# Memes: Universal Acid or a Better Mouse Trap?

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Among the many vivid metaphors in *Darwin's Dangerous Idea*, one stands out. The understanding of how cumulative natural selection gives rise to adaptations is, Dennett says, like a "universal acid"—an idea so powerful and corrosive of conventional wisdom that it dissolves all attempts to contain it within biology. Like most good ideas, this one is very simple: Once replicators (material objects that are faithfully copied) come to exist, some will replicate more rapidly than others, leading to adaptation by natural selection. The great power of the idea is that the resulting adaptations can be understood by asking what leads to efficient, rapid replication. Given that ideas seem to replicate, it is natural that Dawkins (1976, 1982), Dennett (1992), and others have explored the possibility of using this idea to explain cultural evolution.

Natural selection wasn't Darwin's only powerful, far-reaching idea. Ernst Mayr (1982) has argued that was what he calls "population thinking" was also among Darwin's foundational contributions to biology. Before Darwin, species were thought to be essential, unchanging types, like geometric figures and chemical elements. Darwin saw that species were populations of organisms that carried a variable pool of inherited information through time. To understand the evolution of species biologists had to account for the processes that changed the nature of that inherited information. Darwin thought that the most important processes were natural selection, sexual selection, and the "inherited effects of use and disuse." We now know that the last process is not important in organic evolution—unlike Darwin, modern biologists do not believe that the sons of blacksmiths inherit their father's mighty biceps. Nowadays biologists think many processes that Darwin never dreamed of are important including segregation, recombination, gene conversion, and meiotic drive. Nonetheless, modern biology is fundamentally Darwinian because its explanations of evolution are rooted in population thinking, and. If Darwin were to be resurrected tomorrow through some miracle of cloning, we think he would be quite happy with his legacy.

In this paper we want to convince you that population thinking, not natural selection, is the key to conceptualizing culture in terms of material causes. This argument is based on three well-established facts:

1. *There is persistent cultural variation among human groups.* Any explanation of human behavior must account for how this variation arises and how it is maintained.

2. *Culture is information stored in human brains.* Every human culture contains vast amounts of information. Important components of this information are stored in human brains.

3. *Culture is derived.* The psychological mechanisms that allow culture to be transmitted arose in the course of hominid evolution. Culture is not simply a byproduct of intelligence and social life.

Most culture is information stored in human brains—information that got into those brains by various mechanisms of social learning. It follows that to explain the distribution of information stored in the brains of the members of current generation, any coherent theory will have to account for the cultural information in the brains of the previous generation. The theory will also have to explain how this information, together with genes, and environmental contingencies caused the present generation to acquire the cultural information that it did. Unfortunately, we do not understand how this process works. It may be that cultural information stored in brains takes the form of discrete memes that are replicated faithfully in each subsequent generation, or it may not. This is an empirical question which at present is unanswered, and we will see that other models are possible. In every case, the Darwinian population approach will illuminate the process by which the cultural information that is stored in a population of brains is transformed from one generation to the next.

We also want to convince you that population thinking can play an important, constructive role in the human sciences. The fact that population thinking is logically necessary for a materialist theory of culture, doesn't necessarily mean that such a theory will be useful. Thus, we know that human culture must be consistent with quantum mechanics, but it is unlikely that such a connection will help us understand, say, ethnic conflict. However, we think Darwinian models of culture *are* useful for two reasons: First, they serve to connect the rich models of behavior based on individual action developed in economics, psychology, and evolutionary biology with the data and insights of the cultural sciences, (anthropology, archaeology, and sociology). In doing so, we think that it can help shed light on important unsolved problems in the social sciences. Second, population thinking is useful because it offers a way to build a mathematical theory of human behavior that captures the important role of culture in human affairs. Population thinking is not a universal acid that will dissolve existing social science. But, it is a better mousetrap, providing useful new tools that can help solve outstanding problems in the human sciences.

