The Cultural Evolution of Cultural Evolution

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Abstract: What makes fast, cumulative cultural evolution work? Where did it come from? Why is it the sole preserve of humans? We set out a self-assembly hypothesis: cultural evolution evolved culturally. We present an evolutionary account that shows this hypothesis to be coherent, plausible, and worthy of further investigation. It has the following steps: (0) in common with other animals, early hominins had significant capacity for social learning; (1) knowledge and skills learned by offspring from their parents began to spread because bearers had more offspring, a process we call CS1 (or Cultural Selection 1); (2) CS1 shaped attentional learning biases; (3) these attentional biases were augmented by explicit learning biases (judgements about what should be copied from whom). Explicit learning biases enabled (4) the high-fidelity, exclusive copying required for fast cultural accumulation of knowledge and skills by a process we call CS2 (or Cultural Selection 2), and (5) the emergence of cognitive processes such as imitation, mindreading and metacognition – 'cognitive gadgets' specialised for cultural learning. This self-assembly hypothesis is consistent with archaeological evidence that the stone tools used by early hominins were not dependent on fast, cumulative cultural evolution, and suggests new priorities for research on 'animal culture'.

How did human cultural evolution get off the ground? It would be an exaggeration to say there is nothing at all like it elsewhere in the natural world. Cetaceans[1-4], great apes[5, 6] and other animals[7-11] also pass skills down the generations through social learning, leading to stable differences between sub-populations. These differences are often called "traditions."[2, 10] Young bottlenose dolphins learn foraging techniques from their parents[12], young chimpanzees learn from older group members how to extract ants and termites from their mounds with sticks[13]. But human cultural evolution (see Table 1) is different. It is *cumulative*: small improvements to skills and technologies accumulate, resulting in products of such complexity that no one individual could possibly have designed them alone, without any learning from others[14-17]. Examples include canoes, spears, fire control, detoxification of bitter manioc, and, more recently, steam engines, computers, and satellites. Moreover, the accumulation is fast: improvements spread rapidly through populations, no longer tied to the timescale of biological generations. What makes fast, cumulative cultural evolution work? Where did it come from? And why is it the sole preserve of humans?

There is an emerging consensus that fast cultural accumulation draws on a suite of cognitive mechanisms including selective social learning, imitation, language, mindreading (or theory-of-mind) for teaching, metacognition and normative cognition, and that humans have evolved uniquely sophisticated versions of these mechanisms[18, 19]. But what explains the origin of these mechanisms?

A popular, influential type of answer appeals to gene-culture co-evolution. This occurs when the genetic composition of a population responds to changes in the cultural environment, leading to yet further changes in the cultural environment, and so on. The idea is often illustrated by the case of lactose tolerance: genes for lactose tolerance followed the spread of dairy farming, and enabled yet more dairy farming. Boyd and Richerson [20] proposed that some of the cognitive mechanisms involved in human cultural evolution— including the mechanisms mediating conformist bias—evolved, like lactose tolerance, by gene-culture co-evolution. This has remained a central tenet of the "California school" of cultural evolution that Boyd, Richerson, Henrich and their collaborators have built over the past thirty years.

While gene-culture co-evolution has received a great deal of attention, much less has been given to its purely cultural counterpart. We call this (borrowing a term from Muthukrishna and Henrich [21]) culture-culture co-evolution. As we define it here, culture-culture co-evolution occurs when a *culturally inherited* cognitive mechanism evolves in

response to a cultural environment, altering that environment and enabling further evolution of the cognitive mechanism, without any underlying genetic change.

Our aim here is to explain the basic idea of culture-culture co-evolution and to argue that it is worthy of sustained empirical investigation. Indeed, when it comes to explaining the origins of cumulative culture, we think it may even provide a better explanation than gene-culture co-evolution.

Cultural selection, fast and slow

At the core of our hypothesis about the origins of cumulative culture is a distinction between two types of cultural selection. A Darwinian process is one that relies on blind variation and selective retention (Supplement 1). In genetic evolution, "selective retention" always involves the differential survival and/or reproduction of individuals. But in cultural evolution, there are two different types of "selective retention" operating at different timescales.

The first, slower type is natural selection on culturally inherited variation [16, 22]. We will call this Cultural Selection 1 or CS1. CS1 is closely analogous to natural selection on genetic variation. When offspring spend a long time learning practical skills and ecological knowledge from their parents, valuable skills and knowledge will tend to spread through the population for the simple reason that their bearers will tend to have more offspring. Just as in a traditional process of natural selection, change is driven by differences in the number of biological offspring an organism produces. However, unlike in a traditional process of natural selection, the differences in reproductive output are caused by inherited differences in cultural variants, not genes, and they are transmitted from parents to offspring through social learning rather than genetic inheritance.

