Research Article

Necessity Was the Mother of Human Cultural Invention

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The unique intellectual capabilities of Homo sapiens are often attributed to positive, physical evolutionary developments such as increased cranial capacity, upright posture, dexterous hands and an articulate oropharynx, despite the occurrence of similar features in other species that have not developed such capabilities. Humans are also unique, however, in lacking or ignoring instincts that define the social structures and behaviors of other animals. Genetically driven behaviors evolved to improve effectiveness in exploiting specific environmental niches. In nonhuman species, social structures, food choices, mating behaviors, child-rearing, etc. are driven strongly by pheromones and hormones and their neuronal targets, whose physiology evolves very slowly. Humans can rapidly invade new environments because they invent rather than inherit such behaviors, which cumulatively we call a culture. The invention of niche-specific social behaviors enables cultural evolution, which would otherwise be limited by the inflexibility of instinctual behavior. I explore the obverse hypothesis that down-regulation of instincts makes the invention and learning of cultures necessary, which imposes both an opportunity and a burden on individuals and societies. Cultural evolution enables human societies to invent, promulgate, compete and evolve their social structures in a generation or two rather than the hundreds of generations required for significant genetic evolution. Novel cultures and their social structures may conflict, however, with residual instincts. Such conflicts and their resolution will continue both to drive and to constrain cultural evolution.

Introduction

Modern man has intellectual and cultural attributes that are sufficiently distinct from all other animal species that we have little difficulty thinking of ourselves as *sui generis*. Science only recently rejected the notion that humans were a divine creation in favor of the reality that Homo sapiens represents just

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another, relatively small step in the genetic evolution of all animals (Irvine, 1955). This begs the question of how such qualitatively distinctive attributes arose – the problem of human uniqueness (Bingham, 2000). Many physical enhancements to the body and brain of humans have been identified but they are more quantitative and gradual, with precedents in other hominids, primates and mammals.

Human uniqueness manifests as the rapid evolution of highly variable social behaviors and technological capabilities in the genus Homo and its several species, a few of which are identified along the logarithmic timescale in Figure 1. Both the rapid appearance and the systematic variability of most of these attributes are inconsistent with genetic evolution. They are the consequences of cultural evolution, in which individuals and societies invent rather than inherit such attributes. But something must have changed genetically that either permitted or perhaps forced humans to invent cultures. This paper hypothesizes that the enabling phylogenetic steps in human evolution included down-regulation of instinctive behaviors that were limiting the potential of prior and concurrent physical enhancements such as increased cerebral development, articulate oropharynx, upright posture and dexterous hands.

First we consider how genetically specified physiology affects and is affected by behavior and interpersonal relationships. Then we consider how down-regulation of some of these effects enables behaviors to shift from instinctual to learned. Particular attention is paid to behaviors that facilitate that learning (cooperative parenting in Fig. 1) and that support metabolically the mental power implicit in the cerebral enlargement that defines Homo sapiens phylogenetically (cooking in Fig. 1). The burden of learning these behaviors and reconciling them with residual instincts is a major theme. Finally we consider how the separate mechanisms of genetic and cultural evolution interact to generate the extraordinary diversity and dynamic competition that we see between human cultures and among individuals within a culture.

