ARTICLES

The Adaptive Nature of Culture

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Some have argued that the major contribution of anthropology to science is the concept of culture. Until very recently, however, evolutionary anthropologists have largely ignored culture as a topic of study. This is perhaps because of the strange bedfellows they would have to maintain. Historically, anthropologists who claimed the focus of cultural anthropology tended to be anti-science, anti-biology, or both. Paradoxically, a segment of current mainstream cultural anthropology has more or less abandoned culture as a topic. It is particularly ironic that in spite of a growing awareness among evolutionary anthropologists that culture is critical for understanding the human condition, the topic of culture has fallen out of favor among many "cultural" anthropologists.[1,2]

The scientific study of culture is made difficult because many of its definitions are ideational in nature. This creates nervousness among material-minded anthropologists because such definitions imply that culture is ethereal, superorganic, and immaterial. This apprehension is unwarranted. Analogous to data that exists physically on the surface of recording media such as a compact disc, culture takes material form as information stored in the gray matter of very material brains. How this happens is beyond the scope of this paper, but neurobiologists are working to show how mental representations are expressed as patterns of firing neurons.[3–5] Notice I do not say that culture can be reduced to nothing but firing neurons, but the work of the cognitive neurosciences provides strong support for the physical existence of mental representations. The Cartesian mind-body duality is clearly wrong.[6]

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It is fair to say that a consensus has been reached among evolutionary anthropologists to define culture minimally as socially transmitted information.[7–12] This definition contrasts social learning with individual learning where individuals learn on their own about some feature of the environment.[13] It has been well documented that most animals, to some extent, can learn on their own through trial and error about important features of their environment.[14] In contrast, cultural information is learned from conspecifics. While this distinction is a simple one, there are a variety of ways that information can be obtained socially, and these differences can have large effects on the nature of evolutionary process and adaptations. Much of the debate in the nonhuman animal literature revolves around various social learning mechanisms and which animal species are capable of each.[15,16] Although the details of the arguments will not be presented here, these definitional battles in the animal-culture literature are important. While there may not be a consensus as to the type of social learning common in various species, the discussion points us at the salient aspects of the phenomenon.

If behavioral variation not attributable to ecological or genetic variation is considered, culture is widespread among animals.[17] For example, Levebre and Palameta[18] give nearly one hundred nonhuman animal examples of what they term cultural variation in foraging behavior. A recent review by Whiten and coworkers,[12] report thirty-nine different behaviors that they argue vary culturally across seven well-established field sites of different chimpanzee communities. Female guppies observe other females and copy their mate choice decisions.[19]

While some of these animal traditions are surely maintained through social transmission, not all such social learning will bring about sustained cultural change. Tomasello, Kruger, and Ratner,[20] and others have spent considerable time showing that the social learning common in nonhuman primates is not imitation in the strict sense. Imitation happens when an individual observes a conspecific and reproduces the behavior of the model.[21,22] Although the words are often used interchangeably, I prefer the more general term "observational learning." Imitation implies behavioral duplication where one observes a behavior and subsequently repeats it. While there are benefits to imitating the behavior of others, valuable information can be obtained via observational learning without repeating the behavior. In fact, much is learned by not imitating the mistakes made by others.

Tomasello[20,22] and others argue that most of what is attributed to imitation or observational learning in primates is better described as local enhancement (also referred to as stimulus enhancement). Different from imitation, local enhancement is an increased probability that individuals will learn a trait on their own because they are exposed to the conditions that make the trait's acquisition more likely.[10,23] Tomasello suggests that young chimpanzees learn tool-use this way. Young chimpanzees follow their mothers to termite mounds where they are in close proximity to both tools and termites, and where the likelihood that they will learn termiting on their own is significantly increased. Tomasello[10,21,22] offers local enhancement to cast doubt on the classic example of animal culture: Japanese Macaque potato-washing.[24,25] Contrary to the predictions of imitation models, potato-washing behavior spread slowly across the population of monkeys. In addition, the rate of trait acquisition did not increase as the number of washers increased. That is, the predicted S-shaped cumulative adoption curve common when innovations spread via imitation was not apparent in the macaque case.[26,27] Boyd and Richerson[28] point out that most of the cultural behavior observed in nonhuman animals, like potato washing, is simple and easily learned by individuals on their own in each generation. This is not the case for most of the behaviors learned culturally by humans. Imitation has also been difficult to demonstrate in controlled laboratory conditions even among animals that are otherwise very intelligent.[29,30] While it may occur in some instances, true imitation among nonhuman animals seems to be exceptional.[31]

The difference between observational learning and local enhancement is important. Via local enhancement, there is no mechanism for innovations to be incorporated and passed on to others. That is, there is no way for cultural complexity to develop if local enhancement is the sole cultural mechanism. Tomasello[21,22] terms the pattern of imitation, modification, and transmission the "ratchet effect." Without imitation, the ratchet effect is not possible. It is readily seen with technological design and use involving a series of complex steps, each dependent on previous steps.[27] Young chimpanzees might learn via local enhancement how to use stones to open palm nuts on their own.[32] It is also possible that an individual might make an innovative improvement; say, sharpen the hammer using a flaking technique. Without direct observational learning, however, this innovation would be lost to future generations of chimpanzees. Kummer and Goodall[33] argue that many creative acts of intelligence are unobserved in chimpanzees because they are not culturally preserved within the population.

It is cumulative cultural adaptation that sets human apart from other animals.[21,22,28] As Tomasello[21] notes "Indeed, the most distinctive characteristic of human cultural evolution as a process is the way that modifications to an artifact or a social practice made by one individual or group of individuals often spread within the group, and then stay in place until some future individual or individuals make further modifications and these then stay in place until still further modifications are made."

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CULTURE AND BEHAVIORAL ECOLOGY

Coinciding with a series of theoretical developments in the fields of biology and ecology, much of it synthesized in E.O. Wilson's book *Sociobiology*,[34] a number of social scientists interested in an evolutionary approach to human behavior delved deeply into the animal behavior literature and developed lines of research focused around subsistence activities and social behavior.[35–37] Among evolutionarily informed anthropologists interested in human behavior, however, there has been a divergence between those who have tended to minimize the role of culture and a group led by Boyd and Richerson[7] who have specifically focused on models of cultural transmission.

