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# Darwinism Extended: A Survey of How the Idea of Cultural Evolution Evolved

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**Abstract** In the past 150 years there have been many attempts to draw parallels between cultural and biological evolution. Most of these attempts were flawed due to lack of knowledge and false ideas about evolution. In recent decades these shortcomings have been cleared away, thus triggering a renewed interest in the subject. This paper offers a critical survey of the main issues and arguments in that discussion. The paper starts with an explication of the Darwinian algorithm of evolution. It is argued that this ‘formula’ is substrate-neutral, which means that biological evolution might not be the only Darwinian process. Other dynamic systems could evolve as well provided that certain conditions are met. In the case of human culture this seems to be the case. The paper then focuses on the notion of niche construction. It is argued that niche construction plays a crucial role in human evolution because it has altered the sources of natural selection and thus the path of evolution. Next two approaches to cultural evolution are discussed: sociobiology and memetics. I will argue that both approaches have flaws because they either underestimate the influence of culture or they stretch analogies too far. Finally two common objections against the idea of cultural evolution are addressed: Lamarckian inheritance and the issue of guided variation. I will argue that although cultural evolution differs from biological evolution in several respects, these discrepancies do not jeopardize the claim that cultural evolution is essentially Darwinian.

**Keywords** Cultural evolution · Universal Darwinism · Niche construction · Sociobiology · Memetics · Lamarckism

The existence of human culture is a deep evolutionary mystery, on a par with the origins of life itself.

Richerson and Boyd (2005, 126)

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## Introduction

Ever since the publication of *The Origin of Species* (1859) and *The Descent of Man* (1871), people have argued that Darwin's theory of evolution does not only pertain to the biological realm of organisms and species but to the realm of human culture as well. Yet the first attempts to cast culture into a Darwinian framework were somewhat hazardous because the theory of evolution was still incomplete, and as a result people held all kinds of erroneous ideas about evolution. The most common mistake was the widely held belief, propagated by Herbert Spencer (1857) amongst others, that evolution is linear (instead of treelike), thoroughly progressive, and that the white European male was the undisputed pinnacle and end point of this process. It was not until the second half of the 20th century, after the realization of the so-called Modern Synthesis in biology, that authors like Popper (1972); Toulmin (1972); Campbell (1974a, b); Wilson (1975); Dawkins (1976); Cavalli-Sforza and Feldman (1981); Boyd and Richerson (1985) and Hull (1988) resumed the thread by providing models which tried to explain cultural, technological and scientific change in terms of Darwinian principles. For the first time, the Neo-Darwinian theory of evolution was fully deployed in order to understand and explain the development of human culture.<sup>1</sup>

The idea is roughly as follows. Darwin's theory can be extended to the cultural domain, either because culture is considered to be an inextricable part of human nature, or because cultural change is a process fundamentally similar to biological evolution. The former approach sees culture as a direct extension of biological evolution, the latter approach sees culture as a process which is essentially analogous to biological evolution. Either way, cultural change is seen as a process which obeys and thus can be described and explained by Darwinian principles. Culture, in short, can be 'Darwinized'. Yet over the years, many critics have argued that any attempt to Darwinize culture is destined to fail because there are just too many obvious differences between biological evolution on the one hand and cultural change on the other. Hence culture can neither be a direct extension of biological evolution, nor a process that is somehow analogous to it. Of course these critics readily admit that culture 'evolves' in the sense that culture develops and that it changes over time. But that is considered a trivial fact, an obvious truth, because there really is not much needed to meet this condition. It is the stronger claim that these critics object to, the claim that culture evolves *according to Darwinian principles*. This claim, they argue, cannot be upheld because the way in which culture 'evolves' is completely different from the way biological species evolve. After all, biological evolution is a blind and mindless process whereas cultural evolution is guided by intentional agents. These, and other, differences between the two processes make any search for direct links or analogies redundant once and for all.

However, against these critics I shall argue that despite several obvious differences between the two kinds of evolution, cultural change nevertheless might still be called 'Darwinian' because it shares a key feature with biological evolution, viz., both kinds of evolution are the result of cumulative selection processes. I will argue that cumulative selection is the distinctive and defining characteristic of Darwinian evolution. So although many dynamic systems might exhibit directional change over

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<sup>1</sup> See Buskes (1998).

time – and thus evolve –, only a few of these systems evolve in a true Darwinian manner. I shall argue that our culture is one of those systems, although culture as a process obviously deviates from biological evolution in several respects. In the past some authors have mistakenly assumed that in order to be called ‘Darwinian’, cultural evolution should be largely similar to biological evolution. Clearly this is not the case. Analogies must not be stretched too far because both kinds of evolution have their own characteristics and idiosyncrasies. For instance, the way in which information is transmitted in cultural evolution might not entirely correspond with the way in which information is transmitted in biological evolution. In biological evolution the flow of information usually is ‘vertical’, when the genetic code is transferred from parents to offspring, while in cultural evolution the flow of information might be ‘horizontal’ as well, as when cultural information is passed on to contemporaries or nonrelatives. Yet to my mind cultural evolution might still be called ‘Darwinian’ even though it differs in several aspects from biological evolution because human culture, as opposed to animal culture, has the unique ability to accumulate. This means that information gradually builds up over successive generations resulting in highly intricate cultural artifacts and practices which never could have been invented from scratch by a single individual. It is this particular feature that makes cultural change, like biological evolution, quintessentially Darwinian. Both kinds of evolution, that is, are characterized by the accumulation of information, resulting in complex adaptations, historical lineages (whether genetic or conceptual), and descent with modification. Both genes and culture are informational entities that are differentially transmitted from one generation to the next.<sup>2</sup>

Here’s an outline of my argument. In “[Darwin’s Formula](#)”, I show how Darwinian evolution is propelled by what we might call ‘Darwin’s formula’, viz., a three-step algorithm comprising variation, selection, and replication. I argue that Darwin’s formula is substrate-neutral, so in principle the algorithm could be working in other domains – like the realm of culture – as well. In “[The Cultural Animal](#)”, I show how human culture differs from animal culture, and how this difference is caused by the way in which we gather and transmit information. It is this difference which makes human culture cumulative. In “[Niche Construction and Human Cumulative Culture](#)”, I argue that the emergence of human culture is closely related to the phenomenon of niche construction. With the rise of culture, human beings not only have radically altered their natural environments but the sources of selection in those environments as well. Thus niche construction alters the path of evolution. In “[Nature, Culture, and Co-evolution](#)” and “[Genes, Memes, and Flawed Analogies](#)”, I raise the question whether culture is a direct extension of biological evolution as is maintained by sociobiology, or rather a process which is analogous to biological evolution as adherents of memetics argue. I shall demonstrate that both schools have their flaws because they either underestimate the influence of culture (sociobiology), or they are inclined to stretch analogies too far (memetics). In “[Culture’s Blind Edge and Lamarckian Flavors](#)”, finally, I discuss two common objections against the idea of cultural evolution, i.e., its alleged Lamarckian character and its apparent directedness (or guided variation). Again I shall argue that cultural evolution indeed differs from biological evolution in these and other respects, but at the same time I believe that

<sup>2</sup> Laland (2002); Mesoudi et al. (2004); Levinson and Jaisson (2006).

these discrepancies do not undermine my central claim that cultural evolution is essentially Darwinian.

### Darwin's Formula

It was Darwin's great merit that he provided an explanation for something that had baffled scientists and philosophers for centuries: the perplexing diversity and complexity of the living world. Before Darwin, scholars and thinkers had no choice but to appeal to the supernatural in order to explain the riddle. It was firmly believed that all species were created by an omnipotent, divine craftsman, someone who thought it all up, drew the design, and then blew life into it. Yet Darwin demonstrated that the diversity and complexity of the living world can be explained by a mechanism which does not appeal to the supernatural or the divine, to wit: evolution. Darwinian evolution is governed by what we might call 'Darwin's formula'. Darwin's formula consists of the three elements variation, selection, and replication.<sup>3</sup> It is quite a simple mechanism, but given enough time and successive generations, it can produce truly awesome effects. Variation, the first element of the formula, might be called the 'fuel' of evolution. Variation means that the members of a particular population always show slight phenotypic differences, for instance in color, in height, or in the way they are able to cope with disease, etc. Some phenotypic variations are useful while others are harmful with regard to survival and reproduction. That brings us to the second element of the formula, selection, which we might call the 'engine' of evolution. Selection means that some individuals are more successful in surviving and reproducing than other individuals. These differences in fitness are generally *non-random* because selection is not a blind lottery. On average, the individuals who are best adapted to their environment will survive and produce the most offspring. Natural selection is a sieving process which retains useful variations and rejects harmful ones. Finally, the third and last element of Darwin's formula, replication, might be called the 'key' of evolution because, in some real sense, it opens the door to immortality. Not for individual organisms because they eventually will die, but for their genetic blueprint, their DNA. Through sexual or asexual reproduction, organisms can transmit their genetic makeup to the next generation, over and over again, and this makes their DNA virtually indestructible. In fact, some genes in our bodies are so old that we share them with insects, flatworms, and yeast. Moreover, replication also entails that the sieving process becomes cumulative in character. In the course of many generations, useful traits will be enhanced whereas harmful traits will gradually disappear. Again, this means that cumulative selection is quintessentially a non-random process. After all, cumulative selection is no single, haphazard event. On the contrary, cumulative selection is a process in which the results of one sieving process are fed into a subsequent sieving, and so on, ad infinitum. The evolving 'entities' are thus subjected to sorting over many 'generations' in succession, thereby giving a direction to evolution. In the biological realm such cumulative sieving mechanisms result in the countless examples of complex design, functional adaptation, and the seemingly miraculous instances of fit between organism and environment.

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<sup>3</sup> See Lewontin (1970).

In sum, Darwinian evolution is a cumulative sieving process in which the output of every selection cycle serves as input for the next cycle, and so on. As a result the makeup of the population will gradually change over time, and the longer the sorting process will last, the more unpredictable the result will be. Over millions of years and many successive generations, the original population might well have turned into something completely new. The strength and creativity of cumulative selection processes should therefore not be underestimated. Such processes might look rather clumsy and wasteful, but yet they are able to produce genuine novelty, increased organization, and stunning examples of fit. Or as Sperber (1996) put it: ‘Darwinian selection is one of intellectual history’s most powerful tools.’<sup>4</sup>

It is now easy to see that if in some dynamic system one or two of the aforementioned ingredients are missing, no Darwinian evolution will occur. As an example of such a non-cumulative selection mechanism, consider the solar system.<sup>5</sup> Our solar system consists of our star, the sun, and a number of satellites comprising solid planets, gaseous planets, dwarf planets, asteroids, comets, and so on. These satellites display ample variation in size, composition, mass, distance to the sun, orbital velocity, etc. Under the influence of the sun’s gravitational pull – our selection force – a real struggle for existence must have taken place, for only those satellites survived whose orbital velocity and distance to the sun were in perfect balance. Otherwise sooner or later a satellite would either have crashed into the sun, collided with another satellite, or vanished into deep space. So the current relatively stable constellation of our solar system is the result of an elementary selection or sorting process. Moreover, one can even say that the solar system has *evolved*. But note that the solar system did not evolve according to Darwinian principles! Granted, there is variation and there is selection, but the third essential ingredient for the Darwinian recipe is missing: replication. Celestial bodies cannot reproduce themselves, and without the cumulative effect of replication no complex and functional designs will emerge. In short, there are a lot of dynamic systems which evolve, yet only in those dynamic systems in which all three essential ingredients are present will *Darwinian* evolution and hence cumulative selection occur. The question we now have to answer is: might human culture be such a system?