### *Culture is heritable at the group level*

One of the striking facts about the human species is that there are important, persistent differences between human groups that are created by culturally transmitted ideas, not genetic differences, or differences in the physical or biotic environment. Sonya Salamon (1992) research on immigrant communities in the U.S. shows how cultural differences can give rise to different behaviors in the same environment. For example, one of Salamon's studies focussed on two farming communities in southern Illinois. "Freiburg" (a pseudonym), is inhabited by the descendents of German-Catholic immigrants who arrived in the area during the 1840's. "Libertyville" (also a pseudonym) was settled by people from other parts of the US, mainly Kentucky, Ohio, and Indiana, when the railroad arrived in 1870. These two communities are only about 20 miles apart and have been carefully matched for similar soil types.

The people in these two communities have different values about family, property and farm practice, and these differences seem consistent with their ethnic origins. The farmers of Freiburg tend to value farming as a way of life, and they want at least one son or daughter to continue as a farmers. In Freiburg, wills specify that the farm will go to a child who will farm the land and use farm proceeds to buy out any non-farming siblings. Parents put considerable pressure on children to become farmers, but place little importance on education. Salomon argues that these “yeoman” values are similar to those observed among peasant farmers in Europe and elsewhere. In contrast, the “Yankee” farmers of Libertyville regard their farms as profit making businesses. They buy or rent land depending on economic conditions and if the price is right they sell. Many Yankee farmers would prefer their children to continue farming, but they see it as an individual decision. Some families help their children enter farming, but many do not, and they generally place a strong value on education.

The difference in values between Freiburg and Libertyville lead to measurable differences in farm practices despite the proximity of the two towns and the similarity of their soils. Farms are substantially larger in Libertyville—the mean size of farm operations in Libertyville is 518 acres compared to 276 acres in Freiburg. The Libertyville farms are larger because Yankee farmers rent more land. The two communities also show striking differences in farm operations. In Libertyville, as in most of Southern Illinois, farmers specialize in grain production. It is the primary source of income for 77% of the farmers in Libertyville. In Freiburg many people mix grain production with dairying or livestock raising, activities that are almost absent in Libertyville. Because animal operations are labor intensive, they allow Germans to accommodate their larger families on their more limited acreage. Yankee farmers decided against dairying and stock raising because grain farming is more profitable and less work.

The fact that culturally distinctive human groups behave differently in the same environment implies that culture is heritable, at least at the group level. Many beliefs and values that are common in a group at one point in time are also common among the descendants of the same group.  Any theory of how culture works must be consistent with this fact. It must explain why a the German farmers of Freiburg hold different beliefs about life and land than their Yankee neighbors lmost 150 years after leaving Europe.

### ***Culture is information in stored human brains***

Every human culture contains an enormous amount of information. Consider how much information must be transmitted to maintain a particular distinctive spoken language. A lexicon requires something like 10,000 associations between words and their meanings. Grammar entails a complex set of rules regulating morphosyntax, and although the extent to which these rules arise from innate, genetically transmitted structures, it is clear that the rules that underlie grammatical differences that separate English and Chinese are culturally transmitted. Subsistence techniques also entail large amounts of information. For example, Blurton-Jones and Konner (1976) showed that the !Kung San have a very detailed knowledge of the natural history of the Kalahari, so detailed in fact that the researchers were unable to judge the accuracy of much of !Kung knowledge because it exceeded that of western biology. As anyone who as ever tried to make a decent stone tool can attest, the manufacture of even the simplest tool requires lots knowledge;  more complex technology requires even more. Imagine the instruction manual for constructing a seaworthy kayak on from materials available on the North Slope of Alaska. The institutions that regulate social interactions incorporate still more information. Property rights, religious custom, roles and obligations all require a considerable amount of detailed information.

The vast store of information that exists in every culture cannot simply float in the air. It must be encoded in some material object. In societies without widespread literacy, the only objects in the environment capable of storing this information are human brains and human genes. It is undoubtedly true that some cultural information is stored in artifacts. It may well be that the designs that are used to decorate pots are stored on the pots themselves, and that when young potters learn how to make pots they use old pot, not old potters, as models. In the same way the architecture of the church may help store information about the rituals performed within. Without writing, however, the ability of artifacts to store culture is quite limited. First, many artifacts are very difficult to reverse-engineer. The young potter cannot learn how to select clay and temper, or how to fire a pot by studying of existing ones. Second, much  cultural information is semantic knowledge—how can an artifact store the notion that Kalahari porcupines are monogamous? Or the rules that govern bride price transactions?.