Many behavioral ecologists, for example, developed a general view that minimized the importance of culture as an independent variable for explaining behavior. Sometimes referred to as the argument from natural origins,[7] it proceeds in several steps. To start with, cultural ability is correctly viewed as a product of natural selection. Learning capabilities and psychological mechanisms that use cultural information would not have evolved if they produced behaviors that were random with respect to biological fitness.[9,38,39] Thus, the argument goes, there should be a direct relationship between cultural norms and what maximizes inclusive fitness (see Irons[40] for an early exposition of this idea). If cultural mechanisms produce behavior that reduces fitness, culture would be selected against. Therefore, the argument continues, behavior will enhance fitness regardless of whether transmission is cultural or biological, and acultural models should make the same predictions as ones that include culture. While such a view does not necessarily argue that culture does not exist, adaptive behavioral variability can be predicted without reference to it.[9]

From this view, the complexities of cultural processes are avoided when cultural variation is attributed to what biologists refer to as phenotypic plasticity. Phenotypic plasticity occurs when one genotype produces an array of adaptive phenotypes depending on environmental context.[41–43] Tooby and Cosmides[44] call such human behavioral variability evoked culture, defined as innate information (content) that resides in human heads, expressed contingently and adaptively in different environments. The school of cultural ecology has a similar approach except that the arguments are not evolutionarily informed.[45,46] Tooby and Cosmides use the term to demonstrate how standard social science has failed to discriminate between variability caused by innate content-specific phenotypic plasticity and that caused by transmitted culture. While it is true that standard social science has discounted an innate human psychological architecture, using the term "evoked culture" is unfortunate and oxymoronic. Culture is critically defined as socially transmitted information rather than innate and emergent. There is much contingently and adaptively emergent behavior found among nonhuman animals that should be not be defined as culture.[47] Such behavior should not be described as cultural for humans either.

Variability in subsistence behavior by children provides an example of human phenotypic plasticity. Blurton-Jones and Hawkes[48] and Blurton-Jones, Hawkes, and O'Connell[49] examined behavioral variability in foraging among hunting and gathering children. Interested in the implications for human life-history evolution, they examined differences in child foraging patterns between the Hadza and !Kung. Both of these groups live in sub-Saharan African savanna, gather with digging sticks, hunt with poison-enhanced bows and arrows, and harvest many of the same types of resources. Observations show that !Kung children forage little until they are well into their teen years. In contrast, Hadza children are active foragers from an early age (<5 years). Using a detailed analysis of empirical and experimental foraging data, these researchers have shown that ecological differences, primarily the spatial distribution of food and water resources, and the differences in the processing requirements of the different foodstuffs gathered by these groups, explain the observed behavioral variability. There is a lack of nearby resource opportunities for !Kung children comparable to the easily accessible Baobab patches available to Hadza children, and return rates for the !Kung children are correspondingly low.[49] !Kung children do not follow their parents to distant mongongo nut patches because younger children interfere with adult efficiency; older children's time is better spent processing nuts back at the camp. In addition, the !Kung landscape is monotonously flat, additionally discouraging children from foraging because they can easily become lost or prey for predators. The Hadza landscape, in contrast, is broken, providing views of the surrounding area and many landmarks to guide wayward children home.

As Cronk[9] has noted, these sorts of optimization models have been very successful at predicting human behavior, especially among small-scale societies. In the preceding study, the data are good and the arguments are convincing. Using Tooby and Cosmides[44] term the variability in child foraging patterns is "evoked" from ecological differences. The behaviors are adaptive within the respective environments in terms of optimizing mothers' and children's return rates.[48,49] If such a research paradigm is successful, why is it important to incorporate culture within an evolutionary approach to human behavior? A primary reason is that, in spite of excellent work like that cited, much behavioral diversity in humans populations cannot be accounted for by genetic or ecological differences.[9,50,51] People in similar environments vary in ways that are unlikely to be the result of genetic differences. People behave in ways that suggest that history provides constraints that must be incorporated into otherwise sound optimization models.

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The strength of culture to maintain differences between groups that share environments is most apparent in contemporary times where mobility is great, yet groups are able to maintain cultural integrity in spite of living in close proximity to others. Some contemporary urban areas are good examples: Ethnic groups such as African-Americans, Chinese, and Hassidic Jews live in close physical proximity yet behave in strikingly different ways with respect to language, religion, and dress.[52] This is the very stuff of cultural anthropology.

A well-studied example examines the greater rates of homicide in the southern compared to the northern United States. The difference is especially apparent for homicides that involve arguments or conflicts rather than those committed as part of a felony. Nisbett and Cohen[53] attribute this difference to the great number of Scotch-Irish herding people who colonized the south in contrast to the farmers that immigrated to the north. In the absence of a state, herders often develop a culture of honor that favors aggressiveness and willingness to kill to protect the loss of herds.[54–56] Although that likely was adaptive in the past, such a preference is unlikely to be optimal in modern twenty-first-century America, yet Nisbett and Cohen show convincingly that modern-day southerners are very different from northerners in their attitudes toward violence and their propensity to engage in violence, as well as their physiological response to insult. Granted that the difference between farmers and herders discussed in Nisbett and Cohen's book can be construed as ecological in origin, it is difficult to understand without invoking cultural processes why such differences persist generations after the subjects' ancestors ceased to engage in their respective subsistence tasks.

