

PERSPECTIVE:
IS HUMAN CULTURAL EVOLUTION DARWINIAN? EVIDENCE REVIEWED FROM THE
PERSPECTIVE OF *THE ORIGIN OF SPECIES*

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Abstract.—The claim that human culture evolves through the differential adoption of cultural variants, in a manner analogous to the evolution of biological species, has been greeted with much resistance and confusion. Here we demonstrate that as compelling a case can now be made that cultural evolution has key Darwinian properties, as Darwin himself presented for biological evolution in *The Origin of Species*. Culture is shown to exhibit variation, competition, inheritance, and the accumulation of successive cultural modifications over time. Adaptation, convergence, and the loss or change of function can also be identified in culture. Just as Darwin knew nothing of genes or particulate inheritance, a case for Darwinian cultural evolution can be made irrespective of whether unitary cultural replicators exist or whether cultural transmission mechanisms are well understood.

Key words.—Cultural evolution, cultural transmission, human culture, Lamarckian inheritance, memes, natural selection, *The Origin of Species*.

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In *The Origin of Species*, Darwin frequently used analogies with cultural change to illustrate his theory of biological evolution. More recently, arguments that insights into cultural evolution are to be gained by appreciating its Darwinian properties have been developed by eminent figures in fields ranging from biology to philosophy to psychology (e.g., Dawkins 1976; Popper 1979; Skinner 1981; Hull 1982; Dennett 1995). In the last few years such efforts have intensified, with an extensive literature proliferating on relationships between biological and cultural evolution (e.g., Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Aunger 2000a, 2002; Plotkin 2002; Shennan 2002; Wheeler et al. 2002).

However, attempts to apply the theory of evolution by natural selection to the origins of the diverse range of beliefs, knowledge, and artifacts that constitute human culture have met with great resistance in some quarters, comparable to that which followed Darwin's insight (e.g., Hallpike 1986; Gould 1991; Pinker 1997). A prime focus of these debates (see Aunger 2000a) is a preoccupation with the possibility of cultural "units of inheritance," sometimes called "memes" (Dawkins 1976), the delineation of which is often (erroneously) seen as a necessary prerequisite for Darwinian evolution. Darwinian models of cultural evolution have consequently been criticized (and are commonly being rejected) on the grounds that culture cannot be divided into discrete particles (e.g., Bloch 2000; Kuper 2000) or that to the extent that such particles exist, they do not faithfully replicate in the way genes do (Sperber 2000). However, when he wrote *The Origin*, Darwin knew nothing of genes, and he had little understanding of Mendelian particulate inheritance. Many contemporary commentators therefore appear to be rejecting Darwinian cultural evolution on grounds that might have led them to reject the fundamental case made for evolution through natural selection in *The Origin*.

In the present paper we suggest that a clearer approach to the essential issues can be made by returning to the basic principles of the theory supported in *The Origin*, and testing these against the rich variety of empirical data concerning human culture that have been garnered in a diversity of human sciences since *The Origin* was published. Accordingly, we shall briefly reprise the key elements of the case for biological evolution through natural selection that were presented by Darwin in *The Origin of Species* (1859) and explore the extent to which a parallel case is justified for the evolution of culture. Just as *The Origin* forced biologists to take the theory of evolution seriously, we hope that a similar treatment for cultural evolution will force those in the social sciences to give the argument serious consideration, and provoke biologists into giving the matter more thought than they perhaps have done in the past.

The comparison with *The Origin* is more than just an intellectual exercise or historical curiosity. It is of considerable significance to biologists if the core evolutionary processes at the heart of their discipline govern an aspect of human life—culture—that is often contrasted with biology. This is not only because the theory, tools, and findings of biological evolution may generalize to other disciplines, rendering the study of evolution far broader and more important than currently conceived, but also because biological evolution would have to be regarded as interwoven into a lattice of interacting evolutionary processes, for which hierarchical, multiple-level, or multiple process models will be required (e.g., Plotkin and Odling Smee 1981; Laland et al. 2000; Hull 2001).

A final justification for our analysis derives from a common criticism of the proliferating "memetics" literature: its reliance on theory over data (Laland and Brown 2002). In this field there is much armchair speculation and little attempt to

integrate multiple sources of existing evidence to make a coherent case. By contrast, the integration of several disparate sources of evidence was instrumental to Darwin's argument (e.g., the fossil record, geographical distribution of species, taxonomy, morphological features, artificial breeding). A similar breadth of sources is drawn on below. If it is accepted that Darwin provided a robust case for biological evolution by natural selection, and an equivalent case can be made for the evolution of culture, then we maintain that either Darwinian cultural evolution should be accepted as a valid theory in the domain of culture, or the burden of proof is being placed unfairly high. This position does not, of course, imply that a Darwinian model is by itself expected to provide a complete theory of a phenomenon as complex as human culture, and we conclude our argument by highlighting some key points of departure of human cultural evolution from the principles of biological evolution.

PRELIMINARY DEFINITIONS

Darwin had the considerable luxury of not being required to define the phenomenon ("life") that he was trying to explain. However, a long history of confusion over how to define "culture" (Kroeber and Kluckhohn 1952) suggests an explicit definition is needed here. Following Boyd and Richerson (1985), we define *culture* as acquired information, such as knowledge, beliefs, and values, that is inherited through social learning, and expressed in behavior and artifacts. *Cultural evolution* is consequently the idea that the information in this cultural domain frequently changes according to a similar process by which species change, that is, through the selective retention of favorable cultural variants, as well as other nonselective processes such as drift. Forthwith, our use of the term "cultural evolution" will imply such a general Darwinian process. First, this should be distinguished from nonevolutionary theories of cultural change, as exemplified in the cultural determinism of Boas (1940), Mead (1928), and Benedict (1934); the structuralism of Levi-Strauss (1963); or the semiotic theories of Geertz (1973), and second from non-Darwinian theories of cultural evolution. This latter distinction is important, because distortions of Darwinian thinking have long been used to bolster erroneous, prejudicial, linear, and progressive conceptions of cultural change (Tylor 1871; Morgan 1877).

We emphasise the distinction between "cultural selection" and "natural selection" (Cavalli-Sforza and Feldman 1981). For example, smoking may increase or decrease in frequency through the differential adoption of the habit (cultural selection) or through the differential survival of smokers (natural selection). Although both processes operate on human cultural variation, it is cultural selection that concerns us here.

THE EVIDENCE

In *The Origin*, Darwin set out his logical case, empirically backed at each step, by first establishing the extent of variation in characters, followed by analyses of the inevitable competitive struggle for existence, and its consequences, through inheritance, for the shaping of forms of life. Likewise we consider in turn variation, competition, and inheritance, followed by other major themes *The Origin* developed, name-

ly accumulation of modifications, adaptation, geographical distribution, convergence, and changes of function.