It is important to note that Darwin’s formula is not necessarily confined to the narrow context of biology. As Lewontin (1970) already noticed, the generality of the principle of evolution means that any dynamic system that has variation, selection and replication may evolve. This idea, subsequently taken up by Dawkins (1976, 1982) and Dennett (1995) amongst others, is that Darwin’s formula is ‘substrate neutral’, a doctrine also known as ‘Universal Darwinism’. This means that the algorithm is neutral with respect to the medium or substrate of evolution, and neutral with respect to the ‘entities’ that evolve. So in principle *any* dynamic system could evolve according to Darwinian principles, as long as the three aforementioned ingredients are present. When we look at culture, this seems indeed to be the case. Apparently, Darwin’s formula reaches beyond the context of biology. Like biological evolution, the evolution of culture seems to be governed by the algorithm of variation, selection, and replication. Put differently, the evolution of ideas, concepts,

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<sup>4</sup> Sperber (1996), p. 100.

<sup>5</sup> Dawkins (1986).

technology, science, etc., is, just like biological evolution, the result of a cumulative selection process in which the output of every selection cycle serves as input for the next cycle, and so on. Thus given enough time and generations, cultural evolution too can produce some truly awesome effects. In “*Nature, Culture, and Co-evolution*”, we will have to ask ourselves how this extension of Darwinism to the realm of culture should be understood. As pointed out earlier, some authors believe that culture is directly linked to biological evolution, while others argue that culture evolves in its own right, analogously to biological evolution. But before we delve into that matter, we first have to look in more detail at some of the idiosyncrasies of human culture.

### The Cultural Animal

It was Darwin who taught us that there is no sharp divide between man and the rest of the animal kingdom. All creatures on our planet share a common ancestry, i.e., they belong to the same natural system, a system that has gradually evolved and diversified for some 3.5 billion years, resulting in a staggering number of species, all beautifully adapted to a particular environment and to the physical properties of our planet. Yet in one way humans do differ dramatically from the rest of the animal kingdom: man is a *cultural* animal, a species which not only accumulates genetic information in successive generations but cultural information as well. Culture thus involved a major transition in evolution: it changed the way in which information is acquired, stored and transmitted to new generations.<sup>6</sup> Hitherto the flow of information was limited exclusively to the genetic level, a transmission channel which already existed for 3.5 billion years. Culture opened up a new medium for evolution. Information could now be passed on through language and imitation, resulting in the rise of culture in all its different guises. Hence ‘culture’ can be defined as: all information that is transmitted to next generations by non-genetic means, i.e., through spoken or written language, teaching, or imitation.<sup>7</sup>

Obviously language plays a pivotal role in human evolution and may even be considered a *conditio sine qua non* for the emergence of cumulative human culture. Hence to do fully justice to the role of language probably would require an extensive study in its own right.<sup>8</sup> Here it may suffice to address two crucial aspects of the human language system, i.e., its innateness and its adaptedness. Firstly, as Chomsky (1972) pointed out, human language has a clear innate component. The infrastructure of language is part of our biology, not in the sense that a particular language (say English) is innate, because particular languages obviously are acquired through a process of learning and education, but in the sense that humans have a general *ability* to learn any natural language, especially when we are young. Chomsky believed that all extant natural languages have deep structural similarities, a so-called ‘Universal Grammar’ (UG) which is hard-wired into our brains. Loosely defined, UG means that the human brain is primed to prefer some syntactic structures above others. Although several aspects of UG are nowadays disputed by linguists, practically everybody still

<sup>6</sup> See Maynard-Smith and Szathmáry (1995).

<sup>7</sup> Similar definitions of ‘culture’ can be found in Richerson and Boyd (2005); Jablonka and Lamb (2005); Plotkin (2010); Distin (2011), and Mesoudi (2011).

<sup>8</sup> See Deacon (1997) for a comprehensive account of the origins of human language, and the co-evolution of language and brain.

agrees that the ability to acquire language is part of our biological make-up. Secondly, so although Chomsky himself argued that some aspects of the human language module are innate, he opposed the idea that the human language system is the result of Darwinian cumulative evolution. In Chomsky's view, language must rather be understood as an accidental byproduct of the hominid's increasing brain. This view has met considerable critique. Chomsky's idea is not very plausible because, as Pinker (1994) has convincingly pointed out, the human language system clearly has all the hallmarks of a complex adaptation, i.e., it consists of many independent (anatomical, physiological, neurological) components that are all adjusted to each other and to the system as a whole. Since complex adaptation can only be understood as the result of cumulative Darwinian selection, it follows that our language system is an adaptation that has evolved gradually and, in each step, must have conferred greater advantage to our distant ancestors, particularly with regard to the transmission of non-genetic, cultural information.

We humans are the first species with this special ability of cumulative social transmission, allowing us to gather and transmit information on an unprecedented scale. This particular ability gave us culture, science, technology and art, and thus transformed the very core of what it is to be human. To be sure, some other animal species can exchange non-genetic information as well, having forms of rudimentary language and the ability to communicate and exchange information with each other. For instance, think of the alarm calls of many species of animal, or the nut-cracking and termite-fishing abilities of wild chimpanzees, or the ways in which some species of songbirds learn their song.<sup>9</sup> Yet, as Jablonka and Lamb (2005) point out, our social transmission system differs from those in animals in that it is a *symbolic* communication system, and it is this particular quality of human thought and language that has changed our world dramatically. Words can act as symbols because they are part of a rule-governed system of signs, and the rules of language allow us to generate and understand an infinite number of varied meaningful sentences. According to Jablonka and Lamb, our symbolic system may have exactly the same basic neural underpinnings as information transmission in other animal species, but the *nature* of the communication is completely different. Our symbolic thought and communication system enabled the construction of a shared imagined reality: a world of culture, symbols, and meaning. So although some animal species do have culture and even cultural traditions like the presence of regional song dialects in songbirds, they evidently lack *cumulative* culture, i.e., there is no gradual built-up of information resulting in cultural artifacts or practices of increasing complexity.

According to Tomasello, human culture is unique in that the products of cultural evolution far exceed anything that a single person could ever invent on his own in a single lifetime. Tomasello et al. (1993) uses the metaphor of a ratchet and argues that what distinguishes human culture from that of chimpanzees and other species is its 'ratchet effect'. Cumulative cultural evolution not only requires creative invention but also faithful social transmission that can work as a ratchet to prevent the newly acquired information from slipping back. The ratchet thus preserves information, for example a newly invented or improved artifact, from being lost, and it ensures that modifications gradually accumulate over time. Animal culture does not accumulate in

<sup>9</sup> See Whiten et al. (1999).

this way, and rather surprisingly, it is probably not sheer creativity that is the obstacle in animal cultural cumulative evolution, but the stabilizing ratchet effect. Many primate species are capable of creative invention, but they lack the ability to faithfully transmit such innovations to other individuals. Hence new information will get lost, forcing individuals to start from scratch again and again.

So human culture differs dramatically from animal culture since only the former is truly cumulative. Human beings are able to pool their cognitive resources in ways that other animal species are not. According to Tomasello (2000), we probably owe this fact to some properties of the human psyche. Human cultural learning and accumulation are made possible by our ability to understand other individuals as beings like ourselves with their own intentions and mental lives. This attribution of beliefs and desires to other individuals, also known as ‘theory of mind’, is crucial in human cultural learning because it enables humans not only to learn from the other, but also through the other’s perspective.<sup>10</sup> A theory of mind thus facilitates a process of sociogenesis in which multiple individuals create something together that no individual could have created on its own. Understanding others as intentional agents like oneself creates a ratchet by faithfully preserving newly innovated strategies in the social group until there is another innovation to replace them. But there is probably more than one reason why human culture gradually builds up whereas animal culture does not. I already mentioned our generative language as an effective means of information transfer. Another, but related, aspect might be teaching. Human beings possess a communication system that is modeled by natural selection to effectively transmit information and knowledge between individuals, particularly between adults and children. Human adults are predisposed to teach human children by adjusting their speech and actions as to maximize the chance of learning, while human children in turn are predisposed to take the adults’ speech and actions really seriously. The predisposition thus manifests itself particularly in early stages of life where it facilitates the acquisition of language and other skills that are difficult to learn at an older age. The teaching system has therefore been appropriately dubbed ‘natural pedagogy’.<sup>11</sup> Mesoudi (2011) lists several other possible causes for the difference between human culture and nonhuman culture, one of which is the apparent ‘stickiness’ of the latter. Animals like chimpanzees do not possess the ability to easily switch to a newly encountered, better way of doing something. Instead, they show an inclination to stubbornly stick with their existing solution to a problem, however inefficient or unpractical.

As Mesoudi points out, the distinction between cumulative and noncumulative culture is extremely important, because only the former constitutes the gradual evolutionary change that Darwin coined ‘descent with modification’. Put differently, only cumulative culture evolves in a true Darwinian manner. As is the case in biological evolution, in the domain of culture it is possible, at least in principle, to identify different cultural lineages, like branches of a tree, in each of which small modifications have been replicated and accumulated, resulting in cultural artifacts and practices which display intricate design beyond a level that could be achieved by any individual designer. Consider the level of technological wizardry we have achieved,

<sup>10</sup> See also Tomasello (2006).

<sup>11</sup> See Csibra and Gergely (2009); Feldman and Cavalli-Sforza (2002).

or the myriads of complex human cultural practices we encounter on our planet. It is precisely this baffling level of complexity and design which suggests the need of a Darwinian account. As Richerson and Boyd (2005) put it: ‘Even the greatest human innovators are, in the great scheme of things, midgets standing on the shoulders of a vast pyramid of other midgets.’<sup>12</sup> The evolution of language, artifacts, and institutions, Richerson & Boyd argue, can be divided up into small steps, and during each step the modifications are relatively modest. For no single innovator contributes more than a small portion of the total, just as any single gene contributes only marginally to a complex organic adaptation. The history of technology shows that complex artifacts like watches, cars and computers have not been created *ex nihilo*. They have been built up gradually by the cumulative improvements of many innovators, each contributing a small improvement to the present state. According to Richerson & Boyd, this insight holds even for simple modern artifacts like forks, paper clips and zippers. They too have evolved through the accumulation of many trials, some variants being selectively retained, while others were discarded as inadequate. And what holds for technological knowledge and material artifacts also holds for our languages, practices, and institutions. They too are far too complex for even the most gifted innovator to create from scratch. Again, such intricate levels of complexity and design suggest the necessity of a Darwinian explanation, or as Jablonka & Lamb put it: ‘What we are interested in are complex cultural practices that did not emerge in one single step, but are the result of cumulative historical processes. With such complex cultural practices, we can see no alternative to the assumption that the historical changes involved some form of selective retention of cultural variants that allowed the elaboration of the cultural practice.’<sup>13</sup> In short, if we want to understand and explain the vast and wonderful complexity of human cumulative culture, we seem to have little choice but to invoke a Darwinian account.

