, field anthropologists, sociologists and experimental economists to adapt some of these tools and methods developed in biology to the study of cultural microevolution.

Third, there is currently a limited correspondence between our understanding of molecular genetics and the molecular or neural basis of cultural inheritance. This is primarily due to limitations in the tools of neuroscience, such as imaging techniques, which cannot yet reveal exactly how information is acquired by and stored in the brain, nor the relationship between models of social learning and models of memory. Much potential exists, however, to develop further cognitive models of social learning.

4. Differences between biological and cultural evolution

Despite the plethora of studies reviewed above, which we have argued can be viewed as part of a larger field of cultural evolution, many of these studies, as well as the evolutionary approach in general, have yet to gain acceptance by mainstream cultural anthropology and related social sciences. One reason for this resistance is that many social scientists see a number of fundamental differences between biological and cultural change that they argue invalidate an evolutionary analysis of culture. We have already seen that a number of these purported differences, upon closer examination of either the biological or the cultural evidence, become either illusory or unimportant to the validity of the comparison (e.g. the horizontal transfer of cultural information causing cultural lineages to blend and merge (Section 2.1.2); the apparent lack of discrete particles in culture equivalent to genes (Section 3.5.2); and the lack of a clear equivalent to the genotype-phenotype distinction and the related issue of Lamarckian inheritance (Section 3.5.3)).

Another putative difference, not yet discussed, is the frequent argument that, while biological evolution is 'blind' with respect to long-term goals (i.e. mutation is independent of selection), cultural change is often intentionally directed toward some specific goal (e.g. Bryant, 2004; Pinker, 1997, pp. 208-210). However, the extent to which culture is intentionally directed and the precise effect of this intention on long-term cultural change are empirical issues. In fact, studies of technological innovation (e.g. Basalla, 1988) and creativity (e.g. Simonton, 1995) suggest that successful inventions and discoveries are frequently either the result of trial and error or the unintended by-products of attempts to solve unrelated problems. Conversely, biological evolution is also to a degree directed in the sense that potential mutations, particularly the minority that will be subject to selection, are heavily constrained by a species' history of selection (see Hull, Langman, & Glenn, 2001; Mesoudi *et al.*, 2004). This is not to suggest that there are no differences here – on the contrary, 'smart variants', biologically evolved biases in cognition and other cultural traits, may guide behaviour in a non-random direction (Laland, Odling Smee, & Feldman, 2000). There is evidence of both directed and undirected variation in human culture, and the relative importance of each is currently unknown. We maintain that critics must empirically demonstrate that the existence of intent does in fact invalidate an evolutionary account of human culture, and moreover explain why many of the evolutionary methods discussed above (e.g. the phylogenetic analyses) work equally well for both biological and cultural evolution despite this alleged difference.

One potentially valid criticism of some accounts of cultural evolution is the treating of all cultural traits as equivalent. In previous sections we have described beliefs, behaviour, technological artifacts, languages and social systems as examples of a somewhat simplistic notion of the 'cultural trait'. Undoubtedly, cultural evolutionary processes will sometimes act differently on different forms of cultural variation, frequently generating distinct evolutionary dynamics for each. It is already well established that vertically and horizontally transmitted traits, conformist transmission, and direct and indirect biases will each exhibit different but characteristic dynamics (Boyd & Richerson, 1985). We have no doubt that the pattern and intensity of selection acting on fads and fashions will be quite different from that acting on established norms and institutions. In a sense, this is not too dissimilar to the biological case, where alternative traits may be subject to different forms of selection, and where multi-level selection models are commonplace.

