Nothing in Human Behavior Makes Sense Except in the Light of Culture: Shared Interests of Social Psychology and Cultural Evolution

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We would hope that at least some readers would already agree with the first part of our chapter's title, paraphrased from the words of evolutionary biologist Theodosius Dobzhansky, who first stated that "nothing in biology makes sense except in the light of evolution" (Dobzhansky 1964, p. 449). In the animal kingdom, human culture is extraordinary. Over the past 100,000 years, we have cumulatively acquired the abilities necessary to colonize every terrestrial ecosystem on Earth, profoundly affect those systems (for better or worse), escape the embrace of Earth's gravity, and alter our own evolutionary trajectory. Culture permeates our lives profoundly. It affects, for example, some of our most basic psychological processes—many thought to be human universals—such as how our eyes take in information (Chua et al. 2005; Kitayama et al. 2003), how we reason about objects in space (Henrich et al. 2010), and how we recall our memories (Ross and Wang 2010). In our view, as evolutionary biologists and psychologists, any account of human evolution that did not include culture as a major factor would be necessarily depauperate.

Our field, though fundamentally interdisciplinary, has become generally known as *cultural evolution,* or *gene–culture coevolution,* and is one of the modern fields of scientific research that aims to understand human behavior in the light of evolution. While sharing common descent from human sociobiology with its sibling fields, evolutionary psychology and human behavioral ecology, cultural evolution differs considerably in its approach, methods, and underlying assumptions. In this chapter, our aim is to convince the reader that the second part of our title is true. We outline the cultural evolutionary approach for a social psychology audience, highlighting where it differs from those of evolutionary psychology and human behavioral ecology, and the developing areas where we believe there is fertile soil for interaction, collaboration, and exchange between social psychology and cultural evolution. For readers interested in learning more about the potential for crossovers between cultural evolution and social psychology, we suggest the article "How cultural evolutionary theory can inform social psychology and vice versa" (Mesoudi 2009) as an excellent next step.

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The Cultural Evolution Approach

The social sciences have occasionally had a tense relationship with the word "evolution," largely because of the way Darwinian ideas have sometimes been applied to human societies (Laland and Brown 2011). It is therefore worth beginning our outline of cultural evolution by drawing some clear lines between what cultural evolution is and what it is not. Firstly, the modern field of cultural evolution has nothing at all to do with the nineteenth-century "progressive" conception of cultural evolution sometimes known as *Spencerian,* after its principal articulator Victorian anthropologist Herbert Spencer. Under this empirically untenable view, cultural evolution progressed up a fixed series of steps on a ladder from barbarism to the height of Victorian civilization, handily justifying the ongoing colonial exploitation of "less evolved" societies. Progressivism, the idea that all life is evolving toward some single, perfect, form, and the notion of the Spencerian "ladder of life," have been utterly rejected by modern evolutionary biology and have nothing to do with the field of cultural evolution as we understand it.

More subtly, cultural evolution can and should be distinguished from memetics. The word "meme" was coined by Dawkins (1976) to describe a neatly packaged particle of culture, directly analogous to a gene. Despite "memes" having a lasting legacy as part of internet culture, the science of memetics is not thriving (Laland and Brown 2011; Mesoudi et al. 2004), perhaps because it was overly committed to an inflexible, gene-inspired model of transmission of discrete units and a meme's eye view of cultural change to match the gene's eye view of genetic evolution espoused by Dawkins. In contrast, cultural evolution has adopted a broader approach with fewer a priori assumptions about how culture is transmitted—indeed, this question is one area where cultural evolution can potentially learn a lot from social psychology.

Perhaps the defining feature of cultural evolution, with respect to other contemporary, evolutionary approaches to human behavior, is its treatment of culture as being influenced by pressures that operate at least partially independently from those acting on genes (Boyd and Richerson 1985; Mesoudi 2011). To make this clear, we need to introduce some terminology to distinguish the various evolutionary processes that cultural evolution researchers recognize as occurring in human societies (see also Fig. 17.1). The first process is regular genetic evolution—changes in gene frequencies within a given population over time; this can result from a number of processes, including natural selection, neutral drift, and others (Endler 1986). Through development, a genotype interacts with the environment to manifest as a phenotype, but developing humans also acquire cultural content—their language, their values, knowledge of their environment, various technologies, and their material inheritance. As culture thus constitutes another heritable system, parallel to the genetic system, then, alongside genetic evolution, there is cultural evolution. Cultural evolution is the change in the cultural content of a given population over time as certain practices or ideas become more or less common, new knowledge is generated, retained, and elaborated, and so forth. Understanding the range of processes by which this happens is a major concern of cultural evolution as a scientific field. Finally, we can distinguish a process by which genes and culture interact with each other, with each (sometimes profoundly) influencing the evolution of the other. This process is called *gene–culture coevolution,* and it is a cornerstone of the modern study of cultural evolution (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981).

