1

Gene-Culture Coevolution

> The eye and the animal to which it belongs... are only so many out of the possible varieties and combinations of being, which the lapse of infinite ages has brought into existence... Millions of other bodily forms and other species having perished, being by the defect of their constitution.
>
> William Paley

> Man is nothing else but what he makes of himself.
>
> Jean-Paul Sartre

> He who understands baboons would do more towards metaphysics than Locke.
>
> Charles Darwin

> **C:** How are genes and human culture similar?
> **HG:** Both genes and human culture consist of information passed across generations and subject to mutation and selection.
> **C:** How have humans managed to evolve their extraordinary capacity for speech?
> **HG:** Persuasive and informative speakers were rewarded with higher quality mates and increased reproductive opportunities. Their offspring inherit their cognitive and physiological communicative powers.
> This is gene-culture coevolution.
>
> Choreographer interview

The acclaimed archeologist V. Gordon Childe called his account of human evolution *Man Makes Himself* (Childe 1936). Nothing could be more true, and it is true of our species alone. The reason is that at some point in the remote past our ancestors invented a new form of culture, one that is *transmissible across generations* and therefore capable of *accumulation across time and space*. This means that man makes culture, but how does man thereby make himself? This chapter provides the answer. In brief, the answer is that human culture affects the fitness payoffs to alternative social behaviors, rewarding some and penalizing others. The genes that predispose individuals to behave prosocially, according to the cultural rules of the group, are rewarded by having more copies in the next generation while correspondingly antisocial genes are disciplined by having fewer.

We are the species that we are because genes make culture and culture makes genes. Or, more accurately, genes provide individuals with the capacities and incentives to transform culture, and culture guides the transformation of the gene pool from generation to generation. We call this *gene-culture coevolution*.

The critical point in understanding this dynamic is that DNA is simply a *library of information* passed from parents to offspring, and genes are the books in this library (Noble 2011). Each of our cells contains a complete copy of this library, along with specialized information as to what books to read with the instructions to make the specific cell in question. A liver cell and a neuron are constructed by reading different books in the library and following the directions therein. Brain cells, for instance, open DNA books that provide information through which our mental lives are constructed.

Culture is also a library of information passed across generations. This library includes technical information, such as how to build and maintain fire, how to construct and maintain tools and weapons, how to speak and understand language, and which conventions govern social interaction within the group.

Both culture and genes are subject to the forces of evolution (Dawkins 1976; Mesoudi et al. 2006). Both are transmitted, but with a significant level of mutation, and mutants are selected and incorporated in to the library according to their relative fitness, by which we mean the average number of copies that appear in the next generation. Successful genetic mutations are generally *adaptive*, meaning they improve the long-term success of the population. Successful cultural changes are often maladaptive (Edgerton 1992), but so far, and in the long run, human culture has been extremely adaptive. Whether this will continue in the face of the proliferation of nuclear weapons, climate change, and reduction in biodiversity remains to be seen.

I grew up with the notion that man makes himself not only in the sense of V. Gordon Childe, but also in the sense expressed by Jean-Paul Sartre in the chapter head quote above. Sartre's is the notion that there is no such thing as human nature. Rather, we are the complete product of the choices we make. Our morality is a purely personally and socially constructed morality. This is profoundly mistaken (Cosmides et al. 1992). Just as ducks have duck nature and mosquitoes have mosquito nature, so do humans have human nature. This nature was forged through gene-culture coevolution over hundreds of thousands of years (Brown 1991). This book is an analysis of human nature and a tribute to its wonders.

1.1 Culture Determines Biological Fitness

Because of the importance of culture and complex social organization to the evolutionary success of *Homo sapiens*, individual fitness in humans depends on the structure of social life. Those who are successful according to social norms are differentially rewarded with more and healthier offspring, and violators of social rules are likely to be ostracized or killed.

Because culture is both constrained and promoted by the human genome, human cognitive, affective, and moral capacities are the product of an evolutionary dynamic involving the interaction of genes and culture. Whence *gene-culture coevolution* (Lumsden and Wilson 1981; Cavalli-Sforza and Feldman 1982; Boyd and Richerson 1985; Dunbar 1993; Richerson and Boyd 2004).