It is also clear that much cultural information is not stored in human genes. In one sense this is obvious. The evidence is very clear that very little cultural variation results from genetic differences. We know that genetic differences do not explain why some people speak Chinese and others English, or why the !Kung know a lot more about the biology of porcupines than most readers of this paper.

However, there is a subtle and much more plausible way that genes could store cultural information. It could be that most human culture is innate, genetically transmitted information that is evoked by environmental cues. Pascal Boyer (1992) argues that much religious belief has this character. For example, the Fang, a group in Cameroon studied by Boyer, have elaborate beliefs about ghosts. For the Fang, ghosts are malevolent beings that want to harm the living; they are invisible and can pass through solid objects, and so on. Boyer argues that most of what the Fang believe about ghosts is not transmitted, rather it is based on the innate, epistemological assumptions that underlie all cognition. Once a young Fang child learns that ghosts are sentient beings, she doesn't need to learn that ghosts can see or that they have beliefs and desires—these components are provided by cognitive machinery that reliably develops in every environment. According to this view, cultural differences arise because different environmental cues evoke different innate information. My neighbor believes in angels instead of ghosts because he grew up in an environment in which people talked about angels. However, most of what he knows about angels comes from the same cognitive machinery that gives rise to Fang beliefs about ghosts, and the information that controls the development of this machinery is stored in the genome.

This picture of culture is a useful antidote to the simplistic view that culture is simply poured from one head into another. Evolutionary psychologists are surely right that every form of learning, including social learning, requires an information-rich innate psychology, and that much of the adaptive complexity we see in cultures around the world stems from of this information. However, it is a big mistake to ignore transmitted cultural information. The single most important adaptive feature of culture is that it allows the gradual, cumulative assembly of adaptations over many generations, adaptations that no single individual could invent on their own. Cumulative adaptation cannot be based on innate, genetically encoded information.

Consider the evolution of a relatively simple form of technology, the mariners' magnetic compass (Needham, 1978). First, Chinese geomancers noticed the peculiar tendency of small magnetite objects to orient in the earth's magnetic field, an effect that they used for purposes of divination. Then, Chinese mariners learned that magnetized needles could be floated on water to indicate direction at sea. Next, over several centuries Chinese seamen developed a dry compass mounted on a vertical pin bearing, like a modern toy compass. This type of compass was acquired by Europeans in the late Medieval period. European seamen developed the card compass which allowed a helmsman to steer an accurate course by aligning the bow mark with the appropriate compass point. Compass makers later learned to adjust iron balls near the compass to zero out the magnetic influence from the ship and to gimbal the compass to damp the motion imparted to the card by the roll and pitch of the ship. Even such a relatively simple tool was the product of at least seven or eight innovations separated in time by centuries and in space by the breadth of Eurasia. This sort of adaptation can only occur because novel information can accumulate in human populations, be stored in human brains, and be transmitted through time by teaching and imitation.

Evolutionary psychologists argue that our psychology is built of complex, information-rich, evolved modules that are adapted for the hunting and gathering life that we pursued until the origins of agriculture a few thousand years ago. On this argument, humans can easily and naturally do the things we're really adapted to do like learn a language or understand the feelings of others. Inventing complex modern artifacts like the compass is hard, but what about skills necessary for hunting and gathering? Couldn't we learn these as easily as we learn language? Doesn't our brain contain the information necessary to follow hunting and gathering ways? Our ancestors lived as hunter-gatherers of some kind for the last 2 or 3 million years. If we had to do so, couldn't we be able to reinvent that stuff, just as Fang children invent the properties of their ghosts, or children can invent a grammar?

Good questions, but we think the answer is almost certainly “Are you nuts?!” Consider the following thought experiment. Suppose you are stranded in some not-too-extreme desert environment, not the Empty Quarter or the Atacama, but the Altar Desert between Sonoita, Mexico and Yuma, Arizona. Your task is to survive and raise your kids without modern technology. You will be given the resources to survive a few months to get your feet on the ground before we take away your last tin of food and your last steel tool—a little time to see what comes naturally. Will you make it?

