The gene’s-eye view of culture: vehicles, not replicators

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1. Introduction: Cultural Products as Extended Phenotypes

The gene’s-eye view of evolution contends that the replicatory interests of the genes explain the form and the functioning of organisms. As Dawkins famously put it, “We are survival machines—robot vehicles blindly programmed to preserve selfish molecules known as genes” (Dawkins, 1976). All organisms, including humans, are vehicles (phenotypes) produced by the genes (the genotype) to survive in the next generation (see **Figure 1, top panel**). The gene's-eye view of evolution is closely aligned with the inclusive fitness framework that emerged in the 60's in evolutionary biology (Ågren, 2021; Dawkins, 1976; Hamilton, 1964; Rodrigues & Gardner, 2022; Trivers, 1971, 1974; Wilson, 1975). In the last

50 years, this gene's-eye view of evolution has been applied successfully to all sorts of phenotypes or, as Dawkins put it, to all sorts of vehicles: organs, brains, sexuality, parenting, eusociality, cooperative behaviors (Davies et al., 2012).

Importantly, in this view, phenotypes are not be limited to somatic biological processes such as tissue growth, behaviors, or protein biosynthesis. They include all effects that a gene has on its environment, inside or outside the body of the individual organism. Dawkins called such cases *extended phenotypes.* Examples include beaver dams, spider webs, termite mounds, parasite manipulations of a host, and effects on another individual through signaling (Dawkins, 2016). A cry, a growl, or a light signal are also extended phenotypes (see **Figure 1, Middle panel**).

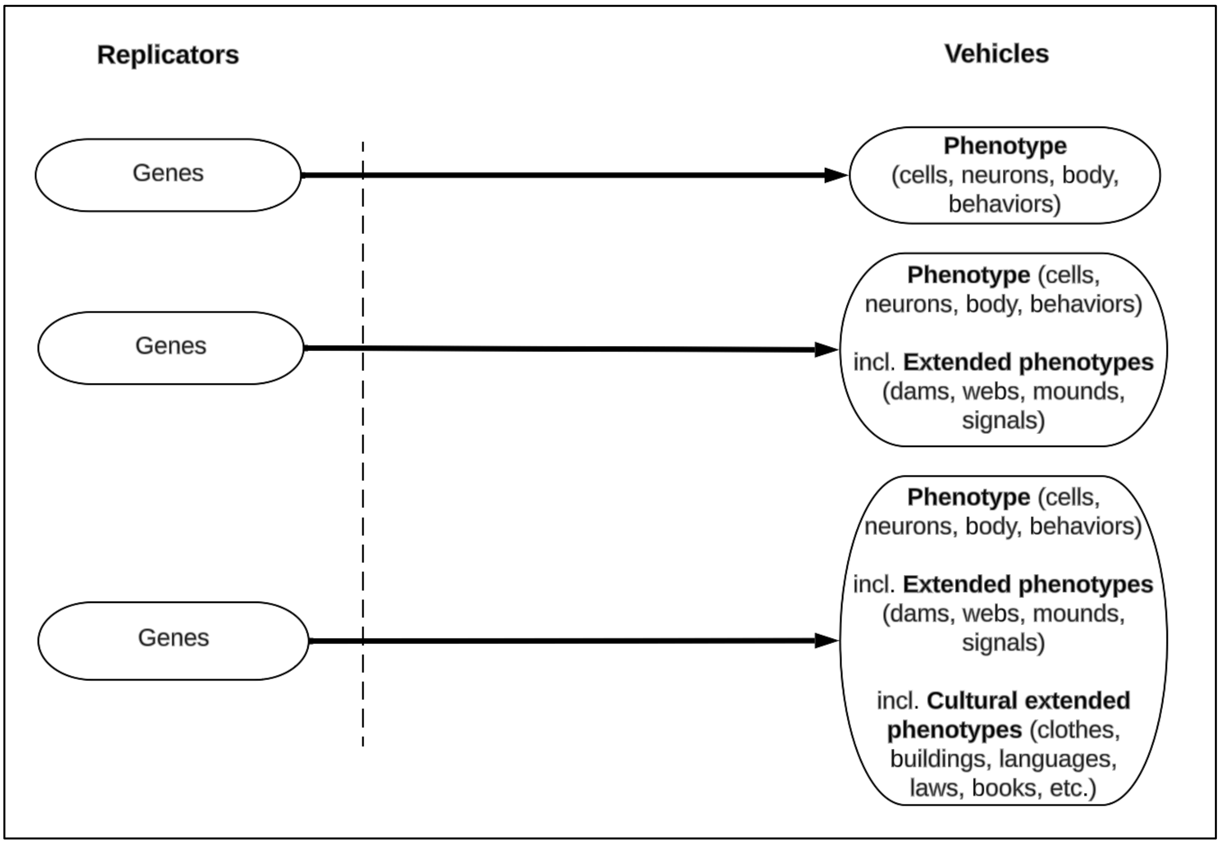

Figure 1. *The gene's eye view of evolution. (Top figure) Standard version. (Middle figure) Version including extended phenotypes. (Bottom figure) Version including extended phenotypes and culturally extended phenotypes.*

The gene's-eye view of evolution thus applies to all kinds of biological phenomena, from parasites to mangroves to fish schools. For Dawkins, and many others after him, there is one famous exception though: culture. He also developed the idea that culture can be approached as a collection of replicators ('memes'). At the end of *The Selfish Gene*, Dawkins put forward the idea that cultural items, unlike other stuff produced by biological organisms, are *not* vehicles, but a new kind of replicator, that he called memes. "Examples of memes are tunes, ideas, catchphrases, clothes fashions, ways of making pots or of building arches. Just as genes propagate themselves in the gene pool by leaping from body to body via sperms or eggs, so memes propagate themselves in the meme pool by leaping from brain to brain" (Dawkins, 1976, p. 230). This idea that cultural products are replicators and evolve like genes contributed to the emergence of a new field, namely *cultural evolution* or *dual inheritance theory*, aimed at modelling the evolutionary change of cultural replicators in the population of their host, namely human brains (Boyd & Richerson, 1985; Henrich, 2015; Mesoudi et al., 2006). While proponents of this view acknowledge some differences between the genetic and cultural cases (Henrich et al., 2008; Mesoudi et al., 2006), they explain cultural productions in terms of very similar mechanisms to those invoked to explain genetic evolution: "cultural mutation," "cultural replication," "cultural inheritance," and "cultural selection." (Henrich, 2015; Richerson & Boyd, 2005) (see **Figure 2**). In practice, cultural productions would thus be beyond "the long reach of the genes" (Dawkins, 2016). Explaining culture would require another explanatory arsenal entirely: cultural evolutionary models, rather than inclusive fitness theory.