Variation

... we have many slight differences which may be called individual differences ... [which] are highly important for us, as they afford materials for natural selection to accumulate ... (Darwin 1859, pp. 101–102)

Essential to Darwin's case was the need to demonstrate the existence of variation between individuals in a population. Without variation there can be no selection of favorable variants, and hence no accumulation of beneficial modifications. Does human culture meet this requirement?

That human culture displays great variation is obvious, but its extent is worth briefly documenting in comparative perspective, through illustrative statistics. A point of contrast is with our closest relatives. In the case of chimpanzees, 39 geographically variable behaviors have been distinguished, such as the usage of different kinds of tools (Whiten et al. 1999; 2001), which are thought to represent distinct cultural variants, with a comparable figure of 24 variants for orangutans (van Schaik et al. 2003). In contrast, Basalla (1988) reports that 4.7 million patents had been issued in the United States alone since 1790, while the latest edition of the *Ethnologue* (Grimes 2002) lists a total of 6800 languages spoken worldwide. Steward (1955, p. 81) reports that an attempt to catalog all "culture elements" (e.g., pottery, the bow, shamanism, polyandry) in various groups of American Indians resulted in the identification of 3000–6000 elements, while the United States military force that landed in Casablanca during World War II was equipped with over 500,000 different material items. Finally, Basalla (1988) notes Karl Marx's surprise at learning that 500 different types of hammer were produced in Birmingham in 1867.

However, what is critically required for the Darwinian process is that variants are of a kind that will compete with each other for differential representation in the future. Thus, among any set of 500 different hammers, it will be important to distinguish between those that vary because they perform different functions, and those that represent alternative designs for the same purpose, for it is between the latter that the "struggle for existence" is expected to be most acute. Although certain cultural phenomena such as alternative religious beliefs would seem to be mutually incompatible and vying with each other, there appears to be surprisingly little systematic documentation of cultural variation that is in competition. One rather whimsical but significant example is provided by Hinde and Barden (1985), who measured the facial dimensions of teddy bears over an 80-year period and found a gradual enlargement of the forehead and shrinking of the snout, which they interpreted as reflecting a human preference for babylike neonatal features. This was interpreted as the result of selection pressure from consumers of teddy bears, acting on the considerable variation on these dimensions that the authors measured at each point along the historical progression.

In general, we might expect that behavioral or technological innovations, such as those indicated in the patent statistic cited above, may be variations on existing patterns, and thus

provide the variation of interest. Competition between new and older variants would then ensue. According to an extensive analysis by Basalla (1988), technological change through gradual modifications of what went before is the rule rather than the exception. Among numerous examples cited by Basalla (1988) are Joseph Henry's 1831 electric motor, which borrowed many features from the steam engine, and Eli Whitney's 1793 cotton gin, designed to remove seeds from cotton plants, which was based on a long line of Indian devices. The new variations thus engendered would be precisely the kind likely to compete with their more long-standing counterparts.

Evidence that two or more cultural variants are indeed competing comes from testing the prediction that over time one variant will increase in frequency while another shows a corresponding decrease. This has been demonstrated by archaeologists using the method of "frequency seriation," in which the frequencies of excavated cultural artifacts are recorded at different time periods, thereby reconstructing lineages of competing artifacts (O'Brien and Lyman 2000). Kroeber (1916) reported that corrugated pottery found in New Mexico gradually decreased in frequency, while the frequency of painted pottery increased. More recently, O'Brien and Lyman (2000) have detailed how lineages of prehistoric projectile points from the southwestern United States show an increase in functional efficiency over time, demonstrating competition of successive forms in one or more lineages, with each new, more efficient variant outcompeting and replacing the older form. In a later section we shall see how other cultural traits, such as stone tools and mathematical systems, show a similar accumulation of successive forms over time, each the result of competition among similar variants.

What are the sources of cultural variation? Darwin had only the vaguest understanding of how the process of biological (sexual) reproduction could give rise to variation, noting only that: "... individual differences. . . are known frequently to appear in the offspring from the same parents . . ." (p. 102). At a similar level of analysis, cultural variation arises through errors or improvisation in learning and distortion in transmission. This distortion has been demonstrated by "transmission chain studies," in which material is passed from person to person, in a manner similar to the childrens' game "Chinese whispers." For example, Bartlett (1932) found a tendency for British participants to distort material originating from a Native American culture according to their own cultural background, whereas Allport and Postman (1947) found that a description of a picture was distorted according to the subjects' racial prejudices. Reviewing the relevant literature, Campbell (1958) listed 21 different systematic biases in human social transmission that introduce novel material, whereas Buckhout (1974) detailed the selective and constructive nature of human memory in the context of eyewitness testimony research. Such studies show that the storage and transmission of cultural knowledge is far from perfect, and much variation is spontaneously introduced.

Darwin proposed that the presence of variation is required for there to be a response to selection pressures, a principle later formalized in Fisher's Fundamental Theorem (Fisher 1930). A similar phenomenon is exemplified in the study of

creativity. In a longitudinal study of teams of molecular biologists, Dunbar (1995, 1997) found that those teams composed of scientists with varied research backgrounds made more key discoveries and breakthroughs than otherwise equivalent teams composed of scientists with similar backgrounds and expertise. The implication here is that the more heterogeneous teams generated a richer variety of ideas upon which cultural selection could work than the more homogeneous teams. There was also a tendency for the successful teams to focus on unexpected findings, suggesting the benefit of introducing novel variation. These results echo more general findings in the human creativity literature (Simonton 1999) that creative individuals tend to be more prolific in their output (irrespective of the quality of that output) and exhibit more divergent thinking compared with less creative individuals, both of which will increase the chances of encountering a successful variant. There is also widespread experimental evidence that groups, especially heterogeneous groups, outperform individuals in tasks of problem solving or decision making (Garrod and Doherty 1994; Moshman and Geil 1998; Schulz Hardt et al. 2000), again suggesting that more variation is generated on which selection can then act.

Darwin argued that biological variation is naturally produced without regard to its consequences (what we now think of as random mutation), favorable variations then being recognized through an independent selection process. In the case of human culture, however, we must contemplate the possibility that foresight may be applied to produce variation channelled towards a certain solution to a problem. This would constitute a departure from a Darwinian model of cultural change, raising the question of how much cultural evolution may be directed in this way, rather than through the Darwinian algorithm of undirected variation coupled with selection.

In fact, the literature on human creativity indicates that much variation in culture is *not* directed in this sense. Simonton (1995) has shown that innovation or discovery is often the result of trial and error, such as when Watson and Crick painstakingly tried to fit molecular models together until they hit on the double helix. Although their intention was to solve this specific problem, intention itself was not sufficient to reach that solution. Other cases demonstrate that intention to solve is also not a necessary condition, such as when William Roentgen, winner of the first ever Nobel Prize for physics, accidentally and unwittingly discovered x-rays in 1895 while studying how cathode rays penetrate different materials. Other serendipitous or accidental discoveries and inventions listed by Simonton (1995) include animal electricity, laughing gas anaesthesia, electromagnetism, ozone, photography, dynamite, the gramophone, vaccination, saccharin, radioactivity, classical conditioning, penicillin, Teflon, and Velcro.