Cultural evolution's emphasis on gene–culture coevolution can be seen as a point of departure from sociobiology. Founding sociobiologist E. O. Wilson famously described culture as being held on a genetic leash (Wilson 1978), with the obvious intention to evoke the image of a person walking a dog and to leave no doubt which is in control. While cultural evolutionists would not dispute that the link between the two—the leash—exists, they would dispute that the implied control is unidirectional. Consider, as an analogy, host–parasite coevolution where two species are engaged in an evolutionary arms

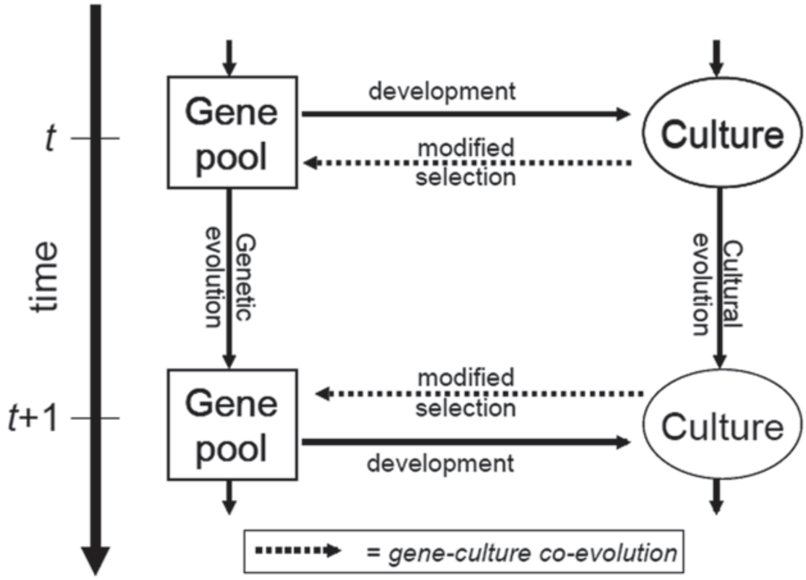

Fig. 17.1 Genetic evolution, cultural evolution, and gene–culture coevolution. Both genes and culture constitute forms of inheritance that are passed down across generations over time. Changes to genes and culture are genetic evolution and cultural evolution, respectively. The influence of genes on culture through development is a classic part of evolutionary theory; however, gene–culture coevolutionary theory extends this model by allowing culture to have an effect upon the gene pool. This occurs by culture modifying the selection acting on genes leading to different future compositions of the gene pool. Several examples of gene–culture coevolution are given in this chapter

race: the parasite evolving to take advantage of the host, the host to repel the parasite. Just as it would be inappropriate to argue that the parasite is controlling the evolution of the host, while ignoring the impact the host is having on the evolution of the parasite, cultural evolution argues that it is inappropriate to focus solely on the influence that genes have on culture, to the extent that the influence of culture on genes is ignored. So it is a central tenet of cultural evolution theory that the relationship between genetic and cultural evolution is mutual in that both forms of inheritance can alter the other's evolution. In support, there is good evidence that culture can alter the rate, dynamics, direction, and steady states of genetic evolution (Boyd and Richerson 1985; Feldman and Cavalli-Sforza 1989; Feldman and Laland 1996; Laland et al. 1995; Laland et al. 2010; Laland 1994; Richerson et al. 2010). A familiar example is the selection of alleles for lactose tolerance following the spread of cultural traits for dairy farming (Tishkoff et al. 2007)—a clear case where cultural evolution subsequently drove genetic evolution. Other examples include the spread of genes for malaria resistance (and in turn sickle cell anemia) following the spread of the cultural practice of yam farming (Durham 1991), and the prevalence of the 230C *thrifty* allele, which impedes the elimination of cholesterol, in Central American populations whose ancestors first domesticated maize. The reliance on maize for dietary proteins was fine when growing conditions were good, but if crops failed, this generated a strong selection for any genetic variants that increased survivability in times of famine, such as the *thrifty* allele. Since then, further cultural evolution has generated a modern nutritional environment rich in fats, with adverse survival consequences for individuals inhibited in their ability to eliminate cholesterol (Hünemeier et al. 2012). Recently, exploration of the human genome has revealed scores of genes that have undergone strong and very recent (i.e., within the past 50,000 years) selection. A good number of these genes have functions likely to have been affected by cultural developments over this period, such as the creation of information-rich environments affecting genes involved in brain development (Laland et al. 2010; Richerson et al. 2010).