The second, faster type of Darwinian process occurs when individuals compete with each other for learners, so that individuals who recruit more learners can be said to have higher cultural fitness [23]. We will call this Cultural Selection 2, or CS2. Roughly, an agent's cultural fitness, with respect to a specific cultural trait, is the number of learners to whom it transmits its variant of that trait through social learning [22-25]. When learners are choosing from a wide range of potential models, and the models are competing for learners, there is potential for fast accumulation of small improvements, because the process need not be tied to the timescale of biological reproduction. We think CS2 lies at the heart of "cumulative culture" as we know it today. Small improvements to existing techniques spread not because they necessarily increase anyone's reproductive success, but because they allow models to attract more learners.

Although we have set out the CS1/CS2 at the individual level, the same distinction can be drawn at the group level. In other words, the CS1/CS2 distinction cross-cuts the distinction between individual selection and group selection. In the group-level version of CS1, change is driven by biological fitness differences between groups, and these differences are due to culturally inherited variation in group-wide patterns of behaviour. In the group-level version of CS2, change is driven by cultural fitness differences between groups— differences in their ability to attract new migrants who will learn their ways. This group-level version of CS2 will be important later on.

The CS1/CS2 distinction allows us to pose our question like this: at some point in human evolution, CS1 began to be supplemented by CS2, allowing fast cultural accumulation. Was this transition driven by gene-culture co-evolution, or did CS1 itself assemble the mechanisms that made CS2 possible? If the latter is the case, then the mechanisms that enable cumulative culture were products of culture-culture co-evolution. Cumulative culture was, in this specific sense, "self-assembling".

A self-assembly hypothesis

According to our self-assembly hypothesis, the role of genetic evolution, though important, was limited. Genetic evolution driven by increasing climatic variability and environmental change gave us larger brains[26], longer childhoods[27], and more powerful domain-general cognitive resources. Associative learning, working memory and inhibitory control were all dialled up, leading, eventually, to a distinctive capacity for slow, deliberative, explicit cognition that made heavy use of working memory [28-31]. These genetically-based upgrades to domain-general cognitive resources enabled early hominins to learn more efficiently the information they needed to hunt and gather in a changing and variable environment. But, on our hypothesis, these genetic changes were not responsible for shaping specialized cognitive mechanisms for accelerating cultural evolution. Cognitive mechanisms like imitation, mindreading and normative cognition emerged later via cultural evolutionary processes. Relatively simple cognition got fast cultural evolution off the ground. Learners were initially driven by attentional processes to copy better models and small improvements in technique; they did not make explicit comparisons between models or consciously recognize improvements. They had "competence without comprehension" [32].

Our hypothesis emphasizes the importance of culture-culture co-evolution. We do not assume that specialized cognitive mechanisms such as imitation have been genetically assimilated to any substantial degree. This is because we think the present-day evidence from

developmental psychology and cognitive neuroscience points towards these mechanisms being culturally inherited now (Supplement 3, [33]). To the extent that this is plausible, it is important to have viable evolutionary hypotheses that do not rely on genetic assimilation.

Our hypothesis has a basic platform—a starting point shared with other great apes— and five steps from that basic platform to fast, cumulative culture (Figure 1).
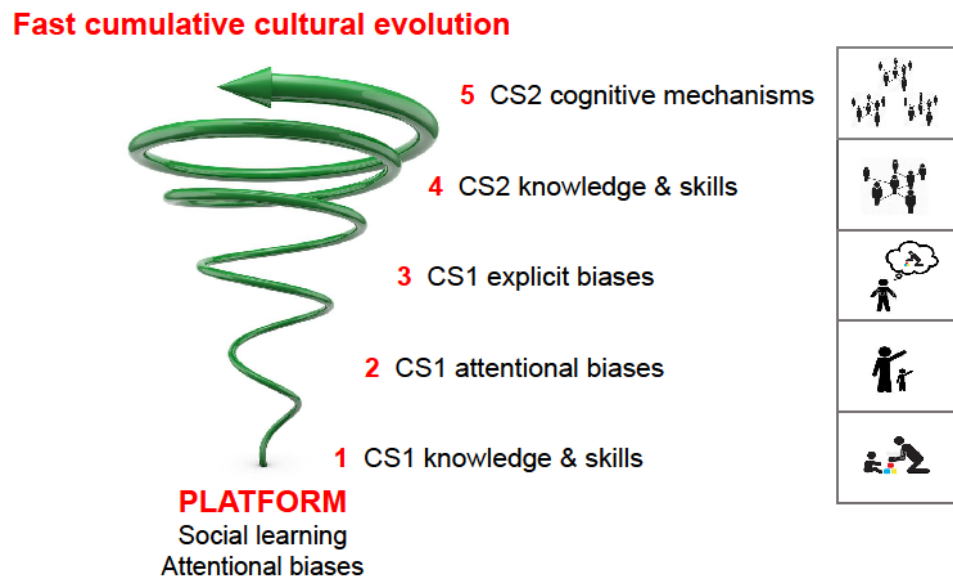

