

Agency and Adaptation: New Directions in Evolutionary Anthropology

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Abstract

Neo-Darwinian evolution is widely acknowledged as the key framework for understanding the form and function of living systems, including myriad aspects of animal behavior. Yet extensions to human behavior and society are perennially challenged; debates are vociferous and seemingly irresolvable, and evolutionary approaches to human behavior are marginalized within much of anthropology and other social sciences. This review explores this contested terrain, arguing that although many critiques of evolutionary analyses of behavior are faulty, some valid concerns must be addressed. Human agency, behavioral plasticity, and the partial autonomy of cultural and historical change present real challenges to the standard evolutionary framework. However, several additions to the standard framework currently employed by evolutionary anthropologists and others address these concerns and provide a more comprehensive understanding of human behavioral evolution and adaptation. These additions include phenotypic adaptation, cultural transmission, gene-culture coevolution, and niche construction.

INTRODUCTION

Neo-Darwinian evolution is widely acknowledged as the key framework for understanding the history and function of living things, from viruses to ecosystems. The explanatory success of this framework extends to myriad aspects of animal behavior, from simple fixed-action patterns to complex life-history patterns and social interactions. Yet the application to human behavior and society is perennially challenged; debates are vociferous and seemingly irresolvable, and evolutionary approaches to human behavior remain minor themes with a taint of illegitimacy within much of anthropology and other social sciences. Although anthropological analyses of human behavioral adaptation have proliferated at a rapid rate in recent years, and have become more methodologically sophisticated and theoretically diverse, one would not imagine this to be the case if reading only the critiques published by nonevolutionary anthropologists (review in Lyle & Smith 2012); instead, these critiques focus heavily on books and magazine articles published for a popular audience and written primarily by nonanthropologists.

Here I review this contested terrain. I argue that although many critiques of evolutionary analyses of behavior are faulty, there are valid reasons for asking if the standard framework is sufficient to analyze human behavioral adaptation. In particular, human agency, behavioral plasticity, and the partial autonomy of cultural and historical change present real challenges for the standard evolutionary framework. However, several additions to the standard framework currently employed by evolutionary anthropologists and others, reviewed herein, provide a more comprehensive approach to analyzing human behavioral evolution and adaptation. These additions include phenotypic adaptation, cultural transmission, gene-culture coevolution, niche construction, and evolutionary game theory. I do not attempt a detailed review of the research accomplishments of evolutionary behavioral anthropologists, as that would require multiple topically focused articles. Instead, I address some key critiques of evolutionary anthropological research on behavior, focusing particularly on issues of agency and determinism, and provide an overview of key conceptual and theoretical developments that are relevant to these issues and critiques.

The term agency has become ubiquitous in the anthropological (and broader social science) literature in the past few decades. Often undefined, it has a variety of meanings and theoretical roles, from the structure-agency debate in sociology to practice theory, subaltern theory, etc. Sociocultural anthropologists and anthropological linguists embed a host of assumptions and agendas in the term; even a minimalist definition—“the socioculturally mediated capacity to act”—is followed by the claim that “all action is socioculturally mediated” (Ahearn 2001, p. 112). Rather than wade into these debates, I use the term simply to indicate intentional, conscious (self-aware) choice, leaving open the question of sociocultural mediation (or social construction). Yet I do share with agency theorists a recursive notion of causality: The world presents people with options and constraints, people make choices, and those choices alter the world (where “the world” is shorthand for relevant aspects of social and nonsocial reality).

This review addresses two related questions that link “agency” and “adaptation”: (a) Why would studies of human adaptation need to consider agency? (b) Why do anthropologists interested in agency need to (re)consider adaptation? In addressing the first question, I start from the premise that humans actively shape important aspects of their social and natural environments, and this in turn affects the adaptive dynamics and outcomes they or their descendants experience. It follows that the study of human adaptation must include explanatory logics that extend beyond (though not necessarily contravening) standard neo-Darwinian ones. And indeed, evolutionary anthropologists are actively engaged in just such research, as discussed below. For the second question, I consider what it would mean to broaden the set of forces that constitute agency beyond the hermetically sealed sociocultural. Doing so involves sketching how one can reconcile agency and the generative,

historical aspects of culture with contemporary understanding of biological and cultural evolution. Put briefly, people act on the basis of beliefs and preferences, norms and values, understandings and goals; but these in turn are generated by complex processes that include genetic, ontogenetic, and cultural adaptation.

The Standard Framework

Darwinian explanation is founded on three basic features of living things:

1. variation (between individuals or other units),
2. inheritance (of at least some of this variation), and
3. fitness effects (some variants are better at reproducing than others).

When these features hold, natural selection will act as an unintentional design force to fit organisms to their environments (i.e., to shape traits in relation to the selective forces that affect their chances of surviving and reproducing).

The neo-Darwinian synthesis refined this scheme, establishing that inheritance was instantiated by Mendelian genes, and new variation arose via genetic mutation that was blind to present or future adaptive benefit. In stark outline, organisms vary blindly, environmental interaction “selects” the winners (with some stochastic noise, to be sure), and adaptive fit evolves from this mechanistic process iterated over time. Evolutionary adaptation is localized, imperfect, myopic, and constrained in various other ways that are abundantly theorized and measured; however, it remains the only explanation for biological design that enjoys scientific consensus. Evolution by natural selection explains why living things exhibit complex design without invoking any designer; it explains how a process without goals can produce goal-directed organisms.