Despite viewing culture as partially independent of genes, cultural evolutionists do not deny that there is any genetic influence on culture. Indeed, such a denial would be clearly untenable. Culture could not exist in a species that had not already evolved brains and cognitive systems capable of acquiring culture and effectively passing it on, such as what Csibra and Gergely (2011) call *natural pedagogy*. Csibra and Gergely argue that natural pedagogy is a human adaptation by which infants acquire, and their adult carers pass on, locally relevant cultural information. For a more specific example of a genetic influence on culture, consider cross-cultural work examining variation in color naming systems. Whilst such systems do show tremendous variation across cultures, cultures that have the same number of terms for different colors tend to show consistency across cultures in which colors relate to which terms (Kay et al. 2009; Regier and Kay 2009). Further work found that the corresponding colors can be understood as providing optimal partitioning of color space given a certain number of partitions (i.e., color names) and human visual processing neuro-circuitry (Regier et al. 2007).

In addition to the instances of genetic influences on the content of a culture, however, cultural evolutionists seek to understand the cultural influences on the evolution of behavior. To illustrate this, consider the evolution of language (Mesoudi 2011). One could explain the evolution of language in terms of the genetic loci involved and relevant selection pressures. However, one could also explain it in terms of why a particular individual speaks Urdu instead of French, the cultural evolutionary histories of the languages involved, how Mandarin has changed over time, or why English more closely resembles German than it does Navajo. These different approaches to the question are complementary, not conflicting, and a central theme of cultural evolution is that a full understanding of the evolution of human behavior will involve both types of answers. From this perspective, culture and genes are both simultaneously proximate and ultimate causes of evolution in humans and possibly other animals (Laland et al. 2011; Whitehead 1998) and, at least in the case of humans, have been for at least the past 100,000 years. This perspective contrasts with others from evolutionary psychology and human behavioral ecology that cast culture as a proximate means to a genetically specified end (Barkow et al. 1992; Mace 2000; Tooby and Cosmides 1989).

How Culture Evolves: An Overview of Social Learning Strategies

Cultural evolution aims to understand the mechanisms by which culture evolves. Part of this process involves considering the extent to which cultural evolution operates like genetic evolution and where the major points of departure can be found (e.g., Strimling et al. 2009). For the purposes of this chapter, however, we focus on the role of cultural evolution in the persistence and spread of the culture of *social learning*—the suite of processes by which an individual's learning is influenced by the behavior or products of another individual (Heyes 1994; Hoppitt and Laland 2013). In particular, we focus on the study of social learning strategies (Laland 2004; Rendell et al. 2011) or transmission biases (Boyd and Richerson 1985; Henrich and Mcelreath 2003); evolved learning rules that guide individual reliance on either social or individual/asocial information and so are central to understanding how culture evolves. Taking an evolutionary perspective, it is also important to understand and show the adaptive value of social learning mechanisms and biases—through, for example, showing their positive effects on the effectiveness and accuracy of decision making—that would favor their evolution and, in turn, the evolution of a human psychology capable of supporting culture as we know it today. The result has been the development of a strong theoretical tradition, using mathematical models of evolution to generate predictions that can then be tested empirically.

In addition to the corpus of theoretical work, we also briefly touch on the burgeoning experimental literature within cultural evolution on social learning strategies. This work bears a great deal in common with studies of conformity from social psychology (e.g., Asch 1956; Jenness 1932; Raafat et al. 2009). The differences typically lie in the specific variables considered by the two fields, but also in the general view of social information use. The view of copying others as an adaptive behavior (if used strategically) contrasts with traditional social psychology, which has often viewed conformity in a negative light—an abandonment of individual beliefs (Asch 1952; but see Krueger and Funder 2004, for a more positive overview). Next, we outline some of the wide variety of social learning strategies that have been considered by cultural evolutionists, both theoretically and empirically.