Another example comes from the whaling communities of Lamalera and Lamakera, Indonesia. Until quite recently, both practiced traditional whaling.[57–59] Lamalera villagers still rely on subsistence whaling for their living; Lamakera villagers occasionally whale, but now are rapidly moving toward a more mixed economy. Traditionally, both practiced cooperative big-game hunting for large-bodied marine mammals, primarily whales and ray. While both hunt whales, in Lamalera the men hunt toothed whales and taboo baleen whales, while in Lamakera toothed whales are taboo and only baleen whales are pursued. The Lamalerans report that baleen whales are too big and dangerous to pursue; paradoxically, the Lamakerans make similar claims about toothed whales. While there are a number of interesting possibilities that might explain this variation in prey choice, it is difficult to imagine an ecological hypothesis independent of cultural transmission to explain these differences. One untested hypothesis is that the difference in prey choice developed as a form of competitive exclusion maintained via cultural transmission.[60]

This example from Lamalera raises an interesting issue. One motivation of optimal foraging theory was to formalize analyses in order to learn if food avoidances were only cultural or, rather, related to adaptive choice. One success of foraging theory has been to show that much of the variation in prey choice is related to return-rate maximization. Hill and Hawkes,[61] for example, argue that some taboos are the result of species falling out of the optimal diet where otherwise pursuing these species would lower return rates. While this argument is convincing for a number of cases, variations in food preferences remain among the most challenging of anthropological problems, and still provide a nagging thorn in the side of an acultural behavioral ecology.[62–65] Most readers know that in Asia dog is eaten with pleasure; in Europe, horse is consumed with gusto, yet maize is relegated to fodder and not considered food fit for humans. In the United States, most people have very different views of these resources.

Smith[66] argued that food acquisition is just the type of activity where one might expect the costs of trial-and-error learning to be low enough that individuals would be able to detect and reject nonoptimal, culturally imposed food choices. This seems a reasonable point, yet we still see anomalous results. Recent work by Aunger[67,68] among horticulturalists and Pygmy foragers living in the Ituri Forest of Zaire, for example, suggests that food taboos are common. While the nutritional burden of observed taboos is small (1% to 2% of lifetime calories are rejected), women are particularly vulnerable. Some women with higher taboo burdens suffer reduced reproductive success.[69] While foraging theory is a powerful tool for understanding resource choice, there is enough uncertainty to warrant consideration of additional independent variables.

Intuitively, because of the its Lamarckian nature, culture transmission allows individuals to adapt more quickly to changing environments than is possible under either a strictly genetic mode of transmission or a system that includes only individual trial-and-error learning. Second, at least among humans, cultural information can accumulate, providing individuals access to information about events they never personally experienced . . .

HOW IS CULTURE ADAPTIVE?

The cognitive mechanisms that allow humans to transmit and receive social information surely evolved via natural selection. From an evolutionary perspective, cultural transmission is a very interesting adaptive strategy and fair game for the adaptationist program.[70] One can hypothesize that cultural ability provides a number of selective advantages. Intuitively, because of the its Lamarckian nature, culture transmission allows individuals to adapt more quickly to changing environments than is possible under either a strictly genetic mode of transmission or a system that includes only individual trial-and-error learning.[71] Second, at least among humans, cultural information can accumulate, providing individuals access to information about events they never personally experienced—both past events (history) and recent events experienced by peers. Finally, the nature of cultural transmission facilitates positive assortment and related benefits obtained via collective action. Using socially transmitted information, people can make predictions about the intent of others, preferentially assort with others who have similar or complementary intentions or capabilities, and reap the advantages of coordinated activities.

In many contexts, it is better simply to copy a successful model than to spend what could be substantial time and energy learning for one's self what is best. It may be better simply to adopt the techniques to make the same type of pottery that your mother makes, for example, than to spend the time and energy learning for yourself the wide variety of pottery techniques and choosing one that you determine to be best. In other words, imitation allows individuals to avoid costly trial-and-error learning.[72]

In a model that examined the frequency-dependent nature of cultural adaptation, Rogers[73] demonstrated that this answer is incomplete. As imitators become increasingly common in a group of learners, the probability increases that imitators will copy other imitators and acquire the wrong behavior. Thus, the advantage that accrues to imitators declines proportionally to their frequency in the population. As Henrich and McElreath (this volume) show in greater detail, Rogers demonstrates that the equilibrium outcome is a mix of learners and imitators who both have the same fitness as learners do in a population where there are no imitators. Since the fitness of learners is independent of the number of copiers, a population of mixed learners and copiers has the same fitness as one composed only of learners. Although natural selection favors imitation, the average fitness of the population does not increase and the species is not more competitive.

CULTURE AND SELECTIVE LEARNING

What then, does culture do? Social learning is adaptive when it makes individual learning more effective, argue Boyd and Richerson.[71] Cultural organisms can engage in individual learning if costs are low and success likely; otherwise, they can imitate others. If learning can be done more selectively, the fitness of individual learners can increase.

This ability can provide many advantages because there is much evidence to suggest that individual learning is not always easy, and human decision making not as rational as economists have led us to believe. In spite of our somewhat vainglorious view of ourselves as cognitively gifted rationalists, much data from cognitive psychology and experimental economics show that humans systematically violate models that assume accurate cost-benefit decisions.[74] An emerging view from economics is that rationality is somewhat more bounded than is assumed of *Homo economicus.*[75,76] For example, people bias their memory in a variety of ways, often overgeneralize from small samples, have trouble detecting covariation and correlation, and are not very good at forecasting a dependent variable given multiple predictor variables.[77–80] Henrich[77] points out that the requisite information is often not available for individuals to learn even if they were to behave rationally. For example, it is often difficult to learn from our personal mistakes because many important decisions occur too infrequently for us to accrue a sufficiently large sample to distinguish the options. The choice of a spouse is good example.[74] Alternatively, a mixed strategy lets us selectively learn on our own when the information is available, and to copy the behavioral strategies of others when information is difficult to obtain.

In order to show how selective learning combined with imitation might work, Boyd and Richerson[71] borrow Rogers[73] basic model, but allow the individuals to switch between individual learning and imitating. Individuals first attempt to learn about the state of the environment on their own, but because learning can be costly and error-prone, individual learners can come to incorrect conclusions concerning the best behavior to adopt. According to Boyd and Richerson's model, natural selection selects a threshold value of d, a parameter that determines the reliance on individual learning (see Box 1). If d is large, individuals require hard evidence that the environment is really one way or the other. If the threshold is not met, they imitate a model. If d is small, individuals are more likely to rely on personal experience.

