

How Cultural Evolutionary Theory Can Inform Social Psychology and Vice Versa

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Cultural evolutionary theory is an interdisciplinary field in which human culture is viewed as a Darwinian process of variation, competition, and inheritance, and the tools, methods, and theories developed by evolutionary biologists to study genetic evolution are adapted to study cultural change. It is argued here that an integration of the theories and findings of mainstream social psychology and of cultural evolutionary theory can be mutually beneficial. Social psychology provides cultural evolution with a set of empirically verified microevolutionary cultural processes, such as conformity, model-based biases, and content biases, that are responsible for specific patterns of cultural change. Cultural evolutionary theory provides social psychology with ultimate explanations for, and an understanding of the population-level consequences of, many social psychological phenomena, such as social learning, conformity, social comparison, and intergroup processes, as well as linking social psychology with other social science disciplines such as cultural anthropology, archaeology, and sociology.

Keywords: conformity, cultural evolution, cultural transmission, intergroup processes, social learning

Over the past few years, an interdisciplinary field of study has emerged that is centered around the theory of Darwinian cultural evolution (Aunger, 2000a; Boyd & Richerson, 2005; Durham, 1991; Henrich & McElreath, 2003; Laland, Kumm, & Feldman, 1995; Lipo, O'Brien, Collard, & Shennan, 2006; Mesoudi, Whiten, & Laland, 2006; O'Brien & Lyman, 2002; Pagel & Mace, 2004; Richerson & Boyd, 2005; Shennan, 2002). These researchers argue that human culture—the body of information that is passed from individual to individual via social learning processes such as imitation, teaching, and language—evolves in a manner that can be described as Darwinian and that thus resembles (but is not identical to) biological/genetic evolution. Consequently, many of the same concepts, methods, theories, and tools that have been developed by biologists to study biological evolution can, suitably modified, be used to study cultural evolution. Although social psychological concepts and findings already play a central role in many cultural evolutionary theories and models, these theories and models tend to be constructed by anthropologists (e.g., Durham, 1991; Henrich & McElreath, 2003; Richerson & Boyd, 2005), archaeologists (e.g., O'Brien & Lyman, 2002; Shennan, 2002), and biologists (e.g., Cavalli-Sforza & Feldman, 1981; Laland et al., 1995) and have received little attention from social psychologists, or indeed psychologists in general. This lack of interest is surprising given that much of this research was inspired and influenced by the work of renowned psychologist and former American Psychological Association President Donald T. Campbell (1960, 1965, 1975), and as Campbell pointed out, there is considerable overlap in the subject matter of these two fields. My aim here is to

show how a closer integration of research in social psychology and research in cultural evolution can be mutually beneficial. Social psychological experiments and theories provide details of the microevolutionary mechanisms through which cultural evolution operates, while cultural evolutionary theory provides details regarding the origins and population-level consequences of many social psychological phenomena. Before providing details of the specific research areas in which this mutual benefit can be observed, the following section outlines contemporary cultural evolutionary theory for a social psychology audience who may be unfamiliar with this work.

An Overview of Cultural Evolutionary Theory

Culture is a notoriously elusive concept that has been defined in many different ways by many different scholars (Baldwin, Faulkner, Hecht, & Lindsley, 2006; Kroeber & Kluckhohn, 1952). Cultural evolutionary theorists tend to adopt a definition of culture similar to the following: “Culture is information capable of affecting individuals’ behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission” (Richerson & Boyd, 2005, p. 5). It is hopefully apparent that this definition of culture as socially transmitted information makes it highly relevant to the traditional subjects of psychological research, and social psychological research in particular. The focus on information incorporates concepts relating to (social) cognition such as attitudes, beliefs, values, practices, opinions, schema, and representations; that this information affects behavior justifies the measurement and manipulation of behavior using psychology experiments; and the requirement that this information must be socially transmitted emphasizes its relevance to social psychology in particular. Culturally acquired information can be contrasted with information that is acquired genetically, which would be the preserve of evolutionary psychology and

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behavioral genetics, and information that individuals acquire through purely individual learning with no social influence, which would be the preserve of cognitive psychology and other more individual-oriented branches of psychology.¹

Cultural evolution is the idea that this body of socially transmitted information changes in a manner that is broadly comparable to the manner in which biological information changes, such that they are both examples of Darwinian evolution. It is helpful to specify exactly what is meant by Darwinian evolution. One hundred and fifty years ago, Charles Darwin (1859/1968) laid out three basic principles that constituted his theory of biological evolution:

1. Variation: Individuals within a species vary in their characteristics. For example, finches may vary in the size of their beaks, with some finches having larger beaks than others.
2. Competition: Resources such as food, nesting space, or mates are limited, and population size increases geometrically, such that not all individuals in each generation will be able to survive and reproduce. There may also be differential fitness, such that the chances of survival and reproduction depend to some extent on the aforementioned variation. For example, if finches with larger beaks can open a wider range of seeds, then larger beaked finches will be more likely to survive and reproduce than smaller beaked finches.
3. Inheritance: Parents produce offspring that resemble them in their characteristics to a greater extent than two randomly selected members of the population. For example, larger beaked finches are more likely to produce larger beaked offspring.

Over successive generations, this variation–competition–inheritance cycle results in evolutionary change. For example, if larger beaked finches continue to have a reproductive advantage over smaller beaked finches, then the mean beak size in this population will increase over successive generations. Indeed, this very trend was documented in Darwin’s finches on the Galapagos Islands during the 1970s (Grant, 1986).

Although typically applied to biological change, these Darwinian principles can be formulated in purely abstract terms (Endler, 1986; Lewontin, 1970), such that any body of information that exhibits variation, competition, and inheritance can be said to evolve in a Darwinian manner. This has led many researchers (e.g., Campbell, 1975; Dennett, 1995; Mesoudi, Whiten, & Laland, 2004; Plotkin, 1995) to argue that human culture constitutes such an evolutionary system, given that it too possesses the necessary Darwinian properties:

1. Variation: Cultural information varies within and between groups of people. Different people hold different beliefs, attitudes, and values; they use different words; they exhibit different skills; and so on.
2. Competition: Cognitive resources (e.g., attention or memory) are limited, such that not all beliefs, attitudes, words, skills, and so on are successfully learned, remem-

bered, and/or passed on to others via social learning. There may also be differential fitness, such that some cultural variants are more likely to be transmitted than others and some cultural models (e.g., parents, celebrities) are more likely to be copied than others.

3. Inheritance: Individuals acquire their beliefs, skills, values, and so on from models via social learning, such that there is a correlation in cultural variation between learner(s) and model(s).

It can be shown that there is good empirical evidence that human culture exhibits these three Darwinian properties (variation, competition, and inheritance) as Darwin himself presented in *The Origin of Species* for biological evolution (Mesoudi et al., 2004). Indeed, I suspect that most social psychologists would find these basic claims—that people vary in their culturally acquired beliefs, knowledge, and so on; that some cultural variants and models are more likely to be copied than others; and that cultural variation is transmitted via social learning—to be quite uncontroversial.

It is important to stress that while both cultural and biological evolution are Darwinian processes in the abstract sense outlined above, many of the details of cultural evolution may be quite different from the details of biological evolution. These details concern the processes that cause new variation to arise, the processes that cause some variants to be selected over others, and the mechanisms by which variation is inherited. In the years since the publication of *The Origin of Species*, evolutionary biologists have

¹ Note that the definition of culture cited here is probably broader than, but encompasses, definitions of culture that have been adopted by many social and/or cultural psychologists. For example, cross-cultural psychologists tend to define culture in terms of large-scale differences between entire nations or societies, such as East–West differences in collectivism–individualism (e.g., Markus & Kitayama, 1991; Nisbett, Peng, Choi, & Norenzayan, 2001). Such national differences would be covered by the broader definition adopted here (unless such differences were shown to be genetically rather than culturally transmitted), but the latter would also include cultural change that occurs within single nations, societies, or groups. Cultural psychologists (e.g., Shweder, 1990) tend to emphasize the symbolic, intentional aspects of culture; this would be included under the category of socially transmitted information, although again the quoted definition would also include nonsymbolic, nonintentional aspects of culture. Most cultural evolution researchers take the position that a broad definition of culture that may later be narrowed by empirical research is strategically better than a narrow definition that excludes a priori potentially productive research topics. For example, defining culture as symbolic and intentional may discourage the study of cultural processes in certain nonhuman species that lack such capacities, potentially excluding useful insights to be gained from comparative psychology. On the other hand, cultural anthropologists might argue that defining culture as semantic information is too restrictive because it excludes behavior and material artifacts. As pointed out by Cronk (1999), however, including behavior and artifacts in the definition of culture is theoretically problematic because human behavior and artifacts are the phenomena that researchers are trying to explain: one cannot define culture as behavior and then explain behavior in terms of culture. To avoid this circularity, most cultural evolution researchers treat behavior and artifacts as the expression or product of culturally transmitted information. This is analogous to the biological distinction between genetic information (represented in DNA) and the expression of that information in phenotypes and extended phenotypes.

devoted their efforts to filling in these details with respect to biological evolution (Futuyma, 1998). For example, new genetic variation is now known to arise through mutation and recombination that is blind with respect to subsequent selection; a range of selective processes have been identified that determine which genetic variants get preserved, such as directional selection, stabilizing selection, disruptive selection, and sexual selection; and inheritance takes the form of the high-fidelity replication of discrete units of information called genes. Another important advance since *The Origin of Species* has been the recognition that genetic variation may change not only due to selection but also due to nonselective processes such as founder effects and sampling bias, collectively known as genetic drift (Kimura, 1983).

Although cultural evolution may exhibit processes that are similar to those listed in the previous paragraph, it is not necessary that it do so to constitute a Darwinian evolutionary system. All that is required is that there is some mechanism that generates new cultural variation, that there is some set of processes that affect cultural variants' differential chances of persistence, and that there are some mechanisms that allow cultural variation to be transmitted. Whether these are similar to the biological case (e.g., whether new cultural variation is random, or whether cultural transmission involves the high-fidelity replication of discrete units of cultural information) is an open question subject to empirical investigation.²

Indeed, one of the central messages of this article is that social psychological research can help to answer such questions by providing an empirically supported set of cultural processes that are analogous to the list of microevolutionary processes identified by biologists. This is illustrated in Figure 1, which shows how both biological evolution and cultural evolution involve a set of processes that alter variation in a population over time. The set of biological processes includes those briefly listed above, while the set of cultural processes includes those described in more detail in the bulk of this article. These include frequency-dependent biases such as conformity, in which the frequency of a trait determines its chances of transmission (Boyd & Richerson, 1985); model-based biases, in which the success, prestige, or expertise of a potential model affects their chances of being copied (Henrich & Gil-White, 2001); content biases, in which the memorability or attractiveness of the cultural trait affects its chances of being copied (Sperber & Hirschfeld, 2004); cultural drift, in which cultural change is affected by random factors such as sampling biases (Bentley, Hahn, & Shennan, 2004); cultural mutation, which may be blind as in the biological case (Cavalli-Sforza & Feldman, 1981) or may take the form of nonrandom *guided variation* (Boyd & Richerson, 1985); migration, in which people carry their cultural knowledge with them as they move through space (Cavalli-Sforza & Feldman, 1981); and finally, biological evolution, in which natural selection alters the frequency of cultural traits if those cultural traits are affected by an individual's survival and reproduction (e.g., the culturally transmitted practice of smoking becoming less common because of the cancer-related deaths of potential smoking models; Cavalli-Sforza & Feldman, 1981). Conversely, biological evolution may be affected by cultural evolution if culturally transmitted knowledge causes changes in gene frequencies (e.g., dairy farming practices facilitating the spread of lactose absorption genes; Feldman & Cavalli-Sforza, 1989). A branch of cultural evolutionary theory known as *gene-culture coevolution* or *dual inheritance*

theory examines how biological and cultural evolution affect one another in this way (Laland et al., 1995).