Sometimes key features of the selective environment consist of members of other species: predators, pathogens, or prey. Because these populations are also subject to evolutionary forces (variation, inheritance, differential success), the resulting evolutionary dynamic is coevolutionary, and models and analyses have been developed accordingly. Additional key interactions are with other members of the same species: allies, competitors, or mates. Here, coevolution occurs within the same population, and the analyses must be modified further to unravel the resulting evolutionary dynamics, using evolutionary game theory (see sidebar) (Maynard Smith 1982) or models of social selection (Nesse 2009, Wolf & Moore 2010). Evolutionary models of cooperation, parental investment and parent-offspring conflict, mating systems, and the like have been developed and extensively tested (Krebs & Davies 1997, Westneat & Fox 2010). On balance, the standard framework crudely outlined above has proven remarkably successful in understanding the diversity of life, including behavioral adaptations.

Yet these elaborations of the neo-Darwinian framework seem insufficient to some, particularly those concerned with understanding variation in human social behavior. Critics argue that the standard framework does not recognize, or may even obscure, the importance of human agency, the generative power of culture, and the ways in which humans transform environments rather than adapt to them (e.g., Fuentes 2009, Goodman & Leatherman 1998b, Joseph 2000, Marks 2012, Schultz 2009, Singer 1996, Smith 2009). Darwinism is castigated for being too deterministic, mechanistic, and reductionist (e.g., Ehrlich & Feldman 2003, McKinnon 2005; review in Laland & Brown 2011).

These criticisms are varied and complex and have themselves been subject to critical examination. Below, I briefly summarize these criticisms, particularly as they are said to apply current evolutionary analyses of human social behavior and institutions—referred to here as evolutionary behavioral anthropology (EBA). I then review key concepts, theories, and representative empirical work in this field, considering to what extent the criticisms accurately portray this body of research.

EBA: evolutionary behavioral anthropology

EVOLUTIONARY GAME THEORY

Game theory is designed to analyze behavior whenever the consequences of actions or choices of one individual or group vary according to the actions or choices of others (Gintis 2000, Maynard Smith 1982). A favored analytical tool in both evolutionary analyses of behavior and several fields of social science, game theory is increasingly utilized in evolutionary behavioral anthropology (Panchanathan 2013).

The basic logic of phenotypic adaptation posits that evolved mechanisms allow individuals to adjust to current conditions (i.e., vary their phenotype in an adaptive manner). In game theory, this is instantiated as a conditional strategy: Under condition X , play α ; under Y , play β , etc. Game theory allows one to analyze the consequences of a wide range of strategic interactions and discover whether there are single or multiple equilibria (or none at all, thus providing an analytical basis for indeterminacy). Anthropological applications include collective action problems in resource management, provisioning of public goods, the emergence of institutionalized inequality, and even variation in marriage systems (e.g., Alvard & Nolin 2002, Fortunato 2012, Smith & Choi 2007). Even when interests do not conflict, adaptive consequences of decisions or strategies may depend on what others are doing (known as a coordination game). The key advantage of evolutionary game theory over classical game theory is that it avoids unrealistic assumptions regarding rationality and information; rather than reasoning one's way to the optimal strategy in any situation, one can let natural selection sort out the winners or cultural dynamics replicate the most successful.

The key focus is on whether and how these analyses address key aspects of human behavior, such as agency, culture, and creativity.

CRITIQUES AND RESPONSES

Anthropological Critiques of Evolutionary Social Science

In his Curl Lecture, Nettle (2009) refers to a “division of labor between biology and the social sciences, whereby biologists agree to not pursue their—generally Darwinian—explanations for behavior into the human realm, because of the phenomenon of culture, and social scientists simply start from the fact of ‘culturality’ and feel no obligation to reconcile their work with the theories of evolutionary biology” (p. 223). This division of labor was institutionalized within anthropology, with an understanding dating at least to the time of Boas: that physical anthropology studies the body, and cultural anthropology the mind (or its manifestations in culture and social behavior), with the boundary between the two carefully respected. But that division is increasingly breaking down, and boundary transgressions occur regularly (although not without cries of trespass by aggrieved parties on each side).

Hostilities along the biology-culture boundary (or the evolution-agency boundary, if the reader prefers) have inspired various proposed resolutions. One is to let parties go their separate ways—to unpack the “sacred bundle” and acknowledge that the dream of a holistic anthropological discipline has outlived its usefulness (Cronk 2006, Segal & Yanagisako 2005). Others call for various reformulations of biological, biocultural, or evolutionary anthropology, including complex systems theory (Lansing 2003), constructivist evolutionary anthropology (Fuentes 2009), developmental systems theory (Schultz 2009), and niche construction (Laland & O'Brien 2010), among others. These alternative proposals share an emphasis on human agency, creativity, and freedom from the constraints of standard evolutionary dynamics. In many cases, they go beyond critiques of

evolutionary anthropology and call for reformation or wholesale rejection of the entire research program in evolutionary biology.