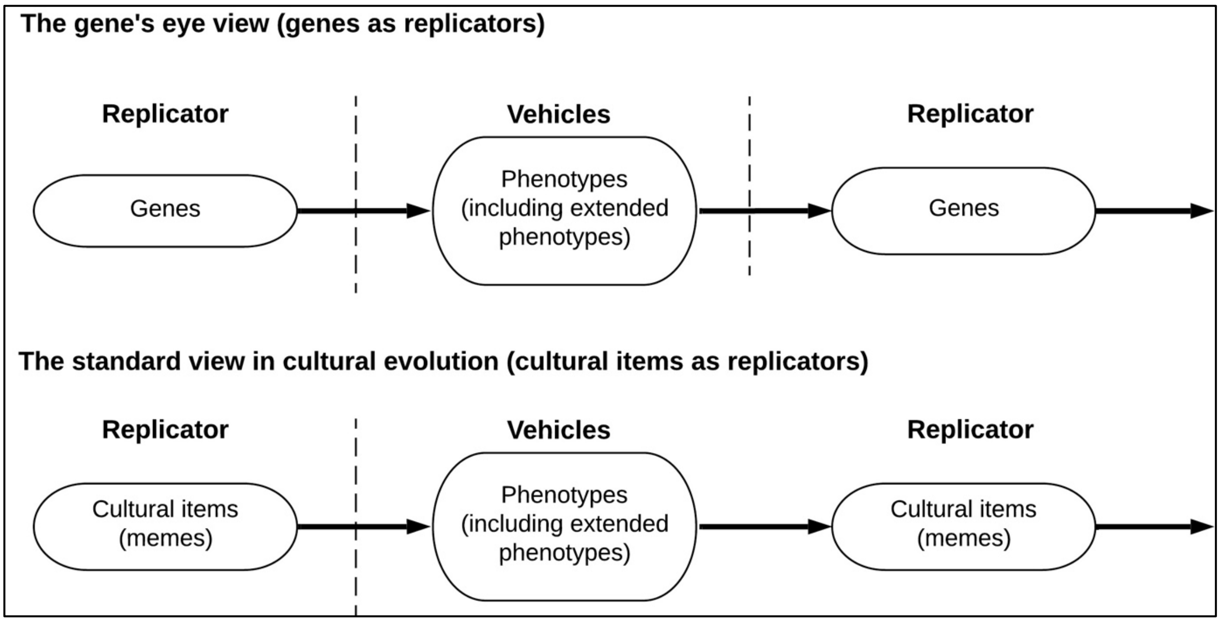

Figure 2. *Genes and culture as replicators in standard evolutionary views.*

In this chapter, we argue for a dissenting opinion, namely that cultural productions are not beyond the long reach of genes. Cultural phenomena are a product of genes: arguably peculiar products, which are located outside the body, created by flexible cognitive mechanisms (rather than being hard-wired), strongly influenced by the environment, and the result not of the genotype of one individual but of many individuals—but a product nonetheless (see **Figure 1 Bottom panel**).

In other words, many cultural products can be construed as humans' extended phenotypes. In evolutionary biology, 'phenotype' is typically characterized as the 'expression' of a genotype—but this is an abstract and flexible notion, with no formal definition (De Vienne, 2022; Mahner & Kary, 1997). Accordingly, it is used pragmatically in different domains, from genetics to whole-organism biology. Just as spider webs and beaver dams, human cultural products such as cosmetics, syntactic rules, religious rituals, and political constitutions, can be construed as extended phenotypes that genes build to maximize their own replication. Despite being produced by genes only very indirectly—through the generative operation of flexible cognitive mechanisms—cosmetics, rituals, constitutions, and syntactic rules are nevertheless produced by genes to achieve typical adaptive goals: communicating information, gaining social status, manipulating others, competing and cooperating, attracting mates and guarding them, acquiring a moral reputation, and so on (André et al., 2023; Fitouchi et al., 2023; Singh, 2022). As tools built to better achieve fitness-relevant goals, cultural products are part of the vehicles that genes build to survive to the next generation (see **Figure 3**).

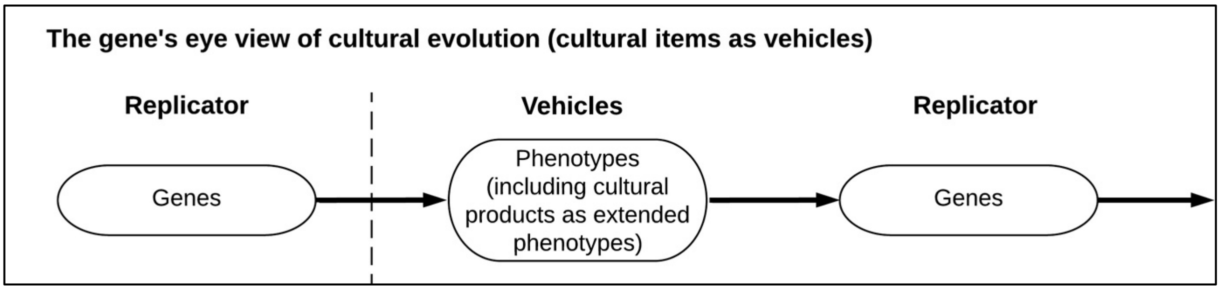

Figure 3. *The gene's eye view of culture.*

To see the idea, consider one area of culture that has already been approached as an extended phenotype, namely body enhancement technologies (Borau & Bonnefon, 2020; Davis & Arnocky, 2020; Etcoff et al., 2011; Luoto, 2019; Miller, 2011). In this field, scholars routinely consider make-up (Etcoff et al., 2011), pets (Luoto, 2019), shoes (Lewis et al., 2017), online avatars (Luoto, 2019) or personal possessions such as cars (Borau & Bonnefon, 2020) as extended phenotypes; that is, as technologies that people invent, use, tweak, and improve to achieve fitness-relevant goals; and eventually give up when they feel a more efficient technology is available. Make-up, for example, naturally appears as a tool people build to increase their mating success, just as beavers build dams to better survive and reproduce. In this field, researchers use the concept of extended phenotype because it helps them understand the existence, forms and function, as well as the variability in the use of these cultural productions (in archaeology, see also Dunnell, 1980; M. J. O'Brien & Holland, 1995; O'Brien & Lyman, 2000).

The idea that culture is an extended phenotype, however, has not caught on in evolutionary social sciences more broadly. We think there are three main reasons for this. First, examples of extended phenotypes in non-human animals, such as dams, webs, and colonies, are often relatively fixed. Cultural phenomena, by contrast, are highly innovative. Unlike the extended phenotypes of ants, spiders, and beavers, human extended phenotypes can be very different from one generation to the next. While it is easy to integrate the extended phenotypes observed in non-human animals into the standard gene's eye view of evolution, it seems much less obvious that genes explain much about, say, the design of Notre-Dame de Paris, the content of *Harry Potter*, and the Universal Declaration of Human Rights. While everyone agrees that, in principle, genes can code for beaver dams and termite signals, which are relatively fixed and hard-wired, there are obviously no genes evolved to code for the particular content of *Harry Potter*. This problem was anticipated by Dawkins, who wrote that "variations in replicators have a causal link to variations in dams, such that over generations replicators associated with good dams survive in the replicator pool at the expense of rival replicators associated with bad dams" (2004, p.377). Since there are no genes 'for' designing buildings, then buildings cannot be extended phenotypes.