Copy When Uncertain

The existence of a bias to copy when uncertain has been a key assumption of many theoretical models of cultural evolution. Boyd and Richerson (1988) constructed a simple mathematical model to demonstrate the utility of this bias, which we describe in conceptual terms here to provide an example of the kind of theoretical work that typically underpins this kind of cultural evolution research. The model simulated an environment inhabited by individuals who could earn payoffs depending on the match between their behavior and the state of the environment, and these payoffs determined their likelihood of reproducing. Individuals died periodically and were replaced with a new generation of offspring such that selection—and hence evolution—could take place. The environment changed between two possible states (which Boyd & Richerson called *habitat 1* and *habitat 2*). Individuals in the model had to determine which habitat they were in at any given time in order to perform the appropriate behavior, and those that got it right received higher payoffs. Individuals were given both imperfect personal information (information that they acquired independently of other individuals) about the habitat and the opportunity to learn from a member of the previous generation. Boyd and Richerson then explored what mix of individual and social learning would be favored by natural selection under varying degrees of imperfection in personal information and rates of switching between the habitat states. They found that when an individual's personal information was unsatisfactory (i.e., it left them uncertain), individuals should adopt the decisions of others. Although uncertainty may be generated through an unsuccessful attempt at collecting personal information (i.e., one that results in insufficient evidence to make a decision), uncertainty in real life could also result from poor performance on the same task on previous occasions or on related tasks. Thus, an individual who makes a poor mating decision may come to doubt their ability to identify high-quality mates and so be more inclined to copy the decisions of others when required to make another decision (i.e., a reduction in confidence). There is strong empirical evidence to support such a role for uncertainty in adult humans. When tested using both a simulated foraging task and a mental rotation task, individuals who expressed higher levels of uncertainty in their individual decision making were more likely to adopt the decisions of others (Morgan et al. 2011). Furthermore, the same study documented that individual certainty correlated with whether or not individuals were correct. Accordingly, this social learning strategy can be seen to improve the accuracy of individual decision making, as it guided individuals who were actually likely to be incorrect to copy the correct decisions of other individuals (Morgan et al. 2011).

Payoff- and Prestige-Biased Social Learning

Payoff-biased social learning refers to any form of selective social learning where an individual's social learning is guided by the payoffs to themselves or to other individuals (Kendal et al. 2009; Schlag 1998). Here, "payoff" is shorthand for what an individual gets as a result of their choice of behavior in a given context (e.g., food, safety).

Theoretical analyses have indicated that strategies where an individual's use of social information is guided by their own payoff ("proportional reservation"), the payoff to demonstrators ("proportional observation"), or the difference between the two ("proportional imitation") can all be highly effective in particular contexts (Schlag 1998, 1999). There is also good empirical evidence that humans are sensitive to such information and do use it to direct social learning (Apesteguia et al. 2007; Caldwell and Millen 2008; Mesoudi and O'Brien 2008; Mesoudi 2008; Pike et al. 2010). For example, in a computer-based tool-design task, in which participants could alter four different parameters before receiving feedback on the efficacy of their design, participants were found to selectively copy the design of the individual who was performing the best in the group (Mesoudi and O'Brien 2008). Similarly, in a pitch-discrimination task, individuals were observed to copy a potential demonstrator in relation to the latter's performance ranking, but were particularly influenced when they themselves were performing poorly (Morgan et al. 2011).

"Prestige" has been defined as noncoerced within-group human status asymmetry, and the idea that prestige might influence social learning biases has been studied by cultural evolutionists (Henrich and Gil-White 2001). The "prestige-bias" hypothesis holds that because specific payoffs are often hard to obtain, individuals have a general tendency to copy the decisions of those who have been successful—though not necessarily in the relevant domain—and who are afforded associated prestige. Prestige is distinguished from dominance on the basis that prestige is noncoercive, whereas dominance is coercive (Henrich and Gil-White 2001), and this mirrors the distinction between hedonic and agonistic social hierarchies observed in nonhuman primates (Barkow et al. 2012). The copying of generally successful individuals may be easier to implement than relying on knowledge of the specific payoffs associated with particular decisions and so could be a widespread phenomenon. For example, a handful of Fijian *yalewa vuku,* or wise women, had a disproportionate impact on the cultural evolution of the population, largely through the high general prestige in which they were held (Henrich and Henrich 2010).