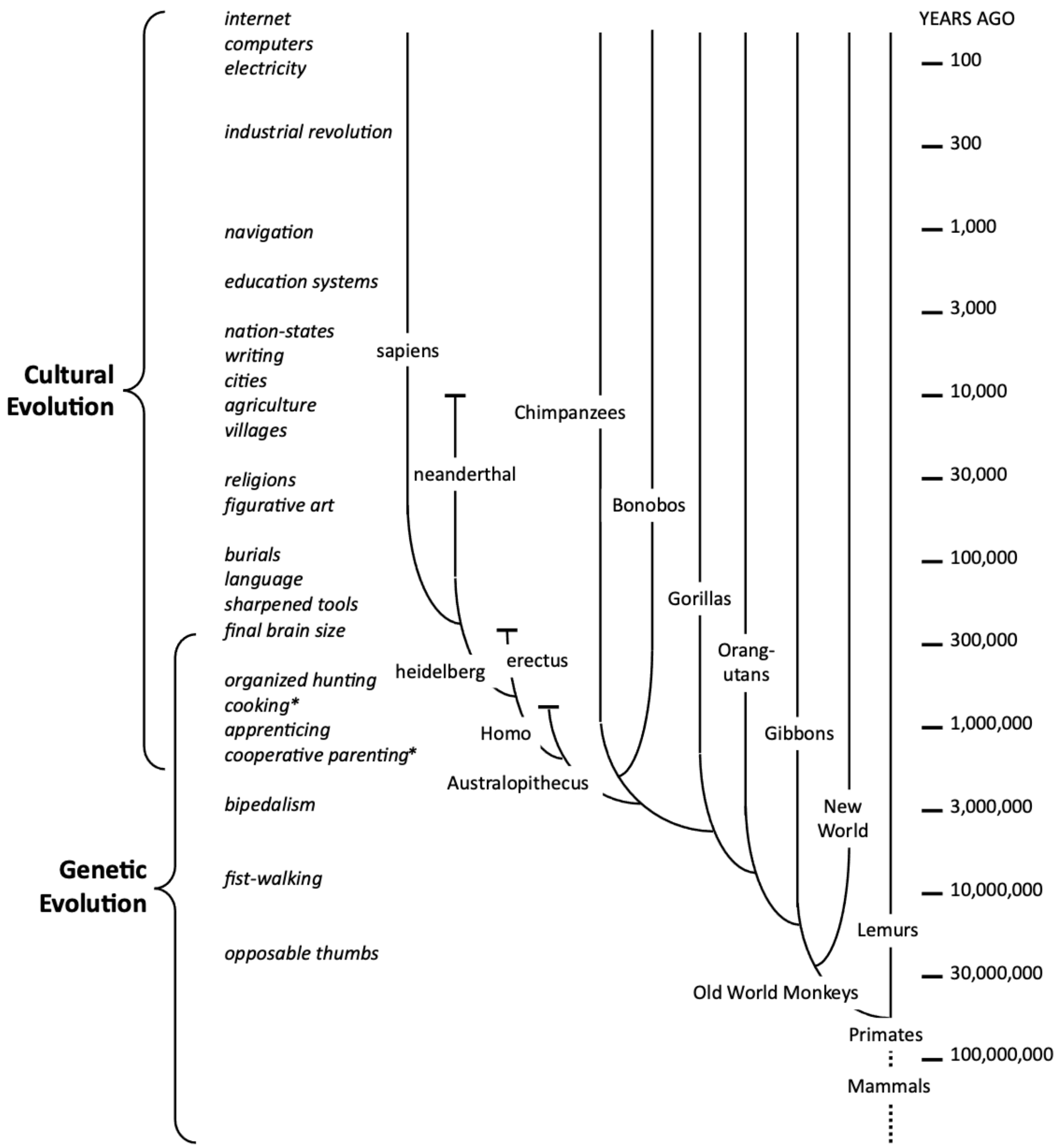

Figure 1. *Major evolutionary steps in hominoid evolution on a log time axis with approximate appearance of associated hominin attributes (Fuentes, 2020). The attributes associated with Homo sapiens are largely the product of cultural evolution, enabled by penultimate steps of genetic evolution that included down-regulation of instinctual behavior that dominates all other animals including non-human primates (* discussed in depth below).*

The Relationship of Genes to Behavior

It is useful to distinguish between the evolution of the body and the evolution of behavior (Ingold, 2006). The physical structure of the body is specified more or less directly by genes while behavior emerges from the interactions between the body and information about the environment in which the body happens to find itself (Kappeler et al., 2013). All spiders make silk and most spin webs that have highly species-specific designs (Petrunkevitch, 1926), but they appear to learn the behavioral patterns of their prey (Japyassú and Laland, 2017). Nest-building birds instinctively build nests with the form associated with their species, but they may learn to refine their designs, for example to accommodate novel sites and building materials (Breen et al., 2016). Humans are particularly in need of shelter but must learn or invent designs and constructions; these will be limited by their individual mental capacity. Note that "instinctual" and "learned" do not correspond to the distinction between "automatic" and "controlled" employed by dual process theory (Schneider and Chein, 2003), which are more concerned with attention and mechanism rather than motivation.

Organisms that evolve more complex nervous systems can accomplish more sophisticated behaviors, increasing their survival and proliferation into novel environments. Thus behaviors might be driven (if not entirely determined) by genetically specified physical circuits similar to the spider or bird (herein called instinctual) and/or they might incorporate or depend on memory of the consequences of previous behaviors or examples (herein called learned). Many behaviors reflect a combination of instinctual (genetic) motivation and learned refinement (Enquist et al., 2016). Furthermore, the learning processes themselves depend on genetically specified intercellular connections and intracellular mechanisms. Disentangling these relationships for any specific observed behavior tends be difficult (Sosa, 2024), but across animal phylogeny, there is a range of behaviors from predominantly instinctual to predominantly learned.

Instinctual behavioral patterns have the advantage of providing an immediate, reliable repertoire of useful behaviors, but they do not provide a way to take advantage of new opportunities. As pointed out by J. Mark Baldwin in the early days of evolutionary theory, a single organism with a new, potentially useful mutation of its body must survive and reproduce for that mutation to persist and evolve further (Baldwin, 1896;1897). That individual will be unlikely to survive if its behaviors are fixed genetically and optimized for a different body or environment. On the other hand, learning behaviors from trial-and-error experience takes time and exposes all individuals of that species to risks that reduce their fitness in the familiar environment.

Genetic evolution provides mechanisms for the development and maturation of the information processing parts of the body. These include both the endocrine system and the nervous system, an anatomically localized elaboration of the same communication scheme based on chemical receptors that generate electrical responses that trigger the release of other chemical transmitters. These mechanisms determine the range of behaviors that might be learned while delimiting the behaviors actually expressed to avoid those that might be immediately fatal either to the individual or to the local breeding population in the case of social species. Tension between instinctual and learned behaviors is inevitable because each may interfere with the other. The evolutionary success of any mutation that affects either type of behavior will depend on how it interacts with the other.

The evolution of social species in which individuals play specialized roles is particularly fraught with potential conflicts between instinctual and learned behavior. If the specializations are genetically specified within fixed subgroups (as in workers, drones and queens in bees), evolution will be constrained within a given breeding population by the complex interactions among the specializations. If the specializations arise in individuals as a consequence of their behavioral experiences and innate physical heterogeneity, then the emergent behaviors are less constrained, presenting both opportunity and danger to the breeding group. The group might be better able to adapt to a novel environmental challenge or the appearance of a mutant individual but it might also self-destruct in its usual circumstances.

The spectacularly rapid evolutionary success of Homo sapiens can be attributed to an extreme ability to take advantage of changed circumstances, including the changes resulting from their own actions. Not only do humans learn to refine their instinctual behaviors during their lives (as do some other animals), humans also create cultures that invent and promulgate new behaviors. The beginnings of such dependence on learned rather than instinctual behaviors can be seen in the extant primates most closely related to Homo sapiens such as orang-utans (Van Schaik, 2013). Van Schaik compared behavioral variability to genetic variability and found that variations in behaviors such as tool use for extracting seeds from fruit were largely due to the inventions of hominoid cultures. Similar analyses for variations in vocal calls distinguish reliably between the learned calls of some bird species and the genetically determined calls of frogs.