Figure 1. The self-assembly hypothesis. Culture-culture coevolution produces fast cumulative culture in five steps. Cultural Selection 1 (CS1) initiates the co-evolutionary process. First knowledge and skills (Step 1), then attentional social learning biases (Step 2), then explicit social learning biases (Step 3), are socially inherited from biological parents and spread through the population because their bearers tend to have more offspring. Subsequently, Cultural Selection 2 (CS2) also contributes. Enhanced knowledge and skills (Step 4) and cognitive mechanisms (Step 5) are socially inherited from unrelated individuals and spread through the population because some models are more successful than others in competition for learners. The five-step process not only produces fast cumulative culture, but is itself cumulative: each step augments, rather than replaces, the previous step (green arrow). The schematic figures on the right represent typical social interactions in each step. See text for details.

Step 0: The basic platform

The human lineage, at the time of its divergence from the other great apes about six million years ago, would have possessed a significant capacity for social learning. Like a wide range of animal species alive today, our earliest human ancestors could learn by observing the behaviour of other agents that some places and objects are worth exploring (stimulus enhancement[34, 35]), while others are either dangerous or rewarding (observational

conditioning[36, 37]). They could also learn socially what the outcomes of actions are likely to be (observational learning[38, 39]): prodding a hive releases bees, and digging in certain areas reveals tubers [40, 41].

These social learning capacities were once thought to depend on specialised cognitive processes, but recent evidence indicates that they are based on the same associative mechanisms as those involved in asocial learning [38, 42-47]. These mechanisms are powerful but, in the form present among our earliest ancestors, they do not allow high fidelity copying of fine bodily movement and technique.

Early hominins would also have possessed structural and attentional social learning biases. A structural bias is a tendency to learn from some models rather than others due to social structure and geography [48-50]. Juveniles would have learned most from their mothers, and to a lesser extent from other members of their immediate residential group, simply because they spent more time in close proximity to these agents than to others. An attentional bias is a tendency to learn from some models rather than others because they are particularly attention-grabbing [30, 51]. These attention-grabbing actors or actions might be intrinsically salient (large, noisy, pungent)[52], close to salient rewards (e.g. close to food [53, 54]) or previously associated with reward (e.g. their actions tend to produce or release food[55]).

Structural and attentional biases, like the social learning they modulate, are based on evolutionarily ancient, domain-general cognitive mechanisms [56, 57]. The social learning biases found in fish, birds and small mammals[48, 58] can be explained by attentional processes that bias social learning in the same way as asocial learning, and that evolved long before hominins appeared on the scene [57]. Nonetheless, we should not underestimate the power of attentional biases. They can produce patterns which, at the population level, fit the description of what cultural evolution theorists call conformist bias, prestige bias and payoff bias [16, 59, 60]. For example, suppose a child learns to associate a particular adult's behaviour with subsequent food rewards and, as a result, attends preferentially to that adult's behaviour. They will end up displaying a simple form of payoff-biased learning without needing to make any explicit judgements about whose behaviour leads to payoffs [55].

Step 1: Cultural Selection 1 of knowledge and skills
A capacity for social learning, and for simple learning biases, can be found in a wide range of species, and is clearly not sufficient for fast, cumulative culture. What made hominins different?

For early hominins, learned knowledge and skills were crucial for survival, and, with the extension of childhood, juveniles had more opportunity to acquire them vertically, primarily from their mothers [61]. Consequently, socially learned knowledge and skills began to spread through populations for the simple reason that their bearers tended to have greater reproductive fitness. Individuals who learned, for example, a more effective foraging technique from their mothers had better nutrition and more viable offspring, and passed the technique on to each of those descendants. CS1 of knowledge and skills became increasingly powerful and important.