Second, because standard extended phenotypes are hard-wired, they do not vary very much from one place to the other within the same species, and in particular they are not very much affected by the extended phenotypes produced by previous generations. Beavers do not build on the dams built by previous generations to create better dams. So there is little causal dependence between generations, unlike in typical cultural phenomena such as kayaks, religions, and artistic productions. Because of that, the standard concept of extended phenotype doesn’t seem to capture the cumulative character of human cultural evolution (Mesoudi & Thornton, 2018).

Third, standard extended phenotypes are often produced by a single individual (e.g., a single spider) or a group of genetically related individuals (e.g., a colony of termites, a family of beavers). It is thus easy to attribute an extended phenotype to a specific genotype or a group of related genotypes that share a common genetic interest. In the case of human culture, things are obviously more complicated. Most of our cultural products, such as laws, cathedrals, and best-selling books, are produced by thousands of decisions made by many individuals whose genetic interests are often unrelated and even conflicting.

In this chapter, we show that these three problems in fact do not undermine the idea that cultural products are extended phenotypes; and hence that approaching cultural products not as replicators—as done by current cultural evolutionary theory—but as extended phenotypes—that is, as expressions of the human genotype—provides a fruitful framework for explaining the existence and design-features of cultural traits. We shall argue that the above-mentioned problems stem from an overly narrow and hard-wired view of extended phenotypes, derived from species with limited cognitive flexibility and behavioral repertoire.

Moving away from hard-wired phenotypes, such as beaver dams and spider webs, we take the example of two extended phenotypes produced by animals with relatively large brains: the bowers produced by bowerbirds as sexual signals, and the nests built by apes to sleep safe from predators and parasites. We show that these extended phenotypes exhibit 1) a high degree of generativity and variability; 2) a form of causal dependence with the extended phenotypes of previous generations, which can include cultural accumulation; and 3) the joint production of a common phenotype by several organisms with potentially conflicting genetic interests. These features can all be explained using the standard tools of evolutionary biology alone, and in particular three key concepts from evolutionary ecology: *generative plasticity*

(§2), *joint phenotypes* (§3), and *ecological legacy* (§4). By applying this conceptual arsenal to the study of human culture, we argue that that there's is no need to add new concepts to evolutionary theory itself—such as secondary evolutionary forces acting on cultural replicators—to explain the existence and design-features of human cultural phenomena. Existing evolutionary theory is already well equipped to study culture, when used alongside key notions from neighboring fields, such as cognitive science or the standard social science of institution formation, among many others.

2. Cultural production as generative plasticity

How could genes 'code' for cultural items, which are variable and innovative? The key notion here is adaptive plasticity, that is the capacity for an organism to tailor its phenotype to the context. A textbook example of adaptive plasticity is the lac operon in *E. coli*, which produces lactose metabolizing enzymes only when lactose is present and glucose is absent. In this case, genes do not code for a specific phenotype, but for a mechanism (the lac operon) that takes into account environmental information (presence or absence of lactose) and, based on this information, execute a specific program and take a decision (produce lactose or not). Genes do not code directly for a *fixed phenotype* (e.g., a specific behavior), but for a *mechanism* that takes as input some properties of the environment and produces an output that is adapted to these properties (**Figure 4**).

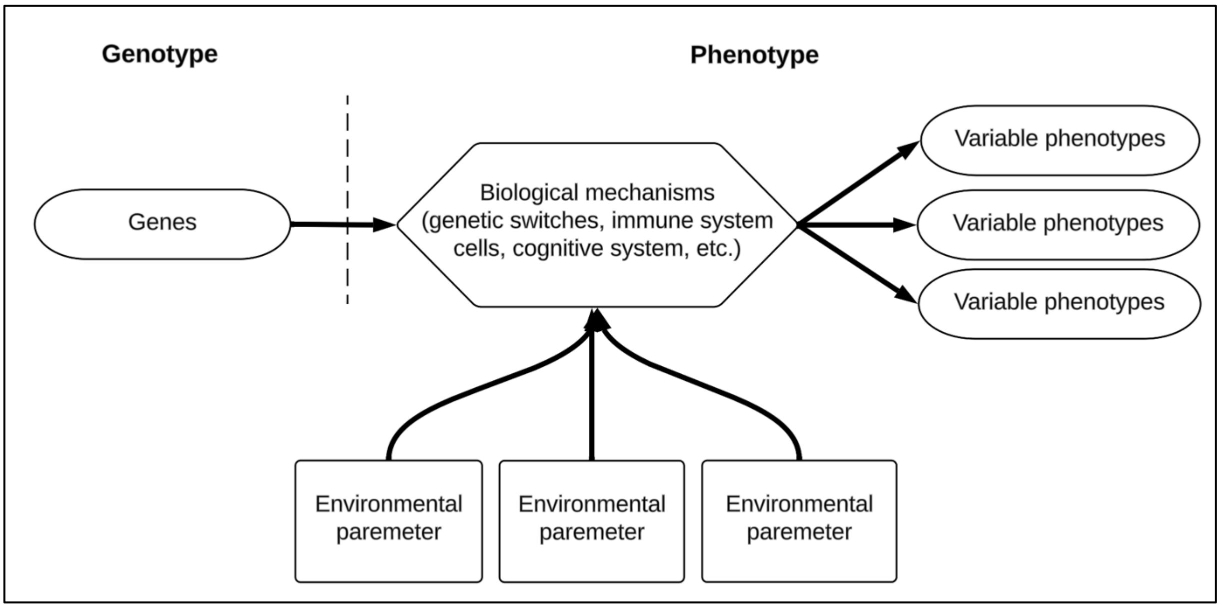

Figure 4. *Adaptive plasticity within the gene's eye view of evolution*

2.1. Adaptive plasticity can be creative and open-ended

The traditional way to conceptualize adaptive plasticity is through the notion of reaction norm (Sultan & Stearns, 2005). A reaction norm describes the pattern of phenotypic expression of a single genotype across a range of environments. But this conceptualization of adaptive plasticity is overly limited. Adaptive plasticity can be much more flexible than the typical on/off switch model. We can contrast *non-generative* forms of plasticity, characterized by a finite range of possible environments and a finite range of possible phenotypes (e.g., growing a protection when predators are present), with *generative* forms of plasticity, characterized by an infinite range of possible environments and an *open-ended* range of phenotypes. In generative plasticity, the adaptive response is not fixed in advance. It can consist of an open-ended mechanism—such as a complex cognitive architecture—capable of generating novel, adaptive responses to environmental conditions that were never encountered in the evolutionary history of the organism (Fawcett et al., 2013; Kolodny et al., 2015; Piersma & Drent, 2003; Taborsky & Oliveira, 2012).

This is the case, for example, of the immune system, a genetic program that creates new antibodies in response to new pathogens. Memory is another example of a genetic program that tailors its expression (the neurons that encode the information) to the new information provided by the environment (where the food patches are, what the conspecifics look like, and so on). The immune system or the memory system produce new responses (new molecular configurations, new neural patterns) by combining and recombining elementary parts.