### Niche Construction and Human Cumulative Culture

Cumulative cultural evolution probably began with modern humans as they first appeared in Eastern Africa some 200,000 years ago. Stringer (2011) argues that, at first, humans probably lived in small populations of hunter-gatherers with little or no contact with other such groups. Local inventions and accumulated knowledge thus might have gone lost quite often. Only after bigger, stable populations emerged with ample connections to others groups could information be preserved and faithfully be transmitted to other individuals. According to Stringer, our ancestors probably reached that crucial threshold some 50,000 years ago. Not surprisingly then, not long after that threshold was reached a genuine ‘cultural big bang’ occurred, with the well-known and beautiful examples of sophisticated Paleolithic cave art and stone-age technology emerging in Europe.<sup>14</sup> From then on culture accumulated bit-by-bit, ultimately resulting in our current complex socio-cultural world which, next to the physical and biological world, constitutes a new and self-created environment into which all humans get immersed from birth. This phenomenon of organisms creating

<sup>12</sup> Richerson and Boyd (2005), p. 50.

<sup>13</sup> Jablonka and Lamb (2005), p. 228.

<sup>14</sup> See Stringer (2011); Chauvet and Brunel Deschamps (2001).

and changing their own environments, and thereby altering the sources of natural selection and the direction of evolution, is called *niche construction*. According to Laland et al. (2000) niche construction is a neglected process in the study of evolution, particularly in the context of human evolution and the emergence of cumulative culture.<sup>15</sup> It is interesting and instructive to realize, for example, that whereas our culture evolves very rapidly, our physical bodies have not noticeably changed in the last 50,000 years or so. During this relatively long period there probably has been no significant biological or genetic modification in humans whatsoever. So everything we call culture and civilization we have built with the same body and brain! A Cro-Magnon child born 50,000 years ago was anatomically and neurologically identical to a child born today in New York, Lagos, or Beijing. The big difference is that our cumulative culture has created a completely new environment – a new niche – into which each new human child is born and to which we all have to adapt. Compared to a Cro-Magnon child, a present-day infant might well live on another planet! In effect, for an average human child to master the basic facts of its culture and society it takes at least 10 to 15 years of intense education, and even then it has barely scratched the surface. Incidentally, the fact that our world has radically changed in the last 50,000 years, whereas our bodies and brains have not, is the reason why evolutionary psychologists argue that we are still stuck with a ‘Stone Age mind’. Because biological-genetic evolution is relatively slow, it could not keep up with the pace of cultural evolution. Thus in our minds we are still Pleistocene hunter-gatherers equipped with physiological propensities and mental modules adapted to a life on the African savannah.<sup>16</sup>

But perhaps this idea is not entirely true, for it is evident that in some cases biological-genetic evolution indeed *did* keep up with cultural evolution because some cultural practices have changed our genetic makeup and hence our physiology. A classic example is the case of adult lactose tolerance. The domestication of cattle and the accompanying practice of dairying, probably first occurring some 10,000 years ago in the Middle-East, did alter the selective environments for some human populations long enough to select for genes that today confer greater adult lactose tolerance. Thus by keeping cattle and using their products, humans have changed their niche in such ways that it became advantageous for adult human beings to be able to digest milk. Niche construction introduced novel selection pressures: by exploiting a new food resource, like dairy products, a new digestive enzyme got selected.<sup>17</sup>

An earlier yet even more important example of the effects of human niche construction is exemplified by the human brain. In the course of hominid evolution the size of the brain has tripled from about 500 cm<sup>3</sup> in *Australopithecus*, 750 cm<sup>3</sup> in *H. habilis* and 1000 cm<sup>3</sup> in *H. erectus*, up to 1500 cm<sup>3</sup> in modern *H. sapiens*. This threefold increase of hominid brain size can perhaps only be made intelligible by invoking the effects of niche construction. Aiello and Wheeler (1995) for instance have suggested that our ancestors could afford a bigger and more ‘expensive’ brain because they switched from being mostly vegetarian to eating meat. Since meat, especially when it is cooked, is much easier to digest than vegetable food, it became

<sup>15</sup> See Odling-Smee et al. (2003).

<sup>16</sup> See Barkow et al. (1992); Mythen (1996).

<sup>17</sup> See Durham (1991), chpt. 5.

evolutionarily affordable to reduce the expensive tissue of the intestines in favor of expensive brain tissue. The hypothesis is therefore appropriately called the ‘gut-brain swap’. The rapid growth of the hominid brain, with all its accompanying consequences, was made possible by the fact that early hominids changed their diets, switched to eating meat, and began cooking their food. With the control of fire and the subsequent invention of cooking, our ancestors changed their niche in such ways that they altered the sources of natural selection, and ultimately, their path of evolution. Thus one of the most sweeping events in hominid evolution, the remarkable growth of the human brain, was initially triggered by a relatively modest change in cultural practice. Laland et al. (2000) argue that this is an example of how a character – the human brain – evolved despite fitness costs by paying for itself by its ‘inventive’ niche construction. Big brains simply would not be adaptive without niche construction.

To be sure, niche construction is not confined to human beings alone. Many other animal species are able to change their environments, thereby creating novel selection pressures and altering the gene frequencies in their populations. But human beings are somewhat special because, unlike most animal niche construction, much of human niche construction is dominated by socially learned knowledge and cultural inherited practices, thus creating a complex interaction between biological and cultural evolution. According to Laland et al. (2000), we can perhaps begin to understand this complex process of co-evolution when we invoke the mechanism of niche construction. They write: ‘[N]iche construction modifies one or more sources of natural selection in a population’s environment and, in doing so, generates a form of feedback in evolution that is not yet fully appreciated.’<sup>18</sup> If the cultural inheritance of a niche-altering human activity persists for enough generations to generate a stable selection pressure, it will be able to influence and direct human biological-genetic evolution. The cultural practice of prehistoric dairy farming, we have seen, provides a case in point. Note incidentally that the phenomenon of niche construction is to some extent reminiscent of Dawkins’ notion of the extended phenotype.<sup>19</sup> Dawkins argued that genes can express themselves *outside* the individual organisms (phenotypes) that carry them, for instance by generating certain behavior like nest- or burrow-building. Thus a bird’s nest and a beaver’s dam are examples of extended phenotypes which increase the chance that the genes responsible for the extended phenotype will be passed on. Like in the case of niche construction, the altered environment influences and modifies the sources of natural selection, thereby changing the path of evolution.

In any case, it is important to realize that niche construction can generate an unusual evolutionary dynamics. In fact Laland et al. believe that niche construction may be of greater evolutionary importance than generally conceived. To their mind, a description of evolutionary change relative only to independent environments is too restrictive: ‘In the presence of niche construction, adaptation ceases to be a one-way process, exclusively a response to environmentally imposed problems; it becomes instead a two-way process, with populations of organisms setting as well as solving problems.’<sup>20</sup> Especially in the case of human evolution, niche construction has important implications for the relationship between biological evolution and cultural change. In human

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<sup>18</sup> Laland et al. (2000), p. 133.

<sup>19</sup> See Dawkins (1982).

<sup>20</sup> Laland et al. (2000), p. 135.

(pre)history our culture has continuously modified natural selection pressures in human environments.

What is also important to realize is that culture has brought about its own transmission channel through which information gets passed on to next generations. As we have seen in “*Darwin’s Formula*”, Darwin’s formula of variation, selection, and replication is substrate-neutral which means that in principle any dynamic system could evolve according to Darwinian principles. Human culture *is* such a dynamic system. The third element of the formula – replication – is realized not by (a)sexual reproduction, i.e., the copying of genes, but by language and imitation, allowing information to accumulate and culture to evolve. So in the case of culture we are dealing with socially learned information and cultural transmission. I will say something about social learning shortly, first I address the complex phenomenon of cultural transmission. As Cavalli-Sforza and Feldman (1981) already pointed out in their seminal work, the transmission of information can depend on several modes of cultural inheritance, including so-called ‘vertical’ transmission (from parent-to-offspring), ‘horizontal’ transmission (among peers from the same generation), and ‘oblique’ transmission (from members of one generation to members of a later generation, as in the case of formal teaching). Note the obvious difference between biological-genetic inheritance and cultural inheritance. Whereas biological-genetic inheritance almost exclusively relies on vertical (parent-to-offspring) inheritance, in cultural inheritance the transmission of information has many different guises because cultural information can be transmitted in lots of different ways. In the realm of human culture vertical transmission can even be reversed as when parents, or even grandparents, can learn things from their (grand)children. But horizontal transmission might be equally important. In fact, if vertical, downward transmission would be the only direction in which cultural information would flow, cultures would probably be very static. For a culture to be innovative, horizontal transmission is needed, i.e., a novel idea should not only spread from parents to offspring but to contemporaries as well. Apart from the different paths, there also are notable differences in speed by which cultural information is transmitted. In small prehistoric groups of hunter-gatherers the mode of transmission was probably often vertical and one-to-few or even one-to-one, resulting in a relative slow stream of information, whereas nowadays with the ever growing influence of the internet and social media, the mode has changed to horizontal and one-to-many, resulting in information racing continuously around the globe with lightning speed. In short, the pioneering work of Cavalli-Sforza & Feldman made it possible to model all these different modes and channels of transmission and to assess the consequences with regard to their respective speeds and directions.<sup>21</sup>

In fact, it is worth mentioning here that the mathematical models and techniques used by Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) amongst others to study cultural evolution were inspired by the Modern Synthesis in biology and the models and techniques employed in the 1920s by scientists like R.A. Fisher, J.B.S. Haldane and Sewall Wright to study biological-genetic evolution. The underlying assumption, of course, is that both biological and cultural evolution are at bottom Darwinian processes. Hence the mathematical tools used to understand,

<sup>21</sup> See also Feldman and Cavalli-Sforza (2002).

explain and predict the effects of micro-evolutionary processes in biological evolution, like natural selection and genetic drift, can be used to study cultural evolution as well. As Mesoudi (2011) explains, in a typical cultural evolution model, a population is assumed to be composed of a set of individuals, each of whom possesses a particular set of cultural traits. Next a set of micro-evolutionary processes is specified that alters the variation in those traits over time. These processes concern the sources of cultural variation, the forms of cultural selection, and the different modes of cultural transmission. Finally variation is transmitted to the next generation, simulating the process of cultural inheritance. The mathematical models and techniques can then be used to understand and predict the long-term (i.e., macro-evolutionary) consequences in cultural variation over time. Employed in a computer simulation, the models for instance could indicate whether some variants might increase in the population or instead go extinct, or whether two or more variants perhaps can coexist indefinitely, etc. Not surprisingly, each of these processes have different macro-evolutionary consequences for how a particular culture as a whole changes over time. In the end the initial make-up of a population might well be totally transformed, having changed a culture into something completely new and different.