We don’t think so. The stretch between Sonoita and Yuma used to be known as El Camino del Diabolo, “the Devil’s Road,” one leg of the main overland route from Old Mexico to California until the coming of railroads. For more than a century it was used by Spanish, Mexican, and American travelers. To get that far, every traveler had to already be an experienced frontiers-person, and no doubt most were hard-bitten, desert-wise, and well equipped with familiar technology. It was the best of several bad routes and was comparatively well known and well marked. Still, it was a infamous leg of the journey, and many travelers ended up in hasty graves that litter the route.

Now, consider that the Camino del Diabolo was also the home to Papago Indians who, with a few pounds of wood, stone and bone equipment, an impressive amount of hard-won knowledge, and a well adapted system of social institutions lived and raised their children in very same desert that killed so many pioneers. We don’t know about you, but if our task was to get to Yuma via the Camino del Diabolo without our accustomed industrial technology, we’d trade a few hours of tutoring by a traditional Papago for any number of months of trying to summon an innate knowledge of the desert.

## *Culture is Derived*

Culturally transmitted traditions occur in many other species of animals. In a review of social transmission of foraging behavior, Levebre and Palameta (1988) give 97 examples of cultural variation in foraging behavior in animals as diverse as baboons, sparrows, lizards, and fish. Much of the evidence for culture in other animals consists of observations of different behavior by populations of the same species living in similar environments. For example, chimpanzees in the Mahale Mountains of Tanzania often adopt a unique grooming posture in which both partners extend one arm over their heads, clasp hands, and then groom one another’s exposed arm pits. These grooming hand-clasps occur often and are performed by all members of the group. Chimpanzees at Gombe, who live less than 100 kilometers away in a similar type of habitat, groom often but never perform this behavior. Sometimes scientists have observed the spread of a novel behavior. One famous example comes from Japan where a group of Japanese macaques, whose range included a sandy beach, were provisioned with sweet potatoes. A young female macaque accidentally dropped her sweet potato into the sea as she was trying to rub sand off it. She must have liked the result, as she began to carry all of her potatoes to the sea to wash them. Other monkeys followed suit. However, it took other members of the group quite some time to acquire the behavior and many monkeys never washed their potatoes. Finally, some evidence for culture in other animals comes from experiments which demonstrate that behavior is socially transmitted. The most famous case is the transmission of song dialects in birds like the white crowned sparrow.

There is little evidence, however, of cumulative cultural evolution in other species. With a few exceptions, social learning leads to the spread of behaviors that individuals could have learned on their own. For example, food preferences are socially transmitted in rats. Young rats acquire a preference for a food when they smell the food on the pelage of other rats (Galef 1988). This process can cause the preference for a new food to spread within a population. It can also lead to behavioral differences among populations living in the same environment, because current foraging behavior depends on a history of social learning. However, it does not lead to the cumulative evolution of complex new behaviors that no individual rat could learn on its own. Thus, in other animals it is quite plausible that most of the detailed information that creates cultural differences is stored and transmitted genetically.

Circumstantial evidence suggests that the ability to acquire novel behaviors by observation is essential for cumulative cultural change. Students of animal social learning distinguish *observational learning* which occurs when younger animals observe the behavior of older animals and learn how to perform a novel behavior by watching them, from a number of other mechanisms of social transmission which also lead to behavioral continuity without observational learning (Galef 1988, Visalberghi and Fragazy1990, Whiten and Ham 1992). One such mechanism, *local enhancement*, occurs when the activity of older animals increases the chance that younger animals will learn the behavior on their own. Imagine a young monkey acquiring its food preferences as it follows its mother around. Even if the young monkey never pays any attention to what its mother eats, she will lead it to locations where some foods are common and others rare, and the young monkey may learn to eat much the same foods as mom.