Underlying some (not all) of these critiques is a political argument. Consider the following statement from the foreword to a collection of essays by biocultural anthropologists advocating a new (and decidedly nonevolutionary) “biocultural synthesis”:

[I]t is naive to suppose that the evolutionary question is what really motivates the struggle between biological and cultural determinism. The real issues are political: Could human life be other than it is? If so, are some social organizations more in accord with “human nature” than others? Is bourgeois society the final completion of a human historical trajectory, embodying the best that human biology allows? The confrontation between biological and social explanations and their various hybrids is, at bottom, a question of constraints and enablements. It should not surprise us that conservatives speak only of constraints while the liberals celebrate flexibility and the openness of possibilities. (Levins & Lewontin 1998, p. xii)

This statement charges evolutionary analysis of human behavior with adherence to several pernicious doctrines: biological determinism, teleological and ethnocentric views of human history, and an underlying political or ideological conservatism. Although authored by biologists, it is not hard to find similar critiques by anthropologists (e.g., Marks 1998, 2012; McKinnon 2005; Pavelka 2002; Singer 1996; Turner 2005).

The question of alleged political/ideological motivation in EBA has been examined recently elsewhere (Lyle & Smith 2012) and is not addressed here. Rather, I focus on whether current scholarship in EBA (as contrasted with pop science writings) is prone to biological determinism, teleology, and ethnocentrism: Do evolutionary analyses of human social behavior deny or minimize agency, history, and cultural variation? But before we turn to these issues, and an examination of what current EBA research actually looks like, it is important to review briefly a key distinction in the explanatory logic of contemporary evolutionary biology.

Proximate versus Ultimate Explanation

The distinction between proximate and ultimate explanations was delineated most influentially by Mayr (1961). Put simply, proximate explanations concern how a trait or feature works, hence a focus on mechanisms (physiological, psychological, etc.). In contrast, ultimate explanations address why traits are designed the way they are. Ever since Darwin, the “why” posits an evolutionary design force, rather than a supernatural or teleological one. Thus, ultimate explanations are also known as functional accounts and ask how a trait of interest contributes to adaptive success or inclusive fitness or otherwise is generated or maintained by evolutionary forces such as natural selection and transmission dynamics.

The proximate–ultimate distinction is critical for this review’s topic for several reasons. First, the two types of explanations complement rather than compete with each other. Much confusion and needless debate concerning the causes of behavior have arisen from a failure to understand this point. When an evolutionary biologist proposes that a given bird species migrates south for the winter because doing so provides better survival prospects than does overwintering in the north, it is not an alternative to an avian physiologist’s account that points to hormonal control over flight patterns. Indeed, the evolutionary explanation is a hypothesis about why such hormonal mechanisms evolved; thus, the explanations are complementary. Similar complementarity exists for explanations of human behavior in terms of fitness maximization (ultimate) versus learning or enculturation (proximate); the evolutionary accounts are hypotheses (which may be right or

wrong—that is an empirical question) about why particular learning mechanisms or behavioral strategies might have been favored in a particular lineage and context.

Agency (intentionality) would seem to offer an alternative (nonevolutionary) answer to “why” questions about behavior in humans and perhaps other species that have complex nervous systems. Indeed, culture itself (or at least an evolutionary or historical process of cultural change) might offer a third ultimate explanatory option. I return to these issues below.

Finally, the proximate-ultimate distinction provides insight into the venerable issue of functional explanation in the social sciences (including anthropology). In outline, classical functionalism sought to account for observed practices and social institutions as devices to maintain some unintended beneficial outcome—often, social order itself. (Why do the Hopi beseech the gods for rain with ceremonies? Because doing so unites them in a common purpose that counteracts the destructive factionalism engendered by clan divisions.) Such explanations are now widely discredited for assuming homeostatic equilibria, system-level goals, and unjustified teleology. This last problem can be termed the functionalist paradox: How can beneficial consequences of a given practice or characteristic explain its existence or maintenance? As explicated by the social philosopher Jon Elster (1983), the solution requires specifying a feedback loop that allows consequences to reinforce the characteristic in question. In functional explanations of the evolutionary (ultimate) variety, that feedback loop is provided by natural selection: An actor A exhibits some characteristic C that produces a benefit B for this actor or her progeny (enhanced fitness); selection causes C to increase in frequency in future generations to the extent that it yields a higher B than some alternative C by another A in the same population (Smith & Winterhalder 1992b, p. 42). Some proponents of classical sociological functionalism alluded to a process of this nature, but most did not, and almost none provided evidence that such a feedback loop existed.

Although widely accepted within biology, and often marshaled to clarify debates about human behavior (e.g., Nettle 2009, Scott-Phillips et al. 2011), the proximate-ultimate distinction has its critics. Thus, Laland and colleagues (2011) have recently argued that the distinction breaks down when selective forces themselves evolve—for example, when sexual selection favors characters in one sex because of evolved preferences in the other sex, or when phenotypic plasticity allows acquired variation to drive evolutionary change. They further propose that developmental or cultural dynamics can drive evolutionary change and thus fall within the realm of ultimate causality. However, they continue to agree that proximate and ultimate explanations are complementary rather than competing and that the distinction remains useful in many contexts. (For more on this debate, see articles in a forthcoming issue of the journal *Biology and Philosophy*.)