This does not mean that CS1 is uniquely human. In fact, CS1 appears to be occurring now among bottlenose dolphins. Some wild dolphins in Shark Bay, Western Australia, use marine sponges, worn on their closed rostrum (beak), to probe the sea floor for food[62]. There is evidence that this foraging technique is transmitted vertically through social learning from mothers to their female offspring[12], and that mothers who forage in this way have more offspring than mothers who do not [63]. If it is confirmed that the technique is spreading by selection on cultural variation, these dolphins could be an excellent model system for studying the very earliest stages of hominin cultural evolution.

Step 2: Cultural Selection 1 of attentional learning biases

CS1 can be cumulative, but the accumulation will be slow (Supplement 2). Since it relies on differential biological reproduction, CS1 occurs on broadly the same timescale as genetic evolution (although the supply of variation may differ: new cultural innovations may appear more or less frequently than genetic mutations). What it provides is a process that can drive the evolution of new cognitive mechanisms that accelerate cultural evolution. In the first accelerating innovation, learned attentional biases—cognitive rather than physical skills—became subject to CS1.

CS1 acting on knowledge and physical skills (Step 1) produced an increasing number of valuable, socially-learnable traits in human populations: knowledge and skills that it would be advantageous for juveniles to learn from models other than one's own parents. Ancient attentional biases (Step 0) were available to guide juveniles when they were learning from unrelated adults and peers (oblique transmission and horizontal transmission), but their choice of models became yet more adaptive when they began to socially learn attentional biases from their parents. For example, they no longer had to learn for themselves, by trial-and-error, that it is beneficial to attend more to females for foraging skills and males for hunting skills (if indeed it was), or to go to elders rather than peers for rare ecological

information. Instead, they could learn these biases by tracking the social attention of their parents in different task contexts.

There is evidence that contemporary humans can socially learn attentional biases. Specifically, we can learn to attend more to some agents than others by following the gaze of third parties [64, 65]. For example, when given choices of foods to consume and objects to manipulate, 3- and 4-year-old children are more likely to learn from an adult to whom they have seen other adults attending than from an adult who was ignored [64]. Nonhuman primates have attentional biases that influence their choice of models[66, 67] but, as far as we are aware, no one has asked whether nonhuman animals can socially learn attentional biases. For example, there is evidence that vervet monkeys attend more to female than male models when learning how to open a box to obtain food[66] but the origin of this attentional bias is not known. Does each vervet learn through its own efforts that the behaviour of females is more likely than the behaviour of males to have a desirable outcome, or can young vervets learn to attend more closely to females by watching the watching behaviour of adults?

The existing evidence leaves a great deal of uncertainty as to when the ability to socially learn attentional biases first evolved. We conjecture that it was in place in Homo erectus well before 700,000 years ago, when the next steps in our account begin. It may have evolved much earlier. Although we suspect that socially learned attentional biases have been far more important for hominins than for other species, we do not rule out the possibility that some other animals do learn attentional biases from their parents, and that these learned attentional biases have been shaped by CS1.

Research on "shared attention" and "joint attention" in contemporary children often assumes that these phenomena require understanding of others' psychological states [68]. In contrast, step 2 in our self-assembly model does not require mindreading. For social learning of attentional bias, learners need to track models looking behaviour, not their mental states.

In so far as attentional biases are transmitted from parents to offspring, they can be targets of CS1. Parents with valuable attentional biases will have greater reproductive success, and the biases will spread.

Step 3: Cultural Selection 1 of explicit learning biases

We come now to the steps that we propose to be unique to the hominin lineage. As noted above, we agree with the received wisdom that human cognitive evolution involved genetically-based upgrades to domain-general cognitive resources, leading to a capacity for slow, deliberative, explicit cognition that made heavy use of working memory. The basic

logic of our self-assembly hypothesis does not depend on any specific assumptions regarding when this happened. We suspect, however, that Late Acheulean lithic technology is a sign that a form of explicit cognition was in place by around 700,000 years ago, the time of *Homo heidelbergensis*. Neuroimaging studies suggest that, in modern humans, success in Late Acheulean toolmaking techniques relies on working memory [69-72]. We cannot be sure that H. heidelbergensis would have learned and executed Acheulean toolmaking skills in the same way we do, but it is a reasonable conjecture.

Once explicit cognition is present, it enables a new type of learning bias on which CS1 can get to work—*explicit* learning biases. Explicit learning biases are internally represented rules of thumb. They may include highly specific rules such as: "find individual *X*, *Y* or *Z* to observe the manufacture of cleavers, and individual *A*, *B* or *C* to observe the manufacture of handaxes." Some rules may refer learners to specific models ("*X*, *Y* or *Z*"), while others may refer learners to a general *type* of model (such as "learn flint knapping from the person who makes the most symmetric shapes"). Explicit learning biases require a capacity for conceptual representation (e.g. possession of concepts referring to specific types of person, tool, and shapes), but it is not clear that they require language. Language could have come along later.