As pointed out above, another important feature of cumulative cultural evolution is social learning. Laland et al. (2000) define social learning as: ‘A general capacity to acquire information from others, regardless of the nature of the information, its function, or the sensory modality involved.’<sup>22</sup> Again, they argue that the increasing reliance of our early ancestors on social learning only becomes intelligible in the light of niche construction. Our ancestors constructed niches in which it ‘paid’ them to transmit more information to their offspring and to other members of their group. After all, vital accumulated knowledge about the environment, prey animals, hunting techniques, edible and medicinal plants, seasonal changes, etc., surely would be worth sharing with tribe members. Thus with the advent of human niche construction, it became more and more advantageous to transmit cultural information via a process of social learning. It might even have triggered an autocatalytic process in which niche construction led to more social learning, while social learning in turn led to more niche construction, and so on. With such a self-enforcing feedback process, culture could easily accumulate and bootstrap itself to higher and more complex levels, and possibly even result in some kind of runaway evolution.<sup>23</sup>

So what should become clear is that niche construction, culture, and the human mind are inextricably tied together in a firm triadic relationship. The modern human mind probably evolved from the more primitive primate mind through a series of major transitions, each of which led to the emergence of a new representational system and corresponding new levels of culture. So our ancestors did not simply evolve bigger brains or an extended memory. First and foremost they evolved new systems for representing reality, i.e., the hominid mind finally managed to grasp the use of symbols. Donald (1991) has distinguished three fundamental stages in the origins of culture and the evolution of the modern human mind. The first stage is the advent of what he calls ‘mimetic culture’ (not to be confused with Dawkins’ *memetic* culture, see “[Nature, Culture, and Co-evolution](#)” below). Mimetic culture was an

<sup>22</sup> Laland et al. (2000), p. 141.

<sup>23</sup> See Laland (2008).

important threshold in hominid evolution because it gave our Stone Age ancestors the ability to represent knowledge through manual or facial gestures, mime, and other voluntary motor acts.<sup>24</sup> This communication system enabled them to share knowledge with group members, with learning taking the form of direct instruction, imitation, and meaningful group rituals. Mimetic culture eventually resulted in sophisticated tool-making, fire use, coordinated seasonal hunting, rapid adaptation to different climates, intricate social structure, burials, and other symbolic rituals. Donald argues that mimetic culture did not require the use of spoken language. High-speed vocal language is probably a relatively recent invention, unique to *H. sapiens*.<sup>25</sup> Mimetic culture, by contrast, is much older and was probably already mastered by *H. erectus*, some two million years ago. This successful Paleolithic hominid cooperated in seasonal hunting, migrated over long distances (i.e., from Africa to the Middle-East, Europe and Asia), used fire, cooked food, and evolved a brain that eventually reached 80 % of the volume of the modern human brain.

A second major step was the evolutionary transition from mimetic culture to what Donald calls ‘mythic culture’. Mimetic skills could only take hominid culture so far, hence language emerged to allow for more precise and extended communication between individuals. Donald calls this culture ‘mythic’ because he believes that myth was the primary function of this ancient, prehistoric language. Mythic culture enabled our ancestors to pass on collective accumulated knowledge much more efficient to other members of the group and to members of the next generation. The ability to convey knowledge through oral tradition and mythic narrative is probably between 100,000 and 200,000 years old, coinciding with the appearance of *H. sapiens* in Africa. In addition to the earlier mimetic era, mythical culture gave our ancestors a new, collective system for understanding and representing the world around them. The full potential of mythic culture revealed itself when *H. sapiens* arrived in Europe, somewhere between 50,000 and 40,000 years ago. Here mythic culture famously gave rise to symbolic art in the form of artistic cave paintings, human and animal figurines, and other delicate artifacts.

The third and, for the moment, latest stage in the evolution of the hominid mind and hominid culture is characterized by the fact that, henceforth, collective accumulated knowledge was no longer restricted to the bounds of the human brain and body, but could now be gathered in ‘external storage systems’. That is, knowledge could now be written down in the form of cuneiforms, hieroglyphs, and other symbolic sign systems. Donald calls this stage ‘theoretic culture’ because for the first time accumulated knowledge, now durably recorded in external media, enabled humans to reflect on their collective wisdom. Theoretic culture probably originated some 10,000 years ago in the Middle-East, and eventually gave our Neolithic ancestors not only the opportunity to reflect upon but also to critically examine their culture, thus establishing the first rudimentary forms of religion, philosophy, and science. Donald argues that this third transition has led to one of the greatest reconfigurations

<sup>24</sup> Apes, monkeys and other primates possess what Donald calls ‘episodic culture’, i.e., they live their lives entirely in the present and are always bound to the concrete situation or episode. The social behavior of non-human primates reflects this situational limitation. Mimetic culture, in contrast, allows the use of abstract symbolic representations and the sharing and accumulation of knowledge.

<sup>25</sup> The hypothesis that communication through manual and facial gestures may have preceded vocal language can also be found in Corballis (2002). See also Deacon (1997).

of cognitive structure in primate history, and again, without much genetic change. While our genome may be 98 or 99 % identical to that of chimpanzees, and even 100 % identical to that of Cro-Magnons, our minds and our cognitive structure clearly are not. Obviously genes do not make the difference, accumulated culture does. In fact, we humans may now have reached a critical point in our cultural and cognitive evolution because we are perhaps on the brink of another major transition in human evolution. More than ever in our hominid past we presently are symbol-using, networked, social creatures, engaged in a seemingly ongoing technological and digital revolution, exemplified *par excellence* by the emergence of populous social media and the ever expanding world wide web. The construction of this new, virtual niche might have a profound and irreversible influence on the future course of human evolution.<sup>26</sup>

### Nature, Culture, and Co-evolution

Now even if we are willing to accept the idea that human culture evolves and accumulates according to Darwinian principles, we still have to explicate in what manner cultural evolution is tied to biological evolution. In principle we can choose between two different and rivaling models. The first model, represented by human sociobiology and kindred research programs like evolutionary psychology, states that human culture is directly linked to biological evolution because what counts in the end is the genetic fitness of the creatures that possess culture, i.e., us. The emergence of culture was rewarded by natural selection because culture must have been advantageous to our ancestors, otherwise culture simply would not exist. Thus ultimately culture must be viewed as a *biological* phenomenon, a complex biological adaptation that allows human beings to cope with the most diverse environments. The second, rivaling model, represented by memetics, states that human culture is no longer (or at least not always) directly linked to biological evolution. Culture may have had its roots in biological evolution, but at some point in history culture took up a life of its own. That is, like biological evolution, culture evolves in itself because it too contains the three ingredients of Darwin's formula: variation, selection, and replication. After all, what holds for genes might also hold for ideas, or 'memes' as Dawkins (1976) has coined the units of cultural evolution. However, despite the fact that both research programs have offered several interesting insights, I also think that both programs are seriously flawed, either because they underestimate the influence of culture, as in the case of human sociobiology, or because they push analogies too far, as in the case of memetics. Let us start with sociobiology. When Wilson (1975) first introduced sociobiology, critics were enraged over the fact that human beings, with all their cultural splendor, were treated as just another animal, apparently completely determined by the instructions of their genes. Clearly, Wilson's seminal ideas did not fall on fertile ground, partly because at that time – the 1970s – many people believed that human behavior was determined by culture rather than nature. Let us call that idea the Culture-First approach. Adherents of the Culture-First approach depicted Wilson as a blunt reductionist and genetic determinist. Yet both charges were ill-founded because Wilson was neither. As we shall see, although he argues that human nature generally

<sup>26</sup> See Schaller et al. (2010).

has the upper hand over culture, Wilson does not deny that culture in turn can change human nature.

Human sociobiologists argue that cultural evolution is a part of and therefore subordinate to biological evolution because all social behavior, including behavior associated with culture, has a biological basis. So inevitably culture will be constrained in accordance with its effects on the human gene pool, or as Wilson (in)famously put it: ‘Genes hold culture on a leash’.<sup>27</sup> Culture has a certain freedom and latitude to develop in all kinds of directions, but if a culture turns itself against human nature, for example by promoting collective suicide or childlessness, it will either be pulled back by the leash and obey the imperatives of human nature, or go extinct. So the margins in which a culture can wander and flourish are determined and limited by the survival of our genes. Hence our biology puts constraints on the ways culture can evolve. In a similar vein, evolutionary psychologists claim that human psychological traits like perception, cognition, language, memory, emotions, etc., are evolved adaptations modeled by natural selection. These and other human characteristics allowed our ancestors to cope with life on the African savannah, an environment where by far the longest part of hominid evolution took place. Recall the evolutionary psychologists’ notion of the Stone Age mind (“[Niche Construction and Human Cumulative Culture](#)”). Because biological evolution allegedly could not keep up with the pace of cultural evolution, we are still stuck with a mind equipped for Pleistocene hunter-gatherers. So sociobiology and evolutionary psychology share the belief that human beings – including their minds, behavior and culture – are foremost biological creatures. We are molded by nature rather than culture, which also means that psychology should become a branch of biology. As the evolutionary psychologists Tooby and Cosmides (1992) put it: ‘Human minds, human behavior, human artifacts, and human culture are all biological phenomena—aspects of the phenotypes of humans and their relationships with one another.’<sup>28</sup> Also notice again the resemblance with Dawkins’ notion of the extended phenotype. Like a bird’s nest or a beaver’s dam, human culture could be viewed as a biological characteristic which extends far beyond the individual human phenotype.

In short, human sociobiologists and evolutionary psychologists both try to understand the human mind and human social behavior, including the behavior that resulted in the origin and evolution of culture, in terms of our biology. Nature overrules culture because, ultimately, culture is a far-extended expression of certain human genes. Let us call this idea the Nature-First approach. The Nature-First approach involves the systematic study of the biological basis of the human mind and human social behavior, and it proclaims that human culture is embedded within the wider and much older framework of human nature. Our evolved psychological dispositions, mental modules, and innate learning capacities, or ‘epigenetic rules’ as Wilson calls them, bias and thus constrain the ways in which culture can evolve.<sup>29</sup> To be sure the Nature-First approach has a certain appeal because nobody would deny that human beings indeed *are* biological creatures without whom cumulative culture would never have emerged. Nor should anybody deny that an understanding of the

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<sup>27</sup> Wilson (1978), p. 167.