However, in other cases cultural variation may not be independent of selection, representing what Laland et al. (2000) have termed "smart variants." Biologically evolved biases in cognition and other cultural traits may guide behavior in a nonrandom direction. What remains to be clearly determined is the relative importance of directed and nondirected variation in actual cultural evolution.

Viewing the comparison between biological and cultural evolution from the reverse perspective, it is also important to note that biological variation is also to a degree directed, insofar as any potential variation is heavily constrained by an organism's present form, which is in turn determined by the species' history of selection. Variation is only random within such boundaries. Indeed, Hull et al. (2001), in a general account of Darwinian selection processes, have argued that

. . . statements about the sorts of variation that function in selection processes need not include any reference to their being blind, random, or what have you. All of the terms that have been used to modify variation are extremely misleading. Hence, we see no reason to put any adjective before variation in our definition of selection. (Hull et al. 2001, p. 514)

In conclusion, human culture has been shown to exhibit extensive variation that is both necessary and conducive to cultural evolution. Although this variation may not be entirely random with respect to selection, ultimately it matters less to the Darwinian process how variation arises, than that variation exists and is exposed to selection.

Competition

A struggle for existence follows from the high rate at which all organic beings tend to increase. (Darwin 1859, p. 116)

Inspired by Malthus's *Essay on the Principle of Population* (1798), which showed how a geometric increase in the world's population will lead to rapid overcrowding and a shortage of key resources, Darwin realized that a similar shortage of resources in nature will lead to *competition* between variants, and hence the selection of favorable variants. Similarly, no individual person can adopt and express all of the immense cultural variability indicated above, so competition for expression in human brains, behavioral repertoires, and material products will occur.

Darwin (1871) himself argued that such competition occurs amongst words.

A struggle for life is constantly going on amongst the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand, and they owe their success to their own inherent virtue. (Darwin 1871, p. 91)

Clearly, the "struggle" Darwin was alluding to here cannot be directly compared to the competition over finite physical resources alluded to by the reference to Malthus. Rather, we have to think in more general terms, of a competition for limited "slots" or functionally equivalent "solutions" to specific "problems." In the case of Malthusian overcrowding the available slots are limited by the carrying capacity of the environment. In Darwin's linguistic example, the slots may instead be semantic categories, which alternative terms compete to label, an example of which would be the successive replacement over recent years in youth culture of the adjectival synonyms "neat," "fab," and "cool."

We suggest that an appropriate way to conceptualize what any set of cultural variations are in general competing over is in terms of functional categories. Thus, synonyms will be in competition for describing the same semantic category; different hammers will be in competition with respect to effective hammering; and different gestures may be in competition to fulfil the same social function. This is analogous to the biological case, for although variations such as those in foraging strategies and territorial defense may indeed subserve competition for limited resources in the narrow Malthusian sense, "competition" considered more broadly is focused on relative functionality, thus extending to characters such as predator defense strategies that are not directly concerned with competition for resources.

Competition between functionally equivalent variants is predicted to lead to the eventual extinction of less favorable forms. Darwin argued against the permanence of species by pointing to fossils of extinct species.

. . . each new variety, and ultimately each new species, is produced and maintained by having some advantage over those with which it comes into competition; and the consequent extinction of less favoured forms almost inevitably follows. (Darwin 1859, p. 323)

The typically faster rate of cultural change compared with biological change potentially makes cultural extinctions much easier to observe. For example, Rivers (1926) detailed how the canoe, pottery, the bow and arrow, and circumcision disappeared from various islands of Oceania. Some cases, such as the canoe, were attributed to the death of all members of the society who had the requisite skills to manufacture the artifact, but some, like circumcision, died out despite the continued survival of its former practitioners. Similar extinction of technology has been documented in Japan, with the loss of the gun and of domesticated animals and wheeled vehicles (Perrin 1979; MacFarlane and Harrison 2000), and in Tasmania, where cultural artifacts such as bone tools and cultural practices such as fishing were lost following isolation from mainland Australian populations (Diamond 1978). There is also at present a very high extinction rate of languages, with Krauss (1992) estimating that half of the 6800 languages worldwide will be extinct within a century if the present rate continues, although estimates as high as 90% are plausible (compared to just 7.4% of mammalian and 2.7% of avian species that are listed as endangered: Krauss 1992).

The latter data illustrate the important point that, as in biological evolution, the scale of competition can vary considerably. At one extreme, whole languages may be in competition, with one replacing the other; at the other end of the scale, individual synonyms for denoting "the same thing" may compete; and in between, as the Darwin quotation above illustrated, there could be competition over the grammar that a linguistic community must share.

Cultural variants are commonly conceived as being passed from brain to brain, in which case the "struggle for existence" can also be construed as overrepresentation in the brain. In one sense, this is simply a reference to the neural counterpart of the functional categories outlined above: it is brains that make the selections between competing cultural variants. However, the properties of the human mind/brain

impose additional competitive pressures on available variants. “Interference effects” on memory indicate competition for finite “brain space.” Interference occurs when recall of previously learned information is disrupted by the learning of new information, with the new information displacing the old. This phenomenon has been shown in countless studies (for a review see Baddeley 1990), although is best illustrated by McGeoch and MacDonald’s (1931) original demonstration. These authors found that recall of a list of previously learned adjectives was greatest when no task was performed during the interval between learning and recall, and decreased when the subjects were given a second list to remember in the interval. Notably, greater interference occurred for synonymous adjectives than for unrelated or nonsense words, suggesting that, as Darwin observed, competition is greatest between similar kinds.

... it is the most closely allied forms—varieties of the same species and species of the same genus or of related genera—which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other. (Darwin 1859, p. 154)

Inheritance

Essential to Darwin’s case was that the favorable variation is preserved along successive generations, or that it is *heritable*: “Any variation which is not inherited is unimportant for us” (p. 75). However, at the same time he admitted that “[t]he laws governing inheritance are quite unknown” (p. 76).

Darwin’s focus on inheritance reflects the fact that biological characters are constrained to being transmitted from parent to offspring, a constraint which does not apply to cultural transmission. Hence, a more appropriate focus for cultural evolution would be between individual “transmission” or “replication,” rather than “inheritance.” Cavalli-Sforza and Feldman (1981) adopted the terms “vertical” to describe transmission of cultural traits from biological parents to their offspring (paralleling biological inheritance), and “horizontal” to describe transmission of traits within a single biological generation (resembling the transmission of pathogens as studied by epidemiologists). Cavalli-Sforza et al. (1982) found evidence of vertical cultural transmission by surveying the opinions and attitudes of Stanford University students and their parents, finding high parent-offspring correlations for religion ($r = 0.71$), politics ($r = 0.61$), superstitious beliefs ($r = 0.49$), and entertainment ($r = 0.44$), traits which are presumably not entirely genetically inherited. Hewlett and Cavalli-Sforza (1986) found even stronger parent-offspring cultural inheritance in the Aka pygmies of central Africa. Seventy-two members of a community of Aka were interviewed to find out from whom they learned a variety of practical skills, such as hunting techniques, tool-making skills, and food preparation. For the 50 traits that were assessed, 80.7% of acquisitions were attributed to parents, 5.2% to other family members, 12.3% to unrelated others, and only 0.9% to independent learning. Similarly, Aunger (2000b) found that among horticulturalists in the Democratic Republic of Congo, children acquire knowledge about food primarily from their parents. Meanwhile, Barry et al. (1976)

showed varying strengths of transmission (“inculcation”) from adults to children of personality traits (toughness, maturity, dutifulness, submission, and sociability) among 182 societies worldwide.