Local enhancement and observational learning are similar in that they can both lead to persistent behavioral differences among populations, but only observational learning allows *cumulative* cultural change (Tomasello et al 1993). To see why, consider the cultural transmission of stone tool use. Suppose that occasionally early hominids learned to strike rocks together to make useful flakes. Their companions, who spent time near them, would be exposed to the same kinds of conditions and some of them might learn to make flakes too, entirely on their own. This behavior could be preserved by local enhancement because groups in which tools were used would spend more time in proximity to the appropriate raw materials. However, that would be as far as it would go. Even if an especially talented individual found a way to improve the flakes, this innovation would not spread to other members of the group because each individual learned the behavior anew. Local enhancement is limited by the learning capabilities of individuals and the fact that each new learner must start from scratch. With observational learning, on the other hand, innovations can be incorporated into others' behavioral repertoires if younger individuals are able to acquire the modified behavior by observational learning.  To the extent that observers can use the behavior of models as a starting point, observational learning can lead to the cumulative evolution of behaviors that no single individual could invent  on its own.

Adaptation by cumulative cultural evolution is apparently not a byproduct of intelligence and social life. Capuchin monkeys are among the world's cleverest creatures.  In nature, perform many complex behaviors, and in captivity  they can be taught extremely demanding tasks. Capuchins live in social groups and have ample opportunity to observe the behavior of other individuals of their own species, yet good laboratory evidence indicates that they monkeys make no use of observational learning. Observational learning is not simply a byproduct of intelligence and the opportunity to observe conspecifics. Rather, it seems to require special psychological mechanisms (Bandura 1986). This conclusion suggests that the psychological mechanisms that enable humans to learn by observation are adaptations have been shaped by natural selection because culture is beneficial.

## *Cultural evolution is Darwinian*

Now, let us consider what these facts imply for a theory of culture. Consider a population of individuals who are culturally interconnected; they speak dialects of a single language, use similar technology, share relatively similar beliefs about the world, and have similar moral values. People in this population think and behave differently from other peoples, in part, because they have different culturally transmitted information stored in their brains. Next consider the descendants of this population, say 100 years later. The culture of the descendant population will be similar in many ways to that of their predecessors. Their language will be similar, and they may often use similar technology, have similar beliefs about the world and subscribe to a similar moral system. The fact that culture depends on behavior stored in the brains of this population requires us to account for how the information that generates these similarities was transmitted from the brains in the first population to the brains in the second.

Of course, there will also be differences between the two populations, sometimes small, sometimes great.  Some of these differences will arise because some behaviors are more common in the second population, what was previously a rare usage or form of pronunciation has become common. Other differences will arise because genuinely new behavior is present, either as a result of borrowing from neighboring populations or genuine innovation. Thus, a complete theory would also have to account for why some forms of cultural information spread,  and why some forms have diminished, and how innovation occurs.

Cumulative cultural change requires observational learning. People (somehow) observe the behavior of others, and acquire the information necessary to produce a reasonable facsimile of the same behavior. In any given time period, each person observes only a sample of the people who make up his population. A very small child is exposed mainly to the people in her family, older children are exposed to peers and teachers, and adults to yet a wider range of people. We will refer to this group of people as an individual's "cultural sample." For most of human history cultural samples were small, but nowadays they may be immense.

The fact that cultures often persist over time with little change means that the commonness of a behavior in an individual's cultural sample must have a positive effect on the probability that the individual ultimately acquires the cultural information that generates that behavior. Such a tendency could arise in several different ways: If observational learning takes the form of approximately unbiased copying, then common-behaviors will be more frequent in cultural samples, and therefore will be more likely to be copied. It could also be that the psychology of observational learning itself predisposes people acquire more common behaviors. Finally, it could be that rare behaviors are typically disadvantageous and less likely to be retained as a result of individual learning and experimentation.

It follows that cultural change is a population process. The argument proceeds in several steps:

a) To understand how a person behaves, we have to know the nature of the information stored in her brain.

b) To understand why people have the beliefs that they do, we must know what kinds of behaviors characterized their cultural sample.

c) To predict the distribution of cultural samples exist, you must know the cultural composition of the population.

d) Therefore, to understand how people behave we must understand why the population has the cultural composition that it does.