Many of the highly labile social behaviors invented by Homo sapiens have precedents in other species (Schradin, 2013), but an individual species usually expresses only one or a small subset of these behaviors, while humans are capable of them all. For humans the specifics of how and when to select a mate, how to and who should raise offspring, what to eat, how to govern, etc. are mostly highly variable inventions rather than instincts. Furthermore, two breeding groups of humans in similar circumstances may chose radically different social structures and then compete against each other for

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dominance. Such cultural inventions can be developed and then proliferate and dominate within a few generations, enabling a form of cultural competition and evolution that occurs at lightspeed compared to the genetic evolution of instinctual behavior (Richerson and Boyd, 2008); note logarithmic timescale in Figure 1. Such cultural evolution requires not just the enlargement of brain capacity for invention but also the down-regulation of instinctive behaviors that would otherwise constrain those inventions.

Examples of Down-Regulated Neural Circuits

The layered structure of the information processing system provides a substrate in which older, more preprogrammed subsystems can persist but be modulated by more recently evolved subsystems for learned behavior. The phylogenetically older endocrine and autonomic nervous systems that we associate with instinctive behaviors are reciprocally connected to the more recent central nervous systems of vertebrates. Hormones released by the former modulate the activity of the latter (Genazzani et al., 2002), providing a basis for instinctually driven behavior. But the central nervous system also modulates the endocrine and autonomic nervous systems, both by generating neurotransmitters that have their own hormonal effects and by direct innervation of endocrine, digestive and immunological subsystems by the hypothalamus and vagus nerve, among other pathways (Levine, 2012). Clinical dysfunctions related to mental stress include hypothalamic amenorrhea (Warren and Fried, 2001) and changes in both adrenocorticosteroids and growth hormones (Brown and Reichlin, 1972). It is difficult to attribute causality during normal function in such feedback systems, which are usually considered from the perspective of maintaining homeostasis or circadian rhythms. The following examples from the sensorimotor system provide clearer examples of the general potential for behavior to evolve phylogenetically by dynamically down-regulating (i.e. modulating) the contributions of older, more automatic pathways.

In mammals the spinal cord preserves reflex connectivity from somatosensory afferents to motoneurons similar to that found even in insects, but it is routed through interneurons that can be biased on or off by descending control from the brains of vertebrates (Loeb et al., 1999). Shifts in the biasing of such interneurons can cause a behavior that is automatic in one species to require learning and voluntary control in another (Alstermark et al., 2007). The spinal cord contains central pattern generation circuits that specify the sequences of muscle activation required for locomotion (Shik and Orlovsky, 1976), enabling a newborn colt to walk almost immediately. Humans start to crawl automatically but then suppress crawling to learn bipedal locomotion slowly and as a novel behavior that is better suited to their anatomy (Adolph et al., 1997). Learning – i.e. "inventing" – how to walk enables humans (but not horses) to learn to play soccer, which requires coordination patterns that are not available in genetically specified central pattern generators.

The hardwired, vertebrate tectoreticular subsystem enables automatic, fast and accurate acquisition of sensory targets in extrapersonal space (e.g. a frog catching a fly with its tongue), but it can be gated on or off or given imagined targets by cerebral cortex in mammals (Contemori et al., 2022;Contemori et al., 2023). Failure to suppress fast, reflexive tectal function in superior colliculus may account for attention deficit hyperactivity disorder (ADHD) in humans (Overton, 2008). ADHD is but one example of the general phenomena of impulsivity, which are known to vary among but be generally weaker in humans than other species under comparable circumstances (Sosa and Dos Santos, 2019).

More complex behaviors such as foraging and mating determine reproductive success but pose immediate risks to the individual. The more highly regulated they are by instincts, the more likely they are to succeed under usual circumstances but to miss opportunities offered by changed circumstances. The instinctual motivators of such behaviors manifest themselves as emotions and desires mediated by the phylogenetically old limbic system, also known as the "reptilian brain". The culturally learned motivators reside in the cerebral cortex, which accounts for almost all increasing brain size in the sequence of species within the genus Homo. The connections between the two are reciprocal, allowing instinctual drives to influence behavior but also allowing cortex to down-regulate the limbic system where they originate.

Successful instincts of social mammals tend to include environmental contingency rules, such as how to change breeding patterns if the relative proportions of males to females changes (Kappeler et al., 2013). The increasingly layered structure of the evolving mammalian brain preserves and modulates robust instinctual behaviors in the lower layers but makes it increasingly difficult for genetic evolution to construct novel instincts there. In addition to the inherent complexity of higher behaviors, they must interact with the other, previously acquired instincts and the subsystems that generate them. Humans have the intelligence to invent such contingent strategies, but their implementation depends also on genetic down-regulation of instincts that might compete with them.

Examples of Down-Regulated but Residual Instincts

One way to identify instinctual mechanisms that have been down-regulated is to examine the behaviors for which humans are more flexible than other animals. Interestingly, most research on such behaviors has focused on identifying vestiges of the genetically programmed mechanisms that still influence those behaviors (Clark and Grunstein, 2004) rather than considering the positive consequences of their down-regulation relative to other animals. It is as if science is still looking for evidence in support of Darwin's *Descent of Man* rather than moving on to the consequences. Human ability to evolve cultures and build large societies has been attributed to the genetic evolution of new instincts such as "pro-social motives" (Boyd and Richerson, 2009). Here we consider instead why hard-won evolutionary instincts that originally enabled increasingly complex social behaviors of vertebrates had to be down-regulated to enable the much more rapid cultural evolution of Homo sapiens. Such instincts can be triggered by any input modality and mediated by a wide range of neural and endocrine mechanisms as noted above. I have chosen here to focus on pheromonal inputs and hormonal mechanisms because these are known to be strong in other animal species and present but relatively weak in humans.