<sup>28</sup> Tooby and Cosmides (1992), pp. 20–21. See also Laland and Brown (2002).

<sup>29</sup> Lumsden and Wilson (1981), p. 370.

basic biological constraints on human behavior is simply indispensable for the study of culture. The problem lies somewhere else.

The main flaw of the Nature-First approach is that it neglects the influence of culture and the ways in which cultural evolution can feedback onto biological-genetic evolution. In “[The Cultural Animal](#)” we have already encountered several examples of such feedback processes, like the case of lactose tolerance and the case of the expanding hominid brain. Both cases are examples of cultural evolution feeding back on biological evolution, thereby changing our genetic blueprint and physiology. The cultural practice of dairy farming altered the human digestive system, and the cultural practice of cooking and eating meat triggered the spectacular growth of the hominid brain. So because culture can change certain selection pressures and hence the path of biological evolution, the Nature-First approach had to be adjusted. Lumsden and Wilson (1981) already rectified this omission by postulating a model of gene-culture co-evolution in which genes and culture are intimately connected. So instead of nature ruling over culture, the two forces are now involved in an intensive and graceful *pas de deux*. Genes (indirectly) influence culture through the working of epigenetic rules, but culture influences epigenetic rules – and therefore genes – as well. Different cultural practices (e.g., dairy farming or cooking food) can lead to shifts in the sorts of epigenetic rules that are useful, and consequently to changes in which genes are passed on.

Next a further major improvement was made by Boyd and Richerson (1985) when they introduced their model of ‘dual inheritance’, i.e., the idea that culture not only feedbacks on our genes, but that culture has its own inheritance system as well. We already encountered this idea in “[The Cultural Animal](#)”. Dual inheritance means that there are two ways in which information can be transmitted to the next generation. The first way is genetic transmission through the replication of DNA, the second way is non-genetic, cultural transmission through imitation or spoken and written word. In both inheritance systems we see Darwin’s formula of variation, selection, and replication at work, which means that some variants (whether genetic or cultural) are selectively retained, resulting in a gradual accumulation of information. Recall that Darwin’s formula is substrate neutral: in principle any ‘dynamic system’ could evolve provided that the three necessary elements are present. Culture, Boyd & Richerson argue, is such a dynamic system. So compared to the model of co-evolution, the dual inheritance model is even more complex because there now are two closely interacting levels at which cumulative selection and thus Darwinian evolution takes place. Richerson and Boyd (2005) argue that the human cultural system arose as an adaptation because it allowed humans to swiftly adapt to lots of different and changing environments, much more swiftly than is possible by genes alone. Or as they put it: ‘Culture would never have evolved unless it could do things that genes can’t.’<sup>30</sup> Laland et al. (2000) have employed mathematical models to examine this claim. These models confirm that culture and social learning are indeed advantageous when environments change too rapidly for the genetic system to keep track of the novel conditions. The genetic system would only be able to cope when environments change very slowly and information updating would not be needed frequently. Reversely, when environments change too quickly, or when sudden environmental

<sup>30</sup> Richerson and Boyd (2005), p. 7.

shifts occur, social learning and vertical (from parents to offspring) transmission would be error prone. In such extreme cases horizontally (within-generation) transmitted information should be favored. So according to Laland et al., cumulative culture and social learning are advantageous only when ‘changes are not so fast that parents and offspring experience different environments, but not so slow that appropriate genetically transmitted information could evolve instead.’<sup>31</sup> Paleoclimatic and geological data seem to confirm that Pleistocene hominids had to cope with such ‘intermediate’ environmental changes.

In any case, social learning by acquiring information from others seems to bring lots of benefits. Amongst others, it allows human beings to swiftly adapt to a wide range of different environments but, as Richerson & Boyd explain, ‘it also opens a portal into people’s brains through which maladaptive ideas can enter – ideas whose content makes them more likely to spread, but do not increase the genetic fitness of their bearers.’<sup>32</sup> So culture (i.e., social learning) solves the problem of living nearly anywhere in the world, but at a price. That price is that we play host to many ‘selfish’ cultural variants like urban legends, chain letters, viral videos, earworms (i.e., a piece of music that keeps going round and round in one’s head), spam, cults, tweets, hypes, and so on. Apparently culture has a certain autonomy – it may sometimes break loose from the leash – because the interests of genes and culture do not always coincide. Culture may even go *against* the biological imperatives of survival and reproduction, for instance when people consume too much high-calorie food, smoke cigarettes, practice celibacy, or get involved in contagious suicide, etc. Such behavior is surely maladaptive from the genes’ eye point of view, so why does it persist? In order to unlock this riddle we have to ask ourselves the ultimate Darwinian question: Who benefits? In the aforementioned cases it clearly are not the genes that profit but certain ideas or habits which reappear again and again because they ‘infect’ people’s minds and thus keep showing up in successive generations. Cultural variants like chain letters and urban legends are selfish because they do not benefit the people who copy them – they benefit their own propagation.

### Genes, Memes, and Flawed Analogies

The idea that human cumulative culture is a process with its own evolutionary dynamics, and that cultural variants often act as to maximize their *own* fitness instead of that of their bearers, brings us to memetics, the study of memes. The idea of memetics was first introduced by Dawkins (1976). His definition of a meme is: ‘A unit of cultural inheritance, hypothesized as analogous to the particulate gene, and as naturally selected by virtue of its ‘phenotypic’ consequences on its own survival and replication in the cultural environment.’<sup>33</sup> Memes (an abbreviation of the Greek word for imitation: *mimeme*) are the cultural analogues of genes. As in the case of genes we can make a distinction between a meme’s ‘genotype’, i.e., its underlying mental (neural) representation in the brain, and the meme’s ‘phenotype’, i.e., its visible (or audible, etc.) expression in the outside world. The phenotypic effects of a meme can

<sup>31</sup> Laland et al. (2000), p. 141.

<sup>32</sup> Richerson and Boyd (2005), p. 150.

<sup>33</sup> Dawkins (1982), p. 290.

manifest themselves in words, music, art, skills, science, etc. These manifestations may then be perceived by other individuals and imprint themselves on their brains, in which case the meme has replicated itself. A meme, in short, is a unit of cultural information which survives and reproduces by leaping from brain to brain. Like genes, memes are involved in a constant and fierce struggle for survival. After all, not every idea that pops up will survive. On the contrary, it is more likely that most ideas are quickly forgotten, but now and again a meme might be selectively retained and then be transmitted to a next generation. And again, because the Darwinian selection process is cumulative in character, information will gradually build up and thus create a huge reservoir of ‘memetic’ information. That immense and ever-changing reservoir of ideas, concepts, fashions and gadgets is our culture.

As we have seen, memes may not always be beneficial to their ‘hosts’, i.e., the individuals in which they reside. Like genes, memes are essentially ‘selfish’: all that counts is that they get transmitted, unaltered, to the next generation. So the survival conditions for memes are essentially the same as for genes, namely: longevity, fecundity, and copying-fidelity.<sup>34</sup> For a meme to be successful and to become part of an established culture it must be long-lasting, capable of making good copies of itself, and get in as many brains as possible. But there are several other interesting parallels between genes and memes, for instance they both are carriers of information. Genes carry information, or instructions, for building proteins and bits of organisms. Memes carry information, or instructions, for building bits of culture. A meme is a piece of symbolic information which resides in a particular neural pattern in our brain and which can be translated into many different mediums. A piece of music, for example, can be performed in a live concert, or just resound in one’s head, but it may also be recorded on hard disc, magnetic tape or vinyl, or written down in sheet music, etc. Notice also that both genes and memes can carry and transmit *latent* information. Like genes, memes do not necessarily have to be expressed or acted upon in order for them to be transmitted. A recessive gene may lie dormant for many generations before it expresses itself again. Likewise, a piece of music can be transmitted through the ages without actually being performed. Or to use a more homely example: granny’s cake recipe may be passed down through the family for several generations without someone actually baking the cake. Again there is a parallel with genes. According to Dawkins, only a change in the recipe (the encoded information or genotype) is heritable, and can therefore be transmitted, a change in the cake (the phenotype) is not. The same principle holds for genes: only genetic information is heritable and transmittable, acquired phenotypic characters are not. Another, but more controversial, parallel between genes and memes is Dawkins’ replicator-vehicle distinction. According to Dawkins a meme, like a gene, is a ‘replicator’, i.e., an entity that is capable of making copies of itself and, by doing so, preserving the information which it contains through successive generations. For three billion years, genes were the only replicators on our planet, but once creatures with language and minds emerged, a new kind of replicator – the meme – took its chance and created a whole new space of possibilities. Human brains (or human beings in general) thus are the hosts or ‘vehicles’ of replicating memes. Memes use us (and our brains) as a

<sup>34</sup> Dawkins (1976), p. 194.

convenient means of transport for their long journey through the generations.<sup>35</sup> However Hull (1988, 1989) has rightly argued that the term ‘vehicle’ has several undesirable connotations, since vehicles are commonly associated with the sorts of things agents ride around in, and what is more, the agents are in control: they steer and the vehicles simply follow. But that is not a realistic picture because the entities in which genes and memes reside (i.e., living beings) are much more than passive vehicles. Hull therefore suggested the term ‘interactor’ which bypasses the negative connotations of Dawkins’ terminology. According to Hull an interactor is: ‘An entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential.’<sup>36</sup> Put differently, because replicators are not directly visible to selection (i.e., they cannot interact directly with their environments), they need interactors that *can*. The ways in which these interactors cope with their environments then will determine the fate of the replicators involved.

We have seen that cumulative cultural evolution has its own inheritance system, a transmission channel that accumulates information which could never have been gathered by any single individual. But such a broadband transmission system also opens a hatch through which maladaptive cultural variants can enter, i.e., memes that do not increase, and even may go against, the genetic fitness of their bearer. But of course the vast majority of memes *is* beneficial, they make up our accumulated culture which determines who we are, what we think, and how we behave. It is cumulative culture, and not our genes, that sets us apart from our closest primate relatives. Cumulative cultural evolution gave us language, art, technology, political systems, law and civilization. Without the ability to transmit and accumulate cultural information we would still be living in caves. In sum, many cultural phenomena are unexplainable by appealing to genes alone, especially those aspects that are not directly linked to one’s genetic fitness. For those cases we have to invoke a model of dual inheritance and co-evolution in which genes and memes each play their respective roles, and in which culture may also evolve for its own sake, without any benefit for the meme’s host. In contrast with the earlier Culture-First and Nature-First approaches, we might call this view the Evolution-First approach because it emphasizes the fact that both our nature and our culture are governed by Darwin’s formula of variation, selection, and replication. Recall that wherever you find these three ingredients, you will find Darwinian, cumulative evolution. So my analysis does not strictly focus on any particular medium of evolution but rather on the process itself.