Attentional biases, of the kind that were important in Steps 1 and 2, are limited in their specificity and accuracy. They lead learners to better than average models from the pool of nearby options, but they will struggle to lead learners to the best models in a sizeable social group. By relating cranial volume to social network size, Gamble, Gowlett and Dunbar estimate that H. heidelbergensis lived in social networks of 100-150 recognized individuals [73, 74]. A more recent estimate, incorporating archaeological data alongside cranial volume, revised this downwards to 60-120 [75]. But even a group size of 60 is enough to create a problem. As group size grows, it becomes increasingly difficult for a juvenile to learn who the best experts are at specific skills purely by tracking the gaze of their parents. Juveniles might learn to attend to elders when uncertain about an important ecological fact, but they will not reliably find their way to the most knowledgeable elder. The problem is that they are not making explicit judgements about who should, and who should not, be copied in particular domains. It is simply that their attention is reliably drawn to some models rather than others by relatively low-level, domain-general psychological processes. Because learners are not reliably able to find the most technically accomplished models in large groups, in Steps 1 and 2 we do not yet have conditions in which small improvements to an established technique can spread reliably and rapidly.

In Step 3, explicit learning biases allow juveniles to reliably access the best models available, and to dedicate their learning efforts to those specific models. A learner who can reliably find the most technically accomplished models will gain biological fitness benefits from doing so, as long as their superior technique can be learned. This provides a selection pressure in favour of explicit learning biases, since they can overcome the limitations of attentional learning biases.

Although genetic changes of some kind will have been involved in the origin of explicit cognition, there is no reason to think that any further genetic changes are required for explicit learning biases, once explicit cognition in general exists. Explicit cognition brings with it a versatile capacity to represent rules. Rules about learning (such as *copy the majority*) can be learned, just like straightforwardly technical rules (such as *strike flint against pyrite to make a spark*). If the learning rules are passed down the generations from parents to offspring, CS1 will be able to shape them, gradually making them increasingly adaptive. We envisage this refinement of explicit learning biases through CS1 as a gradual process taking place over hundreds of thousands of years, beginning around 700,000 years ago.

There is evidence that explicit social learning biases—judgements about who to copy —are crucial to fast cultural accumulation [51, 76, 77]. They are used, in addition to attentional learning biases, by adult humans alive today[78-80], but as yet there is no evidence that they are used by children younger than 4 or 5-years-old[81] or by nonhuman animals.[57]

Step 4: Cultural Selection 2 of knowledge and skills

With accurate, specific, explicit learning biases, assembled by CS1, comes the possibility of fast, cumulative cultural evolution of knowledge and skills. An explicit rule can be highly *task-specific*: it can pertain to the manufacture of a particular tool, for example, and may identify a correlate of success that is very specific to that task, such as the symmetry of the end-product. This task-specificity means high quality models can be reliably identified, leading to greater *exclusivity*. A learner equipped with a model selection strategy that reliably picks out high quality models for particular task-specific skills has more to gain from investing effort in copying the specific technique of a specific individual, rather than hedging their bets and learning from as many different models as possible [51, 82].

High fidelity copying of small improvements is the type of copying that allows fast accumulation. Because learners are very discriminating—they choose only the best models in the relevant task domain, and learn exclusively or nearly exclusively from them—small

improvements in technique can spread reliably and rapidly without being explicitly recognised by the learner as improvements. They spread because they make a substantial difference to the cultural fitness of their bearers: their success in attracting learners who are selecting their models using explicit learning biases. If a small improvement to an existing technique promotes the correlate of success tracked by the learning bias (e.g. the symmetry of the end-product), learners will gravitate towards the innovator. Small improvements to existing techniques will be retained in the population and will spread widely, creating many new sites for new small improvements, which will in turn be retained and copied.

This is a process with a Darwinian character, but one in which change is driven not by differences in reproductive success but by differences between models in the number of learners they attract. This is Cultural Selection 2 (CS2): cultural change driven by culturally inherited differences in cultural fitness. CS2 is the engine of fast, cumulative cultural change. We do not think there was a single, special moment when CS2 "took off", and we do not think that explicit learning biases were the only crucial ingredient. Life history mattered: as juvenile development lengthened, juveniles were able to invest more and more time in learning knowledge and skills, increasing the opportunities for CS2. Demography also mattered: in large, richly interconnected populations, there were more heads in which innovation could occur, more heads in which small improvements could be retained, and more to gain from seeking out the best models for particular skills [83]. We envisage CS2 becoming gradually more important over time, as explicit learning biases become increasingly task-specific and exclusive, as the juvenile period of human life history becomes increasingly long, and as populations become larger and more richly interconnected. Levallois prepared core techniques may be an archaeological signature of cumulative CS2 [19].