2.2. With cognitive control, natural selection can leave it to the organism to generate adaptive solutions on its own

Cognitive mechanisms are a paradigmatic case of generative adaptive plasticity (Barrett, 2014; Tomasello, 2022). Rather than coding for a fixed set of reactions to a fixed set of possible contexts, evolution determines goals to be reached, and builds cognitive mechanisms to find adaptive solution on their own when the problem arises (Fawcett et al., 2013; Nettle & Scott-Phillips, 2023; Osiurak & Reynaud, 2020; Singh, 2022; Taborsky & Oliveira, 2012; Tooby & Cosmides, 1992). As Dawkins put it in *The Selfish gene:*

> Here the program may take the form of the following instructions to the survival machine: 'Here is a list of things defined as rewarding: sweet taste in the mouth, orgasm, mild temperature, smiling child. And here is a list of nasty things: various sorts of pain, nausea, empty stomach, screaming child. If you should happen to do something that is followed by one of the nasty things, don't do it again, but on the other hand repeat anything that is followed by one of the nice things. The advantage of this sort of programming is that it greatly cuts down the number of detailed rules that have to be built into the original program; and it is also capable of coping with changes in the environment that could not have been predicted in detail (Dawkins, 1976, p. 85).

In contrast to rigid reaction norms, the organism behaves as an *agent*: evolution set up a set of adaptive goals and left it up to the organism to find the best way to achieves those goals in each peculiar circumstance (Tomasello, 2022). This kind of plasticity is very ancient, and dates back to at least the first vertebrates (Tomasello, 2022). The fundamental innovation consists in creating a system of feedback control with three key components: (i) a reference value or goal, (ii) a sensing or perception device, and (iii) a device for comparing perception and goal to monitor whether the behavioral decision implemented managed to achieve the goal. As Tomasello (2022) puts it, "With feedback control organization, Nature can still hardwire the most important goals but at the same time empower the individual to pursue them flexibly by attending to relevant situations and making informed behavioral decisions." The history of vertebrates is a succession of cognitive refinements (spatial cognition, object concepts, causal cognition, domain-specific intuitive theories, etc.) evolved to process ever more information, generate ever more behavioral flexibility, and build ever more abstract goals relevant for fitness maximization. Humans are, we shall shortly argue, an extreme case of this trend.

2.3. The generative plasticity of extended phenotypes in non-human animals

Crucially, the generative production of extended phenotypes is not specific to humans. Take the examples of the bowers produced by bowerbirds, and the nests produced by apes. Bowerbirds are well known for building elaborate nests, which they then decorate with up to several thousand items (Madden, 2008; Walsh et al., 2010). These nests are sexual displays that are built to attract and signal the quality of the builder to the female bowerbirds. They thus need to tap into the visual system of the female bowerbird, and to signal some cognitive and physical qualities. Bowers are a good example for our discussion because it is clear that bower architecture is not rigidly coded by the genome (Breen, 2021; Healy, 2022). There's a huge amount of variation from one individual to the next, and from one population to the next, and a great variability in the materials used, as well as in the choice of colors and visual effects (Madden, 2008; Walsh et al., 2010). And yet bower nests are, just like other sexual displays, undeniably adaptive and a result of natural selection.

The reason is that evolution did not select for one fixed extended phenotype, but for proximate mechanisms that can generate many kinds of adaptive phenotypes. A range of evidence suggests that the building of these nests is not achieved through a fixed action pattern or behavior that would be hard-wired but rather through flexible cognitive programs that constantly generate and evaluate new solutions to attract females based on the material available in their environment (Madden, 2008) (see **Figure 5**).

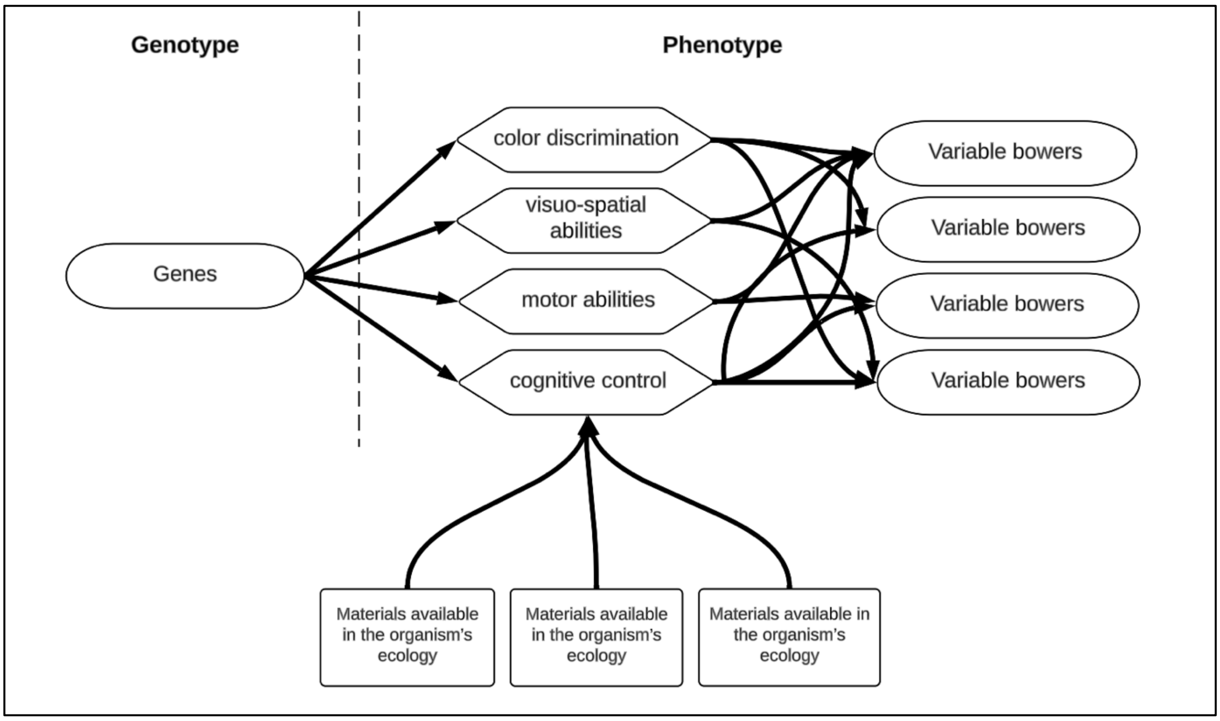

Figure 5. *Generative programs produce a variety of extended phenotypes.*

Another example comes from great apes. Great apes, such as chimpanzees and gorillas, create nests on a nearly daily basis. Typically, these nests are built for temporary use, either for resting during the day or for a single night. Once used, they are typically abandoned and left to decay, although sometimes they are reused. The primary purpose of these ape nests is to provide a comfortable sleeping platform, enabling better-quality rest and longer periods of rapid eye movement sleep by minimizing disturbances throughout the night (McGrew, 2004; Stewart, 2011; Van Casteren et al., 2012). Other complementary functions of nests have been proposed, such as an anti-predation role—where the height of nests and the camouflage they provide may reduce the incidence of night predation—, protection from airborne parasites such as mosquitoes, an aid to thermoregulation by providing a layer of insulation during sleep (McGrew, 2004; Stewart, 2011; Van Casteren et al., 2012). Thus, nests can be construed as extended phenotypes selected by evolution to increase sleep quality, thermoregulation, and protection from predators and parasites. Yet just like bowerbird, nestbuilding in primates is not a rigid, hard-wired behavior. On the contrary, evidence suggest that these artifacts are generated by very flexible cognitive capacities, generatively taking whatever is available in their environment to satisfy their adaptive motivations to sleep well or avoid mosquitos (Van Casteren et al., 2012).