This coevolutionary process has endowed us with preferences that go beyond the self-regarding concerns emphasized in traditional economic and biological theory, and with a social epistemology that facilitates the sharing of intentionality across minds. Gene-culture coevolution is responsible for the salience of such other-regarding values as a taste for cooperation, fairness and retribution, the capacity to empathize, and the ability to value such character virtues as honesty, hard work, piety, and loyalty (Bowles and Gintis 2011; Wilson 2012; Tomasello 2014).

Gene-culture coevolution is the application of *sociobiology*, the general study of the social organization of biological species, to humans—a species that transmits culture in a manner that leads to quantitative growth across generations. Gene-culture coevolution is a special case of *niche construction*, which applies to species that transform their natural environment so as to facilitate social interaction and collective behavior (Odling-Smee et al. 2003). Examples are the beaver's dam and the bee's hive. In the case of gene-culture coevolution, the environmental change is that of *the social structure within which individuals live out their lives*. The natural environment may be involved as well, as when settled agriculture alters the ecology of disease-carrying insects, and hence selects for individuals who are relatively immune to these diseases (Laland et al. 2000).

The genome encodes information that is used both to construct a new organism and to endow it with instructions for transforming sensory inputs into decision outputs. Because learning is costly and time-consuming, efficient information transmission will ensure that the genome encodes those aspects of the organism's environment that are constant, or that change only very slowly through time and space, as compared with an individual lifetime. By contrast, environmental conditions that vary rapidly can be dealt with by providing the organism with *phenotypic plasticity* in the form of the capacity to learn. For instance, suppose the environment provides an organism with the most nutrients where ambient temperature is highest. An organism may learn this by trial and error over many periods, or it can be hard-wired to seek the highest ambient temperature when feeding. By contrast, suppose the optimal feeding temperature varies over an individual's lifetime. Then there is no benefit to encoding this information in the individual's genome, but a flexible learning mechanism will enhance the organism's fitness.

There is an intermediate case, however, that is efficiently handled neither by genetic encoding nor learning. When environmental conditions are positively but imperfectly correlated across generations, each generation acquires valuable information through learning that it cannot transmit genetically to the succeeding generation, because such information is not encoded in the germ line. In the context of such environments, there is a fitness benefit to the *epigenetic transmission* of information concerning the current state of the environment; i.e., transmission through non-genetic channels. This is called *cultural transmission*.

Several epigenetic transmission mechanisms have been identified (Jablonka and Lamb 1995), but cultural transmission in humans and to a lesser extent in other animals (Bonner 1984; Richerson and Boyd 1998) is a distinct and extremely flexible form. Cultural transmission takes the form of vertical (parents to children), horizontal (peer to peer) and oblique (elder to younger), as in Cavalli-Sforza and Feldman (1981), prestige (higher influencing lower status), as in Henrich and Gil-White (2001), popularity-related as in Newman et al. (2006), and even random population-dynamic transmission, as in Shennan (1997) and Skibo and Bentley (2003). The parallel between cultural and biological evolution goes back to Huxley (1955), Popper (1979), and James (1880)—see Mesoudi et al. (2006) for details.

The idea of treating culture as a form of epigenetic transmission was pioneered by Dawkins (1976), who coined the term "meme" in *The Selfish Gene* to represent an integral unit of information that could be transmitted phenotypically. There quickly followed several major contributions to a biological approach to culture, all based on the notion that culture, like genes, could evolve through replication (intergenerational transmission), mutation, and selection. Cultural elements reproduce themselves from brain to brain and across time, mutate and are subject to selection according to their effects on the fitness of their carriers (Parsons 1964; Cavalli-Sforza and Feldman 1982). Moreover, there are strong interactions between genetic and epigenetic elements in human evolution, ranging from basic physiology (e.g., the transformation of the organs of speech with the evolution of language) to sophisticated social emotions, including empathy, shame, guilt, and revenge-seeking (Ihara 2011; Zajonc 1980,1984).