Step 5: Cultural Selection 2 of cognitive mechanisms
CS2 is not limited to selection of small improvements to knowledge and skills. Small improvements to cognitive mechanisms that accelerate cultural accumulation, including imitation, mindreading and metacognition, can also increase in frequency.

How might this work? The idea is that the cognitive mechanisms of cultural learning are themselves learned skills, or "cognitive gadgets" (Supplement 3[30]), and learners are selective in who they learn these skills from. Let us focus on the case of imitation—copying the topography of body movements. Imitation involves learning associations between how movements feel from the inside and how they look from the outside, solving the

correspondence problem. An adult can help a child to develop imitation in various ways: by copying their own movements (i.e. by imitating them) in their sight, by giving them opportunities to practice copying bodily movements with appropriate feedback, and by seeding the child's environment with reflective surfaces that allow the child to see what they are doing [84].

In contrast to some other skills, a child will not learn imitation from a *single* model. More plausibly, the child will learn it gradually from a wide range of adults and peers in their residential group. Because of this, we think a process of model selection operating at the group level may have been particularly important. Provided migration between residential groups is possible (and, in contemporary hunter-gatherers, it is common) the migrating parent can choose the group in which they live, and can therefore choose the child's set of models. The parent will choose using learned explicit rules, such as *move where people look healthiest*, which they can put into practice at large seasonal aggregations of many residential groups [85]. The parent's choice will be influenced by, among other factors, the imitative abilities of the group, in so far as groups with better imitative abilities will be more cooperative and have better ecological knowledge and skills. Groups with better imitative abilities will attract more migrants, and therefore more learners. This is a form of CS2, since it relies on model selection, but the model selection involves evaluations of whole groups rather than individuals. Moreover, since imitation is transmitted in part through models imitating learners, we predict that models who are better imitators will also be better at transmitting their superior imitative abilities to those who spend time around them—a positive feedback loop.

In short, groups whose members have better cognitive mechanisms for high-fidelity, selective copying will attract more migrants and grow in size at the expense of others. As groups get larger, there are more and more heads in which a new, small innovation might occur. This has the potential to further accelerate the CS2 of knowledge and skills at the level of individuals within those groups, making the group as a whole yet more attractive to new migrants—another positive feedback loop.

Conclusion

The self-assembly hypothesis offers three new answers to the question: Why is cumulative culture uniquely human? They are not mutually exclusive, and each answer is empirically testable.

First, it is possible that CS1 of knowledge and skills (Step 1) has rarely evolved because few species have had a social structure that gives juveniles the opportunity to learn a lot from their parents with high fidelity [48, 86]. This would be supported by evidence—perhaps modelled on recent work with dolphins[2, 4, 12, 63]—showing that CS1 of knowledge and skills is more common in species where juveniles spend most of their time with biological relatives of the previous generation.

Second, it may be difficult to transition from CS1 of knowledge and skills to CS1 of attentional biases (Step 2) because variants required to track parental attention are rarely available. In humans, attention tracking is enhanced by inborn tendencies to orient to faces[87] and voices[88] and possibly by reduced scleral colouration [89]. A priority for future research is to find out which extant species are capable of socially learning attentionally biases (for example, to learn *copy females* by observing the orienting behaviour of third parties[66]), and whether, in human and nonhuman populations, such biases can be vertically inherited in a way that enhances biological fitness.

Third, there may be a roadblock at the emergence of explicit social learning biases (Step 3). These require explicit cognition of a kind that may or may not be dependent on language [51]. To find out, we need research with nonhuman animals that does not merely document social learning biases, but is designed to distinguish biases mediated by implicit (attentional) from explicit cognition.[57]

The self-assembly hypothesis suggests that fast, cumulative culture emerged slowly by means of CS1. In this respect, it is consistent with archaeological evidence that the stone tools used by early hominins (Oldowan and Acheulean) were not dependent on fast, cumulative culture [70, 90, 91].

The search for animal culture[9, 11] has been dominated by the idea that patterns of geographical variation in socially learned behaviour, and in particular the diffusion of qualitative novelty, are the most important things to investigate [3, 7, 8, 46]. There has been interesting developmental work on opportunities for social learning in free-living primates, e.g. [92, 93], but relatively little attention has been given to vertical cultural inheritance: How much do offspring learn from their parents? Are small improvements retained or not? The self-assembly hypothesis suggests that these questions matter, because the roots of fast cumulative culture are more likely to be found in species that, due to their social structure, have significant potential for high-fidelity vertical cultural inheritance under free-living conditions. This would be evident in family-specific behaviours: techniques passed down the

generations of a family group and varying between families, with small improvements being retained.