Interpersonal Behavior Driven by Pheromones

Pheromones are chemicals secreted by one animal that are transmitted to other animals as smells that affect their behavior (Wyatt, 2003). Research on human pheromones has been controversial and often inconclusive, at least in part because humans have sparse connections to and weak perception by under-developed olfactory systems (Halpern, 1987).

The pheromones that influence mate selection and bind mothers to their infants (Vaglio, 2009) are just some of many olfactory cues that persist but have become faint in humans (Grammer et al., 2005). The hormones that drive virility in males and fertility in females have strong odors, which is why the enzyme that converts androgens to estrogens is called aromatase (Santen et al., 2009). They are easily detectable in sweat and urine and drive reproductive behavior in most species. They seem to change human perceptions of attractiveness (Thorne et al., 2002) and actual sexual behavior in both men (Cutler et al., 1998) and women (McCoy and Pitino, 2002), but only modestly (in both senses of the word).

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Fear almost instantly changes the nature and odor of human sweat. Dogs are good at detecting this in humans (D'Aniello et al., 2018). So are humans, even when they don't know it. Sweat collected from other humans under fearful conditions (skydiving) elicited changes in the metabolic activity of parts of the brain associated with fear, even when the subjects reported no perceptible difference in smell (Mujica-Parodi and Strey, 2006). Overt behavioral effects of fear pheromones have been well-documented in various mammals, but little is known about their exact chemical composition in humans (Ackerl et al., 2002).

Distinctive body odor results from a combination of kinship genes, dietary habits, hygiene and the microbiome of the skin (Havlíček et al., 2017). One of the cues that promotes friendship relationships among humans appears to be that they smell similarly (Ravreby et al., 2022). Body odor was likely one of many cues that promoted the instinctive tribalism that was useful for competing bands of hunter-gatherers (Lundström and Olsson, 2010), but it is generally counterproductive for multi-ethnic nation-states that are a recent and uniquely human invention.

Pheromones drive the extraordinarily diverse behaviors of various species of ants (Vander Meer Robert and Alonso, 2019). They determine the various roles of individuals in the colony, they distinguish members of the colony from intruders and they paint a target on the nests of competing ant colonies and species. They mark the trails that allow one scout to summon thousands of its brethren to partake of a windfall. Subtle changes in these pheromones and their behavioral effects account for the great variety of social organization and daily behavior seen in the >13,000 different species of ants. Most ant species form individual colonies that aggressively protect their territories and war frequently with the adjacent colonies, something like the small, inbred human tribes that have survived in remote places like the Amazon river basin and the mountain jungles of New Guinea (Keeley, 1996). In his book *The Social Conquest of Earth*, the naturalist Edward Wilson detailed the many parallels in the social behavior of ants and humans (Wilson, 2012). Argentine ants, an invasive species that is dominant in the US Southwest, appear to have lost the tendency to develop unique pheromones when they establish new colonies. This results in "supercolonies" that extend over hundreds of miles and millions of nests that live in peace with each other (Sunamura et al., 2009), something like the human citizens of a large, multi-ethnic nation. This more gregarious culture was enabled for both species – ants and humans – by a down-regulated component of their instinctual behaviors.

Anyone who has ever walked a dog knows that they depend on scent to identify other dogs and their territories (Black et al., 2000). Dogs are a large step up from ants in that they can associate smells with their rich, multi-sensory experiences of individual dogs (and humans) that they have encountered. But they are a step below humans in being unable willfully to ignore olfactory cues.

Genetic evolution has left humans with a notably impoverished sense of smell. We start with unusually few olfactory receptors (less than 5% of a dog's or even a rabbit's) connected to a relatively small patch of brain (Smith and Bhatnagar, 2019). Upright posture takes our noses away from the ground and the genitals, where the most interesting and useful odors tend to be found. This is perhaps why evolution endowed humans with hairy armpits that become smelly as the rising sex hormones in adolescence interact with the mostly odorless secretions of young children (Stoddart, 1998). Nevertheless, loss of most body hair and a fondness for immersing ourselves in water makes us less smelly than the rest of the apes. Modern culture reinforces this by regular bathing, scented soaps, deodorants and perfumes. Thus both genetic and cultural evolution have conspired to reduce the salience of olfactory cues, probably because they would otherwise drive the instinctive behaviors that humans must suppress to develop large, multi-ethnic societies.

Child Rearing Driven by Hormones

Vertebrates exhibit a great range of parenting behaviors, including species in which neither or only the female or only the male or both provide physical protection or nourishment or both (Clutton-Brock, 1991). These species-specific behaviors are largely instinctual and driven primarily by hormones released during mating, pregnancy and lactation. Human relationships are complicated by the fact that successful human reproduction requires an unprecedented duration of parenting compared to other animals. Selecting a mate whose appearance and courtship behavior suggests that he or she could be an effective parent is not the same as actually getting him or her to do so after a demanding and smelly infant arrives. Another layer of motivating instincts is required.

Instinctive behaviors of the human infant trigger useful instinctive behaviors in the parents. An infant reacts to the hovering human face with a reflexive smiling response that adults find irresistible (Messinger and Fogel, 2007), mediated by a serotonin-oxytocin circuit through the adult hypothalamus (Strathearn et al., 2009). Both the sound of crying and the tactile sensations of suckling induce oxytocin and prolactin release, reinforcing lactation in mothers (McNeilly et al., 1983). Fathers also respond to infant crying with increased testosterone and prolactin production (Fleming et al., 2002).