Crucially, bowerbirds and apes (as well as by many other cognitively flexible species) have been shown to be very innovative when they live in ecologies enriched by human activity (Sol et al., 2008; Tuomainen & Candolin, 2011; Wright et al., 2010). For instance, bowerbirds reuse plastic chips, coins, nails, rifle shells, or pieces of glass to build their bowers (Madden, 2008), and apes reuse cotton sheets, and shredded newspaper to build their nests (Anderson et al., 2021). Obviously, plastic chips and shredded newspapers are recent, and birds and apes did not evolve to use them. In Dawkins' words, replicators associated with the use of plastic chips did not survive in the replicator pool at the expense of rival replicators. Should we say then, that bowers made of plastic chips and nests made of shredded newspapers are not "extended phenotypes" because they have emerged only recently? Obviously not. The proper function specified by evolution is not "to use leaves and pebbles to impress females", but "to use any instrumentally relevant tool to attract females." From this point of view, plastic chips, coins, nails, rifle shells, or pieces of glass are completely within the proper domain of the evolved motivation to build bowers, because what has led to the survival of genes of bower building is their ability to orchestrate in a flexible and innovative way the generative search for solutions to fulfill a higher-level goal: attracting the attention of females.

2.4. The generative production of extended phenotypes in humans

Armed with this more sophisticated view of adaptive plasticity, can we consider human cultural products as extended phenotypes? Recall that, for Dawkins, animal products (e.g., beaver dams) qualify as extended phenotypes if and only if "*variations* in replicators have a causal link to *variations* in dams such that, over generations, replicators associated with good dams survive in the replicator pool at the expense of rival replicators associated with bad dams."

The problem with this view is that, for highly flexible organisms like birds, primates or humans, there need not be a one-to-one mapping between the genotype and the phenotype. In reality, genes do not code for specific behaviors, but for relatively general goals or preferences (e.g., for food, status, partners, children, information) and for cognitive capacities that are also relatively general (e.g., memory, planning, inhibition) whose function is to enable individuals to achieve their goals flexibly. What evolution does is to set fitness-good objectives (implemented as goals or preferences), leaving the individual some freedom to select the best low-level, instrumental way to meet these objectives, using the cognitive tools at its disposal. Depending on the organism's degree of cognitive sophistication, these goals can range from the relatively specific (e.g., avoiding heat, liking glucose) to the very general (e.g., attract mates, increase status, treat cooperative partners fairly). In fact, this was well expressed by Dawkins himself in *The Selfish gene*:

> Animal behaviour, altruistic or selfish, is under the control of genes in only an indirect, but still very powerful, sense. By dictating the way survival machines and their nervous systems are built, genes exert ultimate power over behaviour. But the moment-to-moment decisions about what to do next are taken by the nervous system. *Genes are the primary policy-makers; brains are the executives.* But as brains become more highly developed, they took over more and more of the actual policy decisions, using tricks like learning and simulation in doing so. (p. 89, our emphasis)

Tomasello (2022) makes a similar point:

> Because it cannot predict the particularities of the future situations that an individual might encounter, Nature has constructed an underlying psychological organization of agency enabling the individual to make its own decisions and self-regulate its own actions in pursuit of goals that, ultimately, Nature has built in (p. 134)

With that in mind, let us return to Dawkins' argument: that cultural products would not be extended phenotypes because there are no genes coding specifically for any particular cultural products such as a given tool, a given building, or a justice code. This argument can be reformulated using the notion of the “proper domain" of a cognitive adaptation i.e. the function it was designed to solve, by virtue of its past successes (Sperber, 2005; Sperber & Hirschfeld, 2004). The question is, what is the proper domain of the mechanisms that produce cultural products? For animals with relatively simple cognition, the proper function of cognitive mechanisms is often narrow and concrete: detecting light, catching a fly and so on. For vertebrates, however, most cognitive mechanisms have very broad and abstract functions: obtaining food (whatever it may be), improving one's appearance (in whatever way possible), maintaining a good reputation (in all situations), and so on. From this point of view, cultural products are undeniably part of the proper domain of human adaptive mechanisms: they correspond to flexible, innovative solutions that have been generated in specific environments to achieve adaptive goals such as obtaining food, improving one's appearance, and so on.

From this perspective, cultural products are extended phenotypes. Tools, for example, are nothing special from an evolutionary point of view. They are innovative solutions like any other. The cognitive flexibility of humans means that they are constantly inventing tools to solve local problems: using a piece of wood to drop a piece of fruit, a leaf to collect water, a stone to break a bone, and so on. All these solutions are extended phenotypes: they are, *by design*, produced by the combination of evolved preferences (for food, for example) and innovative instrumental abilities.

2.5. The generative production of culturally extended phenotypes

Finally, let us consider phenotypic traits like writing, which clearly necessitates cultural input. Visual cognition did not evolve to enable humans to write. But writing is a technical innovation like any other. It is made possible because humans are able to put their brains to work (e.g., visual cognition, linguistic understanding) to find innovative solutions (e.g., graphic codes) in order to satisfy their evolved preferences (e.g., communicating ideas or memorizing) (Changizi et al., 2006; Dehaene, 2009; Morin, 2023). From this point of view, writing is an extended phenotype of the human genes that control the brain in such a way as to detect any innovation capable of achieving evolved goals (e.g., communication). Writing requires a particular cultural ecology (the existence of specific tools), but this is no different from the plastic chips used by bowerbirds to achieve their goal of attracting mates. Again, evolution didn't select "genes to produce paleolithic tools", but genes that code for cognitive capacities "to use anything in the environment that can help achieve specific adaptive goals".

Thus, writing is not an extended phenotype in the sense that there would be genes evolved for reading specifically. Writing is an extended phenotype in the sense that humans have evolved preferences for communication or managing resources and evolved instrumental capacities to detect that using graphic codes can satisfy these genetically evolved goals. Because replicators associated with higher level of communication or higher level of resource management survived in the replicator pool at the expense of rival replicators associated with lower level of communication or lower level of resource management, then it can be said that graphic codes are the extended phenotypes of these replicators.

In sum, with the gene's-eye view of culture, we’re obviously not arguing that genes control cultural expression the way they control protein expression. The gene's-eye view of culture is that genes have built 'survival cognitive machines’ (Nettle & Scott-Phillips, 2023; Tooby & Cosmides, 1992) which, equipped with cognitive control, flexibly and creatively satisfy high-order evolutionary goals (e.g., mating, status-seeking, communicating).

3. Cultural “inheritance” as ecological legacy

A second apparent problem for the gene's eye view of culture—that sees cultural products as vehicles rather than replicators—is that cultural artifacts outlive their producers, exhibit some kind of historical continuity, and are present in the environment generation after generation, and thus seem to be “transmitted” form individual to individual. At first glance, this feature lends some support to the idea that cultural products are more akin to replicators that jump from host to host rather than vehicles themselves used by genetic replicators to maximize their own reproduction.

