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# The Encultured Primate: Thresholds and Transitions in Hominin Cultural Evolution

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Received: 30 November 2018; Accepted: 28 January 2019; Published: 1 February 2019



**Abstract:** This article tries to shed light on the mystery of human culture. Human beings are the only extant species with cumulative, evolving cultures. Many animal species do have cultural traditions in the form of socially transmitted practices but they typically lack cumulative culture. Why is that? This discrepancy between humans and animals is even more puzzling if one realizes that culture seems highly advantageous. Thanks to their accumulated knowledge and techniques our early ancestors were able to leave their cradle in Africa and swarm out across the planet, thereby adjusting themselves to a whole range of new environments. Without culture this would have been impossible. So we may ask once again: if cumulative culture is so useful, why don't other animals have it? In order to explain this mystery I won't appeal to the major transitions in human evolution—like walking upright, crafting stone tools and controlling fire, etc.—because that would be question begging. Instead I try to unearth the mechanisms that caused those evolutionary turning points to occur in the first place. It seems that unlike other animals, humans are predisposed to efficiently acquire, store and transmit cultural information in such ways that our cultures can genuinely evolve.

**Keywords:** cultural evolution; cumulative culture; gene–culture coevolution; dual inheritance; universal Darwinism; memetics

## 1. Introduction

Why is *Homo sapiens* the only species on our planet with cumulative culture? This issue is a profound mystery because it is obvious that culture has many merits. After all, without cumulative culture we would not have had technology and science and all the conveniences, tools and gadgets we owe to these achievements. Without culture we probably would still live in gloomy caves, growl at each other and be wrapped up in animal hides. So once again here's the riddle: If cumulative culture is so plainly advantageous, why don't other animals have it? Up to now nobody has come up with a satisfactory answer to this question. Indeed, according to Richerson and Boyd “the existence of human culture is a deep evolutionary mystery, on a par with the origins of life itself.” [1] (p. 126). Apparently for a culture to become cumulative several barriers have to be overcome. In this article I argue that the major transitions in human cultural evolution are not accomplished by a few creative innovators which deliberately and kindly helped mankind to ascend the great ladder of civilization. Instead I argue that the emergence and growth of human culture is the result of an evolutionary cumulative process which owes its efficiency not to some special foresight but to the hindsight of a selective system. Most cultural artifacts, practices and institutions are far too complex to be created by a single individual or during a single generation. Complex cultural achievements do not emerge in a single step but evolve gradually due to the selective retention and cumulative improvement of the various elements that constitute a particular cultural artifact or practice.

Although we ourselves are intentional and intelligent agents, much of our culture is not deliberately produced. Compare it with certain aspects of language like pronunciation and word meaning. As Darwin already noticed, most features of a language evolve gradually and almost

imperceptibly through a long chain of small and subtle changes [2]. It is only in the long run that we can see, and hear, that a language or a dialect has dramatically changed or that word meanings have shifted. But even with hindsight it is impossible to say who was responsible for these alterations because they often happen by what Dennett calls ‘subliminal adjustments’ over long stretches of time without anybody noticing them [3] (p. 240). And what holds for language evolution probably holds for other aspects of cultural evolution as well. As Dennett expounds:

Not just pronunciation and word meaning can subliminally shift. In principle, attitudes, moral values, the most emblematic idiosyncrasies of a culture can soften, harden, erode, or become brittle at a pace too slow to perceive. Cultural evolution is lightning fast, compared to genetic evolution, but it can also be much too gradual for casual observation to discern. [3] (p. 240)

There is an interesting parallel with biological evolution here. As in the biological realm, in the realm of culture we encounter system complexity without any (single) designer. As Levinson explains: “Just like organisms, social and cultural systems display intricate designs beyond a level that could be achieved by any individual designer, even if there was one.” [4] (pp. 17–18). According to Levinson, cultural phenomena embody the wisdom of generations: “we inherit the results of millennia of experimentation without any of the costs or dangers.” The results of these millennia of experimentation are, what Henrich calls, *cultural adaptations* [5] (p. 34). Like biological adaptations, cultural adaptations are painstakingly assembled through cumulative selection processes over many generations; they exhibit system complexity and sophisticated design similar to organs of extreme perfection like the eye; and finally, they cannot be invented from scratch at a single moment by any single individual or group of individuals for no single innovator contributes more than a small portion of the total, just as any single gene contributes only marginally to a complex biological adaptation. In sum, the history of culture shows that complex artifacts, practices and institutions have not been invented *ex nihilo* by some clever individuals, but instead evolved over many generations through the gradual accumulation of innumerable trials. In fact, as Petroski demonstrates, this gradual improvement even holds for relatively simple artifacts like forks, pencils, paper clips and zippers [6].

Several authors have argued that cultural evolution roughly adheres to the same Darwinian principles as genetic evolution [1,7,8]. In both cases the process is governed by a mechanism which I earlier dubbed ‘Darwin’s Formula’, i.e., the combined workings of Variation, Selection and Replication, or VSR for short [9]. Together the three elements cause information, whether genetic or cultural, to accumulate and thus enable the ‘system’ or ‘entity’ or ‘population’ which carries the information to evolve. The whole process is cumulative in character because the output of each selection round serves as input for the next selection round and so on, giving evolution a directional effect. Dawkins, Dennett and others have argued that the evolutionary algorithm is ‘substrate-neutral’, i.e., Darwin’s Formula is neutral with respect to the substrate or medium of evolution and neutral with respect to the entities that evolve [10,11]. So in principle any dynamic ‘system’ could evolve in a Darwinian manner, provided that the three elements—VSR—are present. The idea that Darwin’s Formula is substrate-neutral, and thus can operate in completely different media is closely related to what is generally known as ‘Universal Darwinism’, i.e., the notion that the mechanism which causes species to evolve is not confined to the biological domain alone [12]. All that is required for any ‘population’ to evolve in a Darwinian manner are entities which are able to make copies of themselves, entities which Dawkins coined ‘replicators’ [10] (p. 15). In genetic evolution genes are the key replicators whereas in cultural evolution ‘memes’ play this role. In either domain, if such replicators exhibit even the slightest variation in function, appearance, content or whatever, a selection process will ensue which results in the differential proliferation of these replicators. I will return to this issue in Section 8. First we have to address the crucial difference between human and animal culture.