Similarities between descendant and ancestral populations arise because the necessary information has been transmitted from individual to individual through time without significant change. Differences occur because some variants have become more common, others have become more rare, and some completely new variants have been introduced. Thus, to account for both continuity and change we need to understand the population processes by which ideas are transmitted through time.

## ***Memes may not be replicators***

In *The Extended Phenotype*, Richard Dawkins (1982) argues that the cumulative evolution of complex adaptations requires what he calls replicators, things in the physical world that produce copies of themselves, and have the following three additional properties:

1. **Fidelity**. The copying must be sufficiently accurate that even after a long chain of copies the replicator remains almost unchanged

2. **Fecundity**. At least some varieties of the replicator must be capable of generating more than one copy of themselves.

3. **Longevity**. Replicators must survive long enough to affect their own rate of replication.

Replicators give rise to cumulative adaptive evolution because replicators are targets of natural selection. Genes are replicators—they are copied with astounding accuracy, they can spread rapidly, and they persist throughout the life time of an organism directing its machinery of life. Dawkins thinks that beliefs and ideas are also replicators. On the face of it, this is an apt analogy. Beliefs and ideas can be copied from one mind to another, spreading through a population, controlling the behavior of people who hold them.

But there are reasons to doubt that beliefs and skills are replicators, at least in the same sense that genes are. Unlike genes, ideas are not transmitted intact from one brain to another. Instead the information in one brain generates some behavior, somebody else observes this behavior, and then (somehow) creates the information necessary to generate very similar behavior. The problem is that there is no guarantee that the information in the second brain is the same as the first. For any phenotypic performance there are potentially an infinite number of rules that would generate that performance. Memes will be transmitted from brain to brain only if most people induce a unique rule from a given phenotypic performance. While this may often be the case, it is also plausible that genetic, cultural, or developmental differences among people may cause them to infer different memes from the same overt behavior. To the extent that these differences shape future cultural change, the replicator model captures only part of cultural evolution.

The generativist model of phonological change illustrates the problem. According to the generativist school of linguistics, individual pronunciation is governed by a complex set of rules that take as input the desired sequence of words and produce as output the sequence of sounds that will be produced (Bynon 1977). Generativists also believe that as adults people can modify their pronunciation only by adding new rules that act at the *end* of the chain of existing rules. Children, on the other hand, are not constrained by the rules used to generate adult speech. Instead they induce the simplest set of grammatical rules that will account for the performances they hear, and these may be quite different than the rules used by adult speakers. Although the new rules produce the same performance, they can have a different structure, and therefore, allow further changes by rule addition that would not have been possible under the old rules.

The following example (from Bynon 1977) illustrates this phenomenon. In some dialects of English, people pronounce words that begin with *wh* using what linguists call an “unvoiced” sound while they pronounce words beginning with *w* using a voiced sound.

(Unvoiced sounds are produced with the glottis open resulting in a breathy sound while voiced sounds are produced with the glottis closed causing a resonant tone.) People who speak such dialects must have mental representations of the two sounds and rules to assign them to appropriate words. Now suppose that people who speak such a dialect come into contact with other people who only used the voiced *w* sound. Further suppose that this second group of people is more prestigious, and accordingly people in the first group modify their speech so that they too use only voiced *w*'s. According to the generativists, they will accomplish this change by adding a new rule which says "voice all unvoiced *w*'s." So, Larry wants to say *Whether it is better to endure*... The part of his brain that takes care of such things looks up the mental representations for each of the words including *whether* which has an unvoiced *w* (because that is the way Larry learned to speak as a child). Then after any other processing for stress or tone, the new rule changes the unvoiced *w* in *whether* to a voiced *w.* Children learning language in the next generation never hear an unvoiced *w* and, according to generativists, they adopt the same underlying representation for *whether* and *weather*. Thus, even though there is no difference in the phenotypic performance among parents and children, children do not acquire the same memes as their parents. This difference may be important because it will affect further changes. For example, it might make it less likely that the two sounds would split again in the future.