Plotkin (2002) has furthermore argued that 'social constructions', cultural traits such as justice or money that only exist because of shared agreement, require a fundamentally different explanation to concrete traits such as technological artifacts, and have no real equivalent in the biological domain. Like Plotkin (2002), we do not believe that this invalidates an evolutionary approach to culture, rather it requires a different evolutionary treatment to the one developed within biology. An evolutionary consideration of social constructions, as well as a detailed taxonomy of cultural traits, are, however, beyond the scope of this paper. The important point is that deviations from the biological case such as this do not necessarily invalidate an evolutionary approach to culture, they merely require novel treatments of cultural phenomena within a general evolutionary framework.

5. Nonhuman culture

We end by considering the burgeoning literature that has emerged in the last few years regarding non-human social learning and culture (see Avital & Jablonka, 2000; Byrne *et al.*, 2004; Fragaszy & Perry, 2003; Laland & Hoppitt, 2003; Whiten, 2005b; Whiten, Horner, & Marshall-Pescini, 2003), which suggest parallels with the human work discussed above. Irrespective of the similarities and differences between human and animal culture, here we ask whether the above methods can fruitfully be employed to study the behavioural traditions of other species.

First, there is evidence from a number of species of behavioural traditions not obviously attributable to genetic or ecological differences, and hence thought to constitute socially learned cultural patterns. For example, Whiten *et al.* (1999; 2001) documented thirty-nine putative cultural traits in chimpanzees from various regions of Africa, such as tool usage or grooming behaviour. Similar regional differences inferred to be cultural in origin have been observed in orangutans (van Schaik *et al.*, 2003) and capuchins (Fragaszy & Perry, 2003; Perry *et al.*, 2003), as well as in the vocalisations of birds (Catchpole & Slater, 1995) and mammals (especially cetaceans: Janik & Slater, 1997), and behavioural traditions in fishes (Helfman & Schultz, 1984; Warner, 1990). There are obvious parallels here with the databases compiled by cultural anthropologists documenting worldwide geographical variation in human culture.

Second, Mercader, Panger and Boesch (2002) have used traditional archaeological techniques to excavate a site in Africa used by chimpanzees for at least the past 20 years to crack nuts using stone hammers and wooden anvils. Considerable evidence of past nut-cracking behaviour was uncovered, specifically nutshell and fractured stone, the latter of which the authors claimed was indistinguishable from a subset of the earliest and simplest stone tool assemblages left by hominid ancestors. Although the finds were probably very recent compared with the cultural artifacts studied by archaeologists, this study suggests that the same methods can potentially be used to uncover evidence of past non-human cultural behaviour.

Third, a number of studies have tracked the diffusion of innovations within non-human communities, paralleling the research tradition of the same name for human technology (Rogers, 1995). The most famous case is the diffusion of potato washing in a community of Japanese macaques (Kawai, 1965). Lefebvre (1995) found that 16 of 21 reported cases of the diffusion of foraging innovations in primates exhibit a rapid accelerating pattern of adoption characteristic of cultural transmission (an example of which is the S-shaped distribution reported by Rogers, 1995), although Laland and Kendal (2003) and Reader (2004) have expressed reservations about inferring learning mechanisms from diffusion curves. Whiten, Horner and de Waal (2005) have recently employed a more experimental approach to studying the spread of alternative foraging techniques in different groups, creating the potential to track diffusion dynamics more reliably.

Fourth, population genetic modelling has been used to analyse patterns of non-human culture, specifically bird song. Lynch and Baker (1993) found that the geographical distribution of chaffinch songs can be accounted for by a neutral model in which mutation, migration and drift are at equilibrium. Lachlan and Slater (1999) adopted gene-culture coevolution methods to find that vocal learning can be maintained in a ‘cultural trap’ formed by the interaction between genes (which specify the constraints on songs) and culture (the songs themselves). Gene-culture coevolutionary methods have also been used to explore how song learning might affect speciation (Beltman, Haccou, & ten Cate, 2004) and the evolution of brood parasitism (Beltman, Haccou, & ten Cate, 2003).