Pregnancy and delivery are accompanied by massive shifts in hormones that prepare the female body for motherhood but also have deep psychological effects on attitudes and behaviors (Johnson, 2013). Their partners certainly perceive the physical and behavioral changes and they probably detect the associated pheromones subliminally. Behavioral changes in mothers binding with their infants appear to be correlated with persistent decreases in the volume of certain areas of cerebral cortex, which may be one of the many results of the hormonal and other physiological changes associated with pregnancy and lactation (Martínez-García et al., 2021). Perhaps more surprisingly, similar brain shrinkage occurs in fathers (Martínez-García et al., 2022). New fathers generally experience a decrease in their testosterone levels that is associated with greater caregiving. In turn, male infants raised with strong paternal caregiving tend to larger such effects when they become fathers (Gettler et al., 2022). This suggests an intergenerational transmission of parenting style that facilitates the development of cultures that are appropriate for the environment in which humans find themselves. In a high-risk environment, males are more likely to propagate their genes successfully by promiscuously inseminating as many females as possible, a behavior that is known to be promoted by high testosterone levels. In a more stable environment, a man would do better to form a lasting relationship with a fertile woman and a nurturing relationship with prospective heirs.

Long before there were physicians or midwives or nannies or self-help books, hominids were successfully reproducing based on instincts alone, just like all other animals. The unique thing about humans is that we can choose to ignore our instincts, which suggests the need for the professional advice. We can be convinced by external advice that infants must be picked up immediately if they cry or left to cry themselves out, regardless of our instincts. We can override protective instincts and abandon our offspring or engage in physical abuse of our spouse and children. We can force ourselves to leave our infants in the hands of strangers because daycare facilitates providing our offspring with the educational opportunities and material goods of modern society.

Instinctual behaviors for familial nurturing represent an obstacle to the dissolution of parent-child bonds that is necessary for the formation of new and independent family units. The surges of hormones associated with puberty drive aggressive behaviors that are distressing to parents but attractive to potential mates (Buchanan et al., 1992). Such disruptive instincts serve an obvious purpose but advanced societies mandate a greatly extended adolescence to acquire the advanced skills required to succeed. Humans can decide to keep their post-adolescent children under the same roof long after residual instincts encourage their eviction to form new families.

Until recently, the above parental decisions were considered no one else's business. It is only in the past few decades that society has felt not only empowered but even obligated to intervene (Myers, 2008). This is paradoxical in the context of contemporary societal decisions to step back from long-standing interference in life-style choices such as homosexuality, adultery, contraception and abortion. How might we explain this? Since at least Babylon, children were perceived to be assets of their parents (Code of Hammurabi, #209, 210). Most obviously, they were the precious vessel for their parents' genes. In the absence of social insurance schemes, they were the investment whereby parents could hope for a longer life and more pleasant death. As fertility rates plummeted and investment in public education surged in industrialized societies, however, children suddenly became an asset of society at large. There are other primates that care for their offspring communally (Tardif et al., 1990), but they do so instinctively, not politically.

The decisions that remain delegated to parents depend to some extent on subjective personal instincts rather than objective cultural practices. The hormones associated with biological motherhood exert powerful and (usually) useful effects on the mother's judgment and interactions with her offspring. Biological fathers and adoptive parents experience some similar effects but they are inevitably weaker and conflated with mating rather than parenting (Marlowe, 2000). Societies are now experimenting with progressive policies such as equal parental leave from employment for mothers and fathers, but their uptake has been slow and limited (Gnewski, 2019). It remains to be seen how much of these behavioral tendencies are cultural effects that society can change, at least gradually, and how much they reflect residual animal instincts driven by our virtually immutable genes. But the mere fact that such experiments are possible is evidence of the profound down-regulation of instinctual behavior in favor of cultural invention.

Examples of Compulsively Learned Behaviors

Animals that must learn from experience with their environments require motivation to expend effort and take risks while doing so. Young cats learning to hunt will spend hours "playing" with captured prey, presumably to learn their moves and refine their own responses (Biben, 1979). Cats do so when satiated, suggesting that what we call "curiosity" is a preprogrammed tendency of higher nervous systems to seek out and respond to random reinforcement schedules (Baxter and Schlinger, 1990).

Learning something as complex as social behaviors requires even more complex and lengthy trial-and-error practice, during which the immature human is relatively ineffectual and vulnerable. A curiosity drive seems to motivate all humans when young and many throughout life. It is particularly likely to manifest itself in those activities that are important for survival and procreation but for which the genetically defined instincts available to other animals have been down-regulated or even suppressed. An anthropologist from another world comparing humans to other primates would immediately notice that humans have an almost obsessive interest in activities that other primates mostly ignore or take for granted.

Mating Behavior

All social animals have a large stake and take great interest in who mates with whom, but the mating behavior itself is stereotyped. The development of novel courtship and copulation strategies is an important mechanism of speciation, leading to great variety in the animal kingdom but little or none within a given species. Jared Diamond explored the evolution of human sexuality, identifying animal precedents for many human behaviors (and their culturally defined perversions) while noting some that are rare or novel among other animals, including our closest phylogenetic relatives (Diamond, 1998). Perhaps more remarkable, but unremarked upon, is the human obsession with studying the courtship and copulation strategies of other humans, i.e. pornography. My hypothesis is that humans are attracted to pornography because they do not instinctively know what constitutes acceptable sexual relations in their own or other cultures.

