



Review

Replication and emergence in cultural transmission

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Abstract

Humans are fundamentally defined by our socially transmitted, often long-lived, sophisticated cultural traits. The nature of cultural transmission is the subject of ongoing debate: while some emphasize that it is a biased, transformational process, others point out that high-fidelity transmission is required to explain the quintessentially cumulative nature of human culture. This paper integrates both views into a model that has two main components: First, actions – observable motor-behavioural patterns – are inherited with high fidelity, or *replicated*, when they are copied, largely independently of their normal, effective or conventional function, by naive learners. Replicative action copying is the unbiased transmission process that ensures the continuity of cultural traditions. Second, mental culture – knowledge, skills, attitudes and values – is not inherited directly or faithfully, but instead *emerges*, or develops, during usage, when individuals learn the associations between actions and their contexts and outcomes. Mental cultural traits remain stable over generations to the extent that they are informed by similar (replicated) motor patterns unfolding in similar environments. The arguments in support of this model rest on clear distinctions between inheritance and usage; between public-behavioural and private-mental culture; and between selection for fidelity and selection for function.

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1. Human cultural transmission

Human behaviour is extraordinary in nature: we have developed technology and social organization to levels unparalleled among animals, as well as uniquely human traits including art, language and philosophy. The primary specific determinant of human life is, arguably, culture. Human culture has the characteristics of an evolutionary system [37,51,40,24,122,247,227,164,288,188,228,153,47,26]: cultural traits can persist over generations, change and be recombined in novel ways, while new traits come into existence as others disappear. Cultural evolution has given rise to sophisticated, diverse and long-lived traits in myriad domains including technology [230,243,253], language [131,125,126,66,72,62,61], religion [30,5,18], science [37,122], the economy [69,152], social habits [133], and values and attitudes [276,202,203].

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Human cultural evolutionary studies address three broad questions. The first asks what biological, or genetic, evolutionary processes have made us essentially cultural beings (e.g. [24,268,111,112,227]). The second question asks how cultural evolutionary processes such as social learning, interaction and usage explain the structure and distribution of variants of human cultural traits (e.g. [37,51,24,122,218,247,57,153]). The third question asks about the interactions between biological and cultural evolution, in other words, the co-evolutionary dynamics that shapes both humans and our culture (e.g. [63,52,270,107]). This paper is concerned with the second question and, while acknowledging that culture and biology interact, it discusses purely social aspects of cultural evolution.

An essential feature characterizes human cultural evolution: it is cumulative. Human cultural traits build onto prior, existing traits to attain a level of sophistication that is beyond the creative capacity of a single individual [266,261,107,160]. University degrees, credit cards and languages are examples of outcomes of cumulative cultural evolution. Traits occasionally change through processes such as modification (e.g. of the shape of a hammer-head), invention (e.g. of the pinch-to-zoom gesture on a touch-screen) or combination (e.g. of a stone tool and a shaft to make a spear) [65,153]. When modified traits are adopted by new learners, they form new cultural lineages – new branches in the phylogenetic tree of culture – which may subsequently be further modified. When this process is repeated, the result may be highly elaborate or refined traits.

Cumulative evolution is, arguably, unique to human culture. However, a few recent studies claim to show examples of cumulative culture in other species, such as chimpanzees [20] and pigeons [236]. Long-lived songbird dialects within bird species [174,205] as well as experimental results with baboons [44] and zebra finches [67] can also be considered examples. However, the few known uncontroversial cases of long-lived primate cultural traditions do not exhibit accumulation [182,286]. Regardless of whether other species are considered to have it, it is indisputable that cumulative cultural evolution is orders of magnitude greater in humans than in any other species.

Different factors have been proposed to support human cumulative cultural evolution, including intention-reading [86,274,275], content-, model- and frequency-based biases [280,223,293,34,185]; and rationality [223,293], among others. Most scholars agree that cumulative cultural evolution requires high-fidelity transmission [273,267,25,36,261,287,166,54,107,114,153], without which modified traits (which could not be re-invented by a new individual) could not be retained for future generations.