ADAPTIVE MECHANISMS AND DYNAMICS

As noted above, several criticisms of EBA (and more broadly of standard evolutionary biology) argue that current approaches need to be augmented by new concepts, models, and mechanisms. In particular, existing approaches are seen as ignoring nongenetic forms of evolution, prioritizing natural selection over other design forces, or short-changing human creativity, culture, and cognition. However, an examination of current EBA research in light of these criticisms reveals that several mechanisms or processes for generating adaptive dynamics in addition to natural selection of genes are employed. In most cases, these are seen as supplements to or enhancements of the standard mechanism of genetic evolution by natural selection rather than as its wholesale replacement.

Phenotypic Adaptation

Phenotypic adaptation refers to changes in phenotype (observable aspects of an individual) that respond to environmental conditions adaptively—i.e., in ways that enhance the responder’s survival

and/or reproductive success. Skin tanning provides a heuristic example. Upon repeated exposure to sunlight, most people exhibit tanning, which provides protection against short-term skin damage as well as skin cancer. If exposure declines (e.g., seasonally), tanning reverses, allowing increased absorption of beneficial ultraviolet rays (Jablonski & Chaplin 2010). This facultative adjustment is adaptive (as outlined) but involves no genetic change (e.g., identical twins exposed to different amounts of sunlight will differ in skin pigmentation); hence, it meets the criterion of phenotypic adaptation. Yet the capacity for tanning is a genetically evolved adaptation and is genetically variable as well. The physiological processes at work are proximate mechanisms, the ultimate explanation of which is a history of differential exposure to sunlight with attendant fitness consequences.

Does this same logic apply to behavioral phenomena? Given the definition of phenotypic adaptation, we can fairly apply the label to behavioral capacities that are guided by genetically evolved mechanisms and respond adaptively to current conditions. At the proximate level, the kinds of mechanisms involved range from quite inflexible (e.g., rapidly learned aversion to novel foods which are followed by nausea, regardless of the actual link) to quite open-ended (e.g., learning processes involving conscious decision making). As a heuristic illustration of the latter, consider the view that technological innovations in subsistence are evaluated according to their effect on labor efficiency (net rates of food procured per unit labor time). Although obviously an incomplete account of what drives technological change, efficiency arguments do have widespread empirical support in archaeology and ecological anthropology (e.g., Winterhalder & Smith 2000). No one claims that “genes for better projectile points” or “genes for agricultural intensification” have undergone natural selection; instead, the argument is that people generally prefer innovations that provide higher returns on their labor, all else equal; this preference (and the perceptual machinery to detect changes in return rates) is the evolved mechanism, and technological innovations are more likely to be adopted if they match this preference. Understood this way, intentional problem solving, even that employing foresight, does not lie outside the purview of evolutionary adaptation, but rather is a particular form of phenotypic adaptation that relies at least in part on evolved cognitive mechanisms. Although direct evidence might be hard to come by, the hypothesis that these mechanisms evolved genetically to facilitate such flexible, creative, and adaptive behavior is highly plausible; in fact, it is difficult to imagine an alternative naturalistic explanation for why they exist. In any case, EBA research on phenotypic adaptation goes well beyond such plausibility arguments; some illustrative examples follow.

Parental investment. Reproduction is central to Darwinian evolution, so parental efforts are an obvious focus. In modern evolutionary biology, such efforts (material and behavioral) are treated as investments that can yield varying fitness dividends (Trivers 1972, Clutton-Brock 1991). The options for investment are myriad, but here I consider just one: investment in sons versus daughters. Our species exhibits a remarkable degree of variation in the presence and degree of sex-preferential investment by parents (and other kin); various lines of evidence make it highly likely that this variation is driven by local circumstances, norms, and beliefs rather than by any underlying genetic variation (e.g., genes for daughter preference or son preference). But evolutionists want to know what explains the variation in these proximate causes—why some norms and practices here, others there?

Abundant research indicates that sex-biased parental investment is often patterned adaptively across human societies (e.g., Borgerhoff Mulder 1992; Cronk 1991, 2007; Pollet et al. 2009; Voland 1998). Factors shaping variation in payoff to parental investment include relative cost (in fitness-related currencies) of raising sons and daughters, patterns of cooperation and competition between same-sex and opposite-sex siblings, and differences between sons and daughters in postmarital dispersal and ability to aid natal households. One important factor appears to be wealth transmission:

In many ecologies, sons who inherit wealth (e.g., cattle, money, political titles) can more readily convert this into offspring (via polygyny) than can daughters (Hartung 1982). However, daughters are never cuckolded (thanks to internal fertilization), so if there is little wealth to invest, daughters can offer a better return on parental investment (of time, care, food, etc.). Holden et al. (2003) present a formal model along these lines and use it to explain why horticultural Africans generally exhibit daughter-biased investment (which they term matriliney), whereas pastoral ones transfer wealth primarily to sons (patriliney), as observed long ago by Aberle (1961). Mattison (2011) has applied this model to a radically different setting in contemporary China and found that it can account for variation in parental investment there as well, even within the same ethnic group. More broadly, research to date supports the idea that sex-preferential parental investment in our species is a great example of phenotypic adaptation—i.e., response to local conditions that relies on evolved mechanisms (in this case, cognitive mechanisms as well as culturally evolved norms and beliefs) to enhance reproductive success.