Conformist Transmission

Although this learning rule is sometimes referred to as *conformity,* we shall use the term *conformist transmission* here, because what cultural evolutionists refer to as conformist transmission differs from the term "conformity" as used in a social psychology context. In social psychology, conformity typically means "yielding to group pressure" (Crutchfield 1955), and there is a long history in social psychology of studying how people will change their expressed views in apparent attempts to "fit in" to a group context. In cultural evolution, conformist transmission is a learning rule by which individuals are *disproportionately* likely to adopt the decisions of majorities at the expense of minorities (Boyd and Richerson 1985; Morgan and Laland 2012). Consider the case of a naïve individual choosing between options A and B who is presented with seven informants advocating option A and three informants advocating option B. In this case, the majority amongst the informants makes up 70 % of the group. If the naïve individual were to use conformist transmission (we shall henceforth refer to such individuals as "conformists," and when we do so, we mean in the cultural evolution sense) they would have a *greater* than 70 % chance of choosing option A. An individual with a 70 % chance of adopting the behavior of the majority would be using unbiased transmission (behaviorally indistinguishable from picking an individual at random from the environment and copying them) and would *not* be said to be conformist even though they might have altered their behavior to match the majority.

Conformist transmission is of particular interest to cultural evolutionists as it results in popular views coming to dominate the population and so can have considerable population-level consequences (Boyd and Richerson 1985). This interest stems originally from a theoretical model in which groups of individuals occupied a spatially variable environment. The model found that if an individual moved from its existing group to a new group in an unfamiliar part of the environment, conformist transmission was a very effective means by which the migrant individual could accurately hone in on locally adaptive behavior (Boyd and Richerson 1985), so effective in fact that the model predicted that anytime social learning itself would be favored, so would conformist transmission. More recent theory (Nakahashi et al. 2012) has added to this, finding that spatial variation, errors in learning, and the number of options between which individuals choose, all favor the evolution of conformist transmission. This is because conformist transmission uses the decisions of a large group of individuals to identify potentially weak signals across multiple decisions. Both errors in learning and a larger number of options to choose between make each individual's decision less reliable, but when offered to a group of individuals the correct option will still most likely be the most prevalent decision in the population and so conformist transmission will be a successful strategy.

Interest in conformist transmission has persisted because of theoretical studies that suggest it offers a framework to help understand the comparatively extraordinary levels of cooperation seen in human societies (e.g., Boyd et al. 2011). To sketch the argument, conformist transmission sharpens and maintains distinctions between groups. This in theory can produce the conditions for what Boyd and Richerson have called *cultural group selection* to operate. Whereas genetic group selection breaks down when individuals move between groups and bring their behavioral genes with them, thus allowing uncooperative behavior to take advantage of a cooperative group, in a cultural context, with conformist transmission, immigrants to the group change their behavioral culture to match the group they are moving into.

On the other hand, a potential pitfall of conformist transmission is that favoring the already dominant view can be an obstacle to the spread of new information or innovations (Eriksson et al. 2007). As even very good ideas must initially start at very low frequencies, the prevalence of conformist transmission can act to block their spread. This is particularly problematic in temporally variable environments where the discovery and spread of new behaviors is essential to success (Eriksson et al. 2007; Kandler and Laland 2013; Nakahashi et al. 2012). Because weak conformist transmission hinders the spread of innovations less than strong conformist transmission, Kandler and Laland (2013) argue that conformist transmission is likely to be weak. Thus, the extent to which conformist transmission is expected to be adaptive is contested, but the theoretical models lead us to expect a broad range of conditions under which conformity will be utilized.

Given the predictions made by evolutionary models concerning the success of conformist transmission, several experiments on adult human participants have been carried out to distinguish a disproportionate tendency to adopt the majority decision from other rules that lack the same population level consequences. Efferson et al. (2008) carried out an experiment in which, over many rounds, participants repeatedly chose between two "technologies." The participants knew the alternative technologies had different expected payoffs, but did not know which was better. Although conformist transmission was found to be an effective strategy in this context, Efferson et al. (2008) found that only some participants used it. They characterize this difference in terms of a mixed population of conformists and "mavericks," the latter being individuals who typically prefer to rely on their own information. However, the data imply that individuals vary continuously in the extent to which they utilize social information and/or are conformist, such that a dichotomy would not be an appropriate way to interpret the data (Efferson et al. 2008). In a similar experiment, Mcelreath et al. (2005) also used a simple two-choice task, where participants were required to choose between planting two types of virtual crop. Although participants did again show some evidence of a conformist tendency, they were better characterized by unbiased transmission when the environment was stable across time, a result at odds with theory that suggests environmental stability over time favors conformist transmission (Nakahashi et al. 2012). More recent empirical work found that although the response of adult participants to consensus alone was consistent with conformist transmission, the additional effects of other variables, such as individual confidence and group size, acted to mask this effect at the behavioral level (Morgan et al. 2011). The data and the theory concerning conformist transmission are therefore complex, but there is good evidence to think that it is a feature of at least some human social learning.