Despite general agreement that cultural traits evolve and that they do so cumulatively, there are important conflicts in terms of focus, assumptions and terminology between schools of thought related to the nature of cultural transmission (see e.g. 1,251,115). Two notable non-orthogonal conflicts are: First, culture is defined either as fundamentally mental, or as fundamentally behavioural, or as an alternation of mental traits and behaviour. Second, for some, the main process in cultural evolution is (biased) transmission, while for others it is transformation.

The remainder of the introduction reviews these conflicting positions and the ensuing sections present a new model of cultural transmission that reassesses and partially integrates those positions as well other theories of learning and social cognition. In the new model, actions – motor, observable aspects of behaviour – *replicate*; in other words, they undergo direct social, faithful and content-indifferent copying by naive learners. In contrast, mental culture *emerges* or develops within each individual when the inherited actions are deployed for their normal function during usage in context.

1.1. Culture as predominantly mental or behavioural

Many scholars interested in human culture have produced definitions of culture that privilege the mental realm. According to these, culture is information stored in human brains that is able to affect behaviour [51,40,24,122,56,247,206,243,111,105,227,113,188,228,107]. This information includes mental states such as ideas, knowledge, beliefs, values, skills, and attitudes [227] acquired through social inheritance including teaching and imitation learning (e.g. [40,24,227]) or inference (e.g. [247,110,105]). In this view, behaviour is merely the public manifestation of the main, mental, aspect of culture. Many academics studying the evolution of the material culture equally prioritize mental aspects of culture. The lineages of artefacts – or features thereof – such as textile patterns [260], basketry patterns [132] or projectile points [33] are but the public manifestations of mental skills learned and taught by successive generations.

In contrast to those mentalist cultural approaches, other scholars, many of whom study social learning in humans and non-human animal culture, produce definitions of culture that prioritize behaviour (e.g. [40,17,84,155,286,289,7,81,153,160,115]). From this perspective, cultural traits include public, motor-behavioural actions that can be learned

from observation. Recently, a number of evolutionary linguists have also shifted their focus from formal, mental aspects of language to linguistic behaviour: speech sounds, word-forms and utterances [48,269,229,281,66,210,62,215].

A third view contends that cultural transmission proceeds by alternating mental representations and public productions [247,110,42,195].

1.2. *The transmission of mental culture: biased transmission, attraction and inference*

Mentalist views are interested in the transmission of culture from one mind to another [51,40,24,122,56,206,243,111,227,228]. This process must be mediated by public cultural manifestations, and, many contend, has low fidelity. A question arises here: How can low-fidelity transmission of mental culture support cumulative culture? Two schools of thought, Cultural Attraction Theory and Dual Inheritance Theory, offer different answers.

For Cultural Attraction Theory, both the production of public culture and the acquisition of mental culture are fundamentally transformational and reconstructive [247,110,42,195]. Crucially, however, transformation is constrained: when cultural traits are transmitted, instead of changing randomly, they tend to gravitate towards certain states under the influence of ‘factors of attraction’. These factors originate in our brains, bodies and environments and can be of two types. Cognitive factors of attraction include biases and background knowledge that make some representations easier to invent, learn, process or remember than others [195,241]. Ecological factors of attraction range from the climate to the availability of artefacts and cultural institutions to the efficiency of an artefact or behaviour. Ecological factors of attraction are somewhat similar to the forces operating in Odling-Smee, Laland and Feldman’s ecological inheritance pathway [154,207]. The most likely end states of the transformations are called ‘attractors’ [247,110,42,98,43,195]. These are traits that have a high probability of being reconstructed or re-invented; in evolutionary terms we could say these are the fittest variants.