Lots of scholarly attention has been paid to the invention and importance of novel communications media: realistic painting, written language, the printing press, still photography, motion pictures, videotape, the digital internet, and more to come. The dark secret for every one of these is that widespread promulgation and commercial success came from what was essentially the pornography of its time (Barss, 2010).

Pictorial and sculptural representations of humans engaged in sexual activity are among the earliest artefacts of just about every civilization unearthed by archeologists. The *Kamasutra* (circa 225 CE) contains much advice on how to live but became infamous in sexually repressed Western cultures for its depictions of sexual positions. Gratuitous nudes are a feature of the Renaissance that mollifies high school students dragged to a museum.

Gutenberg's invention of the printing press in Europe (anticipated by centuries in China) premiered with *Biblia Sacra* in 1455, with includes the sexually explicit "Songs of Solomon". This was followed by popular printed editions of Chaucer's *The Canterbury Tales* (1476 from manuscript in 1400) and Boccaccio's *Il Decameron* (1492 from manuscript in 1353). About one third of the tales in each include explicit erotica, usually illicit but generally romantic (Allman and Hanks, 2003;Miller, 2005;Serafini-Sauli, 2011).

Photographic technology became practical in 1839 and was almost immediately employed in the production and sale of pornographic images (Mirabelli, 1985). These were added to the popular and inherently voyeuristic technology of the peep box (Huhtamo, 2006). Edison's Kinetoscope and successors such as the Mutoscope used film strip technology to provide peep shows, often pornographic, to paying customers in the sexually repressed Victorian Age. The short-form peep show was followed by the longer "blue movie" (the actual title of a 1969 film by Andy Warhol). Obsessive interest in the mating habits of other humans was captured in the title of the 1967 Swedish erotic hit film *I Am Curious (Yellow)*.

Still and movie cameras were accessible to amateurs, but the exposed film so produced required specialized processing, mostly by commercial laboratories that returned images deemed salacious as "overexposed" blank prints. The commercialization of the Polaroid instant camera starting in 1948 and Sony's video cassettes in 1971 solved that problem; the clandestine "stag film" industry (dating to 1907) exploded (Coopersmith, 1999). Sophisticated but affordable technology plus an established legitimate cinema industry resulted in the "Silicone Valley," the San Fernando Valley portion of Los Angeles that became the center of the modern pornography industry (Self, 2008). The internet made all this once-illicit pornography and exhibitionism much more accessible. A substantial percentage of internet traffic remains pornography of one sort or another (Wright et al., 2023).

If humans just needed to learn how to make love, this plethora of pornography would be overkill. Sexual practices might differ among cultures, but it wouldn't take much effort to learn a specific behavior that was the norm for a given culture. In fact, many of the highly diverse practices outlined by Jared Diamond coexist within a culture, if not overtly then certainly clandestinely. The down-regulation of instincts that linked sexual behavior to procreation allowed such behavior to be repurposed for social organization, so its importance goes beyond procreation. The high level of heterogeneity in the physical and behavioral attributes of individuals within a society gives rise to a similar level of heterogeneity in the collection of mating rituals and sexual practices that coexist within each society. As each individual approaches puberty, he or she must learn about and select from this sexual smorgasbord, a daunting task. One strategy would be to settle for the first thing that worked reasonably well. That shortcut has been largely foreclosed by the extended adolescence mandated by advanced economies, where it is impractical or even illegal to form a stable union between two underage sexual partners.

Food Preparation

All social animals have a large stake and take great interest in how food is distributed and shared among individuals in breeding groups, but the selection of food is driven largely by subconscious nutritional needs and adventitious availability. Lots of animals spend hours perfecting their behaviors for foraging and hunting, but once a food item has been obtained, it is consumed with little preparation or ceremony and usually immediately. Long after their nutritional needs are satisfied, however, humans devote a huge amount of effort to learning about (and frequently inventing) novel food combinations and preparation methods, i.e. cooking. Humans need to learn food preparation because they do not instinctively know what to do with the ingredients available in their own or other cultures. We speak of humans as omnivores (an instinct of some animal species) but in fact humans are "oligovores". Each human culture develops complex recipes involving a relatively small percentage of available foodstocks and often disdains (e.g. insects, dogs, horses) and or prohibits (e.g. Islamic halal, Jewish kosher, Jainism) other ingredients.

As primate brains and their metabolic demands grew, the extraction of energy from the cumbersome and inefficient digestion of raw foods became a limiting factor in human evolution. What we call foods are the bodies of other animals (meat) and the aspirational progeny of plants (seeds and fruits), all of which evolved to resist the disaster of being digested. They require a great deal of energy to break down into usable sources of energy, making them inefficient and less attractive as foods. If necessity is the mother of invention, then the control of fire was the necessary solution to chronic starvation (Wrangham, 2017). Cooking with fire lets humans supply that energy from external sources, mostly the burning bodies of yet other plants and animals (wood and oil). Cooking is the continuing and competitive elaboration of that fundamental invention of human civilization. But cooking is a learned rather than instinctive behavior. Mastering it requires trial-and-error experimentation that is often wasteful in the moment but rewarding in the long term, making it a target for our curiosity drive.

Communications media have been heavily invested in cooking as well as pornography. There are recipes recorded on clay tablets from ancient Mesopotamia circa 1700 BC (Bottéro, 1987). Printed cookbooks were prized possessions of affluent Europeans in the Renaissance (Fitzpatrick, 2016;Notaker, 2022) and hand-written ones are still passed from mothers to daughters everywhere. Newspapers and magazines devote many column-inches to reviewing the latest restaurants and food fads. Cable television has whole channels devoted to cooking shows and competitions. Cooking and recipe apps are popular on cellphones and personal computers. Food "selfies" are pervasive; Google just returned 633,000,000 search results.