Cultural evolution researchers use a range of biologically inspired methods to study the origins and consequences of these cultural processes (Mesoudi, Whiten, & Laland, 2006). Mathematical models are used to quantify how these processes affect cultural variation over time (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981) just as population geneticists model changes in gene frequencies over time. Ethnographic field studies measure the effects of cultural processes in natural populations (Aunger, 2000b; Hewlett & Cavalli-Sforza, 1986) just as field biologists study biological evolution in the wild. Archaeologists study past cultural evolution (O'Brien & Lyman, 2002; Shennan, 2002) just as paleobiologists study past biological evolution. Phylogenetic methods are used to reconstruct historical relationships between cultural traits (Lipo et al., 2006; Mace & Holden, 2005) just as systematists use phylogenetic methods to reconstruct biological relationships. Finally and most importantly for present purposes, just as biologists simulate biological evolution in the lab using fruit flies, bacteria, or other suitable species, psychology experiments can be used to measure the effects of cultural evolutionary pro-

² Two purported differences between biological and cultural evolution are worth highlighting further, given that they are often used to discredit evolutionary approaches to culture. First, it is sometimes argued (e.g., Gould, 1991) that, whereas biological evolution exhibits a continually branching, treelike pattern of separate lineages due to vertical (parent-to-offspring) genetic inheritance, cultural evolution is not treelike and does not contain separate lineages because cultural inheritance is horizontal (between unrelated individuals and across lineages). However, this distinction between a treelike, divergent biological evolution and a blending, convergent cultural evolution is a distortion of both biology and culture. Much biological evolution involves the horizontal transfer of genetic information across lineages, especially in bacteria (Doolittle, 1999) and plants (Abbott, James, Milne, & Gillies, 2003), to the extent that many biological species' evolutionary histories are not at all treelike (Rivera & Lake, 2004). Empirical studies of cultural evolution, meanwhile, have found that historical data sets may in fact exhibit a branching, treelike pattern (Tehrani & Collard, 2002), and a systematic comparison of biological and cultural data sets revealed no significant difference in the extent to which each can be described as treelike (Collard, Shennan, & Tehrani, 2005). Thus, the difference between biological and cultural evolution in this regard is likely to be a matter of degree rather than kind and, in any case, does not invalidate the basic proposition that cultural evolution is a Darwinian process of variation, selection, and inheritance. A second commonly cited objection to cultural evolution is that culture does not exhibit discrete units of transmission (sometimes labeled *memes*) that are equivalent to genes because the boundaries between ideas, beliefs, and so on are fuzzy and difficult to define (e.g., Bloch, 2000). However, genes too have fuzzy, difficult-to-define boundaries (Stotz & Griffiths, 2004), and understanding of how information is stored in the brain is not sufficiently advanced to say with any certainty whether culturally transmitted information is stored in a discrete fashion. As argued in the text, however, the key point is that cultural evolution does not have to be identical in every respect to biological evolution for Darwinian methods to be useful in the analysis of culture. Indeed, mathematical models analyzed by Henrich and Boyd (2002) have shown that discrete genelike replicators are not necessary for cultural evolution; all that is required is some form of inheritance, whether it is particulate or nonparticulate. For further discussion of these and other objections to cultural evolutionary theory, see Mesoudi, Whiten, and Laland (2004, 2006).

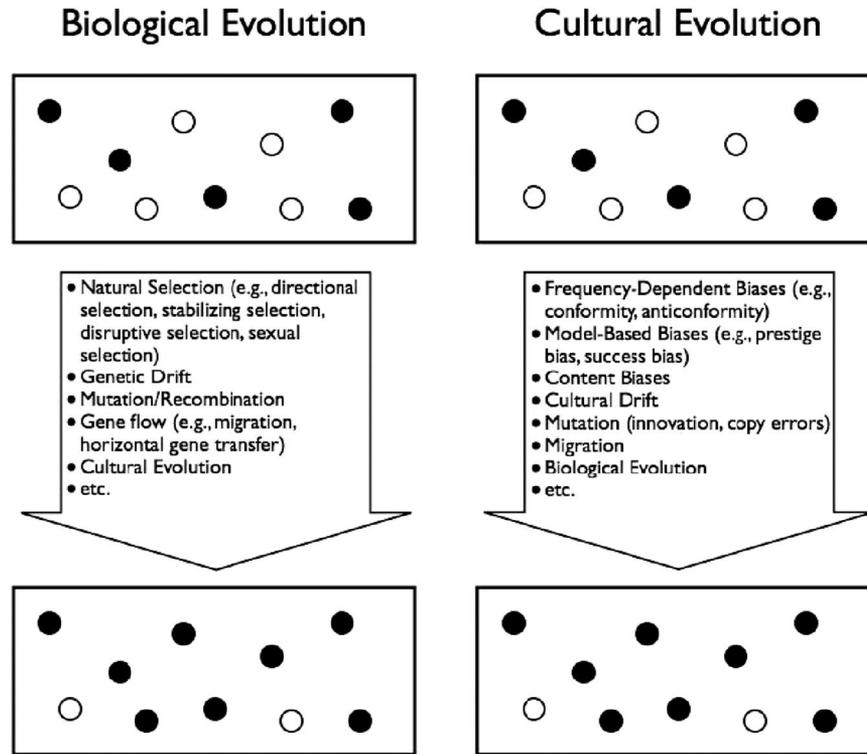


Figure 1. A schematic representation of biological and cultural evolution. Filled and unfilled circles represent two alternative variants, for example, two different genetic alleles in the biological case or two different beliefs in the cultural case. In both biological and cultural evolution, a set of microevolutionary processes acts to alter the variation (genetic or cultural, respectively) in the population over time. See text for descriptions of these processes.

cesses in the lab using small groups of participants. This final parallel is explored further in the following section.

How Social Psychology Can Inform Cultural Evolutionary Theory

Social psychology can inform cultural evolutionary theory by providing empirically supported details of the microevolutionary processes that drive human cultural change. These details might concern who people tend to acquire cultural information from (e.g., their parents, the majority, prestigious models), when people learn socially rather than individually, and what kind of information they copy. Several microevolutionary processes have been the subject of extensive mathematical modeling (e.g., Boyd & Richerson, 1985, 2005; Cavalli-Sforza & Feldman, 1981; McElreath & Henrich, 2006), models that have generated important insights. However, while the authors of the models (who are typically biologists or anthropologists, not psychologists) have made every effort to base the assumptions of their models, and of cultural evolutionary theory in general, as much as possible on empirical evidence, extensive experimental tests of the models' predictions and assumptions remain lacking. This is acknowledged by cultural evolution modelers themselves:

Formal theoretical analysis is a useful tool for clarifying logic but an arid exercise in the absence of well-designed empirical

studies. . . . Micro-level data are needed to understand the properties of cultural transmission and to make estimates of the population-level consequences of these properties. (Boyd & Richerson, 1985, p. 296)

While some effort has been made by these anthropologists and biologists in the ensuing years to conduct experimental tests of predictions that arise from cultural evolutionary theory (e.g., Baum, Richerson, Efferson, & Paciotti, 2004; Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; McElreath et al., 2005), there remains little interest from psychologists in conducting such tests. This is lamentable, as there is real opportunity for social psychologists to contribute to an exciting, truly interdisciplinary area of study, especially given that much work within social psychology already addresses the cultural evolutionary processes in question, such as conformity, social comparison, and intergroup relations, as shown below.

Moreover, much cultural evolutionary research (both models and experiments) remains quite psychologically impoverished, often making highly simplifying assumptions concerning the way in which people process information that they acquire from others. Although making simplifying assumptions is to some extent necessary to build tractable models of complex real-world phenomena, it is shown below how findings from social psychology, particularly social cognition, can valuably inform cultural evolutionary theory by providing more psychologically accurate assumptions regarding social information processing.

How Cultural Evolutionary Theory Can Inform Social Psychology

Cultural evolutionary theory can benefit social psychology in two ways: first, by providing ultimate explanations concerning the possible origin and adaptive basis of various proximate social psychological phenomena. This is typically done by constructing gene-culture coevolutionary models that track both genetic and cultural evolution and examining the conditions under which a particular cultural process enhances an individual's chances of survival and reproduction (i.e., the individual's genetic fitness). For example, in the section on conformity below, I show how cultural evolutionary models suggest that whenever cultural or social learning has (genetically) evolved, one might expect that this social learning will take the form of conformity (Henrich & Boyd, 1998). This fits well with a wealth of evidence from social psychology that people show a powerful propensity to conform (e.g., Asch, 1951), as well as providing further predictions that might be tested experimentally regarding the cost of learning or environmental fluctuation. While social psychology is replete with theories that offer explanations for social behavior (social comparison theory, social identity theory, self-categorization theory, self-perception theory, attribution theory, etc.), these explanations typically remain at a fairly proximate level and fail to explain why people's behavior should be consistent with such theories (why people compare themselves to others, why people readily identify with ingroups and differentiate themselves from outgroups, etc.). It is important to recognize in this context that behavior can be explained at multiple explanatory levels (Tinbergen, 1963): Traditional social psychological explanations tend to explain behavior in terms of proximate situational cues or internal motivations, while evolutionary theories provide ultimate explanations in terms of when and why a behavior may have emerged in a species' evolutionary past. These levels of explanation are entirely complementary: An explanation at one level does not invalidate an explanation at another level. As such, ultimate evolutionary explanations are intended to complement, not replace, proximate social psychological explanations.

A second advantage of cultural evolutionary theory for mainstream psychology is the *population thinking* that links micro- and macroevolutionary phenomena. In biology, ever since the evolutionary synthesis of the 1930s and 1940s (Mayr & Provine, 1980), biologists have recognized that small-scale microevolutionary processes such as selection, mutation, and drift that affect individuals within populations can, when extrapolated up in time and space, explain large-scale macroevolutionary trends and patterns such as speciation, adaptation, and extinction. An equivalent evolutionary synthesis for the social sciences has yet to occur (Mesoudi, 2007a). Such a synthesis would link the cultural microevolutionary processes that affect individuals alone or in small groups (as studied by psychologists) to cultural macroevolutionary trends and patterns in time (as studied by historians and archaeologists) or space (as studied by cultural anthropologists and sociologists). In contrast, it is rare for social psychologists to formally consider the population-level consequences of individual-level or small-group-level psychological phenomena (although notable excep-

tions include the social decision scheme theory of Davis, 1973; the dynamical systems theory of Nowak & Vallacher, 1998; and the dynamical evolutionary psychology of Kenrick, Li, & Butner, 2003). Evolutionary theory provides a ready-made set of tools and concepts for exploring the population-level consequences of individual-level phenomena (Richerson & Boyd, 2005). Furthermore, as a result of the interdisciplinary nature of cultural evolutionary theory, there is a growing body of cultural evolution research in anthropology, archaeology, and sociology that provides hypotheses and data that can be tested and simulated using psychological experiments.

Points of Clarification

Before discussing specific areas of intersection, certain points are worth clarifying regarding cultural evolutionary theory in general. First, the Darwinian theory of cultural evolution outlined above should not be confused with the Spencerian (and non-Darwinian) theory of cultural evolution that was prominent in the late 19th century and that influenced cultural anthropology well into the 20th century. Herbert Spencer (1896) saw biological change—incorrectly—as the progressive unfolding of life-forms along a series of discrete stages of increasing complexity, from what he viewed as simple microorganisms to higher or more evolved organisms such as mammals and, ultimately, humans. This progressive view of biological evolution has been long discredited in biology as both empirically and theoretically untenable (Gould, 1997): Species undergo change and diversify in a manner that is treelike and not ladderlike; almost all species that have ever existed have gone extinct and this rate of extinction shows no evidence of slowing down; there is no known guiding force that might be driving an increase in complexity; and it is unclear how complexity might be defined. Unfortunately, Spencer (1896) also espoused a progressive theory of cultural evolution, in which human societies were seen as progressing along a fixed series of discrete stages of increasing complexity, from savagery to barbarism to various classes of civilization (with, of course, Spencer's own Victorian English society at the apex). This Spencerian, progressive theory of cultural evolution became quite influential within sociology and anthropology during this period (Morgan, 1877; Tylor, 1871), as well as a period during the mid-20th century (Sahlins & Service, 1960; White, 1959). Just like their biological counterparts, however, progressive theories of cultural evolution are both theoretically and empirically untenable: There is no historical or ethnographic evidence that societies pass through discrete, predetermined stages; societies do not form cohesive wholes because skills, customs, words, and technology frequently diffuse across societies; there is no explanation of where these stages came from or what drives societies from one stage to the next; and it is again unclear how complexity might be defined. Progressive theories were often used to justify the exploitation of supposedly "less evolved" societies during the time of British colonialism, perhaps explaining their popularity during this period. It should be emphasized that the modern Darwinian theory of cultural evolution discussed in this article bears little resemblance to these earlier progressive Spencerian theories of cultural evolution (Campbell, 1965; Mesoudi, 2007a), with the

former making no claims of fixed, predetermined stages of increasing complexity.³

Second, cultural evolution should be partially distinguished from perhaps the dominant contemporary evolutionary approach to human behavior, that of evolutionary psychology (Buss, 1995; Pinker, 1997; Tooby & Cosmides, 1992). Evolutionary psychologists typically argue that human cognition, and thus human behavior, has evolved to maximize genetic fitness in ancestral environments and have amassed an extensive body of empirically supported findings that suggest an evolutionary basis for various aspects of human behavior, such as aggression, mate choice, and reciprocity. However, much of this work is commonly criticized by cultural and social psychologists because it does not fully address the possibility that behavior might be additionally shaped by culturally transmitted information (Caporael & Brewer, 1995; Eagly & Wood, 2006; Norenzayan, 2006; Scher, 1999). While evolutionary psychologists acknowledge the existence of transmitted culture (Cosmides & Tooby, 1992), research in the evolutionary psychology tradition has tended to focus instead on the notion of *evoked culture* (Gangestad, Haselton, & Buss, 2006), which explains cultural variation as resulting from universal genetic programs responding differently to varying environmental conditions. In contrast, cultural evolutionary theory treats culture as an evolutionary system in its own right that potentially plays a role as equally important as genetic evolution in shaping human behavior. Indeed, in certain cases, cultural evolution is predicted to lead to the spread via cultural transmission of genetically maladaptive behavior (see Richerson & Boyd, 2005, Ch 5), and gene-culture coevolution models predict that culture may influence genetic evolution as well as vice versa (Laland et al., 1995). Consequently, as shown below, cultural evolutionary theory might be considered more theoretically and empirically compatible with the findings and theories of social psychology.