Examples of horizontal cultural transmission include aspects of language acquisition (Tomasello et al. 1993; Pinker 1995), where children acquire the features of a specific language, from phonemes to complex rules of grammar, from other adults and children. Nagell et al. (1993) and Whiten et al. (1996) showed that two- to four year-olds imitate tool use and other manipulative behavior modeled by nonkin, even when individual learning would have been more efficient. Bandura’s social learning experiments (e.g., Bandura et al. 1961) also demonstrate children’s wide-ranging imitative capacity. Finally, the vast literature on the diffusion of innovations reviewed by Rogers (1995) constitutes evidence for the transmission of a wide range of inventions and practices. For example, Ryan and Gross (1943) traced the diffusion of hybrid seed corn use through a community of Iowan farmers, and Coleman et al. (1966) the diffusion of a new antibiotic among doctors.

Although parent-offspring correlations could in principle be generated through individual adaptation to similar environments rather than inheritance, there is considerable evidence for the role of descent in culture. There are many instances when environmental conditions change but culture does not, due to the lag caused by the inheritance process. For example, McGovern (1981) describes the case of a Viking colony in Greenland which failed to relinquish their Scandinavian farming methods and adapt to their new climate. The colony ultimately died out when conditions deteriorated during the Little Ice Age that began in the 13th century, while the Inuit, living under even harsher conditions but using better adapted technology, survived. Cultural inheritance can also be observed in the different responses to the same environmental changes by societies with different cultural histories. For example, LeVine (1966) found that Nigerian tribes categorized as scoring high on a “need for achievement” trait, such as the Ibo, were more successful than tribes low in this trait, such as the Hausa, when Western capitalist societies became more influential.

In other cases, the transmission biases of cultural inheritance may lead to the spread of traits that fulfil a specific function less well than other competing traits. A familiar example is the spread of the VHS format of video recorder at the expense of the supposedly technically superior Beta-max recorder. Arthur (1990) has argued that this was due to a process of positive feedback in which consumers chose not the best product but the most popular product, a possible example of Boyd and Richerson’s (1985) frequency-dependent conformist bias.

The issue of inheritance, however, gives rise to an immediate and common objection to the application of Darwin’s theory of evolution to culture: that culture sometimes exhibits Lamarckian inheritance, or the inheritance of acquired phenotypic characteristics. Indeed, as Orr (1996, pp. 469–470) has pointed out, the mode of inheritance is critical to the relative importance that selection will have relative to other processes.

Clearly cultural inheritance is not *literally* Lamarckian, in-

sofar as acquired cultural knowledge is not transmitted genetically to the next biological offspring (a position held by early writers such as Semon 1921), thus in this sense the application of the term “Lamarckian” does not discredit or disprove cultural evolution. A more common characterization is that people often adopt a cultural trait, modify it, and then transmit that modified trait to someone else. Whether this is regarded as Lamarckian, however, depends on how the replicator-interactor distinction is drawn (Hull 2000), and it is generally unclear whether the term “Lamarckian” can be meaningfully applied outside of its original context. This also does not mean to say that all cultural evolution occurs through the individual modification of transmitted cultural variants, and it is quite possible that the inheritance of some cultural traits resembles Mendelian inheritance, in a strict analogy with biological evolution as it is now understood.

Accumulation of Modifications

It is one thing to demonstrate the transmission of culture from parent to offspring, or child to child, but quite another to demonstrate the long-term accumulation of modifications (Tomasello et al. 1993; Boyd and Richerson 1996) that is characteristic of biological evolution.

If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down. (Darwin 1859, p. 219)

Curiously, the accumulation of material culture was demonstrated shortly after publication of *The Origin*. Pitt-Rivers (1875) used a wide collection of archaeological artifacts to illustrate the gradual changes that occurred for stone tools and spears. Each new specimen can be recognized as a slight modification on the one before, much as the fossil record shows a succession of related biological forms. A detailed quantitative analysis of the cultural selection and drift processes responsible for changes in lithic technology can be found in Cavalli-Sforza and Feldman (1981).

A similar case for the evolution of technology has been made more recently by Basalla (1988), who amassed extensive historical evidence against the commonly held “great leaps by great minds” view of technological change. That is, rather than single “genius” inventors making unprecedented advances, technological change is more accurately seen as a series of successive modifications. For example, the idea of the steam engine did not spontaneously emerge from James Watt’s inventive mind, but was actually a modified version of the existing Newcomen steam engine, with which Watt had had extensive experience, and which in turn was a modification of a previous model, and so on back through history (Basalla 1988).

Mathematics, like technology, has evolved through the accumulation of successive innovations by different individuals in different societies over vast periods of time, with each new innovation paving the way for the next. Wilder (1968) details how even the basic base 10 decimal system took over 4000 years to emerge. Only after the Sumerians began to use written symbols to represent numbers in around 2400 BC could the Babylonians invent the place value system, in which the

position of a digit with respect to the decimal place determines its value. This then allowed the Hindus and Mayans to invent a written symbol for zero, which in turn allowed calculations to be performed. This accumulation of directly related successive inventions proceeded for centuries, with major additions from the Greeks (e.g., geometry), Arabs (e.g., algebra), and Europeans (e.g., calculus), through to present day mathematics.

Adaptation

We see these beautiful co-adaptations. . . in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world. (Darwin 1859, pp. 114–115)

Darwin’s theory aimed to explain the fit between organisms and their environments. Cultural traits, such as clothing or farming practices, also commonly show a functional appropriateness to environmental conditions that has allowed humans to exploit an unprecedented range of habitats across most of the planet. The work of human behavioral ecologists has been to show that many cultural differences act as adaptations to different environmental conditions (e.g., Smith and Winterhalder 1992). By contrast, some evolutionary psychologists argue that cultural diversity is largely the result of a (biologically) evolved universal human cognition responding to different environmental conditions, characterized as “evoked culture” (Cosmides and Tooby 1992, pp. 209–210). Approaches such as these would not be fruitful if there were no correspondence between human cultural practices and ecological variations.

Darwin knew only too well, however, that perfect biological adaptation is not to be expected.

Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature. (Darwin 1859, p. 229)

It is, in fact, the imperfections in organisms that gave Darwin’s theory some of its greatest support. We have already seen evidence that cultural evolution also does not inevitably lead to perfect adaptation, in those cases where cultural inheritance prevents culture from changing in response to environmental flux. Further instances are seen in the existence of cultural vestiges, outlined further below.

Another consideration, when discussing human adaptation, is that cultural traits will not necessarily promote the inclusive fitness of the humans expressing them (Cavalli-Sforza and Feldman 1981). In the same way that parasites can manipulate behavior to their own ends (Moore 2002), cultural variants that exhibit high rates of (nonvertical) transmission (such as smoking) can spread whether or not they enhance fitness and promote adaptation in the individuals who adopt them.

Geographical Distribution

... neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions. (Darwin 1859, p. 344)

Darwin realized that the geographical distribution of species could often better be explained by descent than by environmental conditions per se. To illustrate this he compared species at the same latitude in Australia, Africa, and South America, finding great differences despite similar environments. Is cultural variation similarly predicted by descent?

Hallpike (1986) found that East African and Indo-Iranian cattle pastoralists shared the same ecology and means of subsistence, but differed in their social organization and religious beliefs (the East African societies were structured around age and were monotheistic, whereas the Indo-Iranian societies had no age-based rank structure and were polytheistic). Conversely, Hallpike (1986) also found essentially identical social institutions, religious beliefs, and cultural values between two Ethiopian societies, the Konso and the Borana Galla, despite very different ecologies and means of subsistence. These observations led Hallpike (1986) to conclude that “[r]ather than ecology, it seems that historical relationship ... is a more reliable predictor of social organisation and religion.” (p. 181). Similar observations concerning Melanesian and Polynesian societies had earlier been made by Sahlins (1963).

Further evidence of descent was found in an analysis of the geographical distribution of 47 cultural traits in 277 African societies by Guglielmino et al. (1995). First, it was found that ecology alone could not account for the distribution of any of the traits. Second, family and kinship traits (e.g., the degree of polygamy or how property is inherited by kin) were found to follow the geographic pattern of language, suggesting descent from a common ancestor. Third, sexual division of labor, religious beliefs, sexual behaviors, and house structure were found to cluster around specific geographical areas, suggesting the role of cultural diffusion. This also fits with potential inheritance mechanisms. For example, family and kinship traits tend to be inherited vertically from parents to offspring and therefore change slowly, allowing descent to be more easily observed. A similar study by Hewlett et al. (2002) found that, in 36 African populations, 20 cultural traits (called “semes” rather than “memes” by the authors, to underline their semantic or symbolic aspect), predominantly kinship, family, and political traits, correlated with genetic and/or linguistic similarities, suggesting vertical transmission. Twelve traits, including house building and sex taboos, correlated with geographical proximity, suggesting cultural diffusion. Only four traits correlated with ecological variations.

A second way to test for descent is by constructing cross-cultural phylogenies for cultural traits, as is done in comparative analyses of biological traits. Mace and Pagel (1994) presented a phylogeny for nine Kenyan pastoralist cultures, suggesting that the distribution of camel keeping can be explained most parsimoniously by just two independent adoptions of camel keeping, with all other similarities being due

to diffusion or descent. Gray and Jordan (2000) similarly found that the distribution of 77 Austronesian languages could most parsimoniously be accounted for with a phylogenetic tree branching from a single common ancestor in Taiwan. Barbrook et al. (1998) and Tehrani and Collard (2002), also using the phylogenetic method, found evidence for cultural descent in manuscripts of *The Canterbury Tales* and the decorative patterns of Turkmen textiles respectively.

Darwin also recognized the importance of barriers, such as oceans, to evolutionary change:

... barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions. (Darwin 1859, p. 345)

Just as Darwin used the flora and fauna of island ranges, such as the Galapagos, to illustrate his point, Cavalli-Sforza and Wang (1986) studied differences in the languages of the Caroline Islands in Micronesia. It was found that the degree to which languages shared words declined according to a negative exponential of the distance between those islands, in a manner directly equivalent to biological traits. This suggests that the islands originally shared a common linguistic ancestor and have since diverged, just as species on island ranges have diverged from a common ancestor in relation to distance.

Darwin realized that where migration does not occur, such as on isolated oceanic islands, the resultant paucity of introduced species and loss through drift may result in proportionately fewer species than in mainland areas.

The species of all kinds which inhabit oceanic islands are few in number compared with those on equal continental areas. (Darwin 1859, p. 379)

The same observation for culture has been made for the indigenous population of Tasmania (Diamond 1978). When first contacted by European settlers in 1798, the Tasmanians had been isolated from any other society for 12,000 years. As a result, the Tasmanians had the simplest material culture of any modern humans, lacking agriculture, domesticated animals, bone tools, bows and arrows, and effective clothes, dwellings, or fire technology. The archaeological record even shows a *reduction* in material culture since isolation, with the loss of bone tools and fishing.

Convergent Evolution

Of course, an evolutionary approach does not preclude the independent invention of identical cultural traits, just as it does not preclude the convergent evolution of similar biological traits in distinct lineages. This very point was recognized by Darwin, who noted that

... in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection ... has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor. (Darwin 1859, p. 223)

Darwin himself famously confirmed this when he and Alfred

Russel Wallace independently proposed the theory of natural selection. Better examples might involve more isolated cases, such as the independent inventions of writing by the Sumerians around 3000 BC, the Chinese around 1300 BC, and the Mexican Indians around 600 BC (Diamond 1998). A striking case of convergent evolution in action is the tendency for Mickey Mouse to become increasingly neotenus over successive cartoons (Gould 1980), in precisely the same way, and over the same period, as teddy bears (Hinde and Barden 1985).

Convergent evolution occurs because of similar selection pressures, which in the case of culture might be due to universals of human cognition, such as a preference for neoteny, or the result of other cultural traits in the population (in the case of writing, for example, the trading of material goods necessitated some method of stocktaking, which makes up the vast majority of early manuscripts: Diamond 1998).

Change of Function

Darwin also used morphological evidence to demonstrate descent with modification, specifically when a trait originally used for one function is modified to perform another function or to perform no function at all.

I believe that disuse . . . has led in successive generations to the gradual reduction of various organs, until they have become rudimentary—as in the case of the eyes of animals inhabiting dark caverns, and of the wings of birds inhabiting oceanic islands, which have seldom been forced to take flight, and have ultimately lost the power of flying. (Darwin 1859, p. 431)

With respect to culture, Darwin himself drew a linguistic analogy:

Rudimentary organs may be compared with the letters in a word, still retained in the spelling, but become useless in the pronunciation, but which serve as a clue in seeking for its derivation. (Darwin 1859, p. 432)

As well as vestigial letters, language provides many other instances of vestiges, such as irregular verbs (Pinker 1999). Vestigial features are also common in technological artifacts, especially when new raw materials become available. Indeed, Basalla (1988) notes that such cases are common enough to merit their own label, namely a “skeuomorph,” which is defined as an “element of design or structure that serves little or no purpose in the artifact fashioned from the new material but [which] was essential to the object made from the original material” (Basalla 1988, p. 107). Stone columns, for example, retained the masonry joints of their wooden precursors, despite no longer serving a function. A familiar vestige is the QWERTY keyboard layout, designed in the 19th century to reduce jamming of the hammers in typewriters by making typing as slow as possible (Rogers 1995). This layout has nevertheless been preserved in modern computer keyboards, despite no longer serving its original purpose.