Before we take a more critical look at the idea of memes in a moment, a brief aside might be instructive because the idea that culture evolves is not confined to memetics alone. In the past authors like Toulmin, Popper and Hull amongst others already have proposed similar ideas, albeit that they focused on one special aspect of our culture: natural science. In talking about the development of science as ‘evolutionary’ these philosophers were not employing a mere *façon de parler* or metaphor, but took the claim quite seriously. Toulmin (1967, 1972) evolutionary approach was meant as a

<sup>35</sup> According to Dennett (1995, 2002) and Blackmore (1999, 2000) memes are viruses of the mind: they spread by infecting us and turning us into their ‘meme machines’. When memes have entered our brains, they act as body snatchers by controlling our behavior in such ways as to produce even more memes.

<sup>36</sup> Hull (1988), pp. 408. Italics in original.

reply to Kuhn's (1962) controversial claim that the history of science is punctuated by conceptual revolutions which cause science to break up into incommensurable paradigms. In contrast Toulmin emphasized the rational coherence and apparent continuity that underlie these changes: the development of science is evolutionary rather than revolutionary.<sup>37</sup> In a similar vein Popper (1972) has stressed that the growth of scientific knowledge is a rational and progressive process governed by Darwinian selection mechanisms. Here is a well-known quote from Popper:

[T]he growth of our knowledge is the result of a process closely resembling what Darwin called 'natural selection'; that is, *the natural selection of hypotheses*: our knowledge consists, at every moment, of those hypotheses which have shown their (comparative) fitness by surviving so far in their struggle for existence; a competitive struggle which eliminates those hypotheses which are unfit.<sup>38</sup>

Popper argued that absolute truth is not be attainable for us, fallible creatures, but we may nevertheless improve our knowledge by a process of trial and error in which theories that stand the test of falsification are selectively retained. Finally Hull (1988, 2001) showed that natural science is propelled by a process of cumulative selection, and that scientific evolution results in conceptual lineages which can be traced back through time. Hull's analysis is mainly genealogical in character. Like Toulmin he shows how dynamic systems (e.g., natural science) may evolve into something radically new and different while at the same time retaining their rational coherence and identity. Like biological species, scientific disciplines and research programs are historical, evolving entities which do not necessarily retain a distinctive and everlasting core or essence.

Now returning to our discussion of memetics, we have to wind up this section by addressing the critique that the meme idea has provoked.<sup>39</sup> I believe that memetics certainly has merits, but I also think that the analogy is frequently being stretched too far because in some aspects memes seem to be very different from genes. In fact the main and most common objection against memetics is that it is not at all clear what memes really are. Supposedly they are mental representations in the mind or neural patterns in the brain, but unfortunately up to now nobody has been able to back up such claims. So we *do* know what genes are (a functional and hereditary bit of DNA), but we have no clue what memes are. On the other hand, perhaps future science may unravel this issue, thus making it an empirical question whether memes have a physical basis in the brain or not. And we should not forget that in the nineteenth century Gregor Mendel postulated the existence of genes and inferred the laws of genetics from his experiments with pea plants, although at that time nobody knew whether genes existed, let alone how they are physically realized. Perhaps we are now at a similar juncture with regard to memes. Another objection against memetics is that the analogy between genes and memes falls short because genes are discrete, particle-

<sup>37</sup> Surprisingly, in an attempt to rebut the charge that he was a relativist, in 1970 Kuhn added a postscript to his book, arguing that there are indeed certain remarkable parallels between biological evolution and the development of natural science. In the postscript Kuhn seems to admit that there is more continuity and progress in science than he previously suggested.

<sup>38</sup> Popper (1972), p. 261. Italics in original. See also Munz (1993).

<sup>39</sup> See Aunger (2000) (Ed.) for a critical appraisal of memetics.

like entities whereas memes apparently are not. After all, memes seem to come in all sorts of kinds, shapes and sizes. Memes can be small, discrete cultural units like the song ‘Happy Birthday’ or Pythagoras’ theorem, but they also can be quite complex and diffuse like the Italian cuisine or Christianity. For this reason Richerson and Boyd (2005) say that they prefer the term ‘cultural variant’ instead of ‘meme’.<sup>40</sup> The point is that memes might not have to be discrete, genelike particles in order for Darwinian cultural evolution to occur. Ardent adherents of memetics like Blackmore (1999, 2000) and Dennett (1995, 2002) seem to think that genelike replicators are necessary for cultural evolution, but that might not be the case. Memes, whatever they are and however they are realized, only have to compete and be replicated in order for differential selection – and hence Darwinian evolution – to take place.

Related to the previous issue is the objection that whereas genes are truly replicated, memes are not. Surely memes are being transmitted or imitated somehow, but this process is very different, in execution and in accuracy, from the way in which genetic information is replicated. Memes are ‘replicated’ or ‘copied’ only in a very loose and broad sense. In fact, high-fidelity replication of memes might well be disadvantageous, particularly in fast-changing societies, for as Jablonka and Lamb (2005) point out: ‘It is not a good idea to stick faithfully to your parent’s style of dress, way of speaking, and type of automobile.’<sup>41</sup> The critique that, unlike genes, memes are not truly replicated is mainly due to Sperber (2000). Sperber admits that cultural items are ‘re-produced’ in the sense that they are produced again and again, with a causal link between all these productions, but they are not reproduced in the sense of being copied from one another. After all, cultural information might easily blend or be changed by the people who receive the information and then pass it on. So, according to Sperber, in cultural transmission no true replication or strong inheritance occurs. However against Sperber one might argue that, like the supposed particle-like character of memes, high-fidelity replication might not be a necessary requirement for Darwinian cultural evolution. Of course, nobody denies that the transmission of cultural information differs from the transmission of genetic information, if only because the former process generally does not involve sex. But apart from such obvious differences, what counts is that information – in either realm – is being transmitted in such ways that information, whether genetic or cultural, can selectively be retained and then accumulate. As I have argued earlier, the key feature of Darwinian evolution is that it is powered by a cumulative selection process. In the realm of culture the accumulation of information is obvious. In fact, if cultural transmission would involve the constant blending of information, there would not be any cultural continuity, traditions or folklore at all. Recall Tomasello’s ratchet effect (“[The Cultural Animal](#)”). What prevents accumulated or newly acquired information from being lost is faithful social transmission. Faithful transmission preserves information and it ensures that slight modifications and improvements gradually accumulate over time. So high-fidelity replication is perhaps not necessary for cultural evolution to be Darwinian. Or as Jablonka & Lamb put it: ‘What matters is not the fidelity of transmission, but the *functional adequacy* of any change in

<sup>40</sup> Richerson and Boyd (2005), p. 63.

<sup>41</sup> Jablonka and Lamb (2005), p. 221.

a cultural element.<sup>42</sup> In sum, there might be no strong analogy between genes and memes, but nevertheless the same Darwinian logic applies: we try to figure out what processes cause some cultural variants to survive and flourish and others to go extinct.

### Culture's Blind Edge and Lamarckian Flavors

Over the years critics have raised many objections against the idea that culture (and science) genuinely evolve.<sup>43</sup> In this final section I want to concentrate on two general objections which usually figure at the top of many a critics' list, i.e., the apparent directedness of cultural evolution, and its alleged Lamarckian character. Although these two issues are closely related, it might nevertheless be helpful if we treat them separately. So let us start with the first objection. Several authors have argued that cultural evolution simply cannot be Darwinian because biological evolution involves 'blind' variation while cultural evolutions seems to involve 'guided' variation. Biological variation is blind or 'random' because there is no foresight or purpose involved. Biological variation (mutation and recombination) cannot anticipate any existing selection pressures in a population because it does not come according to need. By contrast, cultural variation is guided or 'nonrandom' because new variants are usually generated consciously and purposively by human beings. Apparently we can actively seek out the variations and inventions that are needed. Thus at its heart cultural evolutions seems to differ from biological evolution: cultural variation is directed whereas genetic variation is not. And what is more, since cultural variation seems to be guided, we have to ask ourselves whether such a process still counts as being genuinely Darwinian.<sup>44</sup>

Apparently this line of critique assumes that blind variation is the essence of Darwinian evolution. But is that really true? Would Darwin's formula not work if the variation were not genuinely random but instead directed or guided somehow? Of course it would. Let me explain. Earlier I have argued that the key feature of Darwinian evolution is cumulative selection. The presence of a cumulative sieving or winnowing mechanism is what distinguishes Darwinian evolution from other kinds of dynamic processes (see "[Darwin's Formula](#)"). Only cumulative selection is capable of producing complex designs and adaptations, and such a mechanism would still be operable even if the variation were not truly random but instead guided somehow. In fact, guided variation would only increase the efficiency of such a process. The phenomenon of artificial selection is a case in point. Darwin discovered the principle of natural selection by reasoning analogically from the way in which farmers and fanciers have improved their stock and crops by constantly selecting the

<sup>42</sup> Jablonka and Lamb (2005), p. 221. Italics in original. See also Richerson and Boyd (2005, p. 60). They write: 'A Darwinian account of culture does not imply that culture must be divisible into tiny, independent genelike bits that are faithfully replicated. Rather, the best evidence suggests that cultural variants are only loosely analogous to genes. Cultural transmission often does not involve high-fidelity replication; nor are cultural variants always tiny snippets of information. Nonetheless, cultural evolution is fundamentally Darwinian in its basic structure.'

<sup>43</sup> For a comprehensive survey of the (dis)analogies between biological evolution and cultural (scientific) evolution, see Buskes (1998). See also Nelson (2007).

<sup>44</sup> This line of critique can be found in Elster (1979); Ruse (1986) and Thagard (1988).

best individuals, to the way in which nature has improved the design of organisms by constantly selecting the individuals that are best adapted to their environment. In other words, in the process of improving cattle or crops both variation and selection are deliberately and consciously guided by human beings. The variation is guided because only a small sample of variants gets selected for further propagation, namely those that are biased towards human preferences. Moreover, with the advent of genetic engineering we can deliberately manipulate the DNA of plants and animals itself, thus directing the variation even more. But even so, guided variation will not automatically save us from time-consuming sieving process. So despite all intentions and manipulations, artificial selection still is a special instance of Darwinian evolution.