But again, these facts are not in fact a problem for the gene’s eye view. Just as human cultural products, “standard” examples of extended phenotypes, such as the mounds built by termite colonies, often outlive their producers and are often used by following generations. New termite colonies often occupy a mound after the original builders’ deaths (Laidre, 2021). Terrestrial hermit crabs architecturally remodel shells and pass these modified shelters to subsequent generations, which reuse them long after the original architect’s death (Laidre, 2019). Squirrels re-use the extended phenotypes of the previous generation when they benefit from the cache of the previous owner (Fisher et al., 2019). Bowerbirds re-use materials, such as colorful stones, from the bowers built by previous generations of bowerbirds (Madden, 2008). Bumblebees often move into old nests previously dug by mice, thus saving excavation costs (Laidre, 2021).

These are all instances of a more general mechanism that ecologists call legacy effects (Cuddington, 2011; Frauendorf et al., 2021; Hastings et al., 2007; N. R. Jordan et al., 2011; Nuttle et al., 2011; Perry et al., 2008). In evolutionary ecology, the term ecological legacy originally refers to the impact of a species on its ecosystems that persist for a long time after the species has been extirpated or ceased activity in the ecosystem (some have also used the term "ecological inheritance" (Erwin, 2008)). Here we are using it in a broader sense to describe any modification of the environment that results from the behavior of an organism (even when the initiating organism is gone) and that affects the behavior of other organisms outside of its evolved function. Ecological legacies include secondary succession, ecosystem engineering, effects of invasive-plant species, effects of past herbivory events, and human impacts on land use. In the African savannah, for example, wildebeest and zebra crossings create animal tracks and release nutrients during bioturbation, while elephant grazing in the riparian zone changes tree density around the water body. Hippopotamuses also alter geomorphology through trampling; their excretion can influence biogeochemistry and trophic ecology (Frauendorf et al., 2021). Obviously, legacy effects include the impact of extended phenotypes on the ecosystem. In fact, one of the classical examples of ecological legacy is the beaver dam. A beaver dam deteriorates in the absence of beaver and leads to the formation of a beaver meadow that can persist for nearly a century and is rarely converted back to the original forested zone (Hastings et al., 2007; Johnston, 2015).

It's important to note that ecological legacy is not an adaptive process. It has no function, neither from the point of view of its producers nor from that of subsequent users. Soil, for example, is a *byproduct* of the activity of plants that lose their leaves and die, and of the fungi, earthworms, and bacteria that degrade them (Van Breemen & Buurman, 2002). These species are often called “engineers” or “niche constructors,” but their adaptive goal is neither to engineer nor to construct anything (Scott-Phillips et al., 2014). They’re simply doing what is best for their fitness—getting nutrients from the leaves—and the species that subsequently use this legacy are simply responding to the presence of soil when fulfilling their own adaptive agendas.

Now, ecological legacy is not necessarily material. It can be informational: previous generations produce some information that can be retrieved from the environment (Gweon, 2021). When birds observed conspecifics on top of milk bottles in England, this was a legacy effect: some birds have changed the environment of other birds by making milk bottles more salient, through their presence near milk bottles, but they didn’t have the specific adaptive goal of doing so (Sherry & Galef, 1984). Here, changing the environment is only a *by-product* of the behavior of the previous generation. It has a causal effect on later generation; but did not evolve for transmitting information to this generation. To go back to the case of ape nests and bowerbirds, many observations and experiments have demonstrated that birds and apes are able to pick up some of the discoveries that older generations have left in the in the environment such as new colors, new shapes, and new materials (Madden, 2008).

Our point here is that human culture is no different. In fact, archeologists have long studies the ecological legacies of past human population on the ecology of later generations (Boivin et al., 2016). Each generation is born in an environment full of the extended phenotypes that previous generations have built to fulfil their own adaptive goals: houses, paths, tools, jokes, novels, songs. These cultural items survive their initial producers, they degrade, and they can eventually disappear. In the meantime, though, other individuals can adaptively choose to reuse some of them, to improve some of them, to transform some of them, to abandon some of them, to use some of them in new ways, and so on, depending on the fitness-costs and benefits of doing so. The whole process can be described as capital accumulation (André & Baumard, 2020).

This last point is crucial. Individuals do not *replicate* existing cultural products (Claidière et al., 2014; Claidière & André, 2012; Morin, 2016; Nettle, 2020; Scott-Phillips, 2017; Sperber, 2000; Sperber & Claidière, 2006). They are only using it, hence the term 'ecological legacy'. Contrary to what some cultural evolutionists have argued (Odling-Smee & Laland, 2011), ecological legacy is not, in fact, a *system of inheritance* in the biological sense (i.e. as an adaptation to transmit information). Ecological legacy only describes the way in which previous generations affect the environment of later generations. What happens next *depends on later generations' own adaptive agendas*. As Michelletti et al. (2023) rightly put it, “whether individuals adopt or reject some trait they have observed in others is driven by their inclusive fitness interests—the need to survive and reproduce, and the subsidiary needs to assist relatives, defend resources, and acquire food.”

Thus, “cultural evolution,” in the broad sense of historical change in cultural products over time, does not occur because individuals would be biologically adapted to pass on information to the next generation (Boyer, 2018; Morin, 2016; Osiurak & Reynaud, 2020; Pinker, 2010; Scott-Phillips, 2022; Sperber, 1996; Tooby & Cosmides, 1992). Individuals are not interested in transmitting or acquiring culture *per se*. They are interested in acquiring food, helping friends, gaining status, manipulating others, signaling their mate-value; and they craft ingenious extended phenotypes, such as make-up and stone tools, to do so as effectively as possible. As a by-product of generative plasticity, these extended phenotypes survive their producers and populate the environment of the next generations. In turn, these new generations can recycle, tweak, and selectively retain part of this ecological legacy to fulfil their own adaptive goals. This process of "phenotypic recycling" can involve perfect retrieval of information, but more often it involves strategic use of only some of the environmental information that is relevant to the current generation's own adaptive goals, which often only partly overlap with those of the previous generations. To recycle a famous formula, the gene's eye view of culture entails that "culture is what happens to organisms while they're busy making other plans" (Morin, personal communication).

The apparent continuity of cultural traits across generations is not explained by the fact that cultural traits would be replicators, but by the fact genes incessantly use the best material at their disposal—which often includes extended phenotypes of previous generations—to maximize their own replication. Sometimes, what is best for one generation is also best for the next one. As a result, individuals end up using the same items as the previous generations—leading to cultural preservation or stability. But most of the time, humans do not use exactly the same items, leading to cultural change. Words are abandoned, syntax changes, fashions fade, technologies are replaced, novels are no longer read, cooler music emerges, and so on (Morin, 2016; Sperber, 1996). Even items that seem very stable, such as cathedrals or national anthems, do actually change: their content is stable, but their use evolve. A cathedral that was once an instrument of religious activity and social control is now used by the new generations as a touristic spot. A novel that was once a source of pleasurable entertainment is now used by the new generations as an instrument of social distinction. And a national anthem that once meant to galvanize soldiers in wartime now serves for social bonding in football competitions.