Finally, another field that is related to, but somewhat distinct from, cultural evolutionary theory is memetics. Dawkins (1976) coined the term *meme* to describe a unit of cultural inheritance that is analogous to the gene and suggested that culture evolves according to neo-Darwinian principles akin to those that govern genetic evolution. However, perhaps because of Dawkins's reluctance to engage with other theories in the social sciences (either mainstream theories or other cultural evolutionary theories), as well as problems with the meme concept (Aunger, 2006), memetics has failed to take off as a serious academic discipline and remains a somewhat fringe pursuit that is separate from the broader and more rigorous cultural evolution research of Cavalli-Sforza and Feldman (1981), Boyd and Richerson (1985), and others. Specifically, memetics appears to make assumptions that are too similar to the genetic case, such as the assumption that memes are discrete units that are transmitted with high fidelity, an assumption that may not apply to cultural evolution (Atran, 2001; Sperber, 2000). There is no reason, however, why memetics could not become a productive research enterprise (Laland & Brown, 2002) as part of a broader science of culture (Mesoudi, Whiten, & Laland, 2006), although probably rooted in neuroscience rather than social psychology (Aunger, 2002), with neuromemeticists studying the neural basis of cultural transmission in the same way that molecular geneticists study the molecular basis of genetic inheritance.

Areas of Interaction

The following sections each address a phenomenon or process that is relevant to both social psychology and cultural evolutionary theory. These processes are summarized in Table 1. In each case, previous work from both fields is discussed, and potential points of intersection are identified.

Social Learning

Not surprisingly, social learning—the transmission of information from one individual to another nongenetically through such processes as imitation, teaching, and spoken or written language—has played a central role in social psychology. Bandura's (1977) social learning theory holds that much human behavior is acquired not through individual trial-and-error learning, in the form of classical or instrumental conditioning, but rather via observational learning (imitation) of others' behavior. Classic experiments by Bandura and colleagues testify to the extent to which social learning is employed, finding that children readily imitate the aggressive actions of an adult (Bandura, Ross, & Ross, 1961), that aggressive behavior is also imitated when the model is on television rather than in person (Bandura, Ross, & Ross, 1963b), that children adopt the behavior of prestigious adults to a greater extent than less prestigious adults (Bandura, Ross, & Ross, 1963a), and that moral judgments can be influenced by the moral judgments of others (Bandura & McDonald, 1963). Participants in these studies (typically children) were found to spontaneously exhibit the modeled behavior without undergoing a lengthy period of trial-and-error learning. Social learning also occurs when the modeled behavior is not directly rewarded, such that social learning cannot be reduced to instrumental conditioning. Bandura (1977) also provided a potential explanation for these findings that social learning is ubiquitous and potent, arguing that social (or observational) learning allows individuals to avoid the costs of individual learning:

³ While it is not the case that human societies inevitably and universally progress along a unilinear ladder of increasing complexity, it is nevertheless possible to discern certain general trends in cultural macroevolution that are indicative of an increase in the apparent complexity of social organization, such as the shift from relatively egalitarian, kin-based hunter-gatherer societies to large-scale, socially stratified, market-based societies with extensive division of labor (Johnson & Earle 2000). Technology can also be seen to accumulate over time, resulting in an apparent increase in efficiency or effectiveness (Basalla, 1988). However, unlike the unilinear stages proposed by early Spencerians, these general trends in cultural evolution are neither inevitable, fixed, nor irreversible. Moreover, these general trends can (at least potentially) be explained in terms of specific microevolutionary processes such as those listed in Figure 1, whereas Spencerian theories offer no explanation for their proposed evolutionary progression beyond a mysterious jump from one stage to the next. An interesting parallel might be drawn here with Maynard Smith and Szathmari's (1997) notion of major transitions in biological macroevolution, such as from unicellular to multicellular organisms or from asexual clones to sexually reproducing populations; like the trends observed by Johnson and Earle (2000), these biological transitions are neither inevitable, fixed, nor irreversible, yet they result over time in a general increase in complexity (defined, for example, as differentiation into specialized parts).

Table 1
Cultural Evolutionary Processes and Their Corresponding Social Psychology Traditions

Cultural evolutionary process	Description	Relevant social psychological research tradition
Social learning	The capacity to acquire information from another individual nongenetically	Social learning theory (Bandura, 1977); social comparison theory (Festinger, 1954)
Frequency-dependent bias (e.g., conformity)	Copying a trait on the basis of its popularity in the population	Conformity (Asch, 1951; Sherif, 1936) and minority influence (Moscovici, Lage, & Naffrechoux, 1969) research
Model-based biases (e.g., prestige–success bias)	Copying particularly prestigious, successful, or knowledgeable models	Social learning experiments (Bandura, Ross, & Ross, 1963a); triadic model of social comparison (Suls, Martin, & Wheeler, 2000); elaboration likelihood model (Petty & Cacioppo, 1986)
Content biases	Preferentially copying certain kinds of information	Social memory studies (e.g., Bartlett, 1932; Kashima, 2000); inductive biases (Griffith, Kalish, & Lewandowsky, 2008)
Cultural group selection	Cohesive, cooperative groups outcompete less cohesive, less cooperative groups	Intergroup processes (Tajfel, Billeg, Bundy, & Flament, 1971); social identity theory (Tajfel & Turner, 1979)

Because mistakes can produce costly, or even fatal consequences, the prospects for survival would be slim indeed if one could learn only by suffering the consequences of trial and error. For this reason, one does not teach children to swim, adolescents to drive automobiles, and novice medical students to perform surgery by having them discover the appropriate behavior through the consequences of their successes and failures. The more costly and hazardous the possible mistakes, the heavier is the reliance on observational learning from competent learners. (Bandura, 1977, p. 12)

Another area of social psychology that makes predictions as to when social learning should be employed is social comparison theory. Festinger (1954) argued that when people are uncertain about the appropriateness of their own behavior, they look to others for guidance as to the correct response:

To the extent that objective, non-social means are not available, people evaluate their opinions and abilities by comparison respectively with the opinions and abilities of others. . . . In many instances, perhaps most, whether or not an opinion is correct cannot be immediately determined by reference to the physical world. (Festinger, 1954, p. 118)

This social comparison frequently results, Festinger (1954) argued, in the modification of one's behavior to match a model's behavior. Subsequent experiments confirmed this prediction, with people frequently modifying their opinions or behavior to match one or more models' opinions or behavior (e.g., Gerard & Orive, 1987; Goethals & Darley, 1977; Latané, 1966; Suls, Martin, & Wheeler, 2000). Other literatures similarly testify to the strength and ubiquity of social learning, such as studies of conformity (Asch, 1951; R. S. Baron, Vandello, & Brunsman, 1996; Bond, 2005; Bond & Smith, 1996; Deutsch & Gerard, 1955; Latané & Wolf, 1981; Sherif, 1936), although this specific form of social learning is discussed in the following section.

Social psychological theories such as social learning theory contain several concepts and findings that are relevant to cultural evolutionary theory. The first and most basic point to take from the social psychological literature is that social learning is ubiquitous: Numerous experiments have shown that people readily and often spontaneously acquire beliefs, knowledge, and opinions from oth-

ers. This provides supporting evidence for the existence of one of the three necessary properties of Darwinian cultural evolution noted above—inheritance—and therefore justifies treating culture as an evolutionary system. Second, the finding that social learning is not reducible to individual learning processes such as instrumental conditioning justifies the distinction between social and individual learning that is commonly made in cultural evolutionary models, in which they are treated as two distinct ways of acquiring information, with different costs and accuracies. Finally, some of the experiments also speak to the specific biases that have been modeled in the cultural evolution literature, such as the prestige bias observed by Bandura et al. (1963a), which is dealt with in a later section.

What might the social learning tradition take from the cultural evolution literature? Prominent social psychologists have suggested that people should rely on social learning when their own individual learning is inaccurate (Festinger, 1954) or costly (Bandura, 1977). These intuitions have been formally addressed by several gene-culture coevolution models that examine the conditions under which social learning is more adaptive than individual learning (Aoki, Wakano, & Feldman, 2005; Boyd & Richerson, 1985, 1995; Feldman, Aoki, & Kumm, 1996; A. R. Rogers, 1988). The results of these models largely confirm Bandura's (1977) and Festinger's (1954) intuitions, although not entirely, and it is productive to examine exactly how the models deviate from these predictions.

A mathematical model constructed by A. R. Rogers (1988) aimed to formally test the intuition that social learning is adaptive because it allows individuals to avoid the costs of individual learning. Evolutionary models typically do this by simplifying the problem down to its most basic elements. In Rogers's model, individuals were assumed to hold one of two beliefs about the world, each of which resulted in different actions. These beliefs differed in the extent to which they matched some aspect of the environment: One of the beliefs was always more accurate than the other and thus generated behavior that was more appropriate in that particular environment. Every so often, the environment changed such that the other action became more adaptive. Indi-

viduals were assumed to inherit genetic predispositions to learn either individually or socially. Individual learners could determine the best action with some specified learning cost, consistent with Bandura's (1977) claim, whereas social learners copied the action of another randomly selected member of the previous generation at no cost. Rogers then tracked the frequencies of individual and social learners over successive generations, where individuals produced offspring at a rate proportional to their fitness (i.e., the appropriateness of their behavior) and the offspring inherited the type of learning (individual or social) from their parents.

The results of A. R. Rogers's (1988) model showed that social learners did indeed spread in the population. This and similar models (Aoki et al., 2005; Boyd & Richerson, 1985, 1995; Feldman et al., 1996) generally support the intuitions of Bandura (1977) and Festinger (1954) that social learning is favored when individual learning is either more inaccurate or more costly than social learning. However, this finding is qualified by a second important factor: environmental change. When the environment (i.e., which belief or behavior is most appropriate) changes too rapidly, then social learning is less effective. This is because social learners cannot track this environmental change and end up copying out-of-date and inappropriate behavior from others. Individual learners, on the other hand, can detect environmental shifts, and where the benefit of this detection exceeds the cost of individual learning relative to social learning, then individual learning will be favored. Indeed, Rogers found that environmental change resulted in stable mixes of individual and social learners that coexisted at equilibrium. When environments change, then individual learners do better because they can detect this change, while social learners are left copying outdated behavior. Once enough of the population become individual learners, social learners can successfully copy the adaptive behavior of the now-*numerous* individual learners at lower cost than the individual learners, so social learners increase in frequency. Then, the environment changes again, and individual learners do better, and so on. The population continues cycling between individual and social learners until it reaches a stable equilibrium at which individual and social learners have equal average fitness. This points to a somewhat counterintuitive outcome of Rogers's model: Populations in which social learning is present could never have a higher average fitness than populations entirely composed of individual learners. This is because individual learners always have a fixed fitness, determined solely by their learning costs. In mixed populations, social learners will also have this fitness given that they are at equilibrium with individual learners. Hence, mixed populations will have an equal average fitness to populations entirely composed of individual learners. This contradicts the claim of Bandura that social learning will result in improved chances of survival. This counterintuitive result also holds under the alternative assumptions that environments vary spatially rather than temporally, when there are more than two possible actions, when individual learning is inaccurate as well as costly, and when social learners copy only individual learners (Boyd & Richerson, 1995).

Boyd and Richerson (1995) showed that there are two ways in which social learning can increase the average fitness of the population. First, rather than assuming that individuals must be either social learners or individual learners, assuming instead that individuals can facultatively switch between individual learning (when individual learning is inaccurate) and social learning (when

individual learning is accurate) results in an increase in average fitness for populations in which social learning is possible. Here, individual learners do not have a constant and limiting fitness; instead, their fitness increases because they can avoid high learning costs by switching to social learning. A second way in which social learning can improve the average fitness of the population is when it is cumulative, such that social learners start off with the behavior exhibited by their parents in the model but then modify that behavior using individual learning. Individual learners, by contrast, learn from scratch in every new generation. If the cost of the small modification made by social learners is smaller than the cost of the large modification made by individual learners, then social learners will have higher fitness than individual learners.