## 2. The Ratchet Effect

As Richerson and Boyd rightly notice, culture can do many things that genes can't because, for one, cultural evolution is much faster than genetic evolution [1]. Culture thus offers relatively swift adaptation to lots of different and changing environments. Thanks to their accumulated culture, knowledge and technology our prehistoric ancestors had tools, clothes, weapons, shelter, (control of) fire and many artifacts, skills and procedures at their disposal that enabled them to swarm out from their original habitat—the African savannah—to the most remote and inhospitable corners of our planet. Without their accumulated culture such a formidable feat would have been impossible. So we may ask once again, if cumulative culture is such a good trick, why didn't other animals discover it? The uniqueness of human culture suggests that it may be quite difficult and perhaps even impossible for other species to accomplish something similar. Apparently for genuine cumulative culture to emerge several thresholds have to be overcome, and up to now no extant animal species besides *Homo sapiens* has succeeded in cracking this problem.

At this point in our inquiry it may be tempting to appeal to several watershed moments in human evolution like our ancestors' ability to craft stone tools [13] and control fire [14], or their invention of cooking food [15] and eating meat [16] which should explain why we humans have diverged from other hominin branches. Apparently we owe our unique features to a few adaptive breakthroughs which radically and irreversibly altered the path of evolution. But with Sterelny [17] (p. xii), I am skeptical about the explanatory power of such 'magic-moment models' because they neither tell us what *caused* these adaptations nor why they apparently only occurred in our own lineage (and maybe a few other chosen branches which are now extinct). So instead of focusing on those 'miraculous' key moments and turning points in human evolution, we should rather focus on the mechanisms through which such innovations are brought about in the first place. That is, a thorough analysis of the underlying process will not only bring us closer to understanding our own evolutionary past but might also solve the riddle of why we are the only species with cumulative culture. I shall argue that human culture is propelled by a similar Darwinian mechanism (VSR-algorithm) as is genetic evolution, and that cultural cumulative evolution is the combined result of several capabilities like social learning, teaching, cooperation, and the use of language which enabled our ancestors to transmit cultural information more and more efficiently. At some point in time, the accuracy by which cultural information was transmitted paralleled the way in which genetic information is passed on to new generations, thus turning human culture essentially into a second inheritance system.

We may define 'culture' as all information that is transmitted non-genetically, i.e., through imitation, social learning or teaching over successive generations [18] (p. 3). To be sure, many animal species do possess culture in the form of traditions which, by copying the behavior of other individuals, may persist during many generations [19,20]. Well-known examples of animal culture are the termite-fishing and nut-cracking abilities of wild monkeys and apes [21,22]. These complex skills have to be learned, through imitation or social learning, and then thoroughly practiced in order to master the technique. But animals typically lack cumulative culture. For all we know, the techniques used by monkeys and apes to crack nuts or to fish for termites may not have changed for decades or perhaps even centuries. Consequently, if for whatever reason such practices would get lost, it would only take a single clever individual during one generation to reinvent and reintroduce the technique. So for some reason these non-human primates are not able to gradually improve or refine their cultural artifacts and practices or to significantly augment their cultural repertoire. As we saw earlier, what separates us from these animals is not our individual intelligence but our *collective* ability to faithfully pass on information over many generations. According to Tomasello, human beings possess a species-unique cognitive adaptation for cultural learning. What distinguishes human culture from that of other species is the presence of a 'ratchet effect':

The process of cumulative cultural evolution requires not only creative invention but also, and just as importantly, faithful social transmission that can work as a ratchet to prevent

slippage backward [ . . . ]. Perhaps surprisingly, for many animal species it is not the creative component, but rather the stabilizing ratchet component, that is the difficult feat. Thus, many nonhuman primate individuals regularly produce intelligent behavioral innovations and novelties, but then their groupmates do not engage in the kinds of social learning that would enable, over time, the cultural ratchet to do its work. [23] (p. 5)

So although many animal species can be creative and inventive, they do not sufficiently engage in social learning through which innovations can gradually accumulate. Tomasello believes that this uniquely human ability for cultural learning stems, among other things, from our ability to understand other individuals as intentional beings with goals, beliefs and desires. In the remaining sections, I will focus more closely on what precisely constitutes the ratchet effect in human cultural evolution.

### 3. Cultural Niche Construction

I have argued that the dawn of culture opened a completely new medium for evolution. After 3.5 billion years the ancient monopoly of genetic evolution came to an end. From now on it had to share its space with a newcomer on the block, cultural evolution, which would soon leave its own distinctive marks. But equally important, cultural evolution also became closely interwoven with genetic evolution, resulting in a complex coevolutionary process in which cultural innovations fed back on our gene pool and vice versa. For example, consider our prehistoric ancestor's ability to control fire and to cook food. This culturally acquired and transmitted technique, which may already have been mastered by *Homo erectus* more than 1 million years ago [14], had a significant impact on our ancestor's genetic makeup and hence our physiology [15]. Among paleoanthropologists it is widely believed that the rapid growth of the hominin brain, which tripled in volume from 500 cc in *Australopithecus* to 1500 cc in modern humans, was made possible by the fact that early hominins changed their diets, switched to eating meat, and began cooking their food. Since meat is more rich in calories and much easier to digest, especially when it is cooked, than vegetable food, it became evolutionary affordable to reduce the expensive tissue of the intestines in favor for equally expensive brain tissue. This hypothesis is aptly called the 'gut-brain swap' [16]. Thus one of the most significant events in human evolution, the explosive growth of the hominin brain, was initially triggered by a relatively modest change in cultural practice. There are many other examples which demonstrate that human genetic and cultural evolution are inextricably tied together [24]. Thanks to their accumulated culture, our early ancestors changed their environment in such ways that they altered the pathways of natural selection, and hence of evolution.