Because of their common informational and evolutionary character, there are strong parallels between models of genetic and cultural evolution (Mesoudi et al. 2006). Like biological transmission, culture is transmitted from parents to offspring, and like cultural transmission, which is transmitted horizontally to unrelated individuals, so in microbes and many plant species, genes are regularly transferred across lineage boundaries (Jablonka and Lamb 1995; Abbott et al. 2003; Rivera and Lake 2004). Moreover, anthropologists reconstruct the history of social groups by analyzing homologous and analogous cultural traits, much as biologists reconstruct the evolution of species by the analysis of shared characters and homologous DNA (Mace and Pagel 1994). Indeed, the same computer software developed by biological systematists is used by cultural anthropologists (Holden 2002; Holden and Mace 2003). In addition, archeologists who study cultural evolution have a similar *modus operandi* as paleobiologists who study genetic evolution (Mesoudi et al. 2006). Both attempt to reconstruct lineages of artifacts and their carriers. Like paleobiology, archaeology assumes that when analogy can be ruled out, similarity implies causal connection by inheritance (O'Brien and Lyman 2000). Like biogeography's study of the spatial distribution of organisms (Brown and Lomolino 1998), behavioral ecology studies the interaction of ecological, historical, and geographical factors that determine distribution of cultural forms across space and time (Winterhalder and Smith 1992).

Perhaps the most common criticism of the analogy between genetic and cultural evolution is that the gene is a well-defined, discrete, independently reproducing and mutating entity, whereas the boundaries of the unit of culture are ill-defined and overlapping. In fact, however, this view of the gene is outdated. We now know that overlapping, nested, and movable genes have some of the fluidity of cultural units, whereas quite often the boundaries of a cultural unit (a belief, icon, word, technique, stylistic convention) are quite delimited and specific. Similarly, alternative splicing, nuclear and messenger RNA editing, cellular protein modification, and genomic imprinting, which are quite common, undermine the standard view of the insular gene producing a single protein, and support the notion of genes having variable boundaries and having strongly context-dependent effects. Moreover, natural selection requires heritable variation and selection, but does not require discretely transmitted units.

In *The Extended Phenotype* Dawkins (1982a) added a second fundamental mechanism of epigenetic information transmission, noting that organisms can directly transmit environmental artifacts to the next generation, in the form of such constructs as ant nests, tree galls, and even social structures, such as mating and hunting practices. A species creating an important aspect of its environment and stably transmitting this environment across generations, known as *niche construction*, is a widespread form of epigenetic transmission (Odling-Smee et al. 2003). Niche construction includes gene-environment coevolution, because a genetically induced environmental regularity becomes the basis for genetic selection, and gene mutations that give rise to novel niche elements will survive if they are fitness-enhancing for their constructors.

An excellent example of gene-environment coevolution is the honeybee, in which the origin of its eusociality probably lay in a high degree of relatedness, but which persists in modern species despite the fact that relatedness in the hive is generally quite low, due to multiple queen matings, multiple queens, queen deaths, and the like (Gadagkar 1991; Seeley 1997; Wilson and Hölldobler 2005). The social structure of the hive, a classic example of niche construction, is transmitted epigenetically across generations, and the honeybee genome is an adaptation to the social structure laid down in the distant past.

Gene-culture coevolution in humans is a special case of gene-environment coevolution in which the environment is culturally constituted and transmitted (Feldman and Zhivotovsky 1992). The key to the success of our species in the framework of the hunter-gatherer social structure in which we evolved is the capacity of unrelated, or only loosely related, individuals to cooperate in relatively large egalitarian groups in hunting and territorial acquisition and defense (Richerson and Boyd 2004; Boehm 1999). While some contemporary biological and economic theorists have attempted to show that such cooperation can be supported by self-regarding rational agents (Alexander 1987; Fudenberg et al. 1994; Trivers 1971), the conditions under which their models work are implausible even for small groups (Boyd and Richerson 1988; Gintis 2009a). Rather, the social environment of early humans was conducive to the development of prosocial traits, such as empathy, shame, pride, embarrassment, and reciprocity, without which social cooperation would be impossible (Sterelny 2011).