Examples of attractors include minimally counterintuitive concepts, such as characters or narratives that possess few non-intuitive features, including animals that can speak and religious and traditional myths [30,204]; social information in narrations, which is more likely to be recalled and re-told than other kinds of information [189]; words and letters, supported by culturally acquired factors such as literacy and orthography [241]; states of affairs such as smoking and not smoking [42]; and certain graphical shapes, for instance those found in coats of arms [196]. The transmission of attractors is ‘self-correcting’: for example, when a person copies a written word [43] or a letter [241], or a drawing of a five-point star [248], she will ignore misspellings and production errors and produce the correct representation. Cultural Attraction Theory’s explanation for the cross-generational stability of culture, therefore, highlights the role of a heterogeneous set of factors of attraction in guiding transformation and reconstruction.

Cultural Attraction Theory, therefore, explains the stability of cultural traits under low-fidelity transmission by applying the idea of attraction. In contrast, Dual Inheritance Theory answers the same question by proposing that variation is constrained by ‘biased transmission’ [24,227,188]. The biases at work are forces that modulate the probability that a cultural trait variant is observed, copied or adopted [24]. We could say that these forces influence the cultural fitness of variants. Three types of bias are proposed: first, direct biases, also called content-based biases, originate in intrinsic properties of the variants (e.g. an observer is more likely to copy the most efficient variant of a tool, or the recipe that produces the tastiest cake). Second, model-based biases depend on properties of the observed models, or producers of a variant (e.g. we are more likely to adopt the traits displayed by models who are prestigious, similar to us, or knowledgeable, [109,103,114]). Third, frequency-based biases operate if the frequency of a variant disproportionately affects the probability of its being copied (e.g. conformist bias makes us more likely to adopt a trait if it is very frequently observed) [24,108]. Biases on transmission are supplemented by a bias on innovation called ‘guided variation’ [24] or ‘directed mutation’ [219], according to which humans tend to produce innovations that are, on average, more effective or efficient for their function (and thus more likely to be copied) than existing variants. In other words, as a consequence of guided variation, innovations tend to have higher cultural fitness than existing variants. Dual Inheritance Theory therefore explains cultural stability not as a result of high-fidelity transmission of traits, but of human cognitive biases that favour the adoption and generation of certain kinds of cultural variants.

In order to explain the cognitive mechanisms supporting the social transmission of mental cultural traits, Cultural Attraction Theory and some work that falls within Dual Inheritance Theory appeal to inferential learning. The transmission of mental culture must involve production of behaviour by models and inference of mental traits by observers [247,248,3,4,29,123,124,144,227]. During this kind of inference, a learner observes others’ behaviour and mentally

attempts to reconstruct or reverse-engineer [145,295] the underlying knowledge, attitude, value or skill that produced it. In Henrich and Boyd's [110] formal model of inferential cultural transmission, two processes are at work: 'inferential transformation', measuring the extent to which different variants of a trait are preferred, and 'selective attention', measuring the strength of (content-, model- and frequency-based) transmission biases. Assuming that inferential transformation is much stronger than selective attention, Henrich et al. [113] and Henrich and Boyd [110] demonstrate that the resulting distribution of variants in a population reflect the inferential transformation biases and are well fitted by replicator dynamics [259]. Somewhat similarly, Kalish et al.'s [135] iterated Bayesian transmission model involves cultural transmission chains in which each agent observes (public, behavioural) data generated by the previous agent and uses it to try to infer the (mental) hypothesis that generated the data; then, the agent uses the hypothesis inferred to generate data that will be observed by the next individual. Kalish et al. [135] show both analytically and experimentally that, after many iterations, the system arrives at a stationary distribution, which is the same as the prior distribution of hypotheses. In other words, the probability that a mental variant spreads to the population is proportional to the prior preference of individuals for that variant. Moreover, in line with the result of Henrich and Boyd's [110] model, the inductive prior bias drowns the effect of selective pressures.