The coevolutionary process in which cumulative culture is able to feedback on genetic evolution and introduce novel selection pressures is closely linked to the notion of 'niche construction' [25,26]. This process takes place wherever organisms change their environment in such ways that they thereby alter the source and targets of natural selection. Niche construction is not an exclusively human affair, but *cultural* niche construction probably is because unlike most animal niche construction (think of the beaver's dam) human niche construction is characterized by social learning and cultural inherited practices. According to Laland, Odling-Smee and Feldman, if a particular cultural niche-altering human activity (e.g., controlling fire, cooking food, eating meat) persists for enough generations to generate a stable selection pressure, it will be able to influence and change the route of human genetic evolution [26]. As we have just seen, the result is a coevolutionary process between genes and culture, also known as gene-culture coevolution. Genes can influence the path of cultural evolution, but also vice versa: culture can influence the path that genetic evolution takes. Thus when human genes are exposed to a culturally modified environment (i.e., to a new cultural niche) they may alter quite rapidly in frequency through natural selection.

A classic example is adult lactose tolerance, i.e., the ability of human adults to digest milk and other dairy products. In most humans, the ability to digest lactose disappears after childhood, but in some (mostly European and Asian) populations the ability persists into adulthood. This adaptive feature arose through natural selection only after our ancestors first domesticated cattle and started

dairy farming some 8000 years ago in Central Europe and the Middle East [27]. From then on adult individuals who could digest milk had a considerable advantage over adults who couldn't. Hence a new digestive enzyme lactase got selected, thus showing the impact of culture on our genetic makeup [24] (pp. 226ff.). More recently discovered examples are the physiological and genetic adaptations found in the sea nomads, the indigenous free-diving and spear fishing Bajau people of South East Asia who are as comfortable underwater as most people are on land. The Bajau people do not only have complete control over their breath but are also genetically adapted to life in the sea. In the course of evolution, the Bajau developed an enlarged spleen which, when it contracts, increases the amount of oxygen-carrying red blood cells in the body [28]. In sum, the phenomena of gene-culture coevolution and niche construction make evolution, whether genetic, cultural or both, a much more dynamic process than previously believed. Adaptation ceases to be a one-way process, solely being a population's response to environmentally imposed problems. Instead adaptation now becomes a dynamic two-way process with populations of organisms setting as well as solving the problems.

#### 4. Hominin Species Competition

In the previous section I argued that animals do not possess genuine cumulative culture. To be sure, many animal species are smart and inventive but they nevertheless lack the ratchet effect which gradually accumulates cultural information and prevents it from getting lost. But what about our early, prehistoric ancestors? Could they possibly have possessed truly evolving cultures? After all, the current gap between humans and animals only exists because all intermediate forms, i.e., earlier species of hominins, have gone extinct. Hence we are forced to use a bit of imagination. Suppose we could time-travel some 200,000 years back into the past and then make a grand tour across Europe, Asia and Africa. It would be a thrilling experience because on our fictitious Pleistocene safari we might encounter not *one* but up to *six* hominin species. That is the stunning conclusion of groundbreaking paleoanthropological and paleogenetic research of the last decade or so [29]. In Europe and the Middle-East we would encounter our distant cousins the Neanderthals, *Homo neanderthalensis*, and in Central Asia we might catch a glimpse of the mysterious Denisovans who probably were closely related to the Neanderthals, both being direct descendants of the then already extinct species of *Homo heidelbergensis*. Also in Asia, on the Indonesian archipelago, we might encounter the last remaining members of the ancient species *Homo erectus* whose ancestors had left Africa 1.5 million years earlier. On the Indonesian island of Flores we might even spot those strange little 'hobbits' named *Homo floresiensis*, who are believed to be an isolated, branched off population of *H. erectus*. Finally, in Africa we would not only encounter early members of our own species, *Homo sapiens*, but also members of a much smaller and more primitive hominin: *Homo naledi* [30]. All these species belonged to the genus *Homo*. They were all hunter-gatherers, used stone tools, were able to control fire, and at least some of them probably had some rudimentary form of language and culture [31]. Yet at the time of our grand tour, some 200,000 years ago, there was no indication whatsoever that 175,000 years later only one hominin species would remain—us—while all others would go extinct. From their small cradle in Africa our ancestors would soon swarm out across other continents, thereby displacing all other members of the genus *Homo*. We became globally dominant while our fellow hominin species perished. So what on earth happened? Why us?

If we compare the six hominin species we notice obvious differences, most prominently with regard to body size and length. *H. sapiens*, *H. erectus* and the Neanderthals were five to six feet (150 to 180 cm) tall, whereas *H. floresiensis* and *H. naledi* would not grow taller than 3 or 4 feet (100 to 120 cm). Were our ancestors in some sense anatomically or physically superior to the other hominin species? That is hard to believe. Actually the Neanderthals and Denisovans were anatomically more robust and physically much stronger and tougher than our own ancestors. So it wasn't our bodies that made the difference. Next consider brains. One might expect that the hominin species with the largest brain would eventually turn out on top and conquer the world, but rather surprisingly that was not the case. The hominins with the largest brains were not the members of our own species but

the Neanderthals and Denisovans. Anatomically modern humans like us have an average cranium capacity of approximately 1500 cc, whereas the Neanderthals and Denisovans had a volume of 1600 cc to possibly 1800 cc respectively [32,33]. So it wasn't our individual brains either that supposedly made the difference. What really *did* make a difference was, what Henrich calls, our *collective brains* [5] (p. 5). They gave us a headstart. That is, shared intentionality, cooperation and cultural learning probably allowed us to gather, store and transmit information much more efficiently than our hominin cousins could. In our species the increasing flow of information eventually led to cumulative cultural evolution. According to Tomasello, cumulative culture apparently only began when modern humans first emerged in Africa [34], as we now know some 300,000 years ago [35], and this unique human feature might explain why our ancestors outcompeted all other hominin species as they migrated from Africa and swarmed out all across the globe.