Fifth, the experimental transmission chain method devised by Bartlett (1932) has been used to study the social learning of mobbing in blackbirds (Curio, Ernst, & Vieth, 1978) and food preferences in rats (Laland & Plotkin, 1990, 1993). Jacobs and Campbell's (1961) replacement method has been used to study the transmission of food preferences in rats (Galef & Allen, 1995) and route preference in guppies (Laland & Williams, 1997, 1998).

The above studies demonstrate that many of the same methods used to investigate biological evolution or human cultural evolution can be applied to non-human culture. Studying human and non-human culture within the same theoretical framework is likely to provide important insights into the evolutionary origins of, and psychological mechanisms underpinning, human culture.

6. Conclusions

The evidence discussed in this paper suggests that much potential exists for a comprehensive science of cultural evolution with broadly the same structure as the science of biological evolution, as outlined in Figure 1. This potential is already being realised for the study of cultural macroevolution and the mathematical modelling of cultural microevolution, with methods developed within evolutionary biology, such as phylogenetic analyses and population genetic models, being applied to cultural data. A number of opportunities exist for psychologists, sociologists and experimental economists to adopt the experimental methods and tools developed in population genetics to simulate cultural microevolution, and detect cultural evolution 'in the wild'. Finally, the study of the neural basis of cultural transmission is seemingly dependent on advances in new technologies that should reveal how culturally acquired information is represented in the brain.

We have also seen some examples where the explicit adoption of an evolutionary framework or evolutionary methods has provided significant advances over traditional non-evolutionary methods. For example, phylogenetic analyses have provided a solution for Galton's problem when comparing societies related by descent, and evolutionary 'population thinking' allows more accurate descriptions of archaeological artifacts than does an essentialist perspective.

One reason why evolutionary biology has been relatively successful is that a unifying evolutionary framework encourages and stimulates cross-disciplinary work. Some cross-disciplinary borrowing has already been seen in the study of cultural macroevolution, with phylogenetic methods increasingly used in both archaeology and cultural anthropology. As more researchers adopt the evolutionary framework outlined here we anticipate the occurrence of more such borrowing. For example, experimental studies of cultural transmission might explicitly test the predictions of theoretical models, and empirical findings in turn used to inform the assumptions of further models. Experimental work might also simulate the findings of archaeologists and anthropologists to determine the possible transmission mechanisms underlying certain historical and geographical macroevolutionary patterns.

Although we advocate the adoption of a number of methods and approaches developed within evolutionary biology, we do not advocate the slavish and dogmatic imitation of evolutionary biology. Cultural inheritance is undoubtedly different in many respects from biological inheritance, and novel mathematical analyses and empirical investigations into cultural dynamics that deviate from the biological case are necessary (Richerson & Boyd, 2005). As noted above, cultural phenomena such as social constructions have yet to be dealt with in evolutionary terms. At the same time, however, these deviations do not invalidate an evolutionary framework. For example, subtle refinements of traditional biological methods have been found to enhance the validity of the mathematical modelling tradition described in Section 3.1.2.

Furthermore, despite the impression perhaps given in this paper, we should also bear in mind that evolutionary biology is, like any other science, far from perfect and is continually changing and updating its methods. Indeed, evolutionary biologists may well benefit from considering alternative evolutionary systems to their own, or from utilising methods developed by social scientists.

In short, we submit that the argument that culture exhibits a number of key Darwinian properties is well-supported, and advocate taking advantage of this in order to use evolutionary biology as a model for integrating a multitude of separate approaches within the social sciences, and, where appropriate, borrowing some of the methods developed by evolutionary biologists to solve similar problems. Putting disparate studies from presently unconnected disciplines together into a broad evolutionary context adds value to each of the individual studies, because it illustrates that the degree of progress in this area is far more impressive than hitherto conceived. We suggest that these studies can now be said to be aligned within a unified ‘movement’, and that if this Darwinian evolutionary movement could be better co-ordinated, a more persuasive and important direction could be put on much work in the social sciences.

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