Risk-taking behavior. People in the same society often differ remarkably in the degree to which they engage in risky behavior: violent altercations, consumption of drugs, exposure to sexually transmitted diseases (STDs), and pursuit of dangerous or uncertain forms of earning a living. Although psychological research may attribute such variation to personality variables (e.g., impulsiveness, time discounting), and social scientists may point to heterogeneity in cultural values and identities, this begs the question of what explains variation in these proximate causes. Viewing risk taking as a form of phenotypic adaptation offers important insights. The relevant evolutionary framework here is life-history theory (Hill & Kaplan 1999). Although the details are complex, the basic prediction is that high extrinsic mortality (i.e., that due to forces beyond the control of the individual) favors “fast” life histories: reproducing earlier and more often, making less effort to live a long life, and generally discounting the future (valuing present rewards relatively more and future costs relatively less).

Although evolutionary biologists generally study life-history variation across species, and emphasize genetic evolution of such parameters as age at first reproduction, the logic of phenotypic adaptation suggests that the same patterns should be found within a population if there is sufficient variation in extrinsic mortality as well as adequate behavioral flexibility. A growing number of EBA studies have taken just this approach. For example, Nettle (2010a) modeled variation in health-related behavior, arguing that because lower socioeconomic groups are exposed to much higher extrinsic mortality (via pollution, faulty infrastructure, bystander homicide, etc.) they should discount the future more and specifically take more health-related risks. He summarizes published evidence (mostly from industrialized societies) indicating that this behavior does occur, as expressed in higher rates of smoking and alcohol and drug abuse, poorer nutritional choices, greater voluntary exposure to STDs, and lower investment in protective health measures (even controlling for ability to pay). As Nettle points out, none of this means that poor people choose to live in unhealthy conditions; however, it does explain why people forced to live in such conditions would invest less time, effort, and money in future health benefits. It also, incidentally, illustrates a connection between what people desire (e.g., prosperity, good health, decent living conditions) and fitness outcomes.

But what about the reproductive side of fast life histories—do people facing high extrinsic mortality direct investment away from future gains in order to reproduce earlier and more often? In a pioneering study, Wilson & Daly (1997) analyzed demographic data from 77 neighborhoods in Chicago and found a strong relationship between mortality and reproductive timing; specifically, life expectancy at birth varied from 57 years (poorest neighborhood) to nearly 75 years (richest), whereas fertility in young women (aged 15–24) varied inversely (from 0.41 to 0.14 births per year).

Fertility rates at later ages (25–44) did not differ among neighborhoods, consistent with the fast life-history hypothesis. Nettle (2010b) analyzed variation in reproductive rates and parental investment across neighborhoods in contemporary England. He found that in poorer neighborhoods, age at first birth is earlier, birth weights are lower, and breastfeeding is curtailed (resulting in earlier return of fecundability). He concludes that “fast life history is a comprehensible response, produced through phenotypic plasticity, to the ecological context of poverty, but one that entails specific costs to children” (Nettle 2010a, p. 387). In follow-up research, Nettle (2011) explored the proximate mechanisms linking earlier reproduction among poor English women to lower life expectancy and concluded that developmental, decision making, and social-learning factors all play a role. Similarly, Placek & Quinlan (2012) analyzed the relationship between population-level adolescent fertility and extrinsic mortality risk in a United Nations database; statistical analysis demonstrated that onset of reproduction was significantly influenced by surrounding mortality rates early in life, as well as by current environmental cues of harsh conditions.

In sum, phenotypic adaptation provides a useful framework for linking evolved mechanisms to facultative responses, including ones involving agency. Note, however, that agency as used here does not mean that actors are necessarily aware of the reasons for their choices, and it certainly does not imply that people (or indeed members of other species) explicitly think in terms of fitness costs and benefits. I mean only that people make choices, taking into account their circumstances and their preferences; those preferences are generated from a complex developmental process with inputs from both genetic inheritance and social learning. Anthropologists generally consider the latter input, often termed cultural transmission, to be crucial.

Cultural Transmission

Although phenotypic adaptation is a flexible and illuminating way of conceptualizing behavioral variation, it has limitations. In particular, it offers little insight into norms and institutions—two undeniably key aspects of human behavior that are best understood as products of cultural evolution. I adopt here the “ideational” (Durham 1991) definition of culture, as referring to socially learned information (e.g., beliefs, preferences, values, knowledge, and norms). A well-developed body of theory discusses the forms, dynamics, and adaptive consequences of cultural transmission (Boyd & Richerson 2005, Henrich & McElreath 2003, Mesoudi 2011, Whiten et al. 2012). This work explores how information about social and ecological strategies is differentially transmitted according to various contexts and transmission biases. I do not attempt to review the extensive literature on this topic but rather focus specifically on aspects most relevant to debates about agency, determinism, and cultural autonomy.