## 5. Group Size and Cooperation

Before I discuss the various adaptive features which are involved in human cultural learning, we first have to look at a more trivial and *non-adaptive* element which nevertheless probably plays a crucial role in cultural evolution. As Stringer points out, early hominins probably lived in small populations of hunter-gatherers with little or no contact with other such groups [36]. Hence local inventions and accumulated knowledge might have been lost quite often. It was only after bigger populations emerged with regular connections to other groups that cultural information could be exchanged and accumulate. There is ample empirical evidence that group size matters, both in biological and cultural evolution. In small populations the differential distribution of variants mostly depends on chance factors like random drift. In larger populations the effects of non-random selection (i.e., the evolutionary VRS-algorithm) become increasingly stronger. So cultural evolution therefore requires a certain population size and density. Large and interconnected populations have bigger cultural repertoires and more diverse technological toolkits than small, isolated populations. A general prediction states that cultural (and technological) complexity increases as population size increases. This seems to be confirmed in cases where small, isolated island populations have lost valuable technology, a process again similar to the phenomenon of random drift in biological evolution. Boyd, Richerson and Henrich offer some intriguing examples [37]. Anthropological and archaeological studies confirm that the toolkit of native Tasmanians gradually became less complex after they became isolated from mainland Australia. Likewise, the isolated Polar Inuit lost the know-how to build kayaks and bows and arrows when all experienced craftsmen died during a severe pandemic. In addition, what also might drive cultural complexity and variation in toolkit structure is the risk of resource failure, as is stated in the so-called 'environmental risk' hypothesis. That is, as the risk of resource failure increases, toolkits tend to become more diverse and complex [38].

But although group *size* is not an adaptation specifically designed for human cumulative culture, our ability to *cooperate* in large groups probably is. The presence of large populations consisting of socially engaged, cooperating individuals is a necessary condition for a culture to evolve. Human beings are a prosocial species. Prosocial behavior is any behavior performed by any one individual to alleviate another's need or improve their welfare. Prosociality is not rare among animals. In many primate species for instance we see voluntary, social behavior intended to benefit other individuals [39]. Yet some authors argue that we are not only a prosocial species but an *ultrasocial* (or eusocial) species as well, a feature which transformed human groups virtually into superorganisms with shared intentionality and collective superpowers which are not available to other animals who have failed to make the leap from prosociality to ultrasociality. Ultrasociality is the highest level of animal sociality characterized amongst others by cooperative care of the young, division of labor, and its extreme rarity: in the history of life it may have evolved only twenty times, scattered across a few species of insects, crustaceans and mammals [40]. One of the main features in the history of hominin evolution has been the steady increase in the scale of populations. Modern complex societies easily comprise tens or hundreds of millions of genetically unrelated yet closely cooperating individuals, which presents

a real puzzle to both evolutionary and social theory. Turchin argues that ultrasociality must have occurred in several stages, one of which was the transition from group membership based on genetic relatedness and ethnicity to group membership based on symbolic markers such as tools, artifacts, dialect/language, song/dance, dress, rituals, cult/religion, etc. [41]. Such 'ethnic markers' would clearly indicate whether somebody is a trusted friend or an alien foe. In later stages the establishment of institutions, hierarchical organization, and the control of defectors by imposition of norms, rules and sanctions allowed even bigger groups to emerge.

Whether the emergence of ultrasociality is the result of cultural group selection is still fiercely debated among theorists. At first glance it seems obvious that cultural group selection must have played a significant role in hominin evolution [42]. After all, groups made up of cooperative, selfless individuals would soon outcompete groups made up of uncooperative, selfish individuals, thus eventually leading to the elimination of the latter type of group [43]. But groups of closely cooperating individuals are vulnerable to within-group defection by free riders who exploit the collaborative practice, causing the cooperation to dissolve. So the question becomes whether, in the long run, collaborative groups are able to avert the parasitism of such individual exploiters [44]. Some authors argue that despite cooperators losing to defectors within groups, the frequency of cooperators may still globally increase because although selfish members win within groups, groups of cooperators beat groups of selfish members [45].

## 6. Human Adaptation for Cultural Learning

Large interconnected groups of closely cooperating individuals are a necessary but not a sufficient condition for cultures to evolve. For Tomasello's ratchet effect to become effective we need something else. Specifically, what we need is a mechanism through which cultural information gets faithfully transmitted up to a point that it can gradually accumulate and evolve. The most common way in which non-genetic information gets transmitted is through social learning, the ability to acquire knowledge or skills from other individuals by copying their behavior. Learning from others is often a better strategy than learning by oneself because it preserves an animal from making costly mistakes. Through copying you can profit from the trials and errors already made by other individuals. Thus through copying, animals can learn what food to eat, where to burrow safely, which predators to fear, and many other things that would significantly favor survival. Animals don't need to be smart to engage in and profit from social learning. Hence social learning is widespread among animals, even among 'lower' animal groups like insects and fish [46,47]. Through copying, adaptive information can spread through a population and be retained during successive generations. Social learning may become particularly profitable when a population contains one or more inventive and creative individuals. By copying the behavior of those individuals, the other members of the group may solve problems and learn tricks which otherwise would have gone unnoticed. A classic example is the trick of pecking open the caps of milk bottles in order to get to the cream, used by several British bird species like tits and robins in the 1920s. The trick was probably first invented by one or a few creative individuals but then soon turned into a widespread habit, through social learning, among British birds [48]. Like social learning, creative invention is common in the animal kingdom and clearly present in such clever animal groups like primates [49], corvids [50] and cetaceans [51] which are all capable of complex problem solving.