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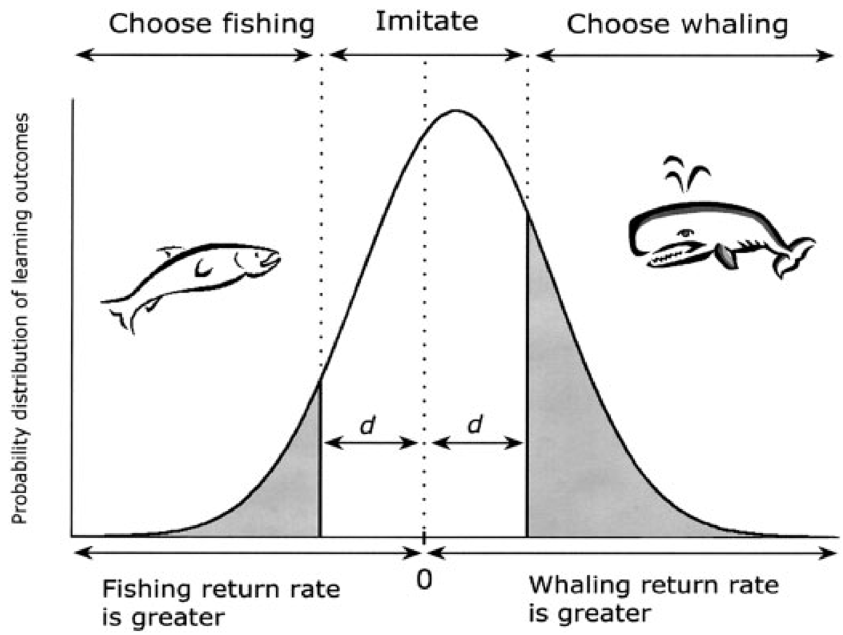
If the environment changes slowly or not at all and social learning is costly (in terms of cognitive machinery, for example), then a genetic system of transmission is sufficient to track the environment. At the other end of the spectrum, if environments change rapidly, then imitation is insufficient because potential models, like parents, are unlikely to possess accurate information for current conditions.[83] Boyd and Richerson conclude that social learning has an advantage when environmental variation is high, but not too high.

An ethnographic example comes from the Indonesian village of Lamalera. Net fishing and cooperative whaling are the two major alternative subsistence strategies for males in the village. Long-term estimates of return rates show that whale hunting provides hunters with greater average benefits than does fishing.[57] Whale harvests vary considerably from year to year, so that a naïve individual would spend years on his own obtaining a sufficiently large sample to determine that whaling is the best strategy in the long term, which the long-term data suggest it is. If a hunter were to rely on just one year's worth of experience, he could easily come to the wrong conclusion. In 1999, for example, Lamalera experienced a very poor whale-hunting year, so that per-capita hunting returns did not differ from those for fishing. Naïve individuals using trial-and-error learning and a small sample of years to determine the best "career" track could easily make an error and decide there is no difference between whaling and fishing. People often do make just this sort of mistake by overgeneralizing from small samples.[84] On the other hand, simply copying the behavior of others in the absence of trial-and-error learning makes individuals unresponsive to changes in the environment. In Lamalera, hunters quickly learned on their own that whaling in 1999 was unprofitable and many switched to alternative activities.[57] Simply imitating the most common strategy would have resulted in many more men whale hunting.

How does the idea that cultural ability is an adaptation to variable environments match with what is known about the state of global environments during the period since the divergence of humans and chimpanzees from a common ancestor? Given the resolution of the archeological record and uncertainty concerning culture's diagnostic features, the discussion is lim-

Box 1. Environment 1 and Environment 2



Boyd and Richerson[28,71,81,82] have us imagine a population that inhabits an environment that switches between two possible states labeled 1 and 2. In our case, let us say environment 1 is one where whale hunting provides greater return rates and environment 2 is one where net fishing provides greater return rates. Hunters can adopt two different behaviors, one that is best in environment 1 (whaling) and one that is best in environment 2 (net fishing), where "best" is defined as leading to greater fitness. In order to adopt the best behavior, an individual must determine the state of the environment. A hunter first uses nonsocial sources of information to do this, including trial-and-error learning. The information obtained this way can be described by a normal probability distribution of learning outcomes, which defines a parameter x. For example, in Lamalera, x might be the difference in return rates between a round of whaling and a round of net fishing. In this case, a positive value of x suggests that the environment is in state 1 (whaling is best) and a negative value of x suggests that the environment is in state 2 (net fishing is best). Also indicated is a threshold value d, which is set by natural selection. If the individual's learning outcome indicates that the return rate from whaling is d greater than net fishing, the individual should whale. If the learning outcome indicates that the return rate from net fishing is d greater than whaling, the hunter should net fish. If however, $-d < x < d$, and a sufficiently large difference between whaling and net fishing cannot be found, the hunter imitates. There is an obvious trade-off. As the threshold d increases, fewer learning errors are made, but the frequency of ambiguous outcomes and reliance on imitation increases as well. (Figure adapted from Henrich and Boyd.[82])

ited to speculation. Nonetheless, knowing broadly when humans evolved the cultural abilities we see today can provide clues as to culture's adaptive nature.

Observational learning was probably not a critical adaptation during the early period of hominid evolution. The australopithecines' lack of stone-tool technology supports this thought. Even after the rise of *Homo* and unambiguous tool technology, culturally transmitted information of the kind seen in modern humans is likely to have been uncommon. While the tool technology commonly used by *Homo erectus* (the Acheulian handaxe) was arguably culturally transmitted from generation to generation, the technology itself remained remarkably unchanged over a million years.[85] This suggests a slight reliance on socially transmitted information of the kind seen in modern humans and perhaps a process more akin to social enhancement.

Agreement is growing that the fully modern, culturally enhanced, human behavioral repertoire did not arise until between 100,000 and 40,000 years ago.[86–92] Traits that occur after this period but not before include blade and microlithic tool technology, the use of bone for making tools, and increasing artifact diversity. Ritual behavior, art, and personal ornamentation become evident. Mobility, geographic range, and long-distance trade increases. It is reasonable to hypothesize that near this point in time humans evolved the ability to transmit information culturally in an observational sense. Subsequently we see a dramatic increase in the archeological record of evidence for cultural diversity, as well as the beginning of cumulative cultural change that is the hallmark of modern humanity. While the exact timing, location, and speed of the change is debated,[93] the transition in the Upper Paleolithic represents a watershed in the course of human evolution. What were the selective forces that favored the development of the traits implicit in such complexity?