### *Replicators are not necessary for cumulative adaptive evolution*

We are also doubtful that replicators are necessary for the cumulative evolution of complex features. Here is an example of a transmission system which does just that. When you speak, the kind of sounds that come out of your mouth depend on geometry of your vocal tract. For example, the consonant *p* in *spit* is created by momentarily bringing your lips together with the glottis open. Narrowing the glottis converts this consonant to *b* as in *bib*. Leaving the glottis open and slightly opening the lips produces *pf* as in the German word *apfel*. Linguists have shown that even within a single speech community individuals vary in the exact geometry of the vocal tract used to produce any given word. Thus it seems plausible that individuals vary in the culturally acquired rule about how to arrange the inside of the mouth when they are speaking any particular word. Languages vary in the sounds used and this variation can be very long lived. For example, in dialects spoken in the northwest of Germany, *p* is substituted for *pf* in apfel and many similar words. This difference arose about 500 AD and has persisted ever since (Bynon 1977).

So how are different rules governing speech production transmitted from generation to generation? Consider two models:

First, suppose that each child learning language is exposed to the speech of a number of adults. These adults vary in the way that they produce the *pf* sound in *apfel*. Each child figures out how she would need to position her tongue to produce the same *pf* sound as each adult model, and then she adopts one of these as her own rule. Here, a mental rule that governs speech production is transmitted from one individual to another. The mental rule is a replicator; it clearly has fidelity. It has longevity because it potentially persists for generations, and it would have fecundity if the rule was more attractive that competing rules. And because it is a replicator, it can evolve.

Now consider a second model. As before children are exposed to the speech of a number of adults who vary in the way that they pronounce *pf*. Each child unconsciously computes the average of all the pronunciations that he hears and adopts the tongue position that produces approximately the average. Here, mental rules are not transferred from one brain to another. The child may adopt a rule that is unlike any of the rules in the brains of its models. The rules (memes) in particular brains do not replicate because no rule is copied faithfully. The phonological system can nonetheless evolve in a quite Darwinian way. More attractive forms of pronunciation can increase if they have a disproportionate effect on the average. Rules affecting different aspects of pronunciation can recombine and thus lead to the cumulative evolution of complex phonological rules. It is true that the act of averaging will tend to decrease the amount of variation in the population each generation. However, phenotypic performances will vary as a result of age, social context, vocal tract anatomy, and so on. Learners will often misperceive a performance. These sorts of errors in transmission will keep pumping variation into a population as blending bleeds it away. In fact, averaging might be necessary to prevent high noise levels from injecting too much variation into the population.

There are still other possibilities that differ even more radically from the replicator model. For example, a propensity to imitate the common type in the population can be coupled with high rates of individual learning to create a model in which there is little heritable variation at the individual level, but substantial heritability of group differences (Henrich and Boyd 1998). In such a model the cumulative evolution of adaptive complexity can occur, and occur rapidly, through selective processes that act at the group level (Boyd and Richerson, 1992, in press). Similarly, in recent models of the evolution of social institutions (Young 1998), there is no cultural transmission at the individual level. Although individuals simply acquire the best response to their social environment by trial and error learning, the structure of social interactions creates persistent, heritable variation at the group level.

We do not understand in detail how culture is stored and transmitted, so we do not know whether memes are replicators or not. If the application of Darwinian thinking to understanding cultural change depended on the existence of replicators, we would be in trouble. Fortunately, memes need not be close analogs to genes. They must be gene-like to the extent that they are somehow capable of carrying the cultural information necessary to give rise to the cumulative evolution of complex cultural patterns that differentiate human groups. They exhibit the essential Darwinian properties of fidelity, fecundity, and longevity, but, as the example of phonemes shows, this can be accomplished by a most un-gene like, replicatorless process of error prone phenotypic imitation. All that is really required is that culture constitutes a system maintaining heritable variation.