Yet because the aforementioned animal species lack cumulative culture, we must conclude that cooperation, social learning and creative invention might be individually necessary but not jointly sufficient for cultural information to accumulate and evolve. What is missing is a mechanism that allows cultural information to be transmitted with such reliability and accuracy that information can gradually accumulate and evolve. Teaching might be such a mechanism. Unlike social learning and creativity, teaching is relatively rare among animals. Apart from us human beings who rely heavily on this mechanism, teaching is only found in a few animal groups like ants, bees, meerkats and two species of bird, and thus, rather surprisingly, *not* in intelligent animal groups like apes, monkeys, corvids and cetaceans [8]. Teaching increases the speed and fidelity in which acquired cultural information can

spread among members of a population and across generations. Note that teaching is essentially a further enhancement of social learning, i.e., teaching is only present in those species which already engage in social learning, the additional difference being that the flow of information now specifically is confined to tutor and pupil, with the tutor actively instructing the pupil. According to Laland, the reason why teaching is not more common among smart animals is that, rather counterintuitively, smart animals rarely have to teach [8] (pp. 165–166). Young apes and monkeys, for instance, learn most of their skills, like nut-cracking, through common social learning or trial and error. In general, animal teaching only pays off when a particular skill is too difficult to learn by oneself; the knowledge taught makes a significant difference to the pupil's fitness; and tutor and pupil are closely related. Obviously teaching among humans deviates from this since humans do not just teach high fitness-yielding skills to close relatives but engage in all sorts of instructive learning, whether tutor and pupil are related or not. This deviance from animal teaching most probably stems from our supposed ultrasociality which, as was noted in the previous section, involves cooperative care for the young amongst other things.

But when we add the capacity of teaching to the three aforementioned qualities, i.e., cooperation, social learning and inventiveness, we must again conclude that these four elements probably are individually necessary but not jointly sufficient for culture to evolve. As we have seen, social learning, creativity and teaching are present in some animal species, yet they nevertheless lack cumulative culture. So obviously we still need something extra for the ratchet effect to operate. For a culture to evolve, that is, you need a reliable medium or channel through which information is conveyed and transmitted among members of a population and across generations. A population may be made up entirely of creative, cooperative and teaching social learners, but without a high-fidelity transmission mechanism that reliably transfers and accumulates information, their culture will not evolve. The most obvious candidate for such a communication system is of course language, which is even more rare than ultrasociality and teaching.

Human language is special, and probably even unique, because it makes high-fidelity social transmission possible. Without our language there probably would be no ratchet effect which causes information to accumulate and prevents it from getting lost. Without language our cultures would not evolve. According to Jablonka and Lamb, human language essentially created a complex symbolic inheritance system which separates us from other animals and which opened the door to our culture and civilization [52]. For the same reason Dennett characterizes language as “the launching pad of human cognition and thinking” [3] (p. 260). Anatomically, physiologically and genetically we humans may closely resemble chimpanzees, bonobos and other great apes, but we also dramatically differ from all other primates because we can think and communicate through words and other types of symbols. That's what sets us apart. According to Deacon, language “offers a means for generating an essentially infinite variety of novel representations, and an unprecedented inferential engine for predicting events, organizing memories, and planning behaviors” [53] (p. 22). Whereas animal communication is always confined and limited, human language is truly open-ended. Our recursive language makes possible an infinite array of sentences and expressions created from a finite set of elements, the alphabet. The range of things we can think and talk about is only limited by our imagination. Thus human language is qualitatively different from animal communication like alarm calls or the song of birds and whales because the latter type of communication is always concrete and concerned with the ‘here’ and ‘now’ whereas human language and thinking can easily transcend our present, manifest world [54].

According to Jablonka and Lamb, language has opened a new portal for evolution. Language allows us to faithfully transmit information from one generation to the next, thus turning our communication system effectively into an inheritance system [52]. (Recall that the evolutionary VRS-algorithm is substrate-neutral, i.e., Darwin's Formula is neutral with respect to the substrate or medium of evolution and neutral with respect to the entities that evolve.) Jablonka and Lamb, like many other theorists in the field of cultural evolution, thus adhere to the theory of ‘dual inheritance’, i.e., the idea that human behavior is the result of two different interacting evolutionary processes: genetic evolution and cultural evolution. The theory of dual inheritance is therefore closely related

to the idea of gene–culture coevolution that I discussed earlier in Section 3. Dual inheritance theory emphasizes the fact that culture is an evolutionary process in its own right, analogous to genetic evolution [1]. The theory is different from earlier sociobiological models which treated culture as a complex biological phenomenon which enhances our genetic fitness [9]. And of course many aspects of culture *are* very useful for our survival, but as we shall see later on, culture can also go *against* our genetic fitness.