Cooking and food preservation required large and phylogenetically recent behavioral changes that were driven by human invention (fire, agriculture, animal husbandry) rather than genetic evolution, but the results are so powerful that they have driven at least some simple genetic selection even within the relatively short existence of Homo sapiens. Perhaps the best known of these relates to lactase, the digestive enzyme for the predominant sugar in milk. The extended childhood of humans, which is necessary to learn non-instinctive social behaviors, necessitated a mechanism to get young children to stop nursing, which imposes a metabolic demand on mothers that suppresses their fertility. The earliest humans stopped producing lactase and could no longer digest milk after early childhood. The inventions of animal husbandry and preservation of milk as yoghurt, butter and cheese drove a genetic reversal of lactase suppression in Euroasian subpopulations (Chenling Xu et al., 2017). Other dietary inventions were facilitated by selection and drift in the microbiome of the gut, which performs much of the digestive work and has its own signaling mechanisms with the human nervous system (Sharon et al., 2016).

Food selections and preparation methods are distinguishing features of human cultures. Infants acquire preferences for the food dishes that they have experienced (Birch, 2002) and their microbiomes adapt to deal efficiently with them (Xu and Knight, 2015). Customary diets may be enshrined in religious laws that help to distinguish competing cultures and their tribal members as well as promoting healthful or efficient behaviors. How well such dietary customs interact with the availability and economic cost of their ingredients in the society's environment becomes another aspect of a culture's fitness.

Implications for Genetic and Cultural Evolution

Genetic evolution is usually studied by comparing the morphology and behavior of variously related species separated by hundreds or thousands of generations. Intermediate forms must have existed but they tend to disappear as useful, stepwise adaptations accumulate. The rate of such adaptations and the appearance of new species both accelerate rapidly when changes in the environment present large opportunities with little competition, i.e. punctuated evolution (Gould and Eldredge, 1977). The hominid explosion still being elucidated by paleontologists and geneticists probably reflects evolution punctuated by changes in the environmental circumstances wrought by the hominids themselves. It would be further accelerated by genetic exchange among incompletely speciated hominids (Sankararaman et al., 2016).

If cultural evolution was enabled by genetic evolution that down-regulated some instinctual behaviors, then this would also create an opportunity for acceleration of genetic evolution. The invention of complex language may be an example of such accelerated coevolution. In the absence of instinctively understood social messages based on pheromones and hormones, individuals who could better convey their intentions verbally would have an important advantage. So, too, would individuals who could better understand complex instructions for the new necessity of food preparation. Put simply, Homo sapiens had more to talk about than other primates. We might then expect rapid genetic evolution to enhance physical capacity for communication and mental capacity for language and other cultural inventions and to further down-regulate other genetically programmed instincts that constrained such invention.

Down-regulation of instinctual behavior in humans presumably started phylogenetically but has been reinforced by complementary steps in cultural evolution. Homo sapiens differs from other great apes in having converted visual cues regarding personal and temporal states of fertility and arousal into permanent displays that facilitate the use of sexual relations as cultural practice (Szalay and Costello, 1991). Most human cultures add at least minimal clothing (e.g. loin cloths and penile sheaths) designed to further hide residual cues such as menstruation and tumescence. Such "modesty" is a uniquely human attribute that the *Bible* marks as one of the main consequences of human enlightenment (*Genesis 3:21*).

The relationship between the genetic and cultural evolution of Homo sapiens can be viewed from the perspective of Aristotle's and Plutarch's causality dilemma – which came first: the chicken or the egg?

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We now understand that a random genetic mutation results in a change of phenotype, so the egg comes first (Fabry, 2016). But we also understand that the survival of the chicken determines whether that mutation persists and, hence, whether other mutations can be added to it to extend the incipient speciation. A genetic mutation that down-regulates an evolved, hence presumably useful, instinctive behavior necessarily reduces the fitness of that individual but might be accommodated if it enables a latent ability to learn a more effective behavior. The learned behaviors of individuals carrying that mutation might then come to dominate the culture, reducing the fitness cost of further mutations that further down-regulated instinctual behaviors (Wilson, 2012). Such iteration would have been particularly strong during the period of overlap between the last major steps in genetic evolution and the first steps in cultural evolution (2 to 0.3 million years ago in Figure 1). Perhaps the most important cultural engine for accelerating these iterative cycles of genetic-cultural coevolution is extended childhood. Young humans lacking instinctive behaviors to survive are sheltered by their parents and the community at large while they learn how to survive and procreate in the culture into which they are born.

Polygenicity Leads to Behavioral Heterogeneity

The most complex social animals benefit from heterogeneity in the physiognomy and behavioral tendencies of individuals within a breeding population (Montiglio et al., 2013), who can take up specialized roles most suited to their individual attributes. Such heterogeneity arises from the random combinatorial effects of the many genes that contribute to those attributes.

Studies of heritability usually assume that the genes responsible for a given phenotype have additive effects. Various types of epistatic interaction between genes are known to confound this assumption (Phillips, 2008). Such epistatic effects seem particularly likely for behavioral traits that depend on a nervous system whose structure and function emerges from experience during development rather than from genes that directly specify that structure and function. A very large number of genes encode the rules for those developmental effects, making the effects of any one of them highly dependent on the other genes and on the unique experiences of the individual possessing the complete genotype. This reduces heritability of behavioral phenotype from these genes, which also favors increasing variance in such genes (Stirling et al., 2002). The down-regulation of relatively fixed, genetically-specified behavioral traits in favor of learned behaviors further weakens the heritability of behavioral phenotype, further increasing genetic variability and unpredictable epistatic interactions. In the extreme, the self-reinforcing cycle of learned cultural evolution and weakened genetic heritability might mean the end of genetic evolution for Homo sapiens. Ironically, that would seal the fate of the failing cultural invention known as eugenics.