These models have several implications for social learning theory in psychology. They predict that the kind of social learning that should have evolved is one in which individuals are selective learners, using social learning when individual trial-and-error learning is costly or inaccurate, when behavioral responses can be accumulated over successive generations, and when the environment (i.e., the appropriate behavior) does not change too rapidly. Some of these predictions receive tentative support from the existing social psychological literature. For example, Deutsch and Gerard (1955) showed that social learning is more commonly observed (in the form of conformity) when the task is more difficult and therefore when individual judgment is more inaccurate. However, few past social psychology studies have systematically varied such factors as task difficulty or environmental change as well as tracking changes in learning frequencies over successive learning episodes to test the specific predictions noted above. In contrast, recent experimental studies that are directly inspired by cultural evolutionary theory have tested these predictions. McElreath et al. (2005) studied social learning in groups of participants playing a similar game to that of A. R. Rogers's (1988) model (i.e., choosing one of two options, one giving a higher payoff), either with or without environmental change. While rates of social learning were lower than predicted by the cultural evolutionary models, the prediction that social learning is employed less often when environments change more rapidly was supported. Other experiments support the prediction that people facultatively switch between individual and social learning over successive cultural generations depending on their success with individual learning (Kameda & Nakanishi, 2003; Mesoudi, 2008). Regarding cumulative cultural evolution, Insko and colleagues (1980, 1983) conducted a series of innovative studies in which groups of participants constructed and traded paper models in exchange for money, with group members gradually replaced with new, naive participants. This replacement allowed the accumulation of increasingly efficient trading rules and manufacturing techniques, resulting in significant increases in productivity and earnings over time, in accordance with cultural evolutionary models. Recent studies using similar experimental methods have similarly found that cumulative cultural evolution generates adaptive traditions (Baum et al., 2004; Caldwell & Millen, 2008).

To summarize, the basic finding from social psychology that social learning is powerful and ubiquitous is an important verification of the importance ascribed to social learning by cultural evolutionary theory. Cultural evolutionary models, meanwhile, provide a formal test of the informal hypotheses of social psychologists regarding the ultimate benefits of social learning relative to

individual learning, generating a set of novel predictions that might be tested using social psychological methods. It might be predicted that social learning should be facultative rather than indiscriminate and should be more common when environments change more slowly. Such predictions can provide a focus for future social learning research, which traditionally does not appear to have been guided by formal theoretical considerations and has become increasingly marginalized within social psychology in recent years.

Conformity

A classic finding in social psychology is that many people show a powerful propensity to adopt whatever behavior or opinion is held by a majority of the members of their local group, even where this behavior or opinion is counterintuitive or incorrect. Classic findings include Sherif's (1936) demonstration that participants adopt the group majority's judgment regarding the ambiguous autokinetic effect, Asch's (1951) findings that a significant proportion of participants forgo their own judgment in an unambiguous line judgment task and adopt the obviously incorrect response of a majority of confederates, and many studies since (e.g., R. S. Baron et al., 1996; Bond, 2005; Bond & Smith, 1996; Deutsch & Gerard, 1955; Latané & Wolf, 1981). Indeed, the tendency for people in groups to conform to a majority opinion or behavior even when the majority exhibits a false or undesirable opinion or behavior has proven to be one of experimental social psychology's most powerful and important messages.

Conformity has also been an important feature of cultural evolution models. Boyd and Richerson (1985) defined *frequency-dependent bias* as a cultural transmission rule in which people use the frequency or popularity of a variant as the basis for deciding whether to adopt that trait. Conformity is thus defined as positive frequency-dependent bias, in which people are disproportionately more likely to adopt the most common trait in their local group. (Negative frequency-dependent bias, not typically considered in cultural evolutionary models, is where people preferentially adopt the least common cultural variant.) These cultural evolutionary models show that over many cultural generations (or learning episodes), conformist cultural transmission has the effect of increasing the frequency of the most common cultural variant (Boyd & Richerson, 1985; Henrich & Boyd, 1998). Hence, the entire population ends up with whatever variant was initially most popular (assuming no other cultural processes are operating). This accords well with the experimental evidence from social psychology, where participants frequently converge on the most common response (e.g., line-length judgment) in the experimental group.

Indeed, the cultural evolutionary models also provide an explanation for why people appear to be so willing to ignore their own judgment and adopt whatever behavior or opinion is most popular in a group. As discussed in the previous section, social learning can evolve when individual learning shows some degree of inaccuracy or cost and when environments do not change too rapidly. Further gene-culture coevolution models (Boyd & Richerson, 1985; Henrich & Boyd, 1998) have examined the conditions under which genetic predispositions for conformist social learning in particular might spread in a population that ordinarily learns individually. These models find that whenever social learning is favored, conformist bias is also favored, and that conformity is more adaptive than simply copying another member of the group at random. This is because con-

formist bias allows cultural learners to benefit from the individual learning efforts of the entire group, and this aggregate response is more likely to be adaptive than the response of a single randomly selected individual. This phenomenon will be familiar to psychologists as equivalent to the benefit of having relatively large sample sizes in experiments: Larger sample sizes reduce the effects of random error and sampling bias that may occur in smaller samples. Similarly, the larger the sample of people that is learned from, the more accurate the behavior is likely to be.

However, the cultural evolutionary models also point to a shortcoming of many social psychology experiments that purport to be studying conformity and suggest how formal cultural evolutionary models might guide future experimental work on conformity in social psychology. Boyd and Richerson (1985) defined conformity as occurring only when people are disproportionately more likely to adopt the most common variant, compared to unbiased, nonconformist cultural transmission. For example, say a participant is in a group with 10 others, and 6 out of those 10 participants choose Option A and 4 choose Option B. An unbiased, nonconformist learner who chooses one of these participants to copy entirely at random would adopt Option A with a probability of 0.6 and Option B with a probability of 0.4. While the most popular choice has a higher chance of being copied here, this is simply because it is more likely to be observed rather than being due to any conformist bias on the part of the learner. A conformist learner, on the other hand, would copy Option A with a probability greater than 0.6, and Option B with a probability less than 0.4. This apparently subtle difference has important implications for long-term cultural change: While the former unbiased, nonconformist transmission does not result in a change in the frequency of choices over the long run, the latter conformist transmission eventually leads to the fixation of Option A, the initially more popular trait (Boyd & Richerson, 1985, pp. 206–209). This can be seen in Figure 2, which illustrates the consequences of unbiased cultural transmission and conformity on the long-term dynamics of two hypothetical beliefs.

Existing research in social psychology is not well suited to determining whether social learning is conformist in this precise sense (Boyd & Richerson, 1985; Efferson et al., 2008). For example, Sherif's (1936) experiments and many of the subsequent experiments that used the ambiguous autokinetic effect (e.g., Rohrer, Baron, Hoffman, & Swander, 1954) suggested that participants adopted the average estimate from all members of the group, rather than the most common estimate. Rather than conformity, this appears to be more of an averaging or blending cultural learning rule. Asch's (1951) line-length experiments typically pitted a single naive participant against a unanimous majority of confederates of varying number (see Bond, 2005). However, this is not useful for studying conformity as defined above: No matter how many confederates there are, if they are unanimous, then the frequency of incorrect responses in the group from a naive participant's perspective is always 100% (given that the naive participant responds after all of the confederates). Both unbiased (nonconformist) transmission and conformist transmission predict that the participant should adopt the confederates' response, such that it is impossible to determine which learning rule the participants are using. In fact, these experiments are typically measuring whether individual judgment favoring the intuitively correct response outweighs cultural learning favoring the intuitively incorrect response. Whether this cultural learning is conformist or nonconformist is indeterminable because these two processes are confounded (Efferson et al., 2008).

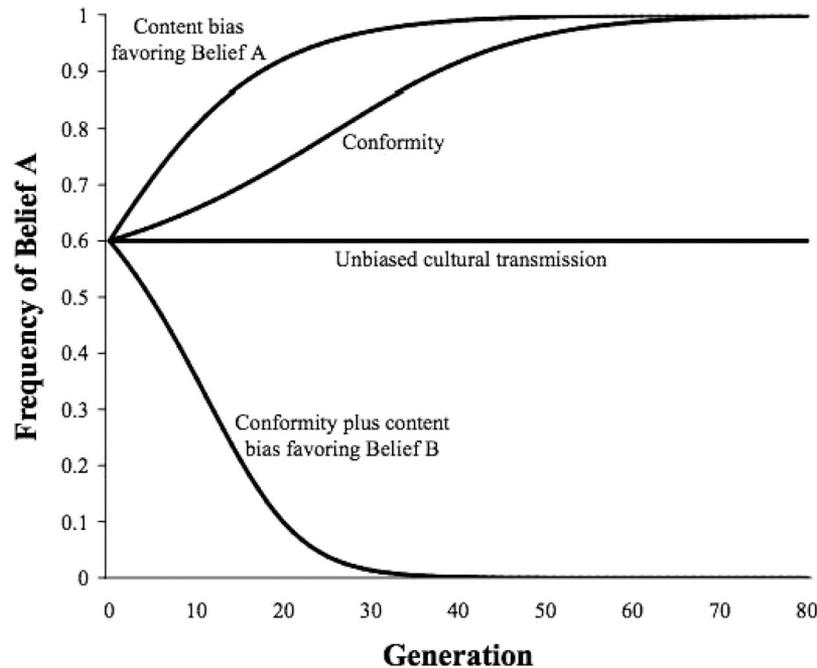


Figure 2. The long-term consequences of different cultural transmission biases on cultural trait frequencies. The y-axis shows the proportion of individuals in a population who exhibit a particular trait, say Belief A, as opposed to an alternative Belief B. Initially, 60% of the population holds Belief A. Unbiased cultural transmission (Boyd & Richerson, 1985, Equation 3.12) does not alter this frequency over time. Conformity (Boyd & Richerson, 1985, Equation 7.1 with $D = 0.1$) causes the entire population to converge on Belief A, the initially most common belief. Content bias in favor of Belief A (Boyd & Richerson, 1985, Equation 5.2 with $B = 0.1$) has the same effect, although convergence is faster. A combination of conformity and content bias in favor of Belief B ($D = 0.1$, $B = -0.1$) causes the population to converge on Belief B, showing how content biases can obscure conformity when both are allowed to operate simultaneously.

An individual's preexisting tendency to prefer one response over another has been modeled by Boyd and Richerson (1985) as content bias (sometimes called direct bias). As shown in Figure 2, the long-term consequence of a content bias is to drive whichever trait is favored by the content bias to fixation. A content bias that favors the most common belief (Belief A in Figure 2) will have the same long-term consequence as conformity, that is, to drive Belief A to fixation. A content bias that favors the alternative Belief B may result in the fixation of the initially rarer Belief B even when conformity is also acting, as shown in Figure 2, highlighting how conformity may be undetectable if other biases are also acting. The key point is that none of the social psychological studies of conformity cited above attempted to tease apart these different cultural processes, which is problematic given their different long-term, population-level consequences.

Studies of minority influence are similarly flawed. For example, Moscovici, Lage, and Naffrechoux (1969) had groups of 4 naive participants judge the color of slides along with two confederates who consistently stated that the blue slides were green. Unbiased (nonconformist) transmission with no content bias would predict that naive participants would respond green with a probability equal to the proportion of group members responding green, or 1/3; conformist transmission would predict that green, being the minority choice, should be chosen with a probability less than 1/3, while anticonformity (roughly equivalent to minority influence) would predict that

green should be chosen with a probability greater than 1/3. Far fewer participants (approximately 8%) in fact chose green, suggesting conformity rather than the anticonformist minority influence suggested by Moscovici et al. Again, however, it is not clear whether this was genuinely due to conformity or to a content bias deriving from the participants' perceptual systems.

Other social psychology studies have presented participants with varying frequencies of behaviors or attitudes and shown better evidence for conformity as defined above. For example, Mackie (1987) found that students' attitudes toward a political issue (whether the United States should increase military spending) shifted on average toward the position said to be held by a majority of their fellow students, irrespective of whether this majority position was for or against the proposition. There did not appear to be a particularly strong content bias here, given that students were initially divided on the issue.

However, even in this latter study, a second problem with traditional social psychology research into social influence remains: Rarely are the long-term, multigenerational consequences of particular social learning biases measured. In Mackie's (1987) study, for example, participants simply recorded their attitudes once before exposure to the stimulus material and once after exposure; it is unknown whether these attitude shifts persisted or whether they returned to preexisting values. Similarly, participants in the Asch-style line judgment experiments may have only been publicly complying

with the other group members' judgments to save face or avoid embarrassment (Deutsch & Gerard, 1955; Sabini, Siepmann, & Stein, 2001). This is a crucial issue from a cultural evolutionary perspective, which is concerned with permanent, long-term changes in beliefs, attitudes, and norms over multiple transmission episodes. Indeed, an important message from cultural evolutionary models is that small biases may, when repeated over several learning episodes and in large groups, have significant population-level consequences (see Figure 2). If social influence is transient, however, then there will be no long-term changes and no population-level consequences.