But there are more ways to restore the analogy between biological and cultural evolution. In general, one could either argue that biological variation is blind but that cultural variation is blind as well, or reversely one could argue that cultural variation is guided but that biological variation is guided as well. The first line of argument is employed by Campbell (1960, 1974b); Munz (1993); Popper (1972); Cziko (1995) and Hull (1988, 2001) amongst others.<sup>45</sup> They argue that cultural (and scientific) variation only *appears* to be guided because, for convenience sake, we quickly tend to forget all those variants which for some reason or other failed to survive. We should not forget that for every successful idea many other ideas have quietly perished. So cultural evolution can be made to *look* directional by careful editing. It is only in retrospect, when all the dead ends, failures and false steps are blotted out, that we get the impression that variation is guided. And even if variation were biased or constrained somehow, the directedness would itself be the product of earlier selection processes. So at bottom real creative evolution always involves fumbling in the dark.<sup>46</sup> Cultural variation is therefore much blinder than people commonly believe. It is blind, random or ‘unjustified’ in the sense that we never can predict *in advance* whether a particular variant will be retained or not. We will always need the hindsight of a selective system to separate the wheat from the chaff. So it is not true that we can actively seek out the variants and inventions that are needed. If that really were the case we already would have found a cure for cancer or a solution to the threat of global warming, etc., a long time ago. Of course nobody denies that cultural evolution usually involves conscious and intelligent agents. But again, the fact that much of culture is consciously and deliberately generated does not guarantee that it will be selectively retained. So the fact that a cultural variant is created intentionally is not a sufficient condition for that variant’s success, and indeed it might not be a necessary condition either because some cultural variants, like certain rumors, customs, or pronunciations, etc., are *not* deliberately generated – they just crop up – but nevertheless may turn out to be highly successful.

But why do people choose one cultural variant rather than another? In the previous section we already saw that a variant – a meme – may for instance increase its frequency over time due to its intrinsic attractiveness. Technically this is called

<sup>45</sup> For a critical comment on this line of argument see Kronfeldner (2010).

<sup>46</sup> As Campbell (1974b, p. 147) put it: ‘[I]ncreasing knowledge or adaptation of necessity involves exploring the unknown, going beyond existing knowledge and adaptive recipes. This of necessity involves unknowing, non-preadapted fumbling in the dark.’ See also Mesoudi (2008).

‘content bias’, i.e., the content of an idea or practice affects its probability of being transmitted. But there are of course many more ways in which selection and transmission can be biased. Let me briefly address two other types here. A second type of transmission bias is called ‘frequency-dependent bias’. This involves using the frequency of a trait as a guide as to whether to adopt it, irrespective of its content. Richerson and Boyd (2005) demonstrate that frequency-dependent bias may result in conformity, i.e., when individuals imitate the *most* common behavior in the population; or in nonconformity, i.e., when individuals imitate the *least* common behavior in the population. Conformity – When in Rome, do as the Romans do – offers an explanation for long-lasting cultural traditions, even when migration numbers are high. A third type of transmission bias is called ‘model-based bias’ or ‘prestige bias’. Here the identity of the person from whom the cultural variant is acquired affects the variant’s success. Prestige bias might not be a bad strategy because by imitating the behavior of successful individuals in the population, you have a chance to become successful yourself. Studies in dialect evolution also support this hypothesis. According to Richerson and Boyd (2005) locally prestigious women tend to be the most advanced speakers of evolving dialects, and popular adolescent girls of the lower middle class are usually the most important leaders of urban language evolution.<sup>47</sup>

Now let us return to the issue of guided variation. So far I have shown that (i) cultural variation is more blind and therefore less guided than people commonly believe; and (ii) that even if variation *were* guided, this would not undermine my central claim that cultural evolution is Darwinian, because cumulative selection – and not random variation – is the key feature of Darwinian evolution. But as pointed out above, there also is another way to resolve the issue of guided variation. One could argue that cultural variation indeed *is* guided, but that biological variation is guided as well. This line of argument is employed by Richards (1981); Dawkins (1986); Wimsatt and Schank (1988); Stein and Lipton (1989) and Kantorovich (1993) amongst others. Their argument boils down to the claim that evolution inevitably puts constraints on both biological and cultural variation. Cultural variation, as we just saw, is random or blind in the sense that we cannot predict in advance whether a variant will survive or not. But obviously, cultural variation is not random or blind in the sense that selection operates on all conceivable variants logically possible. Cultural variation is constrained by tradition, the spirit of the age, the prevailing worldview, and possibly even by innate propensities. So cultural variation is surely guided in this sense, but this will not undermine the analogy with biological variation because we encounter similar constraints in the biological realm. Biological-genetic variation is constrained by a species’ evolutionary history, the constitution of its genotype, and the laws of molecular biology. It is important in this context to realize that constraints are not mere drawbacks which obstruct evolution. On the contrary, constraints channel the variation and by directing it produce much deeper exploration than would otherwise be possible. As Wimsatt & Schank write: ‘Constraints can thus play a creative and, in one sense, ultimately progressive role. This is a deep truth, not only about evolution, but about problem-solving and exploration in general.’<sup>48</sup> Note

<sup>47</sup> Richerson and Boyd (2005), p. 125.

<sup>48</sup> Wimsatt and Schank (1988), p. 235.

incidentally that the two lines of argument discussed above are perfectly compatible. Cultural variation can both be blind (in the sense of unjustified) *and* guided (in the sense of constrained). More in general, both genetic and cultural variation is blind with respect to the problems they have to solve: an ensuing selection process is needed to find out whether some variants are useful or not. But neither genetic variation nor cultural variation is truly random in the sense that they are completely unbiased. It therefore seems that the analogy still holds.

But we still have to address the second main objection raised against the idea of Darwinian cultural evolution. This objection amounts to the claim that cultural (and technological-scientific) evolution cannot possibly be Darwinian because its transmission system is essentially Lamarckian. Lamarckian inheritance means that acquired characters (phenotypic changes) are heritable and thus can be transmitted to an individual's offspring. Lamarckian evolution is therefore swift and progressive: it does not need a laborious and time-consuming Darwinian sieving process which selects, retains and accumulates the rare useful variants. In Lamarckian evolution the variations that occur are already pre-adapted and adjusted to the needs and wants they have to fulfill. As Gould (1996) put it:

[C]ultural change [...] is Lamarckian in basic mechanism. Any cultural knowledge acquired in one generation can be directly passed to the next by what we call, in a most noble word, education. [...] This uniquely and distinctively Lamarckian style of human cultural inheritance gives our technological history a directional and cumulative character that no natural Darwinian evolution can possess.<sup>49</sup>

Now of course it is true that we can hand down ideas, practices and skills, etc., to future generations. But to call this process 'Lamarckian' may be somewhat misleading. As Hull (1988) already pointed out, if cultural evolution were Lamarckian in a *literal* sense, the ideas, practices and skills, etc., that we acquire during our lifetime should somehow become encoded into one's DNA and then be genetically transmitted to one's offspring. Obviously, that is not what Gould and other critics have in mind. They believe that cultural evolution is Lamarckian in a *metaphorical* sense, i.e., ideas, practices and skills, etc., should be viewed as the analogues or counterparts of genes. Just as genes are transmitted to one's biological offspring, so too are memes transmitted to one's cultural 'offspring'. It is important to distinguish these two different types of inheritance because, as we have seen, cultural evolution is propelled by its own Darwinian algorithm of variation, selection and replication. The crucial point is that in both the biological and cultural realm variation is subjected to cumulative selection, a process which – in both realms – will result in perplexing instances of adaptation. As a renowned biologist and paleontologist Gould should have known that of all dynamic processes, Darwinian cumulative evolution is capable of such feats of design. With Hull one therefore suspects that authors who claim that cultural evolution is Lamarckian actually have a caricatured sense of the term in mind, i.e., they want to underline that cultural evolution is *intentional*. But we have already seen that the intentional character of cultural evolution will not save us from a genuine trial and error pursuit. The complex cultural adaptations and designs result

<sup>49</sup> Gould (1996), p. 222.

from indirect Darwinian selection rather than direct Lamarckian instruction. It is only in retrospect that successful cultural variations seem miraculously guided, pre-adapted and premeditated. So cultural evolution may be as intentional as can be imagined, but it is not entirely clear what we would gain by calling it ‘Lamarckian’.

Nevertheless, in the contemporary literature terms like ‘guided variation’ and ‘Lamarckian inheritance’ are still used albeit not in a strict or literal sense. For instance, in the mathematical models of Boyd and Richerson (1985) ‘guided variation’ is a technical term which refers to a mode of transmission in which one individual acquires information from a second individual, and then modifies that information according to his own individual learning processes. This modified information then can be transmitted to other individuals in the population. Here cultural variation is guided by individual experience and the mode of transmission is to a certain extent – i.e., in a metaphorical sense – Lamarckian. As Mesoudi (2011) rightly argues, it is in this sense that cultural evolution can be said to be directed and not blind. But he also stresses the fact that despite these alleged Lamarckian flavors, the basic assumption in most current models of cultural evolution is that all instances of complex cultural design are the result of Darwinian cumulative sieving processes. Not foresighted variation but hindsight selection is the secret to creative Darwinian evolution.

## Conclusion

Let me wrap up the strands of my argument. What I have tried to show in this article is that a case for Darwinian cultural evolution can be made. The claim that culture evolves is not a loose metaphor or mere figure of speech but should be taken quite seriously because cultural evolution generally obeys the same fundamental Darwinian principles as biological evolution. Both instances of evolution are governed by what I called Darwin’s formula: the algorithm of variation, selection, and replication. Together the three elements result in a process of cumulative selection, which is the essential and defining ingredient of Darwinian evolution. Cumulative selection is responsible for the perplexing instances of adaptation and design, both in the biological and the cultural realm. Many aspects of human culture are much too complex to emerge in a single step or to be thought up by an individual human being. Instead these achievements must have been gradually accumulated during a long and historical sieving process in which small adjustments and improvements were selectively retained. We have seen that, so far, only the culture of *Homo sapiens* exhibits this typical cumulative character. Through cumulative culture human beings have constructed a completely novel environment – a cultural niche – which, with regard to complexity and design, easily surpasses anything conjured up by earlier hominids or by any extant primate species. Niche construction, although not uniquely human, played a special role in human evolution because it triggered a complex interaction between cultural and biological evolution. Genes and culture co-evolve, as for instance is demonstrated by the remarkable increase of the hominid brain during the last 3 Ma. Without such cultural innovations as tool use, control of fire, cooking food and eating meat, our ancestors would never have developed bigger brains simply because the appropriate cultural niche was absent. Thus culture changed our genes and thereby the path of human evolution.

I also demonstrated that culture, although constrained by elementary biological imperatives, has its own evolutionary dynamics. Culture has brought about its own variation-selection-and-replication mode through which information is passed to next generations. Culture evolves because Darwin's formula is substrate-neutral, i.e., in principle any dynamic system could evolve according to Darwinian principles as long as the three necessary ingredients are present. As we have seen, in the case of human culture this condition is met. So sociobiologists and evolutionary psychologists are wrong in thinking that human culture wholly takes place within, and therefore can somehow be reduced to, the more fundamental framework of biological evolution. Sometimes culture simply breaks loose from its leash and evolves in its own right. Memetics has picked up this important point, but the alleged strong analogy between genes and memes may be flawed because in some aspects memes are probably very different from genes. So cultural evolution might be a different example of the same type of Darwinian process rather than a simple analogue of it. Future empirical research might settle this matter.