We have argued that the self-assembly hypothesis is coherent, plausible, and empirically testable. It contrasts with a standard gene-culture co-evolution story by giving a central role to culture-culture co-evolution, with a fairly circumscribed role for genetic change. This type of account is favoured by evidence that cultural learning is culturally inherited today (Supplement 3), and can be tested further through empirical research on the behaviour of human and nonhuman animals.

Let us now return to the questions we started with. What makes fast, cumulative cultural evolution work? Our answer is CS2: models varying in the number of learners they attract, with small, unobvious improvements being copied faithfully and more often, allowing those improvements to spread rapidly through populations. Where did it come from? We suggest that CS2 came from CS1: a simpler, slower process in which knowledge and skills, then attentional biases, then explicit biases were inherited by juveniles predominantly from their biological parents. Why is cumulative cultural evolution the sole preserve of humans? Because there are several points along the path from a platform of basic social learning capacities to CS2 where the conditions have to be just right. Other species, throughout the animal kingdom, may be at various points on the path, but only one has made it to the end.

Table 1. Glossary

Attentional bias	A social learning bias mediated by domain-general attentional processes
Asocial learning	Learning without the assistance of other agents. Also known as "individual learning"
Cognitive gadget	A domain-specific cognitive process shaped by cultural evolution
Conformist bias	A social learning bias in favour of variants that are currently prevalent among available models
Cultural evolution	Change in the frequencies of cultural variants over time
Cultural fitness	The number of learners an individual model succeeds in attracting, weighted by the model's degree of influence over the learner
Cultural inheritance	The transmission down the generations of cultural variants, leading to persisting cultural differences between populations
Cultural learning	Social learning mediated by cognitive mechanisms that are specialized for promoting cultural inheritance
Cultural Selection 1 (CS1)	A Darwinian process in which cultural variants spread because they cause their bearers to have more biological offspring, and because offspring learn from their parents
Cultural Selection 2 (CS2)	A Darwinian process in which cultural variants spread because they cause their bearers to attract more learners, giving them higher cultural fitness
Cultural variant	Anything that can be learned socially (e.g. psychological processes, artefacts, skills, habits, customs, rituals, ideas, beliefs, values)
Cumulative cultural evolution	Cultural evolution in which small improvements to existing cultural variants spread through populations, gradually leading to complex adaptive products that no single individual could have designed from scratch
Domain-general cognitive mechanism	A cognitive mechanism that works in the same way across a broad range of tasks and contexts, e.g. social and non-social
Domain-specific cognitive mechanism	A cognitive mechanism that works in one task or context and less efficiently or not at all in others, e.g. social or non-social
Explicit bias	A social learning bias mediated by a domain-specific psychological rule such as *copy the majority*
Genetic assimilation	A process whereby environmentally induced phenotypic variation acquires a genetic basis
Genetic evolution	Change in the frequencies of genes over time
High-fidelity transmission	The learning of a cultural variant with sufficiently few errors that even small, unobvious improvements will be retained
Horizontal transmission	The learning of a cultural variant by a member of one generation from another member of the same generation
Oblique transmission	The learning of a cultural variant by a member of a younger generation from a member of an older generation who is not a biological parent
Payoff bias	A social learning bias in favour of learning cultural variants that effectively yield rewards
Prestige bias	A social learning bias in favour of learning from models who are already successful in attracting learners and have markers of that success
Social learning	Learning assisted by observation of, or interaction with, other agents
Social learning bias	Any mechanism that biases an individual's social learning away from one cultural variant and towards another. Also known as "social learning strategy", "learning bias", and "transmission bias"
Vertical transmission	The learning of a cultural variant from a parent by its biological offspring

Supplement 1 - Cultural evolution and population thinking

Cultural evolution research is currently in a period of rapid development, and various different schools of thought co-exist in the field.[1-8]

Most cultural evolutionists agree on the importance of "population thinking": cultural change can be understood by looking at the dynamics of social learning processes acting on populations. But many population thinkers downplay the importance of Darwinian selection processes.[9,10] For example, Sperber and colleagues[11,12] have developed a non-Darwinian framework based on the concept of a "cultural attractor". These non-Darwinian approaches are not our focus here.