Because behavioral phenotype is highly polygenic and epistatic and those genes are highly heterogeneous, behavior does not "breed true" (Davies et al., 2011). This leads to unusually high levels of heterogeneity in human traits such as personality type and various forms of intelligence. Such heterogeneity persists even in small bands of interbreeding individuals that might otherwise be expected to be subject to rapid selection and gene drift (Bowles and Gintis, 2004). Not coincidentally, it provides the diverse social substrate required for the invention of many, very different patterns of social behavior, i.e. cultures.

Conflict Resolution Constrains Cultural Evolution

The combination of a requirement to learn invented rather than instinctual social behaviors plus irrevocably heterogeneous personalities provides the instability required to drive cultural evolution. Humans counter that instability by rationalizing their culture's inventions (Yong et al., 2021), but not everyone will be convinced. Any given culture is likely to disenfranchise some individuals whose behavioral patterns are "unfit" for that culture. If such misfits persist even after many generations of such societies, they then provide a ready substrate for the invention and success of a new culture within that society. The former misfits and their more appropriate new culture might somehow secede and isolate themselves from their native society, but their now homogeneous personality traits are not strongly heritable, so subsequent generations will become heterogeneous and just as driven to further cultural evolution.

A new culture may arise spontaneously within, be adopted freely by or be imposed upon a society. Any of these will result in both positive and negative effects that may not be immediately apparent. The effects of incompletely suppressed instincts are likely to be negative if they promote behaviors that are anathema to the invented culture. For example, there are many socioeconomic benefits to shifting from a patriarchal to an egalitarian society, but aggressive males who are rejected as mates may become disruptive. The society may then need additional cultural inventions such as early formal education and criminal sanctions, which may themselves conflict with other instincts such as for parenting and autonomy. The contemporary "culture wars" have obvious roots in such conflicts.

Both cultural and genetic evolution are constrained by unintended consequences. The inventors of laws and customs intended to improve a culture often ignore residual instincts, probably because they tend to be unevenly distributed within society and are frequently subconscious. Acceptance of a new law or custom will depend, at least in part, on whether such residual instincts reinforce or conflict with it. Cultures whose inventions maximize benefits and minimize adverse consequences in the long run will appear to be fit and might become prevalent as a result of being adopted by or imposed upon societies with less fit cultures. This assumes that cultural evolution, like genetic evolution, is inexorable and amoral, which fits much human history but ignores more recent human efforts to protect both cultural and species diversity for its own sake.

Cultures themselves differ in how effectively they promote or constrain their own cultural evolution, resulting in a wide range of ability to deal with conflicts within and between societies (Acemoglu and Robinson, 2020). The parallel in genetic evolution would be a mutation in a pathway that regulates the repair of DNA, which would change the rate at which other future mutations could evolve the species. A culture that encourages the invention of new policies could adapt more readily to new challenges and opportunities but might also become inherently unstable. The anthropologists Victor and Edith Turner studied how the public rituals that all human cultures have developed serve to defuse the tension between accepted social behavior and instinctual emotions such as jealousy, ecstasy, anger and grief (note the early appearance of burial and religious rituals in Figure 1). These emotions and rituals tend to be associated with threshold events ("limens" in Turners' lexicon) such as mating, birth and death (Bigger, 2009). When modern societies integrate people from many different cultures, their diverse native rituals may be lost, misunderstood or incompatible, rendering them less effective (Parekh, 1997;Rosenblatt, 2008).

Evolving Cultures Compete Economically

Reinventing mate selection and parenthood leads to the sort of quandaries that humans regularly get themselves into by their cultural ability to overcome their animal instincts. After centuries of worrying that instinctive human fecundity would overrun available natural resources (Malthus and Winch, 1992), the biggest challenge to contemporary socioeconomics has turned out to be rapidly declining birthrates despite unprecedented availability of nutrition ("Global fertility has collapsed, with profound economic consequences" *The Economist*, June 1, 2023). Cultural signals and inventions such as birth control have largely over-ridden instincts as basic as mate selection, mating behavior, pairbonding and child-rearing. The extended adolescence inherent in secondary and tertiary education appears to be delaying mating and procreation (Neels et al., 2017), even as social and/or environmental effects are shifting puberty to earlier ages (De La Rochebrochard, 1999). This seems likely to increase the adverse consequences of residual instincts that are incompatible with modern culture. The hormonally driven adolescent behaviors that were supposed to induce separation from parents now start earlier, must be indulged for longer and may have burned out by the age at which separation becomes economically feasible in modern cultures, resulting in *Failure to Launch* (romantic comedy film from Paramount Pictures, 2006).

The obvious economic rewards of liberated contemporary lifestyles must compete with the costs of residual instincts ignored. Those costs are multidimensional but can be quantified by their net effects on economic productivity. This competition will play out differently among individuals who differ in both their socioeconomic success within a given culture as well as the strength of their residual instincts. If the balance across the whole society or some definable subset of it turns negative, then all or some of the society may invent a new culture (or revert to an old one) that has a better benefit/cost ratio for its members.

There is no going back to instinct. The well-being of modern human societies depends completely on the cultural inventions of large-scale government, finance, trade and technology that are anathema to the unsuppressed instincts of early hominids. Furthermore, Homo sapiens' instincts have become too weak to sustain any level of social organization, even that of early hominids. Humans have transcended the treadmill of genetic evolution and replaced it with the treadmill of cultural evolution. The former comes with a zoo of examples demonstrating how it works; the latter comes without instructions.

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