Neuroscientific studies exhibit clearly the genetic basis for moral behavior. Brain regions involved in moral judgments and behavior include the prefrontal cortex, the orbitalfrontal cortex, and the superior temporal sulcus (Moll et al. 2005). These brain structures are virtually unique to or most highly developed in humans and are doubtless evolutionary adaptations (Schulkin 2000). The evolution of the human prefrontal cortex is closely tied to the emergence of human morality (Allman et al. 2002). Patients with focal damage to one or more of these areas exhibit a variety of antisocial behaviors, including the absence of embarrassment, pride and regret (Beer et al. 2003; Camille 2004), and sociopathic behavior (Miller et al. 1997). There is a probable genetic predisposition underlying sociopathy, and sociopaths comprise about 4% of the male population, but they account for between 33% and 80% of the population of chronic criminal offenders in the United States (Mednick et al. 1977). It is clear from this body of empirical information that culture is directly encoded into the human brain with symbolic representations in the form of cultural artifacts. This, of course, is the central claim of gene-culture coevolutionary theory.

1.2 Reciprocal Causality

Gene-culture coevolution is an empirical fact, not a theory. However, it is a complex and variegated process that takes many forms. Modeling gene-culture coevolution began with Feldman and Cavalli-Sforza (1976), followed by their book (Cavalli-Sforza and Feldman 1981), in which they modeled vertical (parent to child), oblique (non-parental elders to youngers), and horizontal (peer to peer) cultural transmission. Lumsden and Wilson (1981) presented an alternative model, as did Boyd and Richerson (1985). For enlightening contemporary reviews of these pioneers, see Lewontin (1981) and Maynard Smith and Warren (1982).

It might be thought that the complex and intimate interaction of genes and culture outlined above is overdrawn, and that human genetic evolution is the effect of genetic inclusive fitness maximization, culture being an effect of genes that can be factored out in the long run. For instance, the eminent evolutionary psychologist David Buss holds that "culture is not an autonomous casual process in competition with biology for explanatory power" (Buss 1999, p. 407). This denial of gene-culture coevolution can be shown to be *prima facie* untenable. To see this, suppose we have a vector g of genetic variables, a vector c of cultural variables, and a vector e of environmental variables, including the prevalence of predators and prey, weather and the like. In an evolutionary model, the rate of change of variables is a function of the variables, so we have

$$\dot{g} = F(g, c, e) \tag{1.1}$$

$$\dot{c} = G(g, c, e) \tag{1.2}$$

$$\dot{e} = H(e) \tag{1.3}$$

Note that it is plausible for c to affect the nature and pace of environmental change, in which case it should be included in the third equation above. We abstract from this causal path in order to strengthen the case for Buss' argument. The contention that culture is an effect of genetic fitness maximization in this framework is the assertion that c can be eliminated from these equations. Under what conditions can this occur? Taking the derivative of equation (1.1), and substituting equations (1.2) and (1.3) into equation (1.1), we get

$$\ddot{g} = F_g(g, c, e)F(g, c, e) + F_c(g, c, e)G(g, c, e) + F_e(g, c, e)H(e). \tag{1.4}$$

If c is to be absent from this second order differential equation, the derivative of the right-hand side of equation (1.4) with respect to c must be identically zero. Thus, we have

$$0 \equiv F_{gc}F + F_gF_c + F_{cc}G + F_cG_c + F_{ec}H. \tag{1.5}$$

All five of the above terms must then be identically zero, so $Fc = 0$, implying that c does not enter on the right-hand side of the defining equations (1.1)–(1.3); i.e., genes are not a function of culture. This is obviously not appropriate for humans, since both genes and culture are functions of culture. Note that as long as there is high fidelity cultural transmission over multiple generations (signified by the middle row of horizontal arrows), genetic and cultural evolution are inextricably intertwined. By contrast, for species that do not have cumulative learning, these arrows are absent, and despite the fact that genes affect culture in every period, there is no cumulative interrelatedness of genes and culture.