Perhaps inspired by the cultural evolutionary ideas of its second author, a study by Jacobs and Campbell (1961) did attempt to measure the longer term persistence of conformity in successive generations of participants, not just experimenter to participant or confederate to participant. Jacobs and Campbell repeated Sherif's (1936) autokinetic effect experiment but this time used confederates to introduce an exaggerated judgment. Following every group judgment, one member of the three- or four-person group was replaced with a new, naive participant. While initial generations matched the exaggerated judgment introduced by the confederates, once all of the confederates had been replaced, then the judgments of subsequent generations rapidly returned to those observed for individual controls. This suggests that the population-level consequences of conformity are not as striking as suggested by traditional no-replacement experimental designs, probably because of the stronger counterinfluence of a perceptual content bias favoring small judgments. In any case, Jacobs and Campbell's replacement design is more suited to the study of cultural transmission biases such as conformity than traditional one-generation social psychology experiments because the consequences of these biases may only be observable (and, more importantly, distinguishable from other transmission biases) after several generations of learning. Unfortunately, few social psychologists appear to have pursued the multigenerational design pioneered by Jacobs and Campbell; this is another area in which cultural evolutionary models can fruitfully guide social psychological research.

Recently, anthropologists and biologists interested in cultural evolution have begun to conduct their own experiments (Efferson et al., 2008; McElreath et al., 2005) that test for the more precisely defined version of conformity, as well as using a task with no overwhelming default response that may be favored by content biases. Typically, participants have to decide which of two hypothetical technologies to adopt, with one of the technologies giving a higher payoff on average than the other. While the optimal technology can be discovered through individual learning, there is no a priori correct choice, as in the autokinetic effect or line-length tasks, such that content biases should not confound the results. These experiments have yielded mixed results: As predicted by theoretical models, participants who engaged in conformity did indeed do better in the task than nonconformist learners; however, not all participants engaged in conformity, and it is unclear why they did not all follow this optimal learning strategy. Perhaps more interchange of theory and data between cultural evolution researchers and social psychologists might resolve some of these issues by introducing into the evolutionary models such additional phenomena as consistency in responses (Moscovici et al., 1969) and task structure (Steiner, 1972).

Cultural evolution researchers have also attempted to explain actual cultural trends in terms of conformity. Sociologists (E. Rogers, 1995) have repeatedly observed that the diffusion of technological innovations through a society follows a distinctive S-shaped cumulative

distribution curve: a slow initial uptake followed by a rapid increase and then a subsequent slowdown in the rate of diffusion. Henrich (2001) argued that these S-shaped cumulative distribution curves are most likely to result from conformity: The slow initial uptake of an innovation is caused by conformity to existing practices preventing the spread of the novel practice, the increasingly rapid uptake that follows is due to the increasing influence of conformity as the innovation becomes more popular, and the subsequent slowdown results from population saturation. In a later section, the further consequences of conformity in allowing cultural group selection and the evolution of particular forms of intergroup behavior are discussed. The key point, however, is that cultural evolutionary theory allows social psychological concepts such as conformity to be used to explain actual cultural trends and patterns in the sociological record.

In summary, social psychology experiments and cultural evolution models both attest to the importance of conformity, with experimental studies demonstrating strong and ubiquitous conformity in the lab supporting the findings of theoretical models that conformist social learning is highly adaptive relative to nonconformist, unbiased social learning. However, cultural evolution models also highlight important shortcomings of social psychology experiments: their conflation of conformity with other cultural biases (e.g., content bias) and their lack of long-term, multiple-generation transmission episodes.

Model-Based Biases

Another class of cultural transmission biases that may affect cultural evolution is what Richerson and Boyd (2005) called model-based biases, where people preferentially adopt cultural information from models who have particular characteristics rather than on the basis of the characteristics of the cultural information itself. For example, people might preferentially copy models who are particularly successful or prestigious or who are older or richer than themselves. Cultural evolutionary models suggest that copying successful individuals is often a highly adaptive cultural learning strategy, outperforming unbiased cultural transmission (i.e., copying a model at random), conformist cultural transmission, and individual learning (McElreath et al., 2008; Mesoudi & O'Brien, 2008b). The reason for this is fairly intuitive: Copying a successful person's behavior is likely to result in the adoption of adaptive behavior because successful people become successful because of their adaptive behavior. This assumes, however, that there is a straightforward relationship between social success and behavior. In reality, successful models might exhibit many different copyable behaviors or attitudes, and it may be difficult to determine which of these contributed to the model's success and which, therefore, to copy. Is Tiger Woods's success as a golfer due to his swing, his training regime, his clubs, his footwear, or his mental attitude toward his game? It is unlikely that even Tiger Woods himself knows the answer to this question, let alone a novice golfer looking to emulate his or her golfing hero. As might be expected, Boyd and Richerson (1985, pp. 257–258) showed that the adaptiveness of the success-based bias depends on the covariation between the measure of success and the copied trait: The greater the covariation, the more effective is success-based bias. While the simple learning strategy "copy successful individuals" will on average result in the acquisition of adaptive cultural traits, many neutral or maladaptive traits may also be copied along with those adaptive traits. This is why corporations spend huge amounts of money to get sports stars to

wear their branded clothes: People who slavishly copy Tiger Woods will copy not only his swing (which probably covaries with success) but also his choice of branded clothing (which most likely does not covary with success).

In addition, Boyd and Richerson (1985) showed that when the criteria that determine what makes a model successful (e.g., wealth, house size) can also vary and be culturally transmitted, then this indicator trait and the copied trait itself can be subject to a runaway selection process resulting in greatly exaggerated and perhaps maladaptive cultural traits. For example, if house size is used as a measure of success, then people exhibiting success bias will copy the attitudes of people with large houses, including the "large houses are good" attitude; over successive generations, house size and "large houses are good" attitudes will reinforce each other in an upwardly spiraling arms race. Such a process might result, for example, in the enormous mansions of movie and sports stars, far exceeding the space requirements of a single family. Finally, Henrich and Gil-White (2001) argued that another consequence of success bias may be prestige hierarchies, in which less successful individuals grant more successful individuals prestige in the form of gifts or displays of deference in exchange for access to their high-quality information. These prestige hierarchies are widely seen in the ethnographic record and are distinct from dominance hierarchies, which are based on power and coercion.

Experiments from social psychology have to some extent supported the prediction that people should preferentially copy people who possess high success, status, or prestige. As noted above, Bandura et al. (1963a) found that children tend to imitate the behavior of adults who are observed to control access to resources. This is not necessarily indicative of prestige, however; control over resources may also result from coercive power, which Henrich and Gil-White (2001) noted is distinct from prestige. Better evidence comes from Brody and Stoneman (1985), who found that children showed greater imitation of other children who were described as of equal competence to themselves compared to children who were described as of lower competence. This effect was independent of the models' age: Younger equal-competence models were imitated just as much as same-age equal-competence models. Many other experiments have found evidence for success or prestige bias in adult learning tasks. Mausner (1953) found that participants shifted their subjective opinions of art toward those of a confederate introduced as an art director of an advertising firm, while no shift was observed when the confederate was introduced as a fellow student, even where the responses of the expert confederate were typically considered to be incorrect. Similarly, participants' responses in a line judgment task shifted toward those of a confederate previously observed to be successful in a similar line-length task, despite the confederate giving inaccurate responses in the current task (Mausner, 1954). Rosenbaum and Tucker (1962) found that adult participants consistently matched the responses of successful models in a simulated horse-betting task (see also R. A. Baron, 1970; Greenfeld & Kuznicki, 1975), despite being told that they were betting on different races, thus making the models' responses inappropriate. Similar findings have been observed for attitudes as well as behavior. Ryckman, Rodda, and Sherman (1972) found that participants modified their attitudes concerning student activism to match the attitudes of high-status college professors, even where those professors' expertise (e.g., in Chinese history) was unrelated to the issue under discussion.

Other findings, however, present qualifications to the simple claim that people preferentially learn from successful others. For

example, as part of his social comparison theory, Festinger (1954) claimed that people choose to compare themselves with, and consequently learn from, models who are similar to themselves, which would appear to exclude those of higher status or those who are more successful. However, subsequent experimental tests of Festinger's claim have yielded mixed support for this similarity bias and have led to several refinements of social comparison theories of opinion change (e.g., Gerard & Orive, 1987; Goethals & Darley, 1977; Latané, 1966; Suls et al., 2000). For example, Suls et al.'s (2000) triadic model holds that people seek out similar others for matters of subjective preferences, such as tastes in literature or film, while they seek out models who have greater expertise or social status for matters of objective belief in which a factually correct response exists. Even in the latter, however, similarity may still play some role. In a study of attitudes toward science, Mausner and Mausner (1955) found that highly educated, science-literate audiences accepted the factual claims of a science expert without question, while a poorly educated, scientifically illiterate audience demanded that the scientist justify his arguments with evidence before accepting them. Presumably the difference between the poorly educated audience and the science expert counteracted any effect of the latter's greater expertise.

This evidence that subjective preferences are not typically subject to a success or prestige bias casts doubt on Boyd and Richerson's (1985) prediction that people acquire preference traits (e.g., "large houses are good") from high-prestige models. The social psychological evidence also highlights the differences between what in cultural evolution models are typically lumped together as cultural traits: subjective values or preferences, factual beliefs, and skills may each be governed by quite distinct cultural transmission dynamics. The experiments and the wider literature also highlight the many different ways in which success or prestige might be defined: It may be competence or skill at a specific task, knowledge of a specific topic, or a more diffuse social standing or reputation (Berger, Fisek, Norman, & Zelditch, 1977). Cultural evolutionary theory and models would benefit from using these findings from social psychology to construct more specific models that could be more productively applied to specific cases.

The elaboration likelihood model of attitude persuasion (Petty & Cacioppo, 1986) presents another caveat to the claim that people preferentially copy successful others. Research in this tradition has found that while expert, prestigious, or successful models do influence people's attitudes, this only occurs when attitudes are processed via a peripheral route, such as when the person has low personal involvement in the decision or issue in question. Under conditions of high involvement, participants tend to use a central processing route that involves a deeper consideration of the intrinsic qualities of arguments for or against the issue, thus relying more on individual than on social learning. For example, Petty, Cacioppo, and Goldman (1981) found that students were more persuaded by an expert source regarding the introduction of a new exam when the consequences of the decision for them were low (the exam would be introduced in 10 years' time) than when the consequences were high (the exam would be introduced the following year). Subsequent research has found that the central route produces attitude change that is more enduring and more predictive of subsequent behavior than the peripheral route (Petty & Cacioppo, 1986), suggesting that success bias may not be as consequential as sometimes assumed.

The social psychology experiments, however, can also be criticized for not considering the longer term cultural dynamics of a success-biased cultural learning rule, the same criticism that was levied at the conformity experiments above. The runaway effects of success bias, if they emerge, would only be observed after several cultural generations and in groups large enough to observe meaningful differences in success. Perhaps more importantly, social psychology experiments such as those described above are often incapable of determining the adaptiveness of social learning strategies such as success bias due to the deceptive use of confederates to introduce maladaptive behavior. By having successful or prestigious models deliberately exhibiting incorrect responses in tasks, the experiments described above (e.g., Mautner, 1953, 1954; Rosenbaum & Tucker, 1962; Ryckman et al., 1972) were specifically designed to prevent success bias from being adaptive. The fact that the participants typically exhibited success bias anyway suggests that success bias was an adaptive strategy in their everyday lives, as predicted by the cultural evolutionary models, although these were hardly ideal conditions to test such a prediction.

Recent cultural learning experiments directly inspired by cultural evolutionary theory have attempted to address these shortcomings. In a series of studies using the virtual arrowhead task (Mesoudi, 2008; Mesoudi & O'Brien, 2008a), participants in small groups designed their own virtual arrowheads via a computer program by entering values of various arrowhead attributes (length, width, thickness, shape, and color). Participants received feedback regarding the effectiveness of their arrowhead designs, with the objective to find the hidden optimal arrowhead design that gave the highest score. They could improve their design through either individual trial-and-error learning or by copying the arrowhead design of another member of the group. The current scores of those other group members were made publicly available, potentially allowing participants to copy the most successful group member. There was no deception, and groups played over several successive cultural generations to see how learning strategies changed over time. It was found that (a) almost all participants copied the design of the most successful group member, thus readily engaging in success-biased cultural transmission, and (b) groups in which success bias was permitted significantly outperformed groups in which social learning was not permitted, supporting Boyd and Richerson's (1985) prediction that success bias is generally adaptive when measures of success (the participant's score) and copied behavior (the arrowhead design) are correlated, as they were in these experiments. Note also that the copied behavior in these experiments had an objective rather than subjective standard of effectiveness, that is, there was an optimal arrowhead design that gave the highest score. The participants' tendency to copy group experts, then, is consistent with Suls et al.'s (2000) triadic model. On the other hand, model similarity was not manipulated (all participants were college students), which in future studies may be found to qualify these findings.

In summary, social psychological theory and experiments generally support the prediction from cultural evolutionary theory that people should preferentially learn from those of high success, status, or expertise; however, they also provide the caveats that model similarity and task importance may qualify this success bias and that success bias operates primarily on objective beliefs rather than subjective attitudes. For their part, cultural evolutionary models provide the novel predictions that prestige bias is generally adaptive, but only to the extent that indicators of prestige and copied traits covary, and that

when indicator traits are also transmitted, then runaway selection can cause prestige-biased traits to take on maladaptively exaggerated forms due to runaway selection.