Because cultural transmission depends on a set of genetically evolved cognitive/neurological mechanisms, the reasonable expectation is that on average the content of cultural transmission (i.e., culturally variable beliefs and preferences) enhances the fitness of individual bearers. However, “on average” does not mean “in each case,” and existing theory and evidence support the conclusion that cultural variation can be neutral or maladaptive in fitness terms (Boyd & Richerson 2005, Durham 1991). Various transmission biases and dynamics allow cultural variation to produce outcomes that would not arise by standard genetic evolution, including greater possibility for group-level adaptations that are neutral or even harmful to individual fitness interests (Bowles & Gintis 2011, Boyd & Richerson 2005). Differential power and coercion must also affect the direction of cultural evolution, and much work remains to sort out how political economy articulates with cultural transmission theory.

These complexities aside, the adaptiveness of much cultural variation is well established (Cronk et al. 2000, Nettle 2009, Richerson & Boyd 2005, Winterhalder & Smith 2000). But is this due

to genes keeping “culture on a leash” (Wilson 1978, p. 167) via a large set of genetically evolved domain-specific cognitive modules or “Darwinian algorithms,” as many evolutionary psychologists (e.g., Tooby & Cosmides 1992) argue? Or is it produced by a relatively small set of mechanisms governing cultural variation and differential propagation, as cultural transmission theorists (e.g., Henrich & McElreath 2003, Richerson & Boyd 2005) hold? “Adaptiveness on average” does not commit one to any particular position with regard to this debate (Smith et al. 2001). Consider, for example, language: Although humans differ from other species in their language acquisition ability, a difference that undeniably has a genetically evolved basis, it is clear that the content of specific languages is primarily local and historically contingent and yet subject to (cultural) evolutionary processes (Greenhill et al. 2010, Lieberman et al. 2007). Debate currently rages over the Chomskyan view of innate universal grammar and deep structure versus a more developmental view of language learning (e.g., Christiansen & Chater 2008, Dunn et al. 2011). Regardless of how this debate is resolved, linguistic communication in general is clearly a major adaptive tool, and humans rely on it to help fashion myriad other cultural adaptations (Richerson & Boyd 2010, Smith 2010).

Many erroneous notions about cultural transmission and evolution are propounded by its critics (Henrich et al. 2008). One of these is that it leaves no room for agency. But from its inception, the theory has prominently included “decision-making forces” (Boyd & Richerson 1985) or “cultural selection” (Cavalli-Sforza & Feldman 1981, Durham 1991). However, decisions are based on beliefs and preferences, and these beliefs and preferences are not created *de novo*. Rather, we are enculturated into them (i.e., inherit them culturally), or we develop them individually, guided by other elements of our cultural inheritance and by genetically evolved mechanisms. Even when we generate truly novel beliefs (e.g., the world will end on 12/21/12) or goals (e.g., break into a school and murder all the inhabitants), others will evaluate them on the basis of culturally and genetically evolved beliefs and preferences, and most are unlikely to spread far. Thus, an appeal to agency cannot ultimately banish evolutionary explanation.

One example of empirical work in the cultural evolution framework concerns demographic transition to low fertility (and resultant small family size), a historically and regionally variable yet pervasive feature of modernity. As this transition generally accompanies increased material wealth, it presents a Darwinian conundrum. One proposed solution is that reduced fertility is favored when delayed reproduction enhances one’s chance of achieving cultural prominence (e.g., pursuing advanced education and a career before, or even instead of, starting a family). If people learn strategies for economic advancement from such successful individuals (in a “one-to-many” transmission structure), then beliefs and preferences that favor reduced fertility can spread at the expense of parent-offspring enculturation in large families (Boyd & Richerson 2005, Ihara & Feldman 2004). This work has been extended to account for the spread of reduced fertility preference from wealthier to poorer countries via social interaction networks (Borenstein et al. 2006). This example illustrates how cultural evolution might sometimes favor the spread of a trait that reduces its bearer’s biological fitness. Note, however, that cultural evolution in this case is driven in part by preferences for emulating the successful; thus, some argue that it represents an otherwise adaptive strategy that is stretched past its limits in contemporary settings with competitive wage-labor economies (Kaplan et al. 2002). An alternative explanation is that trade-offs between fertility and offspring survival favor increased parental investment in fewer children, which can perhaps optimize fitness over several generations (Lawson & Mace 2010; but cf. Lawson et al. 2012).

Gene-Culture Coevolution

Gene-culture coevolution occurs when cultural innovations alter the selective environment of particular genes or gene complexes or conversely when genetic change alters the probability that

certain cultural innovations will spread (Durham 1991, Laland & Brown 2011). Analysis of gene-culture coevolution demands relatively complex models that track the effects of natural selection and other forces on the various “phenogenotypes” and capture the possible combined genetic and cultural states (Cavalli-Sforza & Feldman 1976, Laland et al. 2010).