Inferential learning is a low-fidelity transmission mechanism for mental traits. It does not guarantee that learners will infer the same hypothesis as the model they observe, as more than one hypothesis could generate the same behaviour. Nevertheless, inductive biases stabilize the process to the point that transmission has the same effects as replication [247,4,28,29,113]. Induction and inference in combination with other biases may thus achieve the fidelity required for cumulative culture. However, analytic and computational models of inference are agnostic as to the actual embodied and cognitive mechanisms that underlie inference, and experimental models of inferential cultural learning (e.g. [97,146,147,68,254]) use enculturated adults as participants, rather than naive learners, so it is not clear to what extent they model cultural transmission to naive learners.

1.3. *The transmission of public culture: imitation and teaching*

A sizeable proportion of the cultural evolutionary literature, including many who privilege mental aspects of culture, propose that cultural inheritance involves reproducing others' observable behaviour (actions) through social learning (e.g. [40,24,267,271,227,153,283,160]). Social learning has many manifestations [284,296,287,81], but here it is most relevant to distinguish between three that involve observation of behaviour, namely emulation, imitation and over-imitation. In *emulation*, an observer sees a model perform some actions and attain an outcome and attempts to reproduce the outcome, but not the behavioural means (the actions) to achieve it [272]. In contrast, *imitation* (see [127]) and *over-imitation* involve copying the actions themselves. Specifically, in *imitation*, the observer copies the actions as well as the outcome; and in *over-imitation*, she copies only the actions, including those that have no relevance to – or even hinder – the attainment of the outcome [186,285,86,120,171,74,162]. Emulation, a low-fidelity cultural inheritance mechanism with a focus on outcomes or goals, cannot support multigenerational cultural lineages [120], but imitation and over-imitation, with their focus on actions, means or process, can [273,25,120,261].

Non-human primates tend to focus on outcomes, and therefore emulate by default [36,285,271], but may also imitate when the relationship between actions and outcomes is opaque [120]. Arguably, there is only one clear instance of significant action imitation in non-human animals in the wild: *vocal learning*, or the ability to copy complex vocalizations. Humans share this ability with a few distantly related species, including some songbirds, whales, dolphins, seals, bats and possibly elephants [130,149,212]. Action imitation in non-human primates has only been attested occasionally, and always copying humans, for instance in orangutans [234,156] and chimpanzees [222]. In humans, in contrast, action imitation is frequent in children [171,184,162], adolescents [200] and adults [183,75,289].

All social learning – and therefore, all cultural transmission – is ultimately inductive [68]. The transmission of actions – purely observable, motor aspects of behaviour through imitation is, therefore, also inductive. It involves the observation of a behavioural pattern in another individual, the inference of the motor responses required to produce the same patterns, and the production of those responses. This is the kind of reverse-engineering that occurs in Bayesian inferential learning, but applied to a very specific type of hypotheses: about the patterns of motor activation that result in a particular action.

Cultural transmission can be supported by teaching, or pedagogy. Combined with language, teaching is an important way to convey cultural mental representations (e.g. [247]) and behavioural skills (e.g. [194]). However, much of the literature on teaching focuses on its role as facilitator of the transmission of behaviour. Teaching involves experts

modifying their behaviour in order to enhance the fidelity of information transmission [76,50] or to facilitate learning [24,38,148], and assumes learners' receptivity to the expert behaviour. Teaching is present in mammal, insect and bird species (see [119] and [148] for reviews). In humans, components of teaching may be innate [49,87] or socially learned [114]; it is supported by cognitive capacities such as theory of mind and joint attention [273,150] and by ostension, reference and relevance [50]. Teaching incurs a cost for the teacher [38], but the advantages of faithfully passing on cognitively opaque or complex traits, such as the products of cumulative culture, outweigh that cost [271,76,153,35].