Content Biases

Another set of cultural transmission biases proposed by Richerson and Boyd (2005) to affect cultural evolution is direct or content-based biases, in which the characteristics of the cultural information itself affect its probability of being acquired, remembered, and passed on to others. This contrasts with the model-based and frequency-based biases, in which factors extrinsic to the cultural informational content—the identity of the model or the cultural trait's popularity—affect its transmission. Content biases have been extensively discussed by cognitive anthropologists (e.g., Atran, 1998; Boyer, 1994; Sperber, 1996), who argue that culturally transmitted representations are distorted or transformed to become more similar to cognitive attractors, which are particularly salient representations that are favored by preexisting cognitive biases. Cognitive psychologists have also recently argued that culturally transmitted information may converge on particular representational forms due to prior cognitive biases (Griffiths, Christian, & Kalish, 2008; Kalish, Griffiths, & Lewandowsky, 2007).

The notion that culturally transmitted information is distorted toward particular preexisting forms receives considerable support from the long-established research tradition in social psychology regarding the social aspects of memory. In classic experiments, Bartlett (1932) passed written text and pictures along linear chains of participants, with the previous participant's recall serving as input for the next participant in the chain. Bartlett and others who subsequently adopted this *transmission chain method* (e.g., Allport & Postman, 1947; Hall, 1951; Maxwell, 1936) found that transmitted material typically suffered a loss of detail, became more abstract, and was distorted according to preexisting knowledge structures, or what Bartlett called schemas. For example, Bartlett showed that unfamiliar elements in a Native American folktale, "The War of the Ghosts," were omitted or conventionalized by his British participants, while Allport and Postman (1947) found that descriptions of pictures were transformed according to participants' racial stereotypes, with descriptions of a White man attacking a Black victim switching to a Black man attacking a White victim in accordance with stereotypes of Black people as dangerous criminals. Since this early research, the notion that memory in general is an imperfect process of biased reconstruction has been repeatedly confirmed by mainstream (nontransmission) memory studies (Loftus, 1996), while recent updated transmission chain experiments have begun to explore the specific directions in which culturally transmitted information is distorted. Kashima (2000) and Bangerter (2000) both found that information is distorted according to gender stereotypes as it is passed along transmission chains, while Mesoudi, Whiten, and Dunbar (2006) found that information concerning social interactions is transmitted with greater accuracy than equivalent nonsocial information. In general, these experiments support the claim that human cultural transmission does not have as high a fidelity as genetic inheritance: It is a process of reconstruction rather than replication (Atran, 2001; Sperber, 2000), with information readily distorted according to preexisting knowledge, stereotypes, attitudes, and beliefs. Consequently, content biases may play an important role in cultural evolution.

Sperber and Hirschfeld (2004) argued just this, explaining actual patterns of cultural diversity and stability as the result of cultural transmission toward preexisting cognitive attractors. For example, the rich and similarly structured ecological knowledge shown by diverse hunter-gatherer societies worldwide may be influenced by a universal folk-biology module, which favors the acquisition of ecological knowledge that fits a specific preexisting structure (Atran, 1998). Similarly, supernatural concepts are argued to spread and persist because they are minimally counterintuitive, that is, they contain a small number of elements that violate certain cognitive expectations but not excessively so. For example, ghosts violate certain intuitions regarding folk physics (e.g., they can pass through walls) but act consistently with other intuitions regarding folk psychology (e.g., they seek revenge). The pervasiveness of minimally counterintuitive religious and supernatural beliefs across the world attests to the strength of this particular content bias (Atran & Norenzayan, 2005; Boyer, 1994), as does the persistence of minimally counterintuitive folktales through history (Norenzayan, Atran, Faulkner, & Schaller, 2006). Barrett and Nyhof (2001) used Bartlett's (1932) transmission chain methodology to test this hypothesis experimentally, finding that minimally counterintuitive concepts were passed along transmission chains with greater fidelity than intuitive concepts (which did not violate any intuitions) and bizarre concepts (which were unusual but again did not violate intuitions). Another example is Heath, Bell, and Sternberg's (2001) investigation of urban legends. A set of experiments, as well as analyses of naturally occurring urban legends, found that the transmission of rumors depended to a large extent on the degree to which the rumor elicited emotional reactions of disgust in the recipient. Rumors involving disgusting actions, such as accidental ingestion of decomposing animal matter, were more prevalent and recalled better than equivalent rumors that elicited disgust to a lesser extent (see Harber & Cohen, 2005, for a supportive real-world test of this emotional-salience hypothesis). Finally, recent experiments and models by Kalish et al. (2007) and Griffiths, Christian, and Kalish (2008) show how culturally transmitted information may converge on the inductive cognitive biases of the individuals in the transmission chains; these inductive biases may be seen as equivalent to content biases, and these experiments found further support for their importance in cultural evolution. Kalish et al. showed experimentally that estimates of mathematical functions converge on linear functions of the form $y = x$ as they are passed along transmission chains, while Griffiths et al. found that transmission chains converge on a method of category learning (using a single dimension) that individuals find easiest to use. These biases reflect prior inductive biases for linear functions and single-dimension category learning found in single individuals.

However, an important qualifier to all of this research comes from social psychological research on cognitive tuning. Zajonc (1960) showed that whether an individual expects to be a receiver of information or a transmitter of information significantly affects the way in which that information is processed. Transmitters activate cognitive structures that are more differentiated into specific and easily identified subcomponents and that are more unified around an integrative theme; such a structure is designed to be more easily processed by the anticipated receiver. Receivers, in contrast, activate cognitive structures that are more general and less organized to more easily incorporate new information that they expect to receive. Relevance theory (Sperber & Wilson, 1995) similarly posits that utterances are designed by transmitters to be maximally relevant to receivers, that is, that they

contain the maximum amount of new information that can be understood by the recipient with the least amount of effort. Such factors as cognitive tuning and relevance have not been considered either in cultural evolutionary models or in the transmission chain experiments described above. In the former, individuals are assumed to exhibit the same traits whether they are transmitters or receivers of information. In the latter, participants are typically not told that they are part of a transmission chain, so there is no way of knowing whether their recall is constructed within a receiving or a transmitting context. Perhaps the frequent finding of transmission chain studies that information becomes schematized into specific subcomponents within a unifying theme (e.g., Bartlett, 1932; Mesoudi & Whiten, 2004) implies that participants are adopting a transmitting mode, although without systematically manipulating and comparing different cognitive tuning styles, this cannot be known for sure. In any case, ignoring cognitive tuning would appear to reduce the validity of these experiments and, by extension, cultural evolution models.

In summary, social psychologists (or researchers from other disciplines using recognizable social psychological methods) have shown that cultural transmission is readily distorted by content biases. Experimental work suggests that cultural information may be distorted to fit preexisting racial and gender stereotypes (Allport & Postman, 1947; Bangerter, 2000; Kashima, 2000) and that cultural transmission favors minimally counterintuitive representations (Barrett & Nyhof, 2001), information concerning social interactions (Mesoudi, Whiten, & Dunbar, 2006), and information that elicits reactions of disgust (Heath et al., 2001). An important aspect of this research is its interdisciplinarity: The above experimental findings are frequently complemented by (or originate in) findings from other social science disciplines such as cultural anthropology, as noted by Sperber and Hirschfeld (2004). The main benefit to social psychologists is the external validity offered by these other, more naturalistic disciplines. Just as evolutionary biology constitutes an overarching interdisciplinary framework that encompasses experimental and naturalistic methods, so too cultural evolutionary theory offers an interdisciplinary theoretical framework that encompasses the experiments of social psychologists and observational methods of cultural anthropologists (Mesoudi, Whiten, & Laland, 2006). A next step might be to measure the quantitative strength of content biases using transmission chain experiments, similar to the way in which biologists use breeding experiments to quantify the strength of various selective processes, as well as explicitly incorporate cognitive tuning into cultural transmission models and experiments.

Intergroup Behavior

One of the most striking findings in social psychology has been related to intergroup relations (Brewer & Brown, 1998; Brewer & Kramer, 1985; Tajfel, 1982): People generally show a strong tendency to view groups with which they identify as superior to other groups and are more willing to help members of their own group than members of other groups. This was demonstrated in Sherif, Harvey, White, Hood, and Sherif's (1961) classic Robber's Cave study, in which boys at a summer camp were arbitrarily divided into two groups and made to perform a series of competitive tasks pitting the two groups against each other. The boys rapidly developed strong ingroup favoritism, viewing their own group as superior to the other group in several aspects, as well as outgroup derogation, exhibiting hostility toward members of the outgroup. Subsequent minimal group

experiments (Tajfel, 1982; Tajfel, Billig, Bundy, & Flament, 1971) showed that ingroup bias arises even when there is no competition or any rationale for favoring the ingroup. In these studies, boys were arbitrarily divided into two groups and asked to allocate money to other participants. Despite the arbitrary and temporary nature of these groups and the lack of any group-based reward or conflict, boys nevertheless awarded more money to anonymous members of the ingroup than to anonymous members of the outgroup. Indeed, participants typically maximized the relative performance of the ingroup relative to the outgroup at the expense of their individual (or their own group's) absolute earnings. Subsequent experimental research has elaborated upon several of these initial findings from the Robber's Cave and minimal group studies. Attitudes toward the outgroup have been found to become increasingly negative in response to threats to the ingroup, either realistic threats, where the outgroup is seen to be taking resources such as land, wealth, or jobs from the ingroup, or symbolic threats, where the outgroup is seen to hold values or beliefs that conflict with those of the ingroup (Riek, Mania, & Gaertner, 2006; Stephan & Stephan, 2000). People have also been shown to emphasize the homogeneity of both the ingroup and the outgroup through the use of positive and negative stereotypes (Boldry, Gaertner, & Quinn, 2007; Rubin & Badae, 2007; Simon, 1992). Lest it be thought that these findings are simply artifacts of experimental laboratory setups, more naturalistic experiments have found similar effects. Hornstein, Masor, Sole, and Heilman (1971) found that residents of a Jewish area of New York City were more likely to help an unknown stranger who held pro-Israel (i.e., ingroup) views than a stranger who held pro-Arab (i.e., outgroup) views, while Levine, Prosser, Evans, and Reicher (2005) found that Manchester United soccer fans were more likely to help strangers in distress when they were wearing Manchester United shirts than when they were wearing shirts of the rival Liverpool soccer team.

Minimal group experiments gave rise to social identity theory (SIT: Brown, 2000; Hornsey, 2008; Tajfel & Turner, 1979), in which ingroup bias and intergroup conflict are said to arise from a desire to achieve or maintain a positive social identity as a member of a group. The subsequent self-categorization theory (SCT: Oakes, Turner, Hogg, Reicher, & Wetherell, 1987) proposes that the desire to maintain a group-based social identity causes people to categorize themselves and others as members of distinct and internally homogeneous groups. While research originating in the SIT-SCT tradition has revealed valuable insights into intergroup processes, the ultimate explanation for such strong ingroup favoritism and outgroup discrimination is less clear. Some SIT researchers argue that ingroup favoritism functions to enhance self-esteem (e.g., Abrams & Hogg, 1988), while others propose that intergroup processes are caused by the "motivation for distinctiveness and self-definition" (Hornsey, 2008, p. 215). However, these explanations—to enhance self-esteem or promote group distinctiveness—remain fairly proximate. The question simply gets moved one step further back: Why does favoring the ingroup boost self-esteem and make people feel good? Alternatively, why do people seek to make their group distinct from others? An ultimate evolutionary explanation is needed to answer such questions.

Classic findings from evolutionary biology highlight just how puzzling the intergroup phenomena observed by social psychologists are. Consider one of the more distinctive social psychological findings, that people help ingroup members more than outgroup members. Evolutionary biologists typically explain altruistic behavior in one of two ways: kin selection or reciprocal altruism. Kin selection models

(Hamilton, 1964) show that genetic predispositions toward helping one's genetic kin are likely to spread, given that those kin are likely to share similar genetic predispositions toward helping kin, and so, helping kin equates to helping to spread kin-altruistic genetic predispositions. While humans obviously show strong altruistic behavior toward kin (e.g., parents care for their children), the intergroup processes noted above have been observed in experiments involving genetically unrelated participants, so it does not appear that kin selection can explain ingroup favoritism. Reciprocal altruism models (Trivers, 1971) show that altruistic behavior can evolve if an altruistic act is repaid back to the altruist in the future with a similar altruistic act from the original beneficiary: "I'll scratch your back if you scratch mine." Again, however, this does not appear capable of explaining the minimal group experimental results in which strangers are brought together and exhibit ingroup altruism with no promise of any future return either in the experiment or after the experiment has ended.