The ratio of oxygen isotopes found in deep-sea cores show a long-term global cooling trend since the middle of the Pliocene.[94] Additional data from Greenland ice cores, pollen data, and loess analyses show increasingly rapid climate fluctuations, especially during the Pleistocene.[95–97] Sometimes strikingly rapid periods of cooling accompanied by prolonged droughts characterized much of this period. Many researchers have suggested that humans were able to adapt successfully to environments that were extremely variable as a consequence of the rapid and extreme climatic oscillations during this period.[83,98–100] This so-called variability selection is hypothesized to have favored increased cognitive abilities and social learning, allowing rapid adaptation to temporally and spatially variable environments. As Richerson and Boyd[83] point out, the rapid changes that occurred in the Pleistocene environments likely put a premium on both the individual and social general-purpose learning mechanisms that currently characterize humans. The correlation between increases in brain size and environmental variability in many mammalian lineages supports this contention, but humans diverged by evolving the ability to acquire and manage cumulative cultural traditions.

CULTURE AND HISTORY

In addition to making learning less costly and more accurate, observational learning also allows information to accumulate; that is, it allows history. Defined broadly, history is a body of information about events that occurred in the past. Defined this way, even nonliterate societies have history consisting of information relating to a wide variety of areas, including ecology, social organization, technology, resource management, and medicine. The selective advantages are great as culture lets individuals access a corpus of information about events never personally experienced. In addition, the ratchet effect allows learners to modify, make innovations, and build on the learning of others. It is this difference that most researchers argue makes human culture different from that of other animals that also learn socially.[10,28] The advantages are most apparent in a technological context. As mentioned, Acheulian handaxes were *Homo*'s tool of choice over a million years and showed extreme conservation of form. At some point, one might imagine that exceptional individuals may have made improvements. Without true observational learning, however, improvements are not incorporated into the cultural history. Stylistic differences, so common in modern human archeological assemblages, cannot be maintained otherwise. In fact, recent reevaluation of handaxe technology has called into question the idea that their makers maintained any sort of shared mental templates. McPherron[101] suggests that some very basic factors, such as raw materials and reduction intensity, are better able to explain what patterns of apparent design and style are observed.

While the exact timing, location, and speed of the change is debated, the transition in the Upper Paleolithic represents a watershed in the course of human evolution. What were the selective forces that favored the development of the traits implicit in such complexity?

With the ability to access accumulated knowledge, individuals can take advantage of a great store of information without having to take the time and effort, metaphorically or actually, to reinvent the wheel for themselves. In addition, access to historical knowledge provides even greater advantage in variable environments. In Boyd and Richerson's[71] model, described earlier, imitators are limited to models in the current or previous generation. History provides much greater depth. If environments are so variable that parents are not good models because they did not experience conditions similar to current ones, perhaps grandparents or great grandparents did. The ability to tap into history allows individuals access to solutions for problems not experienced in generations. In this case, the information from past generations is not transmitted behaviorally but rather symbolically. For example, in an extensive analysis of myths and folk tales Minc[102] presented data to support the idea that the Inuit used oral traditions to transmit information important to mitigate subsistence risk due to variability in whale and caribou availability. Sobel and Bettles[103] make a similar argument for the Klamath and Modoc of the western United States who transmit adaptive strategies in the context of oral myths. Content analysis shows that the stories emphasize reciprocal exchange, skilled hunting and fishing, storage, diversification, mobility, and resource conservation as mechanisms to deal with subsistence stress. Famine myths of the Alaskan Tsimshian and Tanzanian Kaguru have similar content.[104] Cruikshank[105] describes Tlingit oral traditions that recount glacial dynamics and their implication for group mobility over a period of nearly 500 years in what is now Alaska. In each case, exceptional historic environmental events and associated complex adaptive responses accumulate in the minds of individuals, are transmitted from generation to generation orally, and are applied as conditions warrant.

There is a problem, however, with the idea that natural selection directly favored culture ability because of the advantages enjoyed by individuals who could access such accumulated knowledge. Even though the benefits of access to accumulated cultural information are substantial, natural selection cannot favor a capacity for such observational learning when it is rare in a population.[28,71,83] In a population where cultural capabilities are nascent, there are no traditions to learn. Selection is unlikely to favor the cognitive abilities to transmit complexity that does not yet exist. This is especially the case if one supposes that such observational learning requires expensive and complex cognitive machinery. The same goes for language: Language could not have evolved initially to facilitate the passage of a complex database of knowledge because, in the absence of language to produce it, the database did not yet exist. Analogously, natural selection could not have favored the ability to read in an environment where there were no books, in spite of the fact that reading is a very complex and adaptive behavior. Culture, like language and reading, must have been initially epiphenomenal to some other adaptation.

What is suggested here is that to understand complex culture, we need to go back a step and understand it as an exaptation that developed from more fundamental cognitive abilities. The key hypothesis that is emerging is that the human ability to view others as the self is viewed—that is, as intentional agents—was the initial adaptation that subsequently led to the cultural complexity that characterizes humanity. Viewing others as intentional agents involves what has been termed mind reading.[106,107] Mind reading is the ability to reason about the otherwise unobservable mental states of others and make predictions about their behaviors based partly on the awareness that others are intentional agents with general goals similar to one's own. The cognitive ability to glean information from others in this way was selected because of the advantages it provided individuals embedded in complex social contexts.[108–110] It did not evolve at the outset in order to amass and transmit a corpus of cultural data.