A second feature of morphology that suggests descent is the presence of traits that have adopted new functions.

. . . an organ originally constructed for one purpose

. . . may be converted into one for a wholly different purpose . . . (Darwin 1859, p. 220)

Darwin gave the example of the swimbladder in fish becoming the lung in terrestrial animals. Again, Basalla (1988) notes similar cases for technology, such as Edison’s gramophone, originally used for dictation in offices, being turned into jukeboxes and record players, and the derivation of nuclear energy from the atomic bomb. In fact, Basalla (1988) argues that very few technological innovations were originally designed for their eventual function.

POSSIBLE POINTS OF DEPARTURE

It was noted earlier that there is no reason to expect all cultural phenomena to map to biological evolution. Two points of departure, the inheritance of acquired characteristics and the transmission of information between nonrelatives, have already been discussed. In this final section, we outline three others that have been proposed by various authors.

Convergent Lineages

The only diagram in *The Origin* displays the treelike branching of continually separating lineages, seemingly very different to the cross-fertilization that can occur in cultures. Indeed, this has been seized upon by opponents of cultural evolution.

Biological evolution is a system of constant divergence without subsequent joining of branches. Lineages, once distinct, are separate forever. In human history, transmission across lineages is, perhaps, the major source of cultural change. (Gould 1991, p. 65)

However, to elevate this contrast to a dichotomy would be a distortion of both biology and culture. That cultural evolution occurs predominantly through convergence is an assumption. Examining this empirically in the context of Turkmen textile artifacts, Tehrani and Collard (2002) found that, in fact, divergent phylogenesis accounts for much more of the variation in their data than convergent “ethnogenesis” does. Conversely, certain kinds of convergence of biological lineages occur. Symbionts such as lichen represent the converging of distinct biological lineages, as do the symbioses between protoeukaryotes and the alpha-proteobacteria that went on to become mitochondria, and the cyanobacteria that became chloroplasts (Schwartz and Dayhoff 1978). Genetic material may be transmitted across species boundaries (introgression), and horizontal transmission of genetic material occurs through the action of viruses and plasmids. Doolittle (1999) reviews examples of exchanges across archaeal and bacterial lineages, through the process of lateral gene transfer. In all these respects there is, therefore, a less distinct difference between cultural and biological evolution than implied by Gould’s assertions.

The Nature of Selection

If cultural inheritance is sometimes seen as Lamarckian, as noted above, then this inheritance of acquired variation means that human decision-making processes will determine the adoption and expression of cultural traits, and thus affect

the cultural evolutionary process. The idea that cultural evolution is *directed* towards some specific goal has been used to discredit the theory.

Memes such as the theory of relativity are not the cumulative product of millions of random (undirected) mutations of some original idea, but each brain in the chain of production added huge dollops of value to the product in a non-random way. (Pinker, cited in Dennett 1995, p. 355)

Although Pinker talks of “memes”—Dawkins’ (1976) term for a cultural replicator—the criticism that cultural evolution is “directed,” “intentional,” or “conscious” can equally be made for a mechanism-neutral theory of cultural evolution as presented here.

The case of directed selection is analogous to artificial selection as discussed by Darwin in the first chapter of *The Origin*. Darwin described how human selection for certain naturally existing variants over successive generations has led to the emergence of domestic breeds of plants and animals. However, the reason Darwin drew this analogy between artificial and natural selection was that the process—the selective preservation of favourable variants over time—is identical. Darwin further argued that although the immediate selection of the best individual in any one generation may be “intentional” or “conscious,” this need not imply an intention to create the long-term cumulative change that may eventually result in diverse breeds.

. . . a man who intends keeping pointers naturally tries to get as good dogs as he can, and afterwards breeds from his own best dogs, but he has no wish or expectation of permanently altering the breed. (Darwin 1859, p. 93)

The same applies to cultural selection. Indeed, one might argue that dog breeding *is* an aspect of our culture and that in Darwin’s example artificial selection *is* cultural evolution.

Species and Conceptual Lineages

At first sight, culture does not contain separate species. Hull (1982), however, has developed a potential cultural analogue of the species. Hull (1982) believes that scientific communities (e.g., Darwinians) are a collection of interacting scientists that have in common one or more cultural beliefs (e.g., natural selection, Mendelian genetics) that are expressed in an evolving conceptual system (e.g., Darwinism). What unites them is the notion that they derived their beliefs from preceding Darwinians. We can tell whether a scientist is part of a scientific community in exactly the same way we can tell whether an individual organism is a member of a particular species, by determining whether they have inherited shared information from the same source. To belong within the same conceptual lineage, people must have gained their information from each other, rather than merely holding similar views. It follows that “speciation” events can occur when previously sharing conceptual lineages become isolated.

CONCLUSIONS

Even if it has been shown that culture evolves in a Darwinian manner, why is this of any interest or use? First, at a practical level, researchers can borrow sophisticated techniques originally developed for studying evolutionary change in biology to analyze cultural change. Population dynamic models designed to track changes in gene frequencies are already being used to analyze culture by Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985), as are phylogenetic methods (Mace and Pagel 1994; Gray and Jordan 2000).

Second, on a theoretical level, the synthetic framework provided by evolutionary theory (Mayr 1982) has successfully integrated several disparate disciplines into a coherent research program, evolutionary biology, and has the potential to do the same for the study of culture. Just as Darwin drew upon evidence from zoology, botany, geology, palaeontology, and physiology, this paper has incorporated findings from anthropology, psychology, sociology, linguistics, and history, with the hope of integrating these traditionally separate disciplines. Furthermore, since *The Origin*, the synthetic evolutionary framework has resulted in biology becoming an enormously productive scientific discipline. Conversely, the field of cultural (or social) anthropology emerged at about the same time as Darwin’s writings, but has become preoccupied with self examination (Bloch 2000; Kuper 2000) that questions its status as a progressive research discipline comparable to evolutionary biology or genetics.

Finally, an evolutionary perspective gives focus to future empirical work. Some of the studies cited here were specifically designed to test cultural evolution, but most originated from unrelated theoretical perspectives. By recognizing that our current understanding of culture is comparable to that attained by biology in 1859, perhaps some shortcuts can be taken by learning lessons from the succeeding 150 years of biological research. Cultural equivalents of biological concepts such as character displacement can be tested for (Laland and Brown 2002). Studies of social learning are needed, such as more extensive transmission chain studies, in a manner analogous to Mendel’s transmission studies with pea plants. The cultural “Watson and Crick,” meanwhile, are likely to be neuroscientists, looking at how information is stored in the brain. Cultural information may be stored and transmitted in a different way to genetic information, but this just makes the fact that culture evolves more interesting. In short, the unifying framework of Darwinian evolution has the potential to synthesize the social sciences as it has the natural sciences.