Jablonka and Lamb discuss a few interesting parallels between genetic heredity and heredity based on language or symbols which are worth mentioning here [52] (p. 201ff.). First, both inheritance systems can transmit *latent* information, i.e., information which is passed on to next generations without being expressed. Like a recessive gene, a particular bit of symbolic information may lie dormant for many generations before it is ‘switched on’ again. Granny’s cake recipe may be passed down through the family for several generations without anybody actually baking the cake. Moreover, notice that 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. Second, language is modularly organized, i.e., the units of language—words—can be changed one by one, just like the units—or nucleotides—in a DNA sequence, which means that an enormous number of variations can be generated and transmitted, and variation of course being one of the necessary conditions for Darwinian evolution to occur. Without variation no sieving process will ensue [55]. Third and last, like genetic information, symbolic information is encoded and translatable. Each gene encodes a unique protein that performs a specialized function in the cell, and by producing a string of amino acids, a gene can be translated into that particular protein. Symbolic information is encoded and translatable as well, the only difference being that its translatability is probably unlimited. A bit of information, for instance a sentence in English, can be translated into Chinese or Latin, spelled out in Morse code or braille, and be transmitted through poetry, song or sign language, etc. Since we can translate symbols from one form to another and combine them in many different ways, the range, shape and sheer variety of meaningful utterances becomes limitless.

Note that, apart from several interesting analogies, there are also obvious differences between genetic inheritance and cultural inheritance. For instance, whereas genetic inheritance relies almost exclusively on ‘vertical’ (i.e., parent-to-offspring) inheritance, in cultural inheritance the trajectories of transmission are multifarious. In cultural evolution vertical transmission can even be reversed as when parents, or even grandparents, can learn things from their (grand)children. But ‘horizontal’ transmission among members of the same generation might be equally important. In fact, if vertical, downward transmission were to be the only direction in which cultural information would flow, cultures would be very static. For a culture to evolve, horizontal transmission is needed, i.e., a novel idea should not only spread from parents to offspring but to contemporaries as well [7,56].

## 7. Runaway Cultural Evolution

We have seen that for cultural information to accumulate and for cultures to evolve a whole range of conditions has to be fulfilled. That is, for cultural information to accumulate we need the presence of large and interconnected groups, social learning, creativity, cooperation, teaching and language. It is only when these conditions are jointly met that social transmission could result in cultural evolution. In addition, it seems that these conditions, when jointly present, reinforce each other resulting in one or more evolutionary feedback mechanisms. That is, in our ancestors’ emerging cultures (their newly constructed cultural niches) it increasingly ‘paid’ them to transmit more information to their offspring and to other members of their group [25]. 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 one’s tribe members and be worth teaching to one’s offspring. In fact, according to Laland, natural selection may have favored language in our species because it makes teaching much more economical and effective [8]. Thus with the advent of human culture and cultural niche construction, it became more and more advantageous to transmit cultural information

through social learning and teaching. This could have triggered an autocatalytic feedback process in which cultural niche construction led to more social learning and teaching, while social learning and teaching in turn led to more cultural niche construction, and so on. With such a self-enforcing process, culture could easily accumulate and bootstrap itself to higher and more complex levels, and possibly even result in some kind of runaway evolution. In short, the more our ancestors relied on and profited from their accumulated cultural heritage, the greater became the advantage of transmitting this cultural information to the next generation.

As we have seen, at present we human beings are the only extant species on the planet which possess cumulative, evolving cultures. Extinct hominin species like *Homo erectus*, the Neanderthals and Denisovans possibly may have had rudimentary evolving cultures as well, although that is notoriously hard to prove. Recent archaeological findings suggest that Neanderthals may have had a capacity for art, symbolic thought and cultural competence [57]. It probably depends on whether these hominins had some form of rudimentary (proto)language, either spoken or gestural [31,58]. What we *do* know is that our own prehistoric ancestors, the first members of the species *Homo sapiens*, show clear evidence of their evolving cultures during the Middle and Upper Paleolithic, culminating in the cultural ‘big bang’ in Europe some 40,000 years ago exemplified by sophisticated stone tools, cave paintings, and human and animal figurines amongst others. This demonstration of full-blown culture means that our ancestors must have had high-speed vocal language. Donald has called this new stage in human evolution a transition to ‘mythic culture’ because he believes that myth was the primary function of our ancestor’s prehistoric language [59]. Mythic culture enabled our ancestors to pass on collective accumulated knowledge across generations and gave them a collective system for understanding and representing the world around them. The ability to pass on knowledge through oral tradition and mythic narrative could be 200,000 to 300,000 years old, coinciding with the first appearance of our species in Africa [35].

Apart from the various trajectories of cultural transmission, one also could discern differences in *speed* by which cultural information gets transmitted among members of a population. Vertical, parent-to-offspring transmission results in a relatively slow pace of evolution whereas horizontal transmission significantly speeds evolution up. What also contributed to the increasing tempo of evolution was the fact that at some point in time, probably some 10,000 years ago, collective accumulated cultural information was no longer restricted to the bounds of the human brain. From then on accumulated knowledge could be gathered in external storage systems made possible by the invention of writing. Collective cultural information could now be preserved and dispersed in the form of cuneiforms, hieroglyphs and other symbolic sign systems. Donald calls this further evolutionary transition ‘theoretic culture’ because for the first time accumulated knowledge, now durably recorded in external media, enabled humans to reflect on their collective wisdom, thus establishing the first rudimentary forms of religion, philosophy, and science [59]. Since the invention of writing the speed of cultural evolution has further increased as a result of other technological breakthroughs like the art of printing, stenciling and photocopying and, more recently, the advent of social media and the world wide web. According to Bentley and O’Brien the appearance of technology capable of accumulating and manipulating vast amounts of cultural information outside human brains has removed us as bottlenecks altogether, resulting in a seemingly self-perpetuating process of knowledge explosion [60].