CULTURE AND A THEORY OF MIND

Humans develop a theory of mind at an early age.[106,111,112] "An animal with a theory of mind believes that mental states play a causal role in generating behavior and infers the presence of mental states in others by observing their appearance and behavior under various circumstances."[113] In contrast to other types of social learning, observational learning involves an understanding of the intent or goal of the model. Tomasello, Kruger, and Ratner[20] argue that humans are much better than other primates at understanding a model's behavior in intentional terms. Others have argued that humans alone can reason about the beliefs of others.[114] Unlike a parrot, which may mimic sounds but not understand the utterances as communicative, people are very good at predicting the behavior of others not simply based on what others are doing, but inferentially based on the understanding that others are intentional agents.

With the ability to access accumulated knowledge, individuals can take advantage of a great store of information without having to take the time and effort, metaphorically or actually, to reinvent the wheel for themselves.

A series of ingenious experiments demonstrates this ability in fourteen-month-old children.[115] In the initial experiment, an adult sat at a table with a light box on top. With the child watching, the adult leaned forward to illuminate the box by touching it with his forehead. Two-thirds of the children were able to imitate the behavior a week later. They did not use their hands to turn on the light, even though it would have been easier for them to do so. There are two interpretations. One is that the children did not understand the adult as an intentional agent and just mimicked the behavior without understanding the adult's goal.[116] The alternative interpretation is that the children understood the intent of the adult and met the same goal using the same means.[22] This conclusion was subsequently confirmed by experiments suggesting that in some cases observational learning by fourteen-month-old children goes beyond simple imitation. Gergely and Bekkering[117] redid the experiments, but in a new treatment demonstrated to the children that the adult's hands were occupied with a blanket. With this treatment, 79% of the children used their hands when they subsequently imitated the action, as compared to about one-third previously. This result suggests that the children were able to presume the model's intent to illuminate the light, as well as reason that he would have used his hands if they were not otherwise occupied with the blanket. This result reinforces the distinction I made earlier between imitation and observational learning. The children were able to learn the intent of the model via observation and as a result did not simply imitate the adult's actions, but rather improved on them to acquire the goal.

How does having a theory of mind lead to the cumulative cultural complexity seen in modern humans? In terms of social learning, it is clear that knowing that others are intentional agents and being able to predict what others intend to do provides an advantage for manipulating complex social and political situations. Fascinating research on autism shows what a lack of such ability can lead to in humans.[107] If this ability is shifted incidentally to the domain of technology, for example, a mind-reading individual can observe a technique performed by another, infer that the model has a goal, and perhaps apply a modification to the technique that maintains the integrity of the goal yet creates a more efficient process. The ability to attribute intent to others allows individuals, among other things, to observe and innovate while maintaining the goal in mind. The result is an ability that can produce the cumulative cultural evolution that generates the complexity that characterizes even the most simple of human societies.

CULTURE AND COOPERATIVE ADVANTAGE

If this speculative argument is correct, the human ability to generate and access a cumulative corpus of information is an epiphenomenon of a more basic adaptation related to the social transmission of social information. The hypothesis that I explore next is that a having a theory of mind allows individuals to reap the benefits of collective action.

People commonly join together to produce goods that can only be obtained by virtue of being part of a group. Along with our cultural proclivities, the ability of humans to cooperate to achieve common goals is unique and matched in scope only by the social insects.[118] While insects accomplish their collectivity through rigid genetic rules, humans are able to achieve our level of ultrasociality via cultural mechanisms. Exactly how humans accomplish this is one of the key questions of evolutionary anthropology.

Humans are able to form much larger cooperative groups than are seen in any other primate. While cooperation in small groups might be satisfactorily explained as reciprocity or kin selection, it is more difficult for these hypotheses to explain the complex, large-scale cooperation observed in nation states, firms, tribes, political parties, and armies. It is predicted that organization based on genetic kinship easily produces small, nepotistic cooperative groups focused around the nuclear family. It is more difficult for larger groups to form nepotistically because relatedness drops off rapidly as the genealogical distance from the nuclear family increases; conflicts of interest can easily arise.[119–122] While easier to maintain in dyads,[123] it is also difficult to show how reciprocity can maintain cooperation in large groups when defectors cause other cooperatively minded individuals to defect to avoid being dupes.[124,125]

One hypothesized condition that can lead to cooperation in large groups like those seen in humans is positive assortment. Indeed, cooperative kin-selected behaviors evolve because they are preferentially directed at like types.[126] Likewise, the reciprocal tit-for-tat solution to the prisoner's dilemma will spread among a population of defectors only if cooperators can somehow preferentially identify and play with other cooperators.[127] Solutions to larger group cooperative dilemmas also focus around assortative interactions.[128–131] Positive assortment facilitates cooperation because individuals who cooperate without discrimination are vulnerable to noncooperators who take advantage of a cooperator's willingness to act collectively.

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Positive assortment is facilitated by some sort of honest signal that permits fellow cooperators to recognize one another. The classic discussion of this is the "green beard" scenario presented by Dawkins.[128] Imagine that having a green beard was associated with cooperating with other green beards. This would allow cooperators to assort by type and avoid free-riding costs. Similar models have been developed within anthropology and elsewhere to explain the rise of markers that allow individuals to identify group members and assort positively.[132–135] However, the green-beard hypothesis has generally been dismissed because cheaters can exploit cooperators by mimicking the signal (growing a green beard) but withholding cooperation.[136]

This problem is not as disastrous to the hypothesis as it may appear. Most collective action is modeled as prisoner's dilemmas, in which the key feature is that a cooperative strategy is never a player's best response to an opponent in spite of the fact that mutual cooperation is better than mutual defection.[137] Cooperation in such a context is true altruism. There is increasing awareness, however, that there are many alternative paths to cooperation and that solutions can depend critically on how interactions and payoffs are structured.[57,138,139] For example, in contrast to a prisoner's dilemma, coordination games are characterized by players with identical preference rankings of outcomes.[137,140] While gains exist for collective action in a prisoner's dilemma, individuals are nonetheless always better off defecting. In contrast to this scenario, coordination games are structurally mutualism.[141] Individuals are always better off cooperating because there is no benefit to defectors. The classic example of pure coordination involves choosing the side of the street on which to drive. There is no benefit to a cheater who opts to drive on the left while his partners drive on the right. Driving on either side is equally good as long as everyone drives on the same side. Coordination problems abound. Language is good example.[142,143] I utter a sound and others can induce intent based on that sound, unless they do not share my otherwise arbitrary association between sound and meaning. Liberman and Mattingly[144] refer to this as parity. Even slight differences in meaning can have disastrous consequences with respect to collective action.