There are many obvious examples of culture affecting genes. For instance, tribes that raise cattle tend to develop lactose tolerance in place of the default condition for humans, which is lactose intolerance (Gerbault et al. 2011). This development is easy to understand because the ability to digest milk is individually fitness-enhancing, so if the genes that permit lactose processing exist in the population or can be created through high probability mutations, lactose tolerance will evolve. Similar arguments apply to the evolution of the human gut after the control of fire for cooking (Gowlett and Wrangham 2013), the structural transformation of the human hand when social life moved from the trees to the ground (Marzke 1997), and the role of culture in creating a genetic predisposition for cooperative activity in humans (Gintis 2003a). We will use gene-culture evolution to illuminate especially complex issues of this and other physiological changes facilitating linguistic communication in humans (Deacon 1998).

1.3 The Physiology of Human Communication

The evolution of the physiology of speech and facial communication presents a theoretical challenge. It is easy to explain, if everyone else is gabbing away and you can only grunt and pant, why you might be handicapped in finding a spouse and teaching your children. But how could the use of complex phonics begin? When everyone is grunting and panting, what is the fitness benefit of being able to make more complex varieties of sounds? What is the fitness benefit of being able to interpret complex sounds? The answers are far from obvious and go far beyond simple individual fitness, or even inclusive fitness, maximization.

For this reason, the evolution of the physiology of speech is a dramatically complex example of gene-culture coevolution. A most common error in the literature is to consider language as a purely *mental* phenomenon that can be explained simply as a byproduct of brain size and intelligence. In fact, the ability to communicate through facial sign and speech has required major changes in human physiology. These could only have come about because individuals with superior communication capacities were rewarded with more and healthier children. Why might this have occurred?

The increased social importance of communication in human society rewarded genetic changes that facilitate speech. Regions in the motor cortex expanded in early humans to facilitate speech production. Concurrently, nerves and muscles to the mouth, larynx, and tongue became more numerous to handle the complexities of speech (Jurmain et al. 1997). Parts of the cerebral cortex, Broca's and Wernicke's areas, which do not exist or are relatively small in other primates, are large in humans and permit grammatical speech and comprehension (Binder et al. 1997; Belin et al. 2000).

Adult modern humans have a larynx low in the throat, a position that allows the throat to serve as a resonating chamber capable of a great number of sounds (Relethford 2007). The first hominids that have skeletal structures supporting this laryngeal placement are the *Homo heidelbergensis*, who lived from 800,000 to 100,000 years ago. In addition, the production of consonants requires a short oral cavity, whereas our nearest primate relatives have much too long an oral cavity for this purpose. The position of the hyoid bone, which is a point of attachment for a tongue muscle, developed in *Homo sapiens* in a manner permitting highly precise and flexible tongue movements.

Another indication that the tongue has evolved hominids to facilitate speech is the size of the hypoglossal canal, an aperture that permits the hypoglossal nerve to reach the tongue muscles. This aperture is much larger in Neanderthals and humans than in early hominids and nonhuman primates (Dunbar 2005). Human facial nerves and musculature have also evolved to facilitate communication. This musculature is present in all vertebrates, but except in mammals it serves feeding and respiratory functions alone (Burrows 2008). In mammals, this mimetic musculature attaches to the skin of the face, thus permitting the facial communication of such emotions as fear, surprise, disgust, and anger. In most mammals, however, a few wide sheet-like muscles are involved, rendering fine information differentiation impossible, whereas in primates, this musculature divides into many independent muscles with distinct points of attachment to the epidermis, thus permitting higher bandwidth facial communication. Humans have the most highly developed facial musculature by far of any primate species, with a degree of involvement of lips and eyes that is not present in any other species.

In short, humans have evolved a highly specialized and very costly complex of physiological characteristics that both presuppose and facilitate sophisticated aural and visual communication, whereas communication in other primates, lacking as they are in cumulative culture, goes little beyond simple calling and gesturing capacities. This example is quite a dramatic and concrete illustration of the intimate interaction of genes and culture in the evolution of our species.