To sum up, unlike other animals, human beings seem to be carefully adapted to efficiently acquire, store and transmit cultural information. This constant flow of information across generations allowed our cultures to evolve, a trick no other animal has yet mastered. But this great achievement comes with an equally big obligation, namely our duty to teach this colossal and constantly growing body of knowledge—our collective cultural heritage—to each new generation of human infants. Not surprisingly then, our juveniles’ ability to absorb cultural information seems to be carefully modelled by natural selection. Human children are designed by evolution to soak up the culture which they grow up in. Csibra and Gergely have called this adaptive cognitive disposition ‘natural pedagogy’ [61]. Despite the huge variability in cultures and child-rearing practices, all human societies rely on a

particular kind of social learning between adults and infants, i.e., teaching, in which the flow of information from tutor to pupil is accomplished by verbal and textual instruction.

## 8. Memes Reconsidered

As we have seen in the previous sections, there are several interesting analogies between genetic transmission and cultural transmission. In both cases information is passed on from one generation to the next and in both cases information can accumulate through selection processes resulting in complex composite adaptations, whether biological or cultural. Dawkins (in)famously stretched the analogy a bit further by introducing the notion of the ‘meme’, a unit of cultural inheritance equivalent to the unit of genetic inheritance, the gene [10]. 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 it contains through successive generations. Elsewhere I already discussed the alleged (dis)similarities between genes and memes in some detail [9]. I won’t repeat that here. Instead I will briefly focus on what I believe might be some promises of memetics, that is, a few interesting strands of research which might be worth pursuing. For instance, ever since Dawkins coined the term ‘meme’ much of the critical debate has been devoted to the question what memes actually are. Are they ideas, beliefs, traditions, or rather bits of behavior, or perhaps neural patterns in the brain? Nobody could really tell. The biggest problem, at least according to those skeptical about the supposed analogy is that, unlike genes, memes are often quite fuzzy entities which cannot be split up into discrete genelike particles. Surely sometimes memes *are* indeed discrete, particular and clearly outlined like the nursery rhyme *Mary had a little lamb*, the epic poems of Homer’s *Iliad* or the Grimm brothers’ fairy tales, etc., but more often memes cannot be clearly defined because they are hazy, multiform and can widely overlap or easily blend with other memes. Think of fuzzy concepts like ‘Faith’, ‘Philosophy’ or ‘Spirituality’, etc. In short, because memes are often very unlike genes, the analogy obviously breaks down.

Recently Dennett suggested that *words* might be the best examples of memes. According to Dennett, words are salient, well individualized and discrete, and furthermore “they have clear histories of descent with modification of both pronunciation and meaning that can be traced back thousands of years in many cases” [3] (p. 207). Dennett cites Darwin who already noticed a remarkable parallel between species evolution and the evolution of language: “The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously the same” [2] (p. 60). In a similar fashion, Dennett argues that words are culturally transmitted items that evolve by differential replication:

A word, like a virus, is a minimal kind of *agent*: it *wants to get itself said*. Why? Because if it doesn’t, it will soon go extinct. A word is *selfish* exactly the same way a gene is selfish. (italics in original). [3] (p. 189)

Of course, words and all other kinds of memes—Dennett also calls them ‘informational things’—don’t have minds any more than a virus does, so the selfishness should not be taken literally but in a metaphorical sense. That is, like a virus, words and other memes are designed by evolution to provoke and enhance their own replication. Ultimately what counts is a word’s own success, not the success of its user(s). So according to Dennett, words really are discrete, faithfully transmitted entities that are at least somewhat genelike. Perhaps Dennett is right by arguing that the analogy between genes and words might be worth pursuing, but we should not forget that words only constitute a minor part of all ‘informational things’ that can be culturally transmitted. Many memes, or ‘cultural variants’ as Richerson and Boyd call them [1], may not even depend on language at all to be replicated. Think for instance of pictorial symbols like a smiley, the heart symbol or a Christian cross, or bits of behavioral repertoire like (rude) hand gestures, new fashions in clothes or innovative dance steps, etc. All these memes can be copied or imitated without the use of language. So even if words *are* the best examples of memes, they certainly are not the only ones.

My overall suggestion would be that we should be careful not to overstretch the analogy between genes and memes. Culturally transmittable things, whatever they are, need not to resemble genes in every way in order to be faithfully replicated. For as Richerson and Boyd rightly point out, cultural variants need only to be genelike “to the extent that they carry the cultural information necessary to create cultural continuity” [1] (p. 81). And according to the authors, this can be accomplished in most un-genelike ways. Richerson and Boyd expound:

Adopting a Darwinian approach to culture does not mean that you have to also believe that culture is made of minuscule, genelike particles that are faithfully replicated during cultural transmission. The evidence suggests that sometimes cultural variants *are* somewhat genelike, while at other times they are decidedly not. But—and this is a big but—in either case, the Darwinian approach remains useful. (*italics in original*). [1] (p. 80)

What matters is that we can keep track of different cultural variants present in a population and try to understand what processes cause some variants to increase and others to decline. In a similar vein, Mesoudi argues that we should make a distinction between Darwinian and neo-Darwinian evolution [7]. Cultural evolution does not always resemble neo-Darwinian evolution with its strict assumption of particulate genelike inheritance, but it can still be described as Darwinian, given that it exhibits the basic Darwinian properties of variation, selection and replication. Moreover, like genetic evolution, cultural evolution can be depicted by what Darwin called ‘descent with modification’. That is, both in the biological and the cultural domain we can discern lineages and tree-like phylogenetic relationships that can be traced back in time [18].