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LITERATURE CITED

Allport, G. W., and L. Postman. 1947. *The psychology of rumor*. Henry Holt, Oxford, U.K.

- Arthur, W. B. 1990. Positive feedbacks in the economy. *Sci. Am.* 262:92–99.
- Aunger, R. 2000a. *Darwinizing culture*. Oxford Univ. Press, Oxford, U.K.
- . 2000b. The life history of culture learning in a face-to-face society. *Ethos* 28:1–38.
- . 2002. *The electric meme*. Free Press, New York.
- Baddeley, A. D. 1990. *Human memory*. Allyn and Bacon, Needham Heights, MA.
- Bandura, A., D. Ross, and S. A. Ross. 1961. Transmission of aggression through imitation of aggressive models. *J. Abnorm. Soc. Psych.* 63:575–582.
- Barbrook, A. C., C. J. Howe, N. Blake, and P. Robinson. 1998. The phylogeny of *The Canterbury Tales*. *Nature* 394:839–839.
- Barry, H. I., L. Josephson, E. Lauer, and C. Marsall. 1976. Traits inculcated in childhood: Cross-cultural codes: 5. *Ethnology* 15: 83–114.
- Bartlett, F. C. 1932. *Remembering*. Macmillan, Oxford, UK.
- Basalla, G. 1988. *The evolution of technology*. Cambridge Univ. Press, Cambridge, U.K.
- Benedict, R. 1934. *Patterns of culture*. Houghton Mifflin, Boston, MA.
- Bloch, M. 2000. A well-disposed social anthropologist's problems with memes. Pp. 189–204 in R. Aunger, ed. *Darwinizing culture*. Oxford Univ. Press, Oxford, U.K.
- Boas, F. 1940. *Race, language and culture*. Macmillan, New York.
- Boyd, R., and P. J. Richerson. 1985. *Culture and the evolutionary process*. Univ. of Chicago Press, Chicago, IL.
- . 1996. Why culture is common, but cultural evolution is rare. *Proc. Brit. Acad.* 88:77–93.
- Buckhout, R. 1974. Eyewitness testimony. *Sci. Am.* 231:23–31.
- Campbell, D. T. 1958. Systematic error on the part of human links in communication systems. *Inform. Control* 1:334–369.
- Cavalli-Sforza, L. L., and M. W. Feldman. 1981. *Cultural transmission and evolution*. Princeton Univ. Press, Princeton, NJ.
- Cavalli-Sforza, L. L., and W. S.-Y. Wang. 1986. Spatial distance and lexical replacement. *Language* 62:38–55.
- Cavalli Sforza, L. L., M. W. Feldman, K. h. Chen, and S. M. Dornbusch. 1982. Theory and observation in cultural transmission. *Science* 218:19–27.
- Coleman, J. S., E. Katz, and H. Menzel. 1966. *Medical innovation: a diffusion study*. Bobbs-Merrill, Indianapolis, IN.
- Cosmides, L., and J. Tooby. 1992. Cognitive adaptations for social exchange. Pp. 163–228 in J. H. Barkow, L. Cosmides and J. Tooby, eds. *The adapted mind*. Oxford Univ. Press, Oxford, U.K.
- Darwin, C. 1859/1968. *The origin of species*. Penguin, London.
- . 1871/2003. *The descent of man*. Gibson Square, London.
- Dawkins, R. 1976. *The selfish gene*. Oxford Univ. Press, Oxford, U.K.
- Dennett, D. 1995. *Darwin's dangerous idea*. Simon & Schuster, New York.
- Diamond, J. 1978. The Tasmanians: the longest isolation, the simplest technology. *Nature* 273:185–186.
- . 1998. *Guns, germs and steel*. Vintage, London.
- Doolittle, W. F. 1999. Phylogenetic classification and the universal tree. *Science* 284:2124–2128.
- Dunbar, K. 1995. How scientists really reason: Scientific reasoning in real-world laboratories. Pp. 365–395 in R. J. Sternberg and J. Davidson, eds. *Mechanisms of insight*. MIT Press, Cambridge, MA.
- Dunbar, K. 1997. How scientists think: Online creativity and conceptual change in science. Pp. 461–493 in T. B. Ward, S. M. Smith and S. Vaid, eds. *Conceptual structures and processes: emergence, discovery, and change*. American Psychological Assn., Washington, DC.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, U.K.
- Garrod, S., and G. Doherty. 1994. Conversation, co-ordination and convention: An empirical investigation of how groups establish linguistic conventions. *Cognition* 53:181–215.
- Geertz, C. 1973. *The interpretation of cultures*. Basic, New York.
- Gould, S. J. 1980. *The panda's thumb*. W. W. Norton, New York.
- . 1991. *Bully for brontosaurus*. W. W. Norton, New York.
- Gray, R. D., and F. M. Jordan. 2000. Language trees support the express-train sequence of Austronesian expansion. *Nature* 405: 1052–1055.
- Grimes, B. F. 2002. *Ethnologue: languages of the world*, 14th ed. Summer Institute of Linguistics, Dallas, TX.
- Guglielmino, C. R., C. Viganotti, B. Hewlett, and L. L. Cavalli-Sforza. 1995. Cultural variation in Africa: role of mechanisms of transmission and adaptation. *Proc. Natl. Acad. Sci. USA* 92: 585–589.
- Hallpike, C. R. 1986. *The principles of social evolution*. Clarendon Press, Oxford, U.K.
- Hewlett, B. S., and L. L. Cavalli-Sforza. 1986. Cultural transmission among Aka pygmies. *Am. Anthropol.* 88:922–934.
- Hewlett, B. S., A. De Silvestri, and C. R. Guglielmino. 2002. Semes and genes in Africa. *Curr. Anthropol.* 43:313–321.
- Hinde, R. A., and L. A. Barden. 1985. The evolution of the teddy bear. *Anim. Behav.* 33:1371–1373.
- Hull, D. L. 1982. The naked meme. Pp. 273–327 in H. C. Plotkin, ed. *Learning, development, and culture: essays in evolutionary epistemology*. John Wiley, New York.
- . 2000. Taking memetics seriously. Pp. 43–68 in R. Aunger, ed. *Darwinizing culture*. Oxford Univ. Press, Oxford, U.K.
- . 2001. *Science and selection*. Cambridge Univ. Press, Cambridge, U.K.
- Hull, D. L., R. E. Langman, and S. S. Glenn. 2001. A general account of selection: biology, immunology, and behavior. *Behav. Brain Sci.* 24:511–573.
- Krauss, M. 1992. The world's languages in crisis. *Language* 68: 1–42.
- Kroeber, A. L. 1916. Zuni potsherds. *Anthropol. Pap. Am. Mus. Nat. Hist.* 18:1–37.
- Kroeber, A. L., and C. Kluckohn. 1952. *Culture. Vantage*, New York.
- Kuper, A. 2000. If memes are the answer, what is the question? Pp. 175–188 in R. Aunger, ed. *Darwinizing culture*. Oxford Univ. Press, Oxford, U.K.
- Laland, K. N., and G. R. Brown. 2002. Sense and nonsense: evolutionary perspectives on human behaviour. Oxford Univ. Press, Oxford, U.K.
- Laland, K. N., J. Odling Smee, and M. W. Feldman. 2000. Niche construction, biological evolution, and cultural change. *Behav. Brain Sci.* 23:131–175.
- Levi-Strauss, C. 1963. *Structural anthropology*. Basic, New York.
- LeVine, R. A. 1966. *Dreams and deeds: achievement motivation in Nigeria*. Chicago Univ. Press, Chicago, IL.
- Mace, R., and M. D. Pagel. 1994. The comparative method in anthropology. *Curr. Anthropol.* 35:549–564.
- MacFarlane, A., and S. Harrison. 2000. Technological evolution and involution: a preliminary comparison of Europe and Japan. Pp. 77–89 in J. Ziman, ed. *Technological innovation as an evolutionary process*. Cambridge Univ. Press, Cambridge, U.K.
- Malthus, T. 1798/1970. *An essay on the principle of population*. Penguin, Harmondsworth, U.K.
- Mayr, E. 1982. *The growth of biological thought*. Harvard Univ. Press, Cambridge, MA.
- McGeoch, J. A., and W. T. McDonald. 1931. Meaningful relation and retroactive inhibition. *Am. J. Psychol.* 43:579–588.
- McGovern, T. H. 1981. The economics of extinction in Norse Greenland. Pp. 404–433 in T. M. L. Wrigley, M. J. Ingram and C. Farmer, eds. *Climate and history*. Cambridge Univ. Press, Cambridge, U.K.
- Mead, M. 1928. *Coming of age in Samoa*. Morrow, New York.
- Moore, J. 2002. *Parasites and the behavior of animals*. Oxford Univ. Press, Oxford, U.K.
- Morgan, L. H. 1877. *Ancient society*. Henry Holt, New York.
- Moshman, D., and M. Geil. 1998. Collaborative reasoning: evidence for collective rationality. *Thinking and Reasoning* 4:231–248.
- Nagell, K., R. S. Olguin, and M. Tomasello. 1993. Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *J. Comp. Psychol.* 107: 174–186.
- O'Brien, M. J., and R. L. Lyman. 2000. *Applying evolutionary archaeology*. Kluwer Academic, New York.