In spite of its apparent straightforwardness, successful coordination offers its own set of problems. Results of coordination failure in experimental contexts have been widely reported, especially in larger groups.[145–147] The problems revolve around players lacking the confidence that their fellows have shared expectations and will behave in predictable ways; as a result these games are sometimes called assurance games.[137]

People do, however, readily solve coordination problems in many contexts. Understanding the process of how people solve coordination problems can demonstrate the link between culture, a theory of mind, positive assortment, and cooperation. Thomas Schelling in his book *The Strategy of Conflict*[148] noted that people are often able to coordinate around what he called focal points. For example, when asked where to meet with a lost companion in New York City, the majority of people choose the focal point of Grand Central Station. Given that there are a nearly infinite number of possible meeting locations, these results are extraordinary. Sugden[149] suggested that people use shared notions of prominence to solve such coordination problems, in this case drawing on shared information concerning commonly known locations in New York City. Schelling[148] noted that what is prominent depends on the time and place and who the people playing are. What is interesting for anthropologists is that the sorts of solutions Schelling suggested require a cultural mechanism of information transfer to provide people the parity required for coordinating behavior. Schelling's focal points have salience because people share socially transmitted (cultural) information.

It is interesting that for most of the coordination games of interest to economics and political scientists, players are assumed not to communicate before they make their decisions. This is presumably because such communication would provide an uninteresting solution to the problem.[146] Both intuition and laboratory-based experimental coordination game results agree that simple pregame communication (read socially transmitted information), where one or both players can indicate their intent, dramatically increases the likelihood of cooperation compared to control games where no communication is allowed.[150]

Cultural mechanisms provide people the ability to infer each other's mental states and form shared notions. Having shared notions greatly enhances the ability to solve simple yet common and important coordination games. Verbalizing intent may be feasible in small groups, but how do humans communicate intent between members of large cooperative groups like those that characterize most human societies? McElreath, Boyd, and Richerson[151] argue that group markers such as speech or dress function to allow individuals to advertise their behavioral intent so that individuals who share social norms can identify one another and assort for collective action. While cheaters are a problem if interaction is structured like a prisoner's dilemma, these authors' critical point is that group markers are useful if people engage in social interactions structured as coordination games.

Understanding the process of how people solve coordination problems can demonstrate the link between culture, a theory of mind, positive assortment, and cooperation.

As an example, I offer the butchering and distribution of hunted prey as a coordination problem. In Lamalera there are complex norms that precisely describe how an animal should be butchered and distributed. Receipt of a share is contingent on participation as a crew member, a craftsman, or a corporate member. For each prey type, norms explicitly delineate a certain share for each participant. Figure 1 is a diagrammatic representation of the shares, the type of recipients, and the number of recipients for each whole share. While these norms are complex, all participants in Lamalera share general notions of the proper way to butcher and distribute. Members of individual lineages share specific notions of who is to receive shares. Importantly, all participants know that the other participants know the proper way to butcher and distribute. As a result, the process occurs with remarkable swiftness and an absence of contention.[152]

Just as it is important that drivers agree on which side of the road to drive on, it is important that all hunters agree on how a prey item is to be butchered and distributed. It is not a trivial problem, however. There are many ways a whale can be butchered, divided, and distributed to participants. A hunter should be indifferent to most of the ways because in most cases the amount and quality of meat and fat a hunter receives would be independent of the anatomical part of the whale from which it originates. But while a hunter may be indifferent to which particular norm is used, it is critical that all participants share the same norms for butchering and distribution. Just as it does not pay to drive on the opposite side of the road from your partner, it does not pay for hunters to deviate from the common butchering norms. Economists refer to the costs of establishing and maintaining property rights as transactions costs.[153] Without norms of distribution, the transactions costs for determining claims to prey would be so high it is unlikely that individuals would participate in so complex a collective action, and as a result, the benefits of the collective action would remain unrealized.

In such contexts, shared notions of what is right and wrong are critical, even if the final outcome is arbitrary. How do fellow participants know that they share beliefs concerning behavior critical for coordination? How can individuals predict what others think and will do? There are a number of

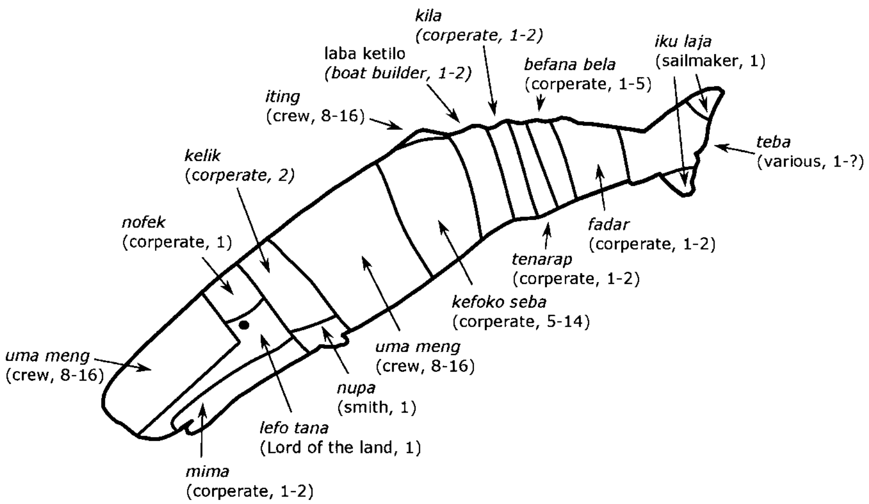

Figure 1. A diagrammatic representation of the shares from a sperm whale at Lamalera, Indonesia. Indicated are the names of each share, the recipient types, and the number of individual shares that typically come from the whole share, assuming only one boat participates in the kill. Each boat that participates in the kill has an equal share in the whale and the whole shares must first be divided between the participating boats before being distributed to individuals. Whole shares can be described by the nature of the recipients, which are clustered into four groups: crew, corporate shareholders, craftsmen, and *tana alep* clans. First, shares called *uma meng* go to the active hunters who were crewmembers on the boat when the prey was captured. Second, certain corporate members receive corporate shares as part of hereditary rights. These consist of the *nofek, kélik, kila, befana bela, fadar, tenarap,* and *kefoko seba* shares. Third, shares go to the craftsmen who may or may not be clan members or crew. The *nupa* goes to the smith, the *laba katilo* goes to the boat carpenter, and the *iku laja* goes to the sail maker. Fourth, there are shares (*lefa tana*) that go to two *tana alep* clans. These shares are given only from sperm whale and represent a historical concession given in exchange for use of the site on which the village now resides. In addition, there are small discretionary shares (*teba*) usually given out by boat manager (see Alvard[152] for more details).