1.4. Integrating public and mental culture

Comparative and human social learning studies have shown that imitation and teaching can support high-fidelity inheritance of behaviour. Some of the authors who defend low-fidelity inferential transmission of mental traits agree that high fidelity is necessary for cumulative cultural evolution, and anecdotally recognize that public behaviour is inherited with high fidelity. Speaking about how to tie a bowline knot, Richerson and Boyd [227] observe that “If we could look inside people’s heads, we might find out that different individuals have different mental representations of a bowline, even when they tie it *exactly the same way*” (2005: 63-64; emphasis added). In the same vein, Claidière et al. [43] argue that while learning meaning requires inferential reconstruction, learning word-forms is mediated by imitation. Hodgson and Knudsen [118] note that “with habits, replicative similarity is necessarily present at the behavioural level” (2004: 288).

At the same time, it is acknowledged that it is not clear exactly what kind of information is transmitted, and how and when it is transmitted so that traits may persist for many generations ([23,27], but see proposed cognitive mechanisms underlying cultural transmission by e.g. [160] and [115,116]; these are discussed below). What seems to be missing is a model that reconciles the attested high-fidelity transmission of public actions with the lower-fidelity transmission of mental traits. This model should explain how cultural transmission can be stable across individuals and over generations, and at the same time be affected by dual inheritance theory’s transmission biases and by cultural attraction theory’s transformation and reconstruction. Finally, it should specify which cognitive mechanisms underlie both faithful and biased or transformational transmission.

The remainder of the paper defends such a theoretical model of cultural transmission, based on two hypotheses. The first (section 3) is that behavioural, public culture is replicated. The second (section 4) is that mental culture is emergent. Before arguing for this model, section 2 makes two interconnected distinctions, the first one between learning cultural traits by naive individuals, and production of cultural traits in order to achieve a function by enculturated individuals, and the second one between selection for fidelity and selection for function. These distinctions are captured by the contrast between inheritance and usage.

2. Inheritance and usage

This section first describes two levels of selection that operates in biology (molecular and organismal) and then argues that the same two levels are found in culture (at the levels of inheritance and usage, respectively). I call them selection for fidelity and selection for function.

2.1. In biological evolution

The beginning of life, before DNA and other complex molecules existed, was characterized by cyclical chemical reactions involving autonomous replication, or “continued growth and division which is reliant on input of small molecules and energy only” [255]. Inheritance, with varying degrees of replication fidelity, occurred whenever molecules begat similar molecules. Variation was brought about by changes in the molecular structure and by recombination or exchange of molecular parts. For the present discussion, the relevant feature of this early life system is that it did not include translation: the molecules did not code for anything in the way DNA today codes for proteins. The only “emergent function” of these systems was self-preservation, as the dynamics of the system selected the most faithfully replicating molecules, those that were better adapted to the replication mechanism, which therefore increased in frequency and produced even more (faithful) copies of themselves, leading to an increasingly permanent *molecular* phylogenetic trace. In the long run, thus, transmission fidelity was maximized. This is *selection for fidelity*.

This process resulted, for instance, in the establishment of DNA as the extremely stable repository of genetic information, and it still operates, in the form of stabilizing selection on the genetic material. Genes are, therefore, adapted to replicate [121,252].

In addition to the stability of early molecules, present-day genes have *functions*; they are, indeed, identified by their functional products [90]. Genes contribute to the fitness of the organism that carries them, for instance by coding for proteins. The more a gene contributes to the organism's fitness, the more, by definition, it propagates in a population. Genes are under natural selection. Since this type of selection is mediated by gene functions, I will call it here *selection for function* (a superordinate of biology's natural selection, applicable across evolutionary systems). The transition that took place when the replicating molecules began to code for proteins is the third of the major evolutionary transitions proposed by Maynard Smith and Szathmáry [178]. For Woese [292], it is *the* major transition of life; he calls it “the Darwinian threshold”, because it marks the beginning of natural selection, enables vertical transfer of genetic information, and leads to an increasingly permanent *organismal* phylogenetic trace.