What about group benefit, in either abstract terms (e.g., enhanced self-esteem) or material benefits (e.g., the rewards in Sherif et al.'s, 1961, study)? Such explanations resemble past arguments in biology for group selection, which similarly purported to explain pro-group behavior in terms of group benefit. Early group selection models (e.g., Wynne-Edwards, 1962) assume that altruism occurs in nature because groups of altruists will, through the mutual benefit accrued from helping one another, be more likely to survive and reproduce than groups in which individuals do not help one another. The problem with group selection models such as this is that groups of altruists are vulnerable to free riders—group members who receive the benefits of other group members' aid but who do not pay the cost of helping others. Free riders thus have higher fitness than altruists, and soon, free riders dominate the group and ingroup favoritism disappears. Social psychological research has demonstrated that people may also free-ride (Kerr, 1983) or loaf on the efforts of other group members (Latané, Williams, & Harkins, 1979) in the absence of an outgroup. Yet free riding and social loafing do not appear to reduce the ingroup bias observed in minimal group experiments. Migration is also a problem for genetic group selection explanations: Migration generally reduces the necessary between-group differences, and free riders can move from group to group taking benefits before being detected (Enquist & Leimar, 1993). Finally, the puzzle deepens when one considers that humans appear to be the only species to exhibit ingroup altruism toward nonkin. This extends even to humans' closest living relative species, chimpanzees. Silk et al. (2005) found that unrelated members of the same chimpanzee group who were given the opportunity to either (a) receive food or (b) receive the same amount of food but also give food to one of their fellow group members did not show a preference for the latter and thus failed to exhibit even this modest (noncostly) form of ingroup bias.

To recap, social psychologists have found that humans exhibit a powerful tendency to help others who are perceived as belonging to the same group. This tendency does not appear to be the result of either kin selection or reciprocal altruism, the standard genetic evolutionary explanations for cooperation, and is unique to humans. These findings have led some researchers to argue that human ingroup altruism is connected in some way to cultural evolution and specifically that it is a result of cultural group selection (Boyd & Richerson, 1985; Campbell, 1975; Richerson & Boyd, 2005). The cultural group selection hypothesis posits that, during recent human evolutionary history, there has been constant

competition between cultural (rather than genetic) groups of people. Those cultural groups that possessed stronger prosocial norms encouraging within-group cooperation would have been more successful in intergroup competition than cultural groups that possessed weaker or no prosocial norms and who were internally uncooperative. Under certain conditions (see below), the more cooperative groups would have gradually replaced the less cooperative groups, resulting in the spread of ingroup altruism norms such as those observed by social psychologists. This intergroup competition may have occurred either militarily, because group-beneficial norms such as self-sacrifice gave cooperative groups an advantage and group-detrimental norms such as desertion put less cooperative groups at a disadvantage, or ideologically, where people living in less cooperative groups voluntarily chose to join more cooperative groups because they were attracted by their prosocial norms. An example of the latter might be the rapid growth of Christianity from minor cult to the official religion of the Roman Empire in just a few hundred years, in part because pagans were attracted to Christian prosocial norms such as caring for the sick and the poor (Richerson & Boyd, 2005, p. 210). Crucially, Richerson and Boyd (2005) argued that cultural group selection is less vulnerable to the problems faced by genetic group selection (i.e., free riders receiving benefits without paying costs and migration eliminating group differences) because cultural processes such as conformity and moralistic punishment of norm violators cause both free riders and immigrants to adopt existing group-beneficial norms.

From this perspective, the findings of social psychologists that people are more altruistic toward members of the ingroup relative to the outgroup is the result of an ultimate evolutionary process of cultural group selection, during which ingroup favoritism norms spread at the expense of selfishness norms (Richerson & Boyd, 2005, pp. 221–222). This hypothesis also accords with specific findings that ingroup favoritism is stronger when the ingroup is threatened by the outgroup in terms of either resources or values (Riek et al., 2006). These are the conditions under which intergroup conflict is most likely to occur, so one might expect that past cultural group selection favored norms that specifically act in response to group threat. Also consistent are the experimental findings that participants maximize relative group success rather than absolute individual or group welfare (Tajfel et al., 1971) given that cultural group selection will act on relative rather than absolute success: It does not matter that groups are doing well, they must be doing well relative to other potentially rival groups. Cultural group selection also crucially requires that different groups are relatively culturally homogeneous to prevent free riders emerging and groups breaking up and that there are significant intergroup differences for selection to act on different groups. This is consistent with findings that people emphasize within-group homogeneity and between-group differences (Simon, 1992; Tajfel, 1982). The finding that this occurs especially in response to group threat (Rothgerber, 1997) also fits the cultural group selection hypothesis. A final point to note is that the SIT–SCT explanations of ingroup altruism (enhanced self-esteem, a desire to promote group identity) discussed earlier can be seen as proximate motivational factors by which culturally group selected prosocial norms operate; as noted previously, these should not be seen as alternative explanations, rather as complementary explanations aimed at different explanatory levels.

An intriguing fit between the social psychological research and the cultural group selection hypothesis concerns the finding from the former that the boundaries that define ingroups and outgroups are often quite flexible. For example, Levine et al. (2005) found that while Manchester United fans helped other Manchester United fans more than fans of the rival Liverpool team, when participants were primed to identify with football fans in general, then Manchester United fans helped both sets of supporters equally (although more than nonfootball fans). Unlike genetic group selection, cultural group selection does not require the physical death of all members of the unsuccessful group, just the extinction of the unsuccessful group's cultural norms. Flexible ingroup–outgroup boundaries would allow people to switch groups in this manner. However, if ingroup–outgroup boundaries are too flexible, then stable cultural groups will not form in the first place, and cultural group selection cannot act. Thus, one might predict some intermediate level of group boundary flexibility.

Specific cultural evolutionary models provide further predictions regarding the way in which group boundaries should be flexible. As well as militaristic conquest, cultural group selection can also act when people selectively copy group-beneficial norms from more successful, more cohesive groups (Boyd & Richerson, 2002) and when people selectively migrate from unsuccessful groups to successful groups (Boyd & Richerson, 2009). Both of these processes can lead to the spread of group-beneficial norms when there is a moderate degree of intergroup diffusion or migration and when the group-beneficial norm of the outgroup is of sufficiently higher payoff than the existing ingroup norm. These models therefore provide a set of novel predictions that might be tested using modified minimal group experiments: that people should be more likely to adopt the group-beneficial beliefs, practices, or ideas of more successful (richer, less violent, less corrupt) groups than their own and that people should be more likely to move to such groups (if such movement is allowed in the experimental setting), with the probability of these occurring varying as a function of the payoff difference between the ingroup and the outgroup.

Minimal group experiments might also be adapted along the lines of Jacobs and Campbell's (1961) multigenerational replacement method to simulate the gradual emergence of prosocial norms in the social psychology lab and test the conditions under which existing prosocial norms are activated. Such studies might resemble the intergroup trading experiments conducted by Insko et al. (1980, 1983), in which groups made and traded paper goods and group members were gradually replaced with new, untrained group members. These studies found that cooperative microsocieties, which contained subgroups that voluntarily traded different types of paper goods, achieved significantly higher payoffs than internally uncooperative microsocieties, in which one subgroup could forcibly confiscate the paper goods of other subgroups. Although not designed as a direct test of the cultural group selection hypothesis, these studies provide suggestive support that internally cooperative groups of people would have outcompeted internally uncooperative groups of people in the past and that (unlike chimpanzees) human social psychological mechanisms allow such a process to occur.

In summary, although it is far from conclusively supported,⁴ the cultural group selection hypothesis offers an intriguing ultimate explanation for the striking ingroup favoritism observed in numerous social psychology experiments, as well as several other specific experimental findings such as tendencies toward intragroup homogeneity and responses to group threats. The cultural group selection hypothesis also makes the specific predictions that intergroup boundaries should be selectively porous to group-beneficial (rather than individual-beneficial) norms of successful outgroups and that people should be more likely to migrate to such groups, but only under certain conditions (e.g., when there is a large payoff difference between the ingroup and outgroup norm).

Links to Other Areas of Psychology

Although this article has focused on the potential links that can be made between cultural evolutionary theory and social psychology, similar links can also be made between cultural evolutionary theory and other branches of psychology. Although space constraints do not allow a full exposition of these links, they are briefly reviewed in the following sections.

Cognitive Psychology

In general, many of the cultural evolution models and experiments discussed so far have been quite psychologically impoverished, typically assuming, for example, that people passively acquire knowledge and beliefs from others with little detail of the cognitive processes that govern this transmission. These models would therefore benefit from incorporating findings from cognitive psychology regarding how information is acquired, processed, stored, and transmitted. Some of the work discussed in the section above on content biases has taken steps toward addressing this shortcoming, showing, for example, how cognitive processes determine the kinds of representations that people can most easily comprehend, remember, and pass on to others (Sperber & Hirschfeld, 2004), such as minimally counterintuitive religious and supernatural beliefs (Norenzayan et al., 2006) and folk biological knowledge (Atran, 1998). Griffiths, Kalish, and Lewandowsky (2008) integrated Bayesian models of human cognition with cultural evolutionary methods and concepts, predicting that cultural representations should in many cases converge on the inductive biases of the cultural learners. Mesoudi and Whiten (2004) found experimentally that culturally transmitted descriptions of everyday events were gradually described at increasingly higher levels of a hierarchical knowledge structure, consistent with script theories from cognitive psychology. In all of these cases, findings from cognitive psychology have been used to predict and explain changes in culturally transmitted information, while a cultural evolutionary framework has encouraged cognitive psychologists to explore the population-level consequences of cognitive processes.

More mechanistic cognitive models can provide insights into the underlying mechanisms of cultural transmission. Much research has been devoted to the correspondence problem of imitation (Brass & Heyes, 2005): How does an observer translate a model's external motor actions into muscle activations within the observer's own body that result in matching motor actions? Brass and Heyes (2005) argued that this problem is solved using general purpose associative learning mechanisms, rather than specialized

mechanisms devoted exclusively to imitation (although see Whiten, 2005). At a neural level, the recent discovery of mirror neurons in monkeys, which fire when specific actions are either observed or executed, has led to speculation that the mirror-neuron system forms the neural basis for imitation (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). Further research in cognitive psychology and cognitive neuroscience will undoubtedly reveal details of the underlying transmission mechanisms that allow and influence large-scale cultural evolution.

Another relevant debate has revolved around the issue of language acquisition. Traditional nativist theories of language assume that universal features of language structure result from strong innate (genetic) biases in language acquisition, as opposed to general-purpose individual learning. Recent cultural evolutionary models, however, have shown that adding cultural transmission to the picture may qualify this earlier conclusion. Kirby, Dowman, and Griffiths (2007) showed analytically that weak inductive biases in the cultural acquisition of language may result in linguistic universals without the need to assume strong innate specification. This is primarily because of the bottleneck that is introduced when children must learn an entire language from a small subset of models; this bottleneck forces languages to adapt to aspects of cognition, rather than vice versa, resulting in a universal language structure. Recent experiments have simulated this process of language adapting to cognition (Kirby, Cornish, & Smith, 2008). This

⁴ It is sometimes argued (e.g., Alexander, 1979; Cosmides & Tooby, 1992) that all human altruism can be explained in terms of standard biological concepts of kin selection and reciprocity. These arguments propose that ingroup favoritism evolved when humans' hominin ancestors were living in small groups of closely related and frequently interacting individuals, such that kin selection and reciprocity would have favored a general predisposition to help most if not all individuals one would have ever interacted with. Since the invention of agriculture, however, modern humans have been living in much larger societies in which they frequently interact with unrelated strangers. Even though it is biologically maladaptive to help these individuals, human "stone-age brains" have not yet adapted to the novel social environments of the present day and so continue to help indiscriminately. While this explanation is plausible, Richerson and Boyd (2005) reviewed ethnographic and paleontological evidence suggesting that ancestral hominin populations were too large and intergroup contact was too frequent for kin selection or reciprocity to have favored the ingroup favoritism observed by social psychologists. The environmental mismatch hypothesis also assumes a tightly genetically controlled and inflexible human cognition that fails to correctly recognize kin and track reciprocal exchanges in modern environments, assumptions that many psychologists might find questionable (see Caporael, Dawes, Orbell, & van de Kragt, 1989, for further arguments against purely egoistic explanations of human altruism). Critics of cultural group selection models also argue that group extinction rates have not been high enough to permit group-level selection. Ethnographic evidence suggests that among precontact, small-scale Papua New Guinea societies, around 10% of groups went extinct every 25 years (Soltis, Boyd, & Richerson, 1995). While this is high enough to permit cultural group selection to occur, at this rate it would take 500–1,000 years for group-beneficial norms to become common (Soltis et al., 1995). While this is too slow to explain recent rapid changes in social norms over years or decades, cultural group selection may have been responsible for the long-term spread of entire religions or empires over the space of several centuries. However, other processes such as the preferential copying of beneficial traits from successful outgroup members (Boyd & Richerson, 2002) and nonrandom migration of people from less successful to more successful groups (Boyd & Richerson, 2009) may speed up this process.

line of research shows how a consideration of cultural evolution might significantly transform the understanding of language structure and acquisition.