Age- and Kin-Biased Social Learning

Another bias that could guide social learning is age. Such a bias is likely to be adaptive to the extent that older individuals have had more time to acquire valuable information, but also have demonstrated, through their survival, that they have not been overly reliant on poor information. Thus, one might surmise that any remaining old individuals are more likely than young individuals to be in the possession of high-quality information. There is also evidence for such a bias in humans. For example, in the case of the Fijian population, although *yalewa vuku* (i.e., wise women) were particularly influential, to a lesser extent, so were *qase*—nonspecific elders (Henrich and Henrich 2010). In the traditional societies of the Solomon Islands, elders are valuable sources of information on the edibility of various plants, which can prove crucial when the gardens that are the usual source of food fail (Diamond 1997).

Individuals may also show a bias to copy the decisions of kin. There are at least three reasons as to why this is likely adaptive and hence favored by selection. First, in a structured population, which most are, related individuals typically live nearer to each other than the average unrelated individual does and so the information they possess may be of greater relevance than that offered by unrelated individuals. Second, kin are readily available, accessible, and tolerant to close proximity. Third, due to the accrual of indirect fitness, individuals may be more likely to donate information to their kin, either by making such information more readily available, or by directly teaching them (Fogarty et al. 2011). In the Fijian population, in addition to the influence of *yalewa vuku* and *qase* (wise women and elders), food taboos were identified as primarily learned from mothers, grandmothers, or mothers-in-law (Henrich and Henrich 2010). Similarly, craftsmen of the New Guinean Langda people report passing on the prized skill of stone-adze construction "only to close relatives" (Stout 2002, p. 702). In the case of vertical transmission from parents to offspring, however, it is possible that such a copying bias may not be the result of a psychological mechanism, but instead the result of behavioral practices concerning childrearing. In species with parental care of offspring, including humans, it is typically the parents with whom offspring interact most frequently. Thus, even unbiased social learning might be expected to lead to a greater cultural transmission between parent–offspring pairs than between other members of the population.

Random Copying

Of course, cultural transmission does not necessarily have to be biased. A number of studies have highlighted areas of human culture where the copying decisions of individuals produce no net effect on the population distribution, consistent with a model in which individuals copy at random. Such models fit observed data for the popularity of baby names, music, and dog breeds very well (Bentley et al. 2007). In spite of all of the thought and care that individual parents put into choosing their child's name, parents, as a group, behave in a manner that is identical to a population of parents who choose names at random—in both cases, new parents are more likely to adopt baby names they have been exposed to more often. Such an approach has also illustrated the interactions between independent decisions and social transmission in the spread of interest in disease pandemics, such as H5N1 and bird flu virus (Bentley et al. 2007). These studies also reveal how the results of apparently random copying can be perturbed by the influence of key events, such as a spike in popularity of the Dalmatian dog breed observed after the rerelease of the film *101 Dalmatians* (Bentley et al. 2007). However, a recently developed model investigating the social transmission of neolithic German pottery designs, which previously had been considered an example of random copying (Bentley et al. 2004), was able to detect collective forces guiding decision making (Kandler and Shennan 2013). This raises the possibility that more sensitive models may yet find trends guiding other decisions currently considered random at the population level.