### ***Darwinian models are useful***

Science on the frontier often has an anarchic, nervy flavor because it must deal with multiple uncertainties. Of course we'd be better off knowing exactly what memes are. Papering over the uncertainties of how culture is stored and transmitted no doubt leads to errors, and conceals areas of fruitful inquiry. But as the psychologists explore one part of the frontier, the evolutionist should probe others. Studying the population properties of cultural information has lots of implications for human cognitive psychology, and vice versa. For example, when a child has the chance to copy the behavior of several different people, does she choose a single model for a given, discrete cultural attribute? Or, does she average, or in some other way combine, the attributes of alternative models? The minute you try to build a population model of culture you see that this question is crucial. However, despite conducting 1000's of experiments on social learning, psychologists apparently have never thought to answer this question. Just as at a four-way stop, it makes no sense for everyone to wait for everyone else. Watch what the other drivers are doing, certainly, but go whenever the road ahead is clear, even though it may turn out to be a dead end.

Many social scientists have reacted to the advent of Darwinian models of culture with palpable distaste (e.g. Hallpike 1986), while others have embraced these ideas with enthusiasm (e.g. Runciman, 1999). Much of this variation can be explained by people's feelings about the current Balkanization of the social sciences. The world of social science is divided into self-sufficient "ethnies" like anthropology and economics that are content to follow the questions and presuppositions that govern their discipline. The inhabitants of this world regard other disciplines with a mixture of fear and contempt, and take little interest in what they have to say about questions of mutual interest. Clearly this is not a satisfactory state of affairs.

We believe that Darwinian models can help rectify this problem. Disciplines like economics, psychology and evolutionary biology take the individual as the fundamental unit of analysis. These disciplines differ about how to model the individual and her psychology, but because they have the same fundamental structure there has been much substantive interaction between them. Nowadays many economists and psychologists work closely together, and a rich new body of work, often called behavioral economics, has rapidly become mature enough to be applied to important practical problems such as the effect of retirement accounts on national savings rates. In the same way, economists and evolutionary biologists have found it relatively easy to work together on evolutionary models of social behavior, a rapidly growing field in both disciplines. Other disciplines like cultural anthropology and sociology emphasize the role of culture and social institutions in shaping behavior, and researchers in sociology, anthropology, and history find interaction relatively comfortable. Bridging the gap between the individual and cultural disciplines has proved much more difficult. Darwinian models are useful precisely because they all both points of view to be expressed within a single theoretical framework in which neither individual nor culture is paramount. In population based models, culture and social institutions arise from the interaction of individuals whose psychology has been shaped by their social milieu.

To see how useful population based modes can be, consider the problem of human cooperation. There is no coherent explanation for the vast scale of cooperation in contemporary human societies, or why the scale of cooperation has increased many 1000 fold over the last 10,000 years. Models in economics and evolutionary biology predict that cooperation should be limited to small groups of relatives and reciprocators. Many theories in anthropology simply assume(often implicitly) that cooperative societies are possible, and that culturally transmitted beliefs and social institutions serve the interest of social groups, but no attempt is made to reconcile this assumption with the fact that people are at least partly self-interested. Darwinian models provide one cogent mechanism to explain human cooperation by identifying the conditions under which groups will come to vary culturally, and predicting when such variation will lead to the spread of culturally transmitted beliefs that support large scale cooperation (Soltis et al. 1995). In such models, the effect of different culturally transmitted beliefs on group prestige and group survival shapes the kinds of beliefs that survive and spread, which in turn effects what people want and what they believe, and therefore their behavior. Other recent work on the evolution of institutions (Young 1998) makes us optimistic that Darwinian models may have widespread utility.

Population thinking is also useful because it offers a way to build mathematical theory of human behavior that captures the important role of culture in human affairs. Mathematical theory has the great advantage of allowing conclusions to be reliably deduced from assumptions. Experience in economics and evolutionary biology also suggests that it leads to a kind of clear understanding that is difficult to achieve with verbal reasoning alone. Of course there is also a cost—mathematical theory is necessarily based on simplified models. However, the combination of mathematical and verbal reasoning is superior to either alone.

Memes are not a universal acid, but they are a better mouse trap. Population modeling of culture offers social science useful conceptual tools, and handy mathematical machinery that will help solve important, longstanding problems. It is not a substitute for rational actor models, or careful historical analysis. But it can be an invaluable complement to these forms of analysis that will enrich the social sciences.

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