To date, empirical evidence for gene-culture coevolution is more readily found for the first category: culture driving genetic change. This evidence includes classic as well as recent findings on genetic adaptation to dietary change: the coevolution of adult lactose tolerance with dairy farming, and of starch metabolism with reliance on domesticated roots and grains (reviews in Durham 1991, Laland et al. 2010). Of course, it can be difficult to tell if a coevolutionary dynamic is driven primarily by changes on one side (e.g., culture); in the lactose case, the circumstantial evidence for dairying as the driver of genetic evolution has been augmented with improved archaeological and genetic evidence (e.g., Burger et al. 2007), as well as phylogenetic analysis of dairying traditions and genetic variation in lactose tolerance (Holden & Mace 1997). So we can be fairly confident that decisions made by hundreds of thousands of individuals to continue consuming milk into adulthood overcame immediate negative feedback from physiology (i.e., digestive upset) and changed the selection coefficient of rare genetic variants sufficiently to cause their rapid spread and near fixation (Gerbault et al. 2011, 2013).

In light of gene-culture coevolution, the view that genes keep culture on a leash (see above) seems simplistic. Rather, genetic and cultural evolution can become coupled, and the resultant effects on human behavior can be markedly different than could be predicted from either system alone (Boyd & Richerson 2005, Durham 1991, Gintis 2011, Laland et al. 2010). To date, this dynamic is more a theoretical possibility (supported by detailed modeling) than an empirically demonstrated reality. Yet it is stimulating research into a variety of anthropologically relevant topics, including coevolution of cultural markers and in-group favoritism (Ihara 2011), in-group favoritism and out-group hostility (Choi & Bowles 2007), and a variety of other social and demographic features (Boyd & Richerson 2008).

Niche Construction

Niche construction (NC) is a term coined to summarize the ways in which the activities of organisms help shape or change their own selective environments (Odling-Smee et al. 2003). It can be defined as “the process whereby organisms modify their own and/or each others’ niches, through their metabolism, their activities, and their choices” (Laland et al. 2009, p. 196). Defined this way, NC is ubiquitous and almost indistinguishable from ecology in general, subsuming predator-prey interactions, host-pathogen interactions, soil buildup from plant decay, etc. One step to narrowing the definition, and thereby increasing its focus and utility, is to say that “the defining characteristic of niche construction is not the modification of environments per se, but rather organism-induced changes in selection pressures in environments” (Kendal et al. 2011, p. 790). Others argue that NC should be restricted to environmental modifications that are adaptive (for the focal organisms or their descendants). Thus, Sterelny (2001) has criticized the broad definition of NC, arguing that “some of these impacts are mere effects; they are by-products of the organism’s way of life,” in contrast to cases in which organisms engage in “engineering” such that “the environment is altered in ways that are adaptive for the engineering organism” (p. 333).

NC has evolutionary consequences because the modified environment and associated alterations in selection pressures constitute an “ecological inheritance” that is passed on to subsequent generations (Laland & Brown 2006, Laland & Sterelny 2006). Thus, organisms help shape the evolutionary destiny of their descendants, although it is important to note that this does not imply conscious agency nor does it necessarily exclude processes by which NC reduces the fitness of

NC: niche
construction

descendants (e.g., environmental degradation). Advocates of the NC perspective go so far as to claim it is a process coequal with natural selection and makes organisms “codirectors of their own and other species’ evolution” (Laland & O’Brien 2010).

The past decade has seen publication of numerous position papers and overviews of NC, many deploying the same well-worn illustrative examples of beavers and earthworms. Some empirical applications of anthropological interest have begun to appear, however. These include studies of habitat modification, subsistence shifts (including domestication), tool kit diversification, and wealth transmission.

The scope and variety of anthropogenic environmental modification have increased dramatically over the long scale from Paleolithic foraging to industrial production. But even small-scale foraging populations regularly modified their landscapes through burning, selective harvesting, and even plant propagation and irrigation (Bird et al. 2005, B.D. Smith 2011, Smith & Wishnie 2000). Of the authors just cited, only Bruce Smith makes use of the NC concept, although Smith & Wishnie employ the related label “ecosystem engineering.”

Shifts in subsistence strategies have occupied considerable ethnographic and archaeological attention for decades. Models from optimal foraging theory, a branch of behavioral ecology congruent with the phenotypic-adaptation approach, have guided many of these efforts and have been tested quite extensively (Winterhalder & Smith 2000). A spate of recent papers recently proposed NC theory as either an addition to or replacement for the behavioral ecology framework in analyzing subsistence change (Broughton et al. 2010; Laland & O’Brien 2010; O’Brien & Laland 2012; Rowley-Conwy & Layton 2011; B.D. Smith 2007, 2009, 2012; Zeder 2012). Whereas those employing foraging-theory explanations for domestication proposed rather precise (and hence falsifiable) predictions, NC proponents have thus far offered broader generalizations, such as domesticators following the rule to “engage in costly niche construction only when you need to” (Laland & O’Brien 2010, p. 317) and engaging in “repeated auditioning of a wide range of species with a constant stream of different forms of management in an effort to identify new and better ways of shaping and enhancing their niche” (B.D. Smith 2007, p. 196). Clearly, domestication and other subsistence shifts often involve active environmental manipulation—a perspective central to NC but not to foraging models. Both approaches stress that humans modify the selective environment for future generations (often in unintended ways). Indeed, the foraging theory–based accounts of domestication and agricultural intensification already stress this recursive causality, where small changes (e.g., in incorporating low-ranked resources and manipulating their yield) can have large long-term consequences that alter settlement patterns, health, demographic dynamics, rates of violence, and political economy (Broughton et al. 2010, Winterhalder & Kennett 2006). Although some real questions about the domestication process arise, much of the debate referenced above seems more concerned with labels and alliance formation than with dispassionate analysis of scientific issues.