Another alleged disanalogy between biological and cultural evolution concerns the supposed Lamarckian character of cultural evolution. I believe that I have demonstrated that cultural evolution is 'Lamarckian' only in some caricaturized sense, i.e., as being purposive and intentional. The impression that cultural evolution is directed – and that cultural variation seems to be guided – arises only in retrospect when we have rubbed out the many mistakes and false starts. Despite all goal-directedness cultural (and scientific) evolution remains essentially Darwinian because humans are fallible creatures: our greatest collective achievements are not due to some mysterious foresight but to the hindsight of a cumulative winnowing process. In sum, although there are obvious differences between biological and cultural evolution, they also have something very fundamental in common since in both processes the same Darwinian logic applies: we try to understand which processes cause some variants to increase in the population and other variants to dwindle. The idea is that when we understand these micro-evolutionary causes, we can try to make predictions about their large-scale and long-term macro-evolutionary effects, predictions which can then be tested in models, and maybe in the real world as well. The science of cultural evolution will then become truly explanatory.

Some adherents of the research program, like Distin (2011) and Mesoudi (2011), go even further. They believe that we are on the eve of a major conceptual breakthrough. That is, they believe that the study of cultural evolution will help to unify the currently still fractionated social sciences in the same way as evolutionary theory has unified the biological sciences in the 1930s and 1940s.<sup>50</sup> The idea of Darwinian cultural evolution thus will provide a common and unifying framework for the social, psychological, behavioral, and economic sciences, disciplines which are currently still divided by different assumptions, approaches and methodologies. Diverse cultural phenomena can then be understood in terms of a handful of common underlying principles and processes. The future will tell whether this promise will be redeemed. What we know at present is that we humans are shaped by Darwinian selection processes, both biological and cultural. The intricate interplay between these two kinds of evolution has resulted in the emergence of a remarkable species of primate

<sup>50</sup> See also Mesoudi et al. (2006).

who has made the transmission and accumulation of cultural information his trademark. From the most casual examples of local folklore to the highest and most sacred instances of human civilization: they all result from the same indefatigable sieving process which dates back at least 3 Ma to our first tool-using ancestors. Since then cultural evolution has never stopped. It is a fascinating thought that cumulative selection processes occur everywhere around us, all the time, and that we are cast in that magnificent play.

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## References

- Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis. *Current Anthropology*, *36*, 199–221.
- Aunger, R. (Ed.). (2000). *Darwinizing culture: The status of memetics as a science*. Oxford: Oxford University Press.
- Barkow, J. H., Cosmides, L., & Tooby, J. (Eds.). (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. Oxford: Oxford University Press.
- Blackmore, S. (1999). *The meme machine*. Oxford: Oxford University Press.
- Blackmore, S. (2000). The power of memes. *Scientific American*, *283*, 52–61.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Buskes, C. (1998). *The genealogy of knowledge: A Darwinian approach to epistemology and philosophy of science*. Tilburg: Tilburg University Press.
- Campbell, D. T. (1960). Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review*, *67*, 380–400.
- Campbell, D. T. (1974a). Evolutionary epistemology. In P. A. Schilpp (Ed.), *The philosophy of Karl Popper* (pp. 412–463). La Salle: Open Court.
- Campbell, D. T. (1974b). Unjustified variation and selective retention in scientific discovery. In F. J. Ayala & T. Dobzhansky (Eds.), *Studies in the philosophy of biology* (pp. 139–161). London: Macmillan.
- Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural transmission and evolution*. Princeton: Princeton University Press.
- Chauvet, J.-M., & Brunel Deschamps, E. (2001). *Chauvet cave. The discovery of the world's oldest paintings*. London: Thames & Hudson.
- Chomsky, N. (1972). *Language and mind*. New York: Harcourt Brace Jovanovich.
- Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton: Princeton University Press.
- Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, *13*, 148–153.
- Cziko, G. (1995). *Without miracles: Universal selection theory and the second Darwinian revolution*. Cambridge (Mass.): The MIT Press.
- Darwin, C. (1859). *The origin of species*. London: John Murray.
- Darwin, C. (1871). *The descent of man*. London: John Murray.
- Dawkins, R. (1976). *The selfish gene. (2nd Second, revised edition, 1989)*. Oxford: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype*. Oxford: Oxford University Press.
- Dawkins, R. (1986). *The blind watchmaker*. New York: W.W. Norton.
- Deacon, T. (1997). *The symbolic species: The co-evolution of language and the brain*. New York: W.W. Norton.
- Dennett, D. (1995). *Darwin's dangerous idea: Evolution and the meanings of life*. London: Allen Lane.
- Dennett, D. (2002). The new replicators. In M. Pagel (Ed.), *Encyclopedia of evolution*, vol. I (pp.E83-E92). Oxford: Oxford University Press. Reprinted in Dennett (2006) *Breaking the spell*, Appendix A (pp. 341-357). New York: Viking.
- Distin, K. (2011). *Cultural evolution*. Cambridge: Cambridge University Press.
- Donald, M. (1991). *Origins of the modern mind: Three stages in the evolution of culture and cognition*. Cambridge (Mass.): Harvard University Press.
- Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.

- Elster, J. (1979). *Ulysses and the sirens: Studies in rationality and irrationality. (Revised edition 1984.)*. Cambridge: Cambridge University Press.
- Feldman, M., & Cavalli-Sforza, L. L. (2002). Cultural transmission. In M. Pagel (Ed.), *Encyclopedia of evolution* (Vol. I, pp. 222–226). Oxford: Oxford University Press.
- Gould, S. J. (1996). *Full house: The spread of excellence from Plato to Darwin*. New York: Harmony.
- Hull, D. L. (1988). *Science as a process: An evolutionary account of the social and conceptual development of science*. Chicago: University of Chicago Press.
- Hull, D. L. (1989). *The metaphysics of evolution*. New York: SUNY Press.
- Hull, D. L. (2001). *Science and selection: Essays on biological evolution and the philosophy of science*. Cambridge: Cambridge University Press.
- Jablonka, E., & Lamb, J. L. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. Cambridge (Mass.): The MIT Press.
- Kantorovich, A. (1993). *Scientific discovery: Logic and tinkering*. New York: SUNY Press.
- Kronfeldner, M. E. (2010). Darwinian ‘blind’ hypothesis formation revisited. *Synthese*, 175, 193–218.
- Kuhn, T. S. (1962). *The structure of scientific revolutions. (Second, enlarged edition, 1970.)*. Chicago: The University of Chicago Press.
- Laland, K. N. (2002). Cultural evolution. In M. Pagel (Ed.), *Encyclopedia of evolution* (Vol. I, pp. 220–222). Oxford: Oxford University Press.
- Laland, K. N., & Brown, G. R. (2002). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford: Oxford University Press.
- Laland, K. N., Odling-Smee, J., & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *The Behavioral and Brain Sciences*, 23, 131–175.
- Levinson, S. C., & Jaisson, P. (Eds.). (2006). *Evolution and culture*. Cambridge (Mass.): The MIT Press.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Lumsden, C., & Wilson, E. O. (1981). *Genes, mind, and culture: The coevolutionary process*. Cambridge (Mass.): Harvard University Press.
- Maynard-Smith, J., & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford: Oxford University Press.
- Mesoudi, A. (2008). Foresight in cultural evolution. *Biology and Philosophy*, 23, 243–255.
- Mesoudi, A. (2011). *Cultural evolution: How Darwinian theory can explain human culture & synthesize the social sciences*. Chicago: The University of Chicago Press.
- Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Is human cultural evolution Darwinian? Evidence reviewed from the perspective of *The Origin of Species*. *Evolution*, 58, 1–11.
- Mesoudi, A., Whiten, A., & Laland, K. N. (2006). Toward a unified science of cultural evolution. *The Behavioral and Brain Sciences*, 29, 329–383.
- Munz, P. (1993). *Philosophical Darwinism: On the origin of knowledge by means of natural selection*. London: Routledge.
- Mythen, S. (1996). *The prehistory of the mind: The cognitive origins of art and science*. London: Thames & Hudson.
- Nelson, R. N. (2007). Universal Darwinism and evolutionary social science. *Biology and Philosophy*, 22, 73–94.
- Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton: Princeton University Press.
- Pinker, S. (1994). *The language instinct: The new science of language and mind*. London: Penguin.
- Plotkin, H. (2010). *Evolutionary worlds without end*. Oxford: Oxford University Press.
- Popper, K. R. (1972). *Objective knowledge: An evolutionary approach*. Oxford: Oxford University Press.
- Richards, R. (1981). Natural selection and other models in the historiography of science. In M. B. Brewer & B. E. Collins (Eds.), *Scientific inquiry and the social sciences: A volume in honor of Donald T. Campbell* (pp. 37–76). San Francisco: Jossey-Bass Publ.
- Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
- Ruse, M. (1986). *Taking Darwin seriously: A naturalistic approach to philosophy*. Oxford: Blackwell.
- Schaller, M., et al. (Eds.). (2010). *Evolution, culture, and the human mind*. New York: Psychology Press.
- Spencer, H. (1857). Progress: its laws and cause. *Westminster Review*, 67, 244–267.
- Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Oxford: Oxford University Press.
- Sperber, D. (2000). A objection to the memetic approach to culture. In R. Aunger (Ed.), *Darwinizing culture: The status of memetics as a science* (pp. 163–173). Oxford: Oxford University Press.
- Stein, E., & Lipton, P. (1989). Where guesses come from: evolutionary epistemology and the anomaly of guided variation. *Biology and Philosophy*, 4, 33–56.
- Stringer, C. (2011). *The origin of our species*. London: Allen Lane.

- Thagard, P. (1988). *Computational philosophy of science*. Cambridge (Mass.): The MIT Press.
- Tomasello, M. (2000). *Cultural origins of human cognition*. Cambridge (Mass.): Harvard University Press.
- Tomasello, M. (2006). Uniquely human cognition is a product of human culture. In S. C. Levinson & P. Jaisson (Eds.), *Evolution and culture* (pp. 203–217). Cambridge (Mass.): The MIT Press.
- Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *The Behavioral and Brain Sciences*, 16, 495–552.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). Oxford: Oxford University Press.
- Toulmin, S. (1967). The evolutionary development of natural science. *American Scientist*, 55, 456–471.
- Toulmin, S. (1972). *Human understanding: The collective use and evolution of concepts*. Princeton: Princeton University Press.
- Whiten, A., et al. (1999). Cultures in chimpanzees. *Nature*, 399, 682–685.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge (Mass.): Harvard University Press.
- Wilson, E. O. (1978). *On human nature*. Cambridge (Mass.): Harvard University Press.
- Wimsatt, W., & Schank, F. (1988). Two constraints on the evolution of complex adaptations and the means for their avoidance. In M. H. Nitecki (Ed.), *Evolutionary progress* (pp. 231–273). Chicago: The University of Chicago Press.