Maladaptive Culture

Culture has typically been viewed as an evolved adaptation, and thus to be highly beneficial to individuals. However, the only requirement is that culture be adaptive as a whole; many specific cultural traits may in fact be maladaptive to the individuals who possess them. Accordingly, the study of the appearance, spread, and persistence of maladaptive cultural practices has been another focus of cultural evolution. For example, Tanaka et al. (2009) modeled the evolution of maladaptive practices for treating disease. They found that the inefficacy of poor treatments, paradoxically, allowed them to spread. Individuals who use effective treatments are likely to seek treatment less frequently than individuals who use ineffective or maladaptive treatments (because effective treatments will cure problems whilst ineffective treatments allow them to persist, causing the individual to seek further bouts of treatment). Provided the ineffective treatments do not immediately lead to the death of their users, undecided individuals will observe the use of ineffective treatments more often than they observe the use of effective treatments. If the relative efficacy of treatments is not obvious then the maladaptive medical treatments may spread throughout the population at the expense of superior ones. As described above, the prevalence of conformist transmission can also lead to maladaptive consequences because it inhibits the spread of beneficial innovations (Eriksson et al. 2007; Morgan and Laland 2012). The view of culture as a blend of adaptive and maladaptive traits evolving both independently and in interaction with genetic evolution can be contrasted with the other subfields studying human evolution and behavior. For example, in evolutionary psychology, the role of what is termed *epidemiological culture*—the transmitted culture studied most often by cultural evolutionists—is de-emphasized. Instead, evolutionary psychology conceptualizes human minds as possessing *evoked culture,* analogous to a jukebox, where "evoked" behavior is selected from a library of genetically determined alternatives according to inputs from the environment in which the individual finds themselves. In this case, culture is generally expected to be adaptive as long as the environment is not too different from that in which the library evolved (Brown et al. 2011). In human behavioral ecology, culture is viewed as a proximate mechanism; a highly flexible strategy allowing individuals to tailor behavioral responses in order to ultimately maximize fitness in any environment, but with little creativity beyond the complex matching of behavior to environment (Brown et al. 2011). Accordingly, it suggests that the vast majority of culture should be adaptive. Both approaches struggle to accommodate empirical phenomena such as the demographic transition (the switch from having many children with low life expectancy, to fewer children with greater life expectancy) seen in populations across the world, that does not increase long-term fitness and seems to result from the prioritization of socioeconomic competitiveness over fitness (Goodman et al. 2012). Cultural evolution, in contrast, expects culture to contain a mix of adaptive and maladaptive behavior, and as a result the demographic transition can more easily be modeled within its assumptions (Kolk et al. 2014).

Comparative Work

A feature of many of the social learning strategies considered by cultural evolutionists is that their adaptive value is likely to be very general. For example, copying other individuals when you are uncertain is likely to be an effective strategy across many different contexts and even for multiple species. Accordingly, there has been much work investigating social learning strategies in nonhuman animals (e.g., Kendal et al. 2005). Such work can help our understanding of the evolution of social learning and culture in two ways. First, it can help piece together the evolutionary history of certain human traits. Studies of nonhuman primates may be particularly informative in this regard. Second, comparative work can give insights into the conditions that favor reliance on social information or the evolution of particular social learning strategies. In this case, a much wider range of species can be fruitfully studied. For example, a bias to copy when uncertain has received empirical support across a variety of nonhuman taxa, including rats (Galef et al. 2008), gerbils (Forkman 1991), capuchin monkeys (Visalberghi and Fragaszy 1995), ants (Grüter et al. 2011), and nine-spined sticklebacks (Kendal et al. 2005). There is also evidence for a bias to copy older individuals in guppies (Amlacher and Dugatkin 2005) where female mating preferences were influenced to a greater degree by the equivalent decisions of older conspecific females than they were by the decisions of younger conspecific females. Other studies have found that young birds (Biondi et al. 2010) and chimpanzees (Biro et al. 2003; Biro et al. 2006) are more reliant on social information than older conspecifics. More recently, vervet monkeys have been observed to adopt group norms when choosing food, going with the group even when the choice contradicts previously acquired preferences (van de Waal et al. 2013). Understanding the functional consequences of social learning across species helps us understand the generality of conditions under which various strategies may or may not be adaptive and feeds into an understanding of the evolution of human culture, even while debates continue about the relationship between cultural processes in humans and nonhumans (Laland and Galef 2009).

Integrating Social Psychology and Cultural Evolution

Cultural evolution has a strong theoretical tradition of mathematical modeling, but has only relatively recently, compared to social psychology, begun experimentally exploring how culture is passed from individual to individual. It is here that we see the clearest opportunities for the two fields to inform each other in developing the science of cultural evolution. Mathematical models of cultural transmission have to incorporate complex cognitive processes and the array of environmental and social factors that potentially affect them. If a model is to be tractable, that is, suitable for analyzing to understand the processes it is designed to represent, then these intricacies must be dramatically simplified. This simplification can often be in tension with the complexities of psychological findings on how people actually acquire cultural information (Barkow et al. 2012). Current models do not, for example, reflect the possibility that different informational domains will favor different learning biases, and that these biases are likely to change over the life-course. Empirical evidence for this possibility exists, however. For example, among the many social learning biases observed in young children (referred to as "trust" by developmental psychologists) are a bias to trust familiar caregivers over strangers and a bias to trust individuals who have shown themselves to be reliable informants over those exposed as unreliable. Whilst 3-year-olds prioritize familiarity over reliability, this changes in 4-year-olds who favor reliability (Corriveau and Harris 2009; Harris 2012).