The other applications of NC listed above have all been treated extensively by anthropologists and others without reliance on the NC concept. More broadly, evolutionary biologists have developed a broad set of models and analytical frameworks that treat the same phenomena as NC under different rubrics (ecosystem engineering, habitat selection, extended phenotypes, phenotypic plasticity, density-dependent selection, interspecific coevolution, etc.). Some researchers have even published dual analyses of the same phenomena as forms of NC and as examples of gene-culture coevolution (e.g., Gerbault et al. 2011, 2013). This has led some to question whether NC contributes new insights or simply offers old wine in new bottles.

A more fundamental issue is whether NC requires a fundamental rethinking of neo-Darwinism. Its proponents insist that NC is “a fundamental cause of evolutionary change” (Laland et al. 2009, p. 195), an “endogenous causal process in evolution, reciprocal to the causal process of natural

selection” (Kendal et al. 2011, p. 785). Some critics agree that the empirical phenomena labeled NC are real, but they argue that the concept simply renames a standard process wherein “natural selection can happen once when a species is shaped to fit an environmental niche, and again when that species . . . so changes that environment that new adaptive problems emerge”—something fundamentally new only if one “considered neo-Darwinian evolution to be a one-shot game” (Dickins 2005, p. 82).

CONCLUSIONS

Evolutionary analyses propose ultimate explanations—that is, answers to why features of living things are designed as they are, a large yet limited domain of inquiry. Natural selection is the force generally credited with guiding evolutionary design, for sound theoretical and empirical reasons. But selection has produced, among other things, creatures that are capable to various degrees of acting as designers. As Daly & Wilson (1991) put it, “Natural selection doesn’t have goals, but it’s the reason organisms do.” In the human case, cultural evolution provides an additional design force, as discussed above.

This review began by faulting the frequent and diverse criticisms of standard evolutionary approaches for ignoring important features of human behavioral adaptation. I hope to have shown that the development over the past three decades of theory and analyses that incorporate agency, culture, and social change provides robust answers to these criticisms. The persistence of the critiques in spite of such work suggests that the critics themselves have too narrow a view of contemporary evolutionary theory and practice and rely on a simplistic stereotype of evolutionary explanation as “genes for trait X.” The work reviewed above demonstrates that this stereotype grossly misconstrues EBA research.

My broader aim is to help steer anthropology away from the unproductive dichotomies that dominate debates about evolution and human social behavior. The mechanisms and processes outlined above are part of the regular tool kit of evolutionary anthropologists who analyze social behavior. They provide principled ways of conducting evolutionary analyses of behavior without positing specific “genes for behavior X” and serve as strong grounds for rejecting the view that evolutionary analyses of behavior deny the importance of human agency, cultural variation, and historical change. In doing so, they might even contribute to a rapprochement between the cultural and biological wings of anthropology. In turn, such rapprochement would reinforce the position of anthropology as the central arena for linking the biological and social sciences, an emerging trend as anthropologists, biologists, economists, psychologists, and others increasingly collaborate in studies of human sociality. But this will require relinquishing the long-standing dichotomy between nature and culture (or the natural and the social, to use terms that go back at least to Marx). This outmoded dichotomy is in turn linked to a persistent view among many social scientists and humanists that “biology” refers to fixed, predetermined attributes, whereas culture/action/history are mutable and agentive. We are too often prisoners of such frozen misconceptions (Slingerland & Collard 2011).

Yet while recognizing the ways in which agency and cultural inheritance can play a significant role in evolutionary analyses, some caution is warranted. Empirical evidence is needed to evaluate each specific claim of agency or cultural direction to human adaptation, and in some cases the evidence may be against such claims. An example would be the results of decades of research on human reproductive ecology, which indicate that fertility control in preindustrial populations is governed primarily by physiological mechanisms, though strategic choice does play some role (Ellison 2001).

More broadly, although beliefs and preferences may play active, crucial roles in human adaptation, they themselves evolve: Agency is not a “prime mover,” and people do not direct their evolutionary destiny as much as nudge it in different directions. As Marx (1978 [1852]) famously

argued, humans “make their own history, but they do not make it just as they please; they do not make it under circumstances chosen by themselves, but under circumstances directly found, given and transmitted from the past” (p. 595). Those circumstances transmitted from the past include genetically and culturally evolved beliefs, preferences, and constraints. Yet within those parameters, agency as well as evolutionary processes helps generate the tremendous diversity of forms that constitutes past, present, and (as yet unknown) future human behavior.

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