2.2. In culture

The two selection processes, for fidelity and for function, are also present in cultural evolution. In order to persist over generations, a cultural trait faces two challenges – it has to be transmitted largely intact to new individuals, and it has to fulfil some desirable function. In other words, it has to survive both inheritance and usage, two processes that the cultural evolutionary theory literature often conflates under “transmission” (but see tests of the distinct contributions of transmission to new learners and communicative usage to linguistic structure by [147] and [225]). Although related, inheritance and usage have different evolutionary causes, mechanisms and consequences.

2.2.1. Selection for fidelity in culture: inheritance

In the real of culture, inheritance relates to the acquisition of a cultural trait by a learner, a naïve individual, often an infant or a child, from one or several models, who are usually expert, enculturated individuals. Inheritance's main variable property is ‘fidelity’, or the degree of correlation of properties of a trait across generations [71]. Cultural inheritance is therefore a cross-generational process that necessarily involves two parties that can be called learners and experts.

In order to be inherited with high fidelity, a cultural trait has to be well matched to the cultural inheritance mechanisms. Cultural inheritance relies on general cognitive and social factors that support copying such as motivation, attention, perception, processing, memory, production, availability of models and appropriate materials, as well as characteristically human traits such as mimesis [58,59,297], teaching (see [148] for review) and learning biases. All of these factors pose constraints on inheritance fidelity. If a trait is not cognitively salient (easy to perceive, process, attend to etc.); if it cannot be produced by the human body (e.g. a gesture that can only be produced with three arms, or with seven fingers per hand); if it requires materials and artefacts that are not readily available; if it is perceived as being unintentional [39] or if it is infrequent or is produced by a model who has no ‘prestige’ in the eyes of the learner [183], it is unlikely to be reproduced with high fidelity. During inheritance, mutation happens when actions undergo unintentional modification that is not motivated by function. Experimental models of the transmission of language show that variants adapt to being transmitted with high fidelity by becoming compressible. This has been observed in the orthographic [146,147], visual [13,44,138,258] and auditory [257,277,224] modalities.

Selection for fidelity favours *novel* variants if they well adapted to the inheritance mechanism; in the case of mature, long-established traits, selection for fidelity is a stabilizing force that makes the trait stay within its adaptive zone. Changes in the inheritance mechanism may shift or enlarge the adaptive zone for fidelity, and when this happens, traits that were previously not socially inheritable can be incorporated into culture. For instance, major changes such as the origin of language, the invention of writing, or the establishment of institutional teaching enabled the faithful transmission of information that had thus far been non-transmissible. This had momentous consequences that can be classed as cultural evolutionary transitions [178].

2.2.2. Selection for function in culture: usage

Cultural traits interact with their environment during usage. ‘Usage’ is the deployment of a trait by expert, enculturated individuals in context, that is, for its normal purpose, in order to achieve its usual function. Examples of usage include producing the sounds of a language or uttering a word to convey its conventional meaning, bringing your

phone to your ear in order to speak to someone, or passing a comb through your hair in order to make it neat. The term ‘usage’, therefore, will not cover instances in which a trait is put into practice for functions other than its normal function, such as when an infant produces the sounds of a language during babbling, when a toddler says “actually” without fully understanding its meaning, or when a child puts a phone to her ear or a comb to her hair during imitative play.

During usage, cultural traits interact with the environment, and traits that are better matched to it have an advantage. The cultural environment comprises functional niches, and these define cultural traits; in consequence, different ways to achieve the same function are cultural variants of a trait [231]. Cultural functional niches are many and varied. Variants for the functional niche of attaching something with a rope include different types of knot; for going from A to B: walking, cycling and driving; for conveying a meaning: synonym words; for greeting someone: kissing, shaking hands and bowing; for standing next to others: from close up to far apart; for bringing food to one’s mouth: using a fork, chopsticks, a spoon or one’s hand. When several variants compete for the same functional niche, fitter variants are those that have increased chances of being observed, adopted and/or deployed. Fitness can correlate with fulfilling the function in a more effective (fit for purpose) or efficient (fast, economical) way, but also with being more attractive, salient, or even more fun. For example, experimental results show the adaptation of signals to communicative function during usage [79,83,147,291] – that is, selection of variants that are more fit for purpose.