options. One could attempt to learn on one's own the beliefs of all the potential cooperative partners. This could prove difficult, time consuming and error prone. In the Lamalera case, there were 290 men who hunted in 1999, and more who participated either as craftsmen or corporate members. There are also numerous prey species that differ in ways that might effect butchering. In addition, even if one could determine what each possible fellow cooperator believes is the correct way to butcher and distribute, unless there is a mechanism that also enhances agreement, each participant may simply learn that others have different views of how to butcher the whale.

One hypothesis is that lineage membership acts as an unambiguous, easily observed marker (like a green beard) that allows individuals to identify and assort with others who have a higher probability of sharing norms. Preferring to assort with someone who shares lineage identity increases the probability that they also share ideas of what is normative; it decreases anonymity, and provides assurance that fellows play by the same rules. Data that show Lamalera hunters assort by lineage membership rather than strict kinship supports this idea.[122]

CONCLUSION

Many evolutionary anthropologists who study human behavior have ignored culture in practice, if not explicitly in theory. Rejecting a lack of scientific rigor on the part of traditional cultural anthropology is appropriate. However, it is a mistake to disregard culture itself, arguably one of the critical watershed adaptations of the human lineage, because its past students have used misguided methods. The real division in contemporary anthropology lies between science and nonscience, not between culture and biology.

Increasingly, the application of evolutionary theory to the problem of culture has brought to bear the analytic tools associated with the adaptationist program.[70] In other words, observational learning can be usefully understood as a complex adaptation that provides selective advantages responsible for its presence. In this paper I have reviewed a number of ideas concerning the adaptive nature of cultural ability. Following the seminal work of Boyd and Richerson,[7] I have discussed how socially transmitted information allows learning to be more selective and cost effective. Social learning, combined with selective individual learning, provides individuals advantages in rapidly changing environments like those that characterized the Pleistocene. Relatedly, culture also allows information to accumulate—the ratchet effect[22]—into complex traditions and oral histories that allow rapid adaptation to changing environments.[83] Not only can innovation be incorporated and maintained in behavioral repertoires, but individuals also have access to historical reservoirs of information otherwise lost with the death of individual innovators. The advantages are most apparent with technological advances that can build on and incorporate historical innovations.[27]

A critical point made by Boyd and Richerson[28] that motivates much of this paper is that the advantages of the social complexity allowed by the ratchet effect cannot have been the selective force that originally produced cultural abilities. As I have highlighted here, accumulated culture needs to be understood as an exaptation derived from other cognitive adaptations that perhaps are related to managing a complex social life. The communication of intent so crucial to the solution of coordination games like cooperative hunting requires a theory of mind and may have been one selective pressure favoring the evolution of language and culture. Coordination problems abound, and their solution is significantly facilitated when partners have the ability to acquire information quickly about others' norms of behavior and then associate with others who share their norms.

While simply speaking to one another is often sufficient to generate complexly coordinated behaviors, evolutionarily speaking, speaking is anything but simple. It is possible that culture solves problems so transparently that we do not see them as problems at all. Among experimental game theorists, pregame communication among subjects is such a simple solution to many games that researchers routinely disallow it, in order for the "truly" interesting solutions to emerge.[146] Not only do people speak but, as discussed earlier, humans also use symbols and markers of group identity to transmit information via mind reading about norms in order for them to assort positively. The adaptive advantages of such positive assortment with others in terms of solving collective action problems are impressive.

As is often the case, theory has outstripped hypothesis testing. Evolutionary anthropologists who have studied cultural processes, while developing a very rich theoretical program, have left untested many of the predictions generated by this theory. Despite the wealth of ideas found in the classic work of Boyd and Richerson's,[7] for example, very few of these ideas have been tested empirically, although this is beginning to change (see the work of Aunger,[67] Henrich,[77] and Gil-White[154]).

How might behavioral ecologists and other evolutionary anthropologists incorporate culture into their analyses? Recent work using signaling theory is one example where behavioral ecology and culture may be used together, although the connection is currently more implicit than explicit. Costly signaling theory argues that individuals often engage in behaviors that are honestly linked to a variety of the signaler's qualities, such as health, intelligence, courage, leadership, or generosity.[155] The signals may act as reliable signals of commitment to intragroup cooperation.[156,157] Honest signals allow observers to learn about otherwise unobservable qualities of the signaler and make decisions beneficial to both. In humans, such displays are not limited to hunting-and-gathering societies or subsistence activities. There is a wide variety of sometimes seemingly maladaptive and otherwise inexplicable behavior that may be understood in terms of signaling theory. Some examples include monumental architecture,[158] expensive public rituals like the potlatch among the Kwakiutl,[159] conspicuous consumption among the wealthy,[160] and elaborate courtship displays.[161] Understanding the signals as culturally transmitted will go a long way toward understanding seemingly arbitrary yet socially important traits.

Finally, bringing culture within the analytic purview of evolutionary anthropology should be considered an integral part of a larger agenda to bring the social sciences in line with the rest of the natural sciences.[9,44,162,163] Understanding that culture is social information in a material world places its study squarely within the realm of scientific inquiry. Admitting that the ability to transmit and acquire cultural information is among the defining human adaptations places it squarely on the agenda of evolutionary anthropologists.

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