A second promise of memetics is that, although it isn’t a mature research program yet, it nevertheless might capture and explain the undeniable fact that a considerable part of our cultural heritage is not adaptive at all. Many memes are not replicated for *our* benefit but for their own sake. That is, like their biological counterparts genes, memes often are ‘selfish’ in the sense that they are only ‘interested’ in their own success. Like nasty parasites they pursue their own fitness rather than the fitness of their hosts. This view has led to the quite disturbing idea that memes are ultimately some sort of evil ‘viruses of the mind’ and that our entire culture is nothing more than the meme’s means for creating and propagating even more memes, like a chicken is the egg’s way for making more eggs [62,63]. Thus seen in the right perspective, we are only temporary, passive vehicles in which potentially immortal memes—the body snatchers—travel through the generations. The memes are in charge, we are their unresisting slaves [64]. This picture might be a bizarre caricature, but it does capture one important facet of human cultural evolution, namely that there is a lot of cultural junk out there that propagates and spreads only for its own sake. To be sure, it is my conviction that most of our culture is highly adaptive. Recall that in the introduction of this article I argued that without our evolved culture we probably would still be primitive troglodytes and that thanks to our accumulated ideas, techniques, tools and institutions, we humans outcompeted other hominin species and eventually conquered the entire globe. So it is an undeniable fact that much of our culture is indeed truly beneficial *for us*.

But not each and every part of our culture is benign in that way. Consider the memes for cigarette smoking, drug consuming and alcohol drinking, etc. Or consider the worrying increase of pro anorexia websites and the recurrent emergence of infectious memes that encourage self-injury or (collective) suicide. Or consider the brainwashed suicide bomber whose grotesque behavior in turn inspires a host of new copycats. And last but not least, consider the incessant and increasing flood of viral videos, earworms, conspiracy theories, chain letters and other internet junk on the world wide web. These are all examples of ‘selfish’ memes that rather pursue their own fitness than the fitness of their bearers. In fact, as we have seen in the previous section, one could argue that human hosts are actually no longer needed for cultural information to disperse itself. But how is it possible that such useless, irritating and even harmful memes can survive and proliferate? To answer that question we need to embrace an evolutionary approach which explains how a novel transmission channel encourages ‘rogue’ cultural variants to emerge. Inevitably the huge benefit of cultural evolution comes

at a price because sooner or later any new transmission channel will play host to parasitical cultural variants. Thus, according to Richerson and Boyd, maladaptive variants are an unavoidable byproduct of cumulative cultural adaptation:

Acquiring information from others allows people to rapidly adapt to a wide range of environments, but it also opens a portal in people's brains, through which maladaptive ideas can enter. [1] (p. 150)

So even if cumulative culture is for the most part highly beneficial, it also makes us vulnerable to selfish memes. That's the price we have to pay. Cultural evolution, learning from others and sharing and accumulating information creates conditions that allow 'selfish' maladaptive cultural variants to spread. And in order to understand the propagation of such variants we need to employ evolutionary models which describe and explain the transmission and differential proliferation of memes in the same way as the science of population genetics describes and explains the transmission and differential proliferation of genes.

In short, I believe that as yet the study of memetics is not a genuine science in the Lakatosian sense that it neither shows significant theoretical progress nor empirical progress. But memetics may nevertheless reveal and perhaps even explain certain aspects of cultural evolution that traditional social sciences like sociology and anthropology have ignored or overlooked. By adopting an evolutionary approach we now might unravel the underlying mechanisms of cultural change. In fact, Mesoudi argues that such an approach might even unify the social sciences in unprecedented ways [7]. Mesoudi foresees an 'evolutionary synthesis' for the social sciences in which the various isolated disciplines will be unified within a single theoretical framework. Dennett foresees a similar future. Up to now social scientists may have uncovered and described many plausible purposes of cultural practices and traditions, but they were unable to explain how such cultural adaptations come into existence [3]. What the social science theories lack is a proper mechanism, i.e., the differential proliferation and cumulative selection of memes. Dennett compares the current situation with Alfred Wegener's theory of continental drift before the discovery of plate tectonics. He writes: "The theory of meme evolution by natural selection can provide the needed mechanism just as plate tectonics provided the needed mechanism for the hypothesis of continental drift to be taken seriously" [3] (p. 212).

## 9. Conclusions

My aim in this article was to shed new light on a highly familiar but still utterly mysterious phenomenon: human culture. In particular, I addressed the question why we are the only species on this planet with cumulative, evolving cultures. The most common explanation for this remarkable feat usually refers to several 'miraculous' turning points and breakthroughs in hominin evolution like our prehistoric ancestor's ability to walk upright, craft stone tools, control fire and cook food, etc. Such an explanation may sound plausible but it does beg the question of what caused such watershed events to occur in the first place, and why they only took place in our own hominin lineage. The mystery even deepens when we realize that cumulative culture is very useful because it enables organisms to swiftly adapt to lots of different and changing environments. So why haven't other animals mastered this trick?

I argued that in order to unravel this mystery we should not so much focus on the major evolutionary transitions themselves but on the underlying mechanism that drives cumulative cultural evolution. Moreover, the enigmatic character of human cumulative culture suggests that the major transitions in hominin evolution were major thresholds as well, and that these barriers were simply too difficult or complex for other species to overcome. Hence only a special and very rare combination of 'key' adaptations could unlock the access to cumulative culture. That is, for cultures to evolve you need the combined presence of relatively big and interconnected populations, cooperation, creativity, social learning, teaching, and language. The ratchet effect, which causes cultural information to gradually add up and accumulate, only happens when these conditions are met, and up to now no non-human

animal species has managed to accomplish this feat. Together the conditions create a transmission system which passes on cultural information reliably from one generation to the next, thus preventing accumulated information from ‘slipping back’ and getting lost. Human language, which is qualitatively different from animal communication, plays a crucial role in this process. Language not only makes high-fidelity social transmission possible but also allows information to be gathered and stored outside the human brain. Language thus effectively creates a novel inheritance system through which cultural information can be faithfully transmitted across generations.

**Funding:** This research received no external funding.

**Acknowledgments:** The author would like to thank three anonymous referees who provided useful and detailed comments on an earlier version of the manuscript.

**Conflicts of Interest:** The author declares no conflict of interest.

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