Usage is, additionally, the stage in cultural evolution in which effective mutation happens. Cultural traits may change, or mutate, either by accident (e.g. through errors in production or copying), or intentionally, through directed mutation (see section 1.2). Accidental mutations may be introduced by anyone at any time, during learning by a naive person or during usage by an expert. For complex cultural traits, however, accidents will almost certainly reduce efficiency or efficacy (e.g. the probability that an accidental change in the production of a computer chip or a space rocket will make it better is vanishingly small). In contrast, intentional, directed mutation is more likely to introduce modifications that may increase the efficiency or effectiveness of a trait and thus contribute to cumulative cultural evolution. Examples include using a new material – e.g. bronze instead of iron for tools, bamboo instead of cotton for fabric – and combining existing technologies to create a new one – e.g. steam power plus pistons and cylinder to create a steam engine. Intentional mutations, unlike an accidental ones, must be generated by experts who fully understand the causal connections between actions and functions. Crucially, expertise and understanding can only emerge through usage.

2.2.3. *The contributions of inheritance and usage to cultural evolution*

Inheritance and usage are closely intertwined – naive learners *inherit* cultural traits by observing experts *using* those traits. Nevertheless, they are distinct processes. The previous two sections have argued that the evolutionary success of a trait variant depends, on one hand, on whether it is well adapted to the inheritance mechanisms, and therefore can be passed on unchanged to fresh individuals and, on the other hand, on whether it is well adapted to its functional niche – whether it fulfils a function effectively and efficiently – and therefore on the probability of its being produced during usage, observed and adopted. Adaptation of a variant to the replication mechanism results in an increase in inheritance fidelity – that is, high similarity between the expert’s and learner’s trait. Adaptation of a variant to its function results in increased trait fitness – that is, an increase in the prevalence of that variant for the relevant trait in a population.

Several questions arise at this point: What is the human cultural inheritance mechanism? What exactly is inherited by that mechanism? Is all of culture inherited in the same way? The following sections address these questions by proposing that public aspects of behaviour – actions – are faithfully inherited, or replicated, while mental goals, knowledge, beliefs and values emerge from interactions between replicated actions on one hand, and its outputs and the contexts in which it is used on the other.

3. Action replication ultimately underpins all culture

This section argues that copying actions by naive learners constitutes replication. Here, ‘actions’ specifically mean observable, motor aspects of behaviour, independent of what function they fulfil and what goal they are intended to achieve. Actions include habits, gestures, linguistic utterances (in spoken language, audible, if not directly observable in all its detail), means or methods to achieve goals, rituals etc. They may involve not only the body, but also interactions between the body and artefacts (e.g. how one pours tea from a teapot). In sum, actions are ways to do things.

The term ‘*naive learners*’ refers to individuals who do not, at the time of learning, know the function that an observed action is intended to fulfil.

This section first reviews the criteria that different authors require to call a transmission process ‘replicative’; it then shows that action inheritance does meet those criteria; finally, it argues that cultural replication in humans happens in naive learners who copy actions independently of their function.

3.1. *Criteria for replication*

Replication is a special kind of copying paradigmatically exemplified by DNA replication. A replicator has been defined as “the entity that passes on its structure largely intact in successive generations” [122]. Williams [290] advocated the view that the unit of replication is defined by its information content (information being any pattern that influences the formation or the transformation of other patterns), while for Dawkins [51] it is the entity that contains the information that is passed on during replication. Replication must fulfil the criteria of longevity, fecundity and copying fidelity (or similarity between original and copy). In other words, the model must exist for long enough that it can be copied; copies must actually be produced; and that copy must resemble the original (in relevant respects).