Defenders of Darwinian (or "selectionist") approaches, pioneered by Donald Campbell[13,14] in the 1960s and 1970s, hold that Darwinian processes have a special role. They argue that, just as in the case of genetic evolution, there are many causes of cultural change, but only a Darwinian process of "blind variation and selective retention"[13] is able to generate complex, well-adapted cultural products without the need for intelligent design.[15,16,17,18]

Darwinian approaches can themselves be divided into meme-centred and individual-centred approaches.[19,20] The meme-centred approach regards the cultural inheritance as particulate, like genetic inheritance, and models the flow of these particles through populations.[6,21] The individual-centred approach does not assume that cultural inheritance is particulate. It focusses on learners and the people from whom they learn ("models"), looking in a more holistic way at the inheritance channel between a model and a learner. Sometimes models that succeed in attracting larger numbers of learners are said to have higher cultural fitness (Supplement 2).

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Supplement 2 - Cumulative and non-cumulative Darwinian processes

A cumulative Darwinian process is one in which very small improvements gradually accumulate. Each small improvement spreads through the population, creating many new sites at which a further small improvement may arise by chance. This next improvement will then itself spread, creating new sites for yet another small improvement, and so on. The result is that complex, adaptive, apparently "well designed" products are gradually assembled without the need for any intelligent design.[1-5]

Both types of cultural selection can be cumulative but will not always be cumulative. Special further conditions are required to turn a selection process into a cumulative one.[6] In particular, the transmission of traits must occur with high fidelity, so that tiny improvements (so small as to be unobvious to their inventors) that arise by chance will be inherited rather than disappearing. It is also crucial that tiny improvements reliably make a difference to fitness, so that selection can "see" them.

We hypothesize that, at an early stage in hominin evolution, cultural transmission from parents to their offspring (vertical transmission) already met the conditions for accumulation: fidelity was high owing to the sheer amount of time offspring spent with their parents, and small differences in cultural variants made a difference to a parent's reproductive success. The result was cumulative CS1. We think cumulative CS1 may even occur in some non-human animals, such as dolphins and chimpanzees.

By contrast, in common with many researchers who study traditions in nonhuman animals[13], we hypothesize that cumulative CS2—the faster, distinctively human type—only came along much later. On our hypothesis, it required exclusive, task-specific copying of models, achieved through explicit learning rules. Only then would tiny improvements to existing techniques have been reliably transmitted to learners, and only then would these tiny improvements have reliably made a difference to a model's ability to attract new learners.

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Supplement 3 - Cognitive gadgets

Cultural learning, the kind of learning that makes cultural evolution possible now, involves imitation, mindreading and language. Since the 1970s and 1980s, it has been assumed that each of these capabilities is a "cognitive instinct"[1] designed by genetic evolution in the Pleistocene era, inherited in the DNA of each human child, and requiring minimal learning for its development. However, recent evidence from developmental psychology and social cognitive neuroscience challenges this assumption by suggesting that, like literacy, the capacities to copy new body movements, to interpret the minds of others, and to communicate using language are all constructed by learning in the context of social interaction. Rather than cognitive instincts, they are "cognitive gadgets".[2]

Imitation was thought to be a cognitive instinct because influential research in the 1970s suggested that newborn human babies can copy facial expressions.[3] This result was recently undermined by a large-scale study that failed to find any sign of imitation in newborns.[4,5] Furthermore, evidence has emerged that the capacity to imitate develops slowly in the course of childhood[6,7] and depends on social experience in which juveniles are exposed to synchronous action, optical mirrors, and imitation by other agents.[8-10]

Mindreading was taken to be a cognitive instinct because it depends on specialised computations and localised areas of the brain, and because people with autism find it particularly difficult to interpret thoughts and feelings. However, these inferences have been weakened by evidence that literacy, a capacity known to be culturally rather than genetically inherited, is also characterised by computational and neural specialisation, and associated with a distinctive developmental disorder (dyslexia).[11] Moreover, positive evidence that mindreading is a cognitive gadget has come from research showing that the rate, sequence and extent of mindreading development depends on how much and in what ways children converse with adults about mental states.[12-15]

The status of language is not so clear. Many linguists and language scientists remain convinced by Chomsky's "poverty of the stimulus argument"; that language has grammatical features that could not be learned from the environments in which language develops.[16] However, this view is being challenging with increasing vigour by research showing that FOXP2 is not a "language gene"[17]; "specific language impairment" is not, in fact, specific to language[18]; computers can learn complex grammatical structures without inbuilt linguistic knowledge[19,20]; and, in their everyday lives, children receive much more language tuition than earlier studies suggested.[19]

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