A second complexity not covered by extant models is membership of individuals to different groups within the same population. The likelihood that an adult will adopt the behavior of a group depends on how strongly they identify with that group (Louis et al. 2007), and individuals might actively reject the influence of a majority if it conflicts with information already learned from a more salient social group (Smith and Louis 2008). Similar behavior has been observed in young children where they preferentially trust an adult informant with the local accent over an informant with a foreign accent (Kinzler et al. 2011). Given that the processes underlying group identification already have a rich literature devoted to them (e.g., Tajfel 1982), this could be a fertile area for integration between cultural evolution and social psychology.

One recent study (Cross et al. 2013; under review) attempted to integrate cultural evolution and social psychology approaches to the question of sex differences in conformity. The finding that women are more susceptible than men to conform to a majority is well demonstrated within social psychology (Bond and Smith 1996), yet was not explicitly addressed within the cultural evolution approach. As noted above, social learning rules are typically assumed to be used similarly by all members of a population, and both men and women did indeed adopt a copy-when-uncertain rule in two different experimental tasks. However, gender stereotypes—well studied in social psychology—about performance on these tasks affected women's confidence independently of any effect of accuracy. That is, women consistently underestimated their ability to perform the task when it was stereotypically "masculine." Using the copy-when-uncertain strategy, they therefore copied the majority more often than men. Conversely, where gender stereotypes about a task were absent, uncertainty related to accuracy similarly for both sexes, such that the copy-when-uncertain rule produced similar levels of copying for men and women.

Incorporating experimental findings from social psychology into general models of cultural transmission is a major challenge for cultural evolution researchers. The modelers are mindful of the likelihood of informational and cognitive intricacy, and work on these kinds of complexities has increased in recent years (Rendell et al. 2011). Nonetheless, we still do not know how general current mathematical models of cultural transmission are. Each model might only be valid for specific domains of information in specific circumstances. A model that works for language transmission and change, for example, may have quite different assumptions, structure, and evolutionary outcomes than a model of religious learning, or cultural transmission of diet, or changes in fashion mediated by mass media. The implication is that we need increased collaboration between social psychologists who study social learning and cultural transmission, and the theoreticians of cultural evolution (Mesoudi 2009), so that model builders are challenged to incorporate the complexities found by cognitive scientists. Culture, after all, can only be the cumulative result of cognitive processes occurring in the brains of a population of individuals, so for a complete understanding of how it evolves and coevolves, a concurrent understanding of human psychology is essential.

Another area where cultural evolution could benefit from collaboration with social psychology is in the details of what cultural transmission involves. Cultural evolutionary models, for simplicity's sake, typically model cultural transmission the same way population geneticists model genetic transmission—the clean and instantaneous transmission of a trait from one individual to another (give or take some chance mutation or learning error). Yet, culture clearly does not "transmit" like DNA or electrons (Strimling et al. 2009); there is no material continuity between the brains in the way that there is when DNA enters gametes and then zygotes. Instead, culture is a melange of information, various types of which may or may not be processed and acquired in different ways. What looks like cultural transmission at the macro level is built at the individual level upon cultural editing and reconstruction processes in the brain that we still understand little about. This should not be taken as a reason to dismiss cultural evolution theory out of hand. Just as the modern evolutionary synthesis was developed using models based on a conceptual understanding of genes before their chemical basis was identified, the success of cultural evolutionary models in predicting behavior is proof that they have been fruitful tools. By implication, there is tremendous opportunity for collaboration between cultural evolution and social psychology as the impact of a proper understanding of cultural transmission on our understanding of culture could be as profound as the impact of the discovery of DNA on evolutionary biology.

Conclusion

Social psychologists continue to generate significant insights into how human behavior is affected by the behavior of others, describing how conformity works, understanding how human cultural acquisition is biased, how it can be fooled, what contexts these biases are sensitive to, and so on. What cultural evolution has to offer is a conceptual and theoretical framework within which to understand these features of human psychology as the product of a complex and ongoing coevolutionary dynamic between genes and culture. We believe that increased interactions between these fields will result in further progress in generating hypotheses that encompass evolutionary timescales and ultimately help to explain those features of modern human behavior that social psychologists are in the process of revealing.

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