Developmental Psychology

One way of determining the cognitive mechanisms that underlie cultural learning is by tracking the emergence of cultural learning in children in relation to other developing cognitive abilities. Heyman (2008) showed how children gradually come to recognize that different models can vary in their knowledge and reliability and, later, that models can hold false beliefs and exhibit intentional deception, with the latter depending on an unfolding theory of mind. Other experimental studies have shown that from a very early age, infants and children take other people's goals and intentions into account when copying their actions, again to an increasing extent as theory of mind abilities develop (Carpenter, Call, & Tomasello, 2005; Gergely, Bekkering, & Kiraly, 2002). Findings such as these suggest that shared intentionality is crucial to human social learning processes and may underpin several aspects of human cultural evolution (Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Evidence from developmental psychology can also address a fundamental issue within cultural evolutionary theory concerning the extent to which people learn from their parents (vertical cultural transmission) or from their peers (horizontal cultural transmission). Developmental psychologists have long emphasized the influence of parents (e.g., within attachment theory: Bowlby, 1969), although subsequent researchers have challenged this assumption and emphasized instead the influence of peers via horizontal cultural transmission (Harris, 1995). Cultural evolutionary models highlight the importance of this debate: Vertical transmission and horizontal transmission are predicted to have quite different population-level consequences (Cavalli-Sforza & Feldman, 1981) and are thought to be adaptive under different conditions (McElreath & Strimling, 2008). Longitudinal developmental studies tracking who children learn from at different stages of development would be crucial to resolving this issue.

Comparative Psychology

Comparative psychologists have used many of the same experimental methods as social psychologists to test for the presence of social learning in nonhuman species, such as the transmission chain method and the replacement method (Whiten & Mesoudi, 2008). The resulting body of experimental findings has shown that social learning is surprisingly common in the animal kingdom, observed in various species of insects, fish, birds, and mammals (Galef & Laland, 2005; Leadbeater & Chittka, 2007). Comparative psychologists have also delineated an array of social learning mechanisms, including imitation, goal emulation, result emulation, affordance learning, observational conditioning, and stimulus enhancement (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Different mechanisms likely have different implications for the fidelity of information transmission yet are rarely explicitly differentiated in human cultural evolution models or experiments.

Despite the widespread taxonomic distribution of social learning and the observation of regional cultural differences in several species (e.g., Whiten et al., 1999), only humans appear to have the

ability to accumulate cultural traits over successive generations (Tomasello, 1999). Indeed, it is this accumulation (in Darwin's terms, descent with modification) that allows one to describe human culture as an evolutionary process. While cultural evolutionary models have addressed the issue of cumulative culture (Boyd & Richerson, 1996; Enquist & Ghirlanda, 2007), the reason for this apparent uniqueness is most likely to come from further comparative studies of cognitive cultural capacities across species. While there is no clear consensus as to the identity of the mechanisms underlying cumulative cultural evolution, candidates include intentionality, teaching, and language (Tomasello, 1999). No doubt future comparative studies will reveal the precise cognitive mechanisms and evolutionary origins of cultural transmission.

Cultural Psychology

Cultural psychologists have documented extensive cross-cultural differences in psychological processes (Heine, 2008; Markus & Kitayama, 1991; Nisbett et al., 2001), yet explanations of these cross-cultural differences remain sketchy (Heine & Norenzayan, 2006). The microevolutionary processes of cultural evolution, such as the cultural transmission biases discussed above and studied empirically by social psychologists, might aid this explanation. For example, models suggest that conformity can act to maintain between-group variation despite the presence of migration (Henrich & Boyd, 1998), which might explain why cross-cultural differences in psychological characters persist despite increasingly porous cultural boundaries brought about by globalization. Furthermore, cross-cultural experimental studies (Henrich et al., 2005) have revealed nontrivial cultural variation in the extent to which people cooperate in economic games, findings that might be explained by the cultural group selection hypothesis discussed above.

Conclusions

In this article, I have outlined five areas—social learning, conformity, model-based biases, content biases, and intergroup relations—in which experimental findings from social psychology can illuminate aspects of cultural evolutionary theory, or cultural evolutionary theory can illuminate social psychological findings, or both. I hope to have shown that experimental findings from social psychology provide valuable details regarding the microevolutionary processes that drive cultural change and that cultural evolutionary theory provides important ultimate explanations for social psychological phenomena as well as ways of linking such proximate phenomena to wider patterns of actual cultural change. In most cases, there is no direct contradiction between cultural evolutionary theory and social psychological theories. Both emphasize the importance of social learning, conformity, intergroup behavior, and so on. There are, however, a number of points at which a mutual appreciation of the other field's findings and theories might benefit both fields and where findings from one field can be used to make specific, novel predictions that can be tested in the other.

Several findings from social psychology challenge the assumptions of cultural evolutionary models and theory. First, what are typically treated in cultural evolutionary models as cultural traits, a uniform and ambiguous category that covers all culturally transmitted information, are actually quite diverse phenomena. Social

psychology experiments have revealed important differences, for example, between factual beliefs and subjective preferences in the extent to which each is vulnerable to social comparison with similar others. Cultural evolutionary models would do well to specify exactly what kind of culturally transmitted trait (belief, attitude, value, skill, ability, representation, etc.) is being modeled, and consider social psychological evidence related to that specific trait. Second, another aspect of cultural evolutionary models that appears too simplistic is how the environment is conceptualized. Typically, cultural evolutionary models and recent experiments specify a set of possible cultural traits (usually two) and an independent environment, with one cultural trait being more effective in a particular environmental condition than the other trait. While this might be appropriate for certain factual beliefs or skills, subjective attitudes often do not have an objective fitness: Attitudes such as a liking for jazz music cannot be correct in any objective sense. Many other behaviors may have an objectively correct form, but this is determined not by an external (ecological) environment but rather by the behavior of others. For example, driving on the left side of the road is clearly adaptive in the United Kingdom, but this is only because everyone else drives on the left. The correct behavior is determined by social agreement rather than any objective standard, given that in most other countries, people drive on the right with no difficulty. Cultural evolutionary models have yet to systematically explore different kinds of environments or standards of cultural fitness, although several evolutionary methods exist that might be useful in pursuing such a task, from evolutionary game theoretic analyses of frequency-dependent behavior (Gintis, 2000) to niche construction, in which behavior may shape environments as well as vice versa (Odling-Smee, Laland, & Feldman, 2003). Third, the section on content biases highlights how cultural evolution models and experiments have neglected the crucial social psychological phenomenon of cognitive tuning: Whether a person expects to be a receiver or a transmitter of information results in significantly different ways of processing information, differences that may have important consequences for long-term cultural evolutionary change. Finally, findings from several social psychology literatures suggest that refinements of a simplistic success bias (preferentially adopting the traits of successful models) might be required. The social comparison literature suggests that success bias may be qualified by similarity—successful models that are too dissimilar are not copied, especially with regard to subjective attitudes—while the elaboration likelihood model suggests that model characteristics are more important in cultural transmission when personal involvement is low and processing is peripheral.

Conversely, cultural evolutionary models have generated a number of formal predictions that can be tested using social psychological methods and, in some cases, suggest refinements of existing social psychological theories. Simple evolutionary models predict that social learning should be employed when environments are stable enough that copied behaviors are not outdated and when individual learning is relatively costly or inaccurate. Although previous social psychology experiments provide tentative support for these predictions, systematic tests remain lacking. Regarding specific social learning biases, both conformity and prestige or success bias are predicted to be adaptive under a wide range of conditions and often provide an effective alternative to both costly or inaccurate individual learning and unbiased, indis-

criminate social learning. This might be seen to challenge the assumption occasionally made by social psychologists that cultural processes such as conformity or social comparison are somehow maladaptive or undesirable, as noted previously by Campbell (1975). Unfortunately, the widespread use in social psychology of participant deception through the use of confederates or misinformation prevents adequate tests of the adaptiveness of cultural learning processes, given that the experiments are set up a priori to demonstrate maladaptive behavior. While contemporary social psychologists now commonly recognize that cultural processes can be adaptive (e.g., Baumeister & Leary, 1995), deception is still in frequent use in experimental social psychology (Hertwig & Ortmann, 2008). Instead, the use of genuine, nondeceptive tasks should be encouraged, tasks in which participants can use social learning strategies in situations that are not biased toward demonstrating their maladaptiveness.

Cultural evolutionary models also provide a more precise and useful definition of conformity than is commonly used in the social psychology literature, one that distinguishes conformity from unbiased, nonconformist cultural transmission. This distinction has important population-level consequences and should be taken into account in future experimental studies of conformity. More specific predictions regarding prestige bias can also be made, for example, that prestigious individuals should be copied to the extent that indicators of prestige and copied behaviors covary. Finally, the cultural group selection hypothesis makes some specific predictions concerning the nature of intergroup boundaries, that is, that under certain conditions ingroups should selectively adopt the group-beneficial norms of successful outgroups and that migration across boundaries should be selectively directed toward successful groups, as a function of payoff differences between ingroup and outgroup norms.

Cultural evolutionary theory also emphasizes the long-term, population-level consequences of various individual-level cultural transmission biases; as such, multiple-generation experimental methods that allow such long-term consequences to be measured are needed, such as the transmission chain method (Bartlett, 1932) or the replacement method (Jacobs & Campbell, 1961). Indeed, neither of these methods has received much attention in recent years except from researchers interested in cultural evolution (e.g., Caldwell & Millen, 2008; McElreath et al., 2005; Mesoudi, Whiten, & Dunbar, 2006). A broader cultural evolutionary framework may encourage renewed interest in such methods within social psychology, as well as reinvigorate branches of social psychology that have become marginalized in recent years but that gain added importance within cultural evolutionary theory, such as social learning theory (Bandura, 1977).

One of the prime benefits of cultural evolutionary theory is its interdisciplinarity, allowing formal links to be made between psychological phenomena studied in the psychology lab and cultural phenomena studied by anthropologists, economists, sociologists, historians, and others. For example, the experimental studies of success bias using the virtual arrowhead task (Mesoudi & O'Brien, 2008a) were explicitly linked to patterns of actual cultural variation in the archaeological record: Prehistoric arrowheads 1,500 years old found in what is now Nevada have been found to exhibit low diversity, consistent with success-biased cultural transmission causing hunters to adopt the single arrowhead of the most successful hunter, while prehistoric arrowheads found in what is now

California exhibit much greater diversity, consistent with individual trial-and-error learning causing arrowhead designs to diverge (Bettinger & Eerkens, 1999). Experimental simulations confirmed that these learning rules do indeed generate these patterns of diversity, but only under certain conditions, such as when there are multiple locally optimal arrowhead designs rather than a single globally optimal design (Mesoudi, 2008; Mesoudi & O'Brien, 2008b). In the latter case, individual learning causes each group member to converge on the global optimum, resulting in similarly low diversity as observed for the cultural learners. This novel prediction could not have been tested using archaeological methods alone, given the difficulty of reconstructing past fitness environments, and highlights the value of social psychological experiments. Other examples where cultural evolutionary theory has been used to link proximate social psychological phenomena to wider cultural patterns include intergroup processes being linked to both ethnographic data regarding ethnocentrism (LeVine & Campbell, 1972; Soltis et al., 1995) and the origin of the state (Insko et al., 1980, 1983) and conformity being linked to sociological patterns of the diffusion of innovations (Henrich, 2001).

Such work provides social psychological research with much needed external validity: If the signatures of social psychological phenomena that are observed in the laboratory can be found in the archaeological, sociological, or ethnographic records, then confidence in both their existence and their importance increases. Conversely, social psychology experiments provide the internal validity—via the isolation and manipulation of variables, controlled environments, random subject assignment, complete data sets, and so on—that is needed to test cultural evolutionary hypotheses (Mesoudi, 2007b). Indeed, experimental methods, with their high internal validity and low external validity, perfectly complement more observational and historical methods employed in cultural anthropology, sociology, history, and archaeology, which offer high external validity but low internal validity. For example, ethnographers cannot assign different communities to different control and experimental conditions, and archaeologists cannot rerun history to see whether a particular trend is significant or just due to chance. Just as the interdisciplinary, multiple-method, synthetic approach of evolutionary biology has paid dividends in the effort to understand the complexities of biological evolution (Mayr & Provine, 1980), so too an interdisciplinary, multiple-method, synthetic approach to the study of cultural evolution can pay dividends in efforts to better understand human cultural change (Mesoudi, Whiten, & Laland, 2006), with social psychology playing a vital role in these efforts. And not just social psychology: In the previous section, it has been shown how mutual links might be forged between cultural evolutionary theory and several other branches of psychology. Given that humans are a truly cultural species (Heine & Norenzayan, 2006; Richerson & Boyd, 2005; Tomasello, 1999), there are likely to be few areas of psychology that would not benefit from a consideration of cultural processes, and cultural evolutionary theory provides the most scientifically rigorous means of conceptualizing and studying human culture that is presently available.

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