Interestingly, the gene's eye view of culture leads to an analytical definition of culture. Cultural phenomena are what genes make of the legacies of the phenotypes of the previous generations. Cathedrals, languages, cosmetics are cultural phenotypes because they cannot exist without previous generations and their legacies. But feet, visual perception and threat avoidance systems are not cultural phenotypes because they do not need ecological legacy to exist. With or without legacy, human genes produce feet, visual perception and threat avoidance systems. Obviously, there are some specific forms of feet, visual perception and threat avoidance that require some legacy. Foot binding, modern myopia (due to increased hours spent reading) and aerophobia require certain specific cultural environments to be expressed. In this sense, they can be considered as cultural phenotypes.

In other words, while we have insisted that many cultural phenomena can be considered as extended phenotypes, this does not mean that all cultural phenomena are extended phenotypes. In fact, many cultural behaviors (e.g. beliefs) happen within the organisms. What makes something cultural is not that it happens outside the body (that it is an extended phenotypes) but that it needs some legacy to exists. To sum up, a phenotype can be extended or not (internal or external to the organism), cultural or not (produced thanks to a legacy or not), and as we will see in section 4, joint or not (produced by several genotypes or just one). All these distinctions are independent, and can be combined, but legacies alone make a phenotype cultural.

4. Joint phenotypes and the question of cultural functionality

The gene’s-eye view of culture faces a third apparent problem. Extended phenotypes are designed by selfish genes for their own replication. Yet many cultural phenomena don’t seem to benefit individual fitness. Many of them, such as social norms, religions, and institutions often appear designed for group-level benefits rather than individual fitness. Many others, such as magical rituals, fake news and other false beliefs appear completely dysfunctional, both collectively and individually. How can we accommodate the gene's-eye view of evolution with this kind of apparent maladaptation? How can we accommodate the gene's-eye view of evolution with this kind of group functionalism?

Again, this apparent problem stems from an overly simplistic view of extended phenotypes, and even of non-extended phenotypes (i.e., the bodies of organisms). We mistakenly assume that the shape and structure of these phenotypes depend on a single group of genes, that of the organism that controls them. But this isn't true in many cases. An insect manipulated by a parasite is a phenotype resulting from two groups of genes, those of the insect and those of the parasite. Trees massively depend on soil fungi for their growth; and humans, of course, are massively influenced by their gut microbiome for their digestion and immunity.

To account for such phenomena, ecologists have coined the notion of "joint" or "shared phenotype" (A. M. O'Brien et al., 2021; Queller, 2014; Queller & Strassmann, 2018). Geneticists also speak of Indirect Genetic Effect (IGE) (Bailey, 2012). Indirect Genetic Effects occur, for example, because an individual's mental health or dietary habits are determined not only by his or her own genes, but also indirectly by the genes of his or her environment, such as his or her spouse (Clarke et al., 2021; Xia et al., 2021) or schoolmates (Sotoudeh et al., 2019). In fact, all individuals are shared phenotypes, partly influenced by their own genes, and by the genes of their kins, friends, rivals, and so on.

Beyond these examples, groups of genes can even share an *extended* phenotype. Consider, again, the bower structures build by bowerbirds. Theft of decorations and destruction of bower structures by neighbors or competitors is common in most species of bowerbird (Madden, 2002). Theft may act to increase the number of decorations on a thief's bower, and destruction of bower may serve to limit the competition. Bowerbirds whose bowers were experimentally provisioned with excess numbers of berries suffered higher rates of destruction (Madden, 2002). Interestingly, males may also modify their own displays to avoid interference from rival males. For example, when given a choice of "free" decorations, male bowerbirds do not increase their number of decorations beyond what they normally have. Therefore, males do not necessarily signal at the maximum level available and individuals maintain their displays at different levels (Madden, 2002). Thus, in birds, as well as in other species producing extended phenotypes (e.g., cichlid fishes: (L. A. Jordan et al., 2016)), the final design of the extended phenotype is the product of a "negotiation" between individuals with conflicting interests.

The joint production of extended phenotypes can be, not only competitive, but also cooperative. In monogamous species, for example, nest building is often cooperative (Hahn et al., 2021). In this case, the fitness interest of the male and the female overlap to produce the best nests to protect offspring from external stressors such as predators and temperature. However, the interests of both sexes do not align exactly, generating sexual conflict (Chapman et al., 2003). The design and the functioning of the nest is the joint phenotype of the mix of shared and opposing interest of the female and the male (Hahn et al., 2021).

Moving up the scale of social interactions, joint phenotypes also describe collective behaviors such as bird flocks, fish schools, or insect swarms. In these cases, the aggregation of the behaviors of many individuals creates a "collective phenotype" (Kuzdzal-Fick et al., 2023) with emergent properties absent from each of the individual phenotypes that compose it. For example, herding behaviors can produce an optical illusion that confuses predators and thereby protects individuals (Olson et al., 2013). In this case, the benefit of an individual behavior arises from a higher-level, "collective phenotype" that emerges from the joint actions of its members. Many studies show that the design-features of these joint phenotypes—from the social structure of fish schools to the collective decision-making of whale pods to the colony performance of social spiders—are determined by the genotypes of their members (for a review, see Cantor et al., 2021; Farine et al., 2015; Jolles et al., 2017).

Very often, human cultural products, we argue, are best conceived as joint extended phenotypes. A house, for example, is the extended phenotype of its inhabitants, just as birds' nests, beavers' dams and rodents' burrows are the joint extended phenotypes of their producers. The design, size, organization, and construction materials of a house are the result of a compromise between the—potentially conflicting—adaptive goals of its inhabitants and the constraints of the environment. Some inhabitants prioritize comfort (e.g., for their children's health), others prefer external appearance (e.g., to signal wealth or good taste), and still others prioritize proximity to social opportunities (e.g., to build and maintain their social capital). Depending on the balance of power and the degree to which individual interests overlap, the shape of the house will vary from one household to another.

The notion of joint phenotype thus makes it possible to analyze a cultural product in a functional and adaptive way, while avoiding the trap of thinking that a cultural object has a group function. On the contrary, what best explains the design-features of a cultural object is often the fact that it results from a compromise between several parties whose genetic interests only partially overlap. Take Notre Dame de Paris. This is an extended phenotype of a considerable number of individuals with different and only partly overlapping interests: the Parisian and French population, who agreed to finance the monument through their contribution to the Church, the ecclesiastical hierarchy, the King of France, the craftsmen's guilds, the Provost of the Merchants, and so on. The ecclesiastical hierarchy undoubtedly had an interest in having the most imposing building possible, while the Parisian population had to make a compromise between financing Notre Dame and other priorities (eating, protecting the city, etc.). Even within the ecclesiastical hierarchy, not everyone had the same interests:

the lower clergy, being poorer, would no doubt have an interest in a less expensive building. And the function of the building was not the same for everyone. Some financed Notre Dame to increase social discipline (via belief in a moralizing god); others aimed at the prestige of the town or the Kingdom; others saw it as a source of income, an opportunity to show off their craftsmanship or their degree of devotion.