- Orr, H. A. 1996. Dennett's dangerous idea. *Evolution* 50:467–472.
- Perrin, N. 1979. Giving up the gun. G. K. Hall, Boston, MA.
- Pinker, S. 1995. Language acquisition. Pp. 135–182 in L. R. Gleitman and M. Liberman, eds. *Language: an invitation to cognitive science*. Vol. 1. MIT Press, Cambridge, MA.
- Pinker, S. 1997. *How the mind works*. W. W. Norton, New York.
- . 1999. *Words and rules*. Basic Books, New York.
- Pitt-Rivers, L.-G. A. L. 1875. On the evolution of culture. *J. Anthropol. Inst.* 4:293–308.
- Plotkin, H. C. 2002. *The imagined world made real*. Penguin, London.
- Plotkin, H. C., and F. J. Odling Smee. 1981. A multiple-level model of evolution and its implications for sociobiology. *Behav. Brain Sci.* 4:225–268.
- Popper, K. R. 1979. *Objective knowledge: an evolutionary approach*. Clarendon Press, Oxford, U.K.
- Rivers, W. H. R. 1926. *Psychology and ethnology*. Kegan Paul, Trench, Trubner, London.
- Rogers, E. 1995. *The diffusion of innovations*. Free Press, New York.
- Ryan, B., and N. Gross. 1943. The diffusion of hybrid seed corn in two Iowa communities. *Rural Sociol.* 8:15–24.
- Sahlins, M. 1963. Poor man, rich man, big-man, chief: political types in Melanesia and Polynesia. *Comp. Stud. Soc. Hist.* 5: 285–303.
- Schulz Hardt, S., D. Frey, C. Luethgens, and S. Moscovici. 2000. Biased information search in group decision making. *J. Pers. Soc. Psychol.* 78:655–669.
- Schwartz, R. M., and M. O. Dayhoff. 1978. Origins of prokaryotes, eukaryotes, mitochondria, and chloroplasts. *Science* 199: 395–403.
- Semon, R. 1921. *The mneme*. Allen and Unwin, London.
- Shennan, S. 2002. *Genes, memes and human history*. Thames and Hudson, London.
- Simonton, D. K. 1995. Foresight in insight? A Darwinian answer. Pp. 465–494 in R. J. Sternberg, ed. *The nature of insight*. MIT Press, Cambridge, MA.
- Simonton, D. K. 1999. Creativity as blind variation and selective retention: Is the creative process Darwinian? *Psychol. Inq.* 10: 309–328.
- Skinner, B. F. 1981. Selection by consequences. *Science* 213: 501–504.
- Smith, E. A., and B. Winterhalder. 1992. *Evolutionary ecology and human behavior*. Aldine de Gruyter, New York.
- Sperber, D. 2000. Why memes won't do. Pp. 163–174 in R. Auger, ed. *Darwinizing culture*. Oxford Univ. Press, Oxford, U.K.
- Steward, J. 1955. *Theory of culture change*. Univ. of Illinois Press, Urbana, Illinois.
- Tehrani, J. J., and M. Collard. 2002. Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *J. Anthropol. Archaeol.* 21:443–463.
- Tomasello, M., A. C. Kruger, and H. H. Ratner. 1993. Cultural learning. *Behav. Brain Sci.* 16:495–552.
- Tylor, E. B. 1871. *Primitive culture*. John Murray, London.
- van Schaik, C. P., M. Ancrenaz, G. Borgen, B. Galdikas, C. D. Knott, I. Singleton, A. Suzuki, S. S. Utami, and M. Merrill. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102–105.
- Wheeler, M., J. Ziman, and M. A. Boden. 2002. The evolution of cultural entities. *Proc. Brit. Acad. Oxford Univ. Press*, Oxford, U.K.
- Whiten, A., D. M. Custance, J. C. Gomez, P. Teixidor, and K. A. Bard. 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 110:3–14.
- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, and C. Boesch. 1999. Cultures in chimpanzees. *Nature* 399:682–685.
- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, and C. Boesch. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481–1516.
- Wilder, R. L. 1968. *Evolution of mathematical concepts*. Open Univ. Press, Milton Keynes, U.K.

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