The notion of joint phenotype finally helps to explain why human culture so often appears harmful or dysfunctional. Part of the explanation comes from the fact that what is dysfunctional for one individual is not dysfunctional for another, just as in biology (André et al., 2023). Rain-making rituals are maladaptive for clients—who spend money buying for inefficient technologies—but they are adaptive for the religious specialists who manage to hack clients' cognitive mechanisms to sell them supernatural services at a high price (Hong, 2021). The same goes for shamans, who manage to convince clients of their ability to communicate with supernatural agents to ward off misfortunes such as illness or crop failure (Singh, 2018). Menstruation huts among the Dogon of Mali are imposed on women by the men of their households to control their sexuality (Strassmann et al., 2012). They are joint phenotypes in the sense that their design-features are best explained as a compromise between two genotypes, the one of the signalers and the one of the recipient.

5. Conclusion: Human cultures as ecosystems

5.1. In the gene-eye's view, genes don't make the decisions; they set the agenda

In a sense, the gene's eye view of culture is not new. It was already defended by E.O. Wilson in *Sociobiology* (Wilson, 1975). But the approach to human culture advocated in *Sociobiology* was inherently defective. As Tomasello (2023) puts it, "The paradigm did not include much psychology—by design, as it dubbed itself 'the biology of behavior'—and virtually no concern with individual agency." *Sociobiology* was inspired by Wilson's own work on social insects, a kind of animal with low behavioral flexibility and cognitive control.

As a result, the evolutionary approach appeared reductionist and deterministic, as if genes had to code directly for behaviors, including cultural behaviors, without individual decisions, cognitive control, behavioral flexibility, and environmental input playing any role.

Yet, since *Sociobiology*, a great deal of work in animal cognition has highlighted the complex cognitive capacities of non-human animals (e.g., spatial cognition, numerical cognition, decision-making) and their capacity to innovate. In birds and mammals in particular, evolution has not selected for a particular fixed behavior, but for a particular cognitive architecture, equipped with internal goals, internal models, and the ability to generate and evaluate new solutions. Again, as Dawkins wrote, "Genes are the primary policy-makers; brains are the executives.” This explains how adaptive genetic programs can lead to diverse and innovative cultural solutions.

5.2. Genetic interests explain the design-features of cultural items

It’s commonly thought that the gene’s-eye view of evolution cannot make sense of cultural phenomena: human culture is too flexible, too creative, and too dependent on the environment to be under the “the long reach of the genes.” We have shown in this chapter that this is not the case. It is possible to explain cultural phenomena as the product of the interaction between adaptive cognitive dispositions and a variety of physical, social, and informational environments. This is obviously true for the cultural products of small-scale societies, such as lithic tools, languages, or kinship systems that have existed for thousands of years and that have co-evolved with human cognition. But it is also true of the cultural products of more recent societies. Recent work has shown that graphic codes (Morin, 2018), imaginary worlds (Dubourg & Baumard, 2021), puritanical norms (Fitouchi et al., 2021) mobilize the same cognitive dispositions as older cultural products and are used by humans to achieve the same adaptive goals. The difference is that in those cases, human adaptive dispositions have at their disposal the much larger amount of physical, social, and informational resources created by previous generations. Thus, to the extent that they are used by humans to satisfy adaptive preferences in a flexible and generative way, graphic codes, imaginary worlds, prosocial religion, and fake news are extended phenotypes, just like older tools.

This conclusion means that it is possible to use standard inclusive fitness theory (e.g., sexual selection, reciprocal altruism, parent-offspring conflict) to understand their form, function, and cultural distribution. Importantly, this does not mean that all cultural products are adaptive. After all, not all decisions made by apes and bowerbirds are adaptive. What is adaptive is the cognitive *system*, not any instance of human behavior, including cultural behavior.

5.3. Emergence and coercion

More generally, the notion of joint phenotype enables us to re-conceptualize human social phenomena. While in non-human societies, social phenomena are easily seen as emergent properties of individual behavior, human social phenomena are often (wrongly in our view) characterized as involving an autonomous layer of social causes, social facts, or social forces. In humans, social phenomena are so spectacular that they seem to involve other kinds of "forces" or mechanisms. The conceptual framework of joint phenotype makes it possible to avoid reference to this layer: it allows us to analyze any social phenomena - a belief, a norm, an artifact - as the result of the joint action of individuals with, or without, the same interests. We often hear "society forces us to do X", "society dictates to individuals to do X", "society is not ready to give rights to X". In reality, this is an elusive shorthand for the net effects of many individual human actions. When an individual criticizes society because he feels that his interests, or the interests of others, are in conflict with "society", he is really only criticizing other individuals, who do not have the same interests as he does. To re-use Sartre's words in *No Exit*, society "is other people".

5.4 Nothing more is needed

The theory of evolution by natural selection was not constructed to study cultural phenomena. As a consequence, evolutionary biology is often perceived as insufficiently equipped to understand cultural phenomena, and it would be necessary to include other mechanisms such as cultural selection (Mesoudi et al., 2006; Richerson & Boyd, 2005), niche construction (K. N. Laland et al., 2000, 2015), epigenetic inheritance or multilevel selection into an “extended evolutionary synthesis” (K. Laland et al., 2014; Pigliucci & Muller, 2010). In this paper, we have argued that the conceptual tools of evolutionary biology—extended phenotype, adaptive plasticity, ecological legacy, joint phenotypes—allow us to think about cultural phenomena without leaving the standard framework of evolutionary theory in its modern form, i.e. inclusive fitness theory. In other words, human cultural products can ultimately be explained through the lens of natural selection (André et al., 2023; Boyer, 2018; Coyne, 2014; Nettle, 2020; Rodrigues & Gardner, 2022; Scott-Phillips et al., 2014). Of course, the conceptual tools of standard evolutionary theory can be enriched with conceptual tools designed for other levels of analysis (e.g. in cognitive science, the representational theory of mind), but within biology itself, the standard tools provide what we need.

What we propose in this chapter is a rather parsimonious or “sober” theory of culture: there is no magic bullet, no missing mechanism, no hidden force. If we want to understand human culture, we have what we need: we just need to work harder to understand the complexity and richness of what is behind our eyes, just as we do for the rest of living organisms. Human culture is made up of extended phenotypes, plus adaptive plasticity, plus ecological legacy, plus shared phenotypes. Or, to be more precise, it consists of an extended phenotype, plus a huge amount of adaptive plasticity (thanks to the human brain), plus a huge amount of ecological legacy (thanks to the long human history), plus a huge number of shared phenotypes (thanks to the increasing size of human societies). In the end, human culture *seems* qualitatively different from animal culture. From the perspective of evolutionary biology, however, this is still a consequence of genes trying to pass on copies of themselves to the next generation.

Incidentally, our chapter points to the underestimated usefulness of an ecological approach to culture. For the past 50 years, the paradigmatic discipline used to understand culture has been evolutionary biology. The field of cultural evolution is based on the idea that culture can be understood using concepts from evolutionary biology (mutation, selection, phylogeny). But there is another evolutionary paradigm, that of evolutionary ecology. Ecology is the science of interactions, between organisms, and between organisms and their environment. What we have argued in this chapter is that culture is best understood as the product of interactions, between organisms and their environment, between organisms and their legacies, between organisms and their conspecifics. Culture are like forests. A forest is not a replicator. It is rather an emergent phenomenon. It emerges from the actions of billions of organisms producing joint phenotypes and extended phenotypes and accumulating legacies. Just as human cultures.

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