Causation is also a requirement for replication: the original must be a causal factor in the production of the copy [122,91]. Whilst we cannot say that a new car, fresh from the factory, is caused by another (identical) car, we can say that a new token of DNA is caused by another (identical) DNA token: the parent token is necessary and causally involved in the production of the child token. Sperber [248] adds the criterion of information transfer (“the process that generates [the copy] must obtain the information that makes [the copy] similar to the original from [the original]” [248, p. 169]). When there is causation and information transfer, had the original been different, the copy would be accordingly different. The cases of the car and DNA also illustrate information transfer: only in the latter case is there information transfer.

Causation and information transfer are important to distinguish between two types of inheritance. Gene inheritance is replicative, but while ecological factors (from the cell cytoplasm to the dams that beavers inherit from their ancestors) can also be inherited, they are not replicated because there is no causation nor information transfer between e.g. mother and daughter cell’s cytoplasm or between the dam during a parent beaver’s lifetime and child’s.

Finally, Millikan [192] additionally demands that a copying mechanism for replication is specified. Even though Millikan’s discussion refers to ‘reproduction’, it can be safely taken to apply to replication, as she explicitly distinguishes ‘reproduction’ from the inheritance of phenotypic traits: “I have blue eyes not directly because my mother and/or father had, but because of my genes, which were copied from their genes, which were not, however, copied from their eyes” [192].

We can now assess whether the inheritance of an action by a naive individual from an expert through observational social learning mechanisms and teaching meet all the required criteria for replication.

3.2. *The inheritance of actions meets the criteria for replication*

Starting with the criteria imposed by Dawkins [51], many socially transmitted actions are extremely long-lived and fecund. History records and museums contain countless examples of ancient artefacts and associated practices that are still present today, including traditional skills such as woodwork or pottery. Extreme cases include lineages of linguistic replicators such as word-forms [95,96,210,22]) and other linguistic features [62] that go back many thousands of years, and the actions involved in making Acheulean stone tools, a tradition that persisted for more than one million years with little change [159,46].

Similarity, or copying fidelity, is evidenced by variation in gestures and other culturally inherited actions that show cross-cultural specificity – they are often consistently and recognizably similar within a cultural community and different between communities. Examples include technological methods, languages, and also less measurable actions like the expression of emotions through body posture [237], nonverbal communication [175] and walking style [128].

Going back to the replication/ecological inheritance distinction mentioned in 3.1, two factors may contribute to similarity, or structural correlation, between different tokens of the same cultural action lineage or type: ecological or environmental factors (which we can equate to ecological factors of attraction), and social transmission. Consider an action: the method of holding a pair of scissors by inserting a finger and thumb in the scissors’ eyes. This aspect of the action is to some extent ecologically inherited, the cultural ecological niche (the scissors) does not easily afford other

options, and so it favours similarity across tokens of the action. Ecologically-mediated similarity does not involve causation or information transfer between the original *action* and its copy. Therefore ecological inheritance of actions does not constitute replication.

In contrast, causation and information transfer can be present in the social transmission of actions. In the gestural examples above, the production of an action variant token in the learner (e.g. a style of walking, a particular bodily stance) is caused by the production of one or more tokens of that action variant observed in the expert. If the observed tokens had been different, the copy would also be different. As for information transfer, the explanation for the structure of the learner's copy is in the expert's original action. In the example of the scissors, ecological inheritance dictates that they must be held with a finger and thumb through the eyes; but causation and information transfer may be present with respect to *which* finger is inserted in the scissors: the first, second or third finger. Because the three variants of this trait are possible and functional, social learning may influence which one a given person uses. Different cultural traits will vary in how much information originates in environmental factors, and how much originates in social inheritance. Touch typing, for instance, can be socially learned and taught, but, given the structure of the keyboard, and of human hands, it is also likely to be discovered asocially. When tying a knot, in contrast, the structure of a piece of string does not guide, direct or suggest the structure of the knot to any significant extent. Learning how to make a knot requires more social learning, or cultural inheritance, and is less influenced by environmental inheritance, or attraction factors, than touch-typing. Arguably, then, replication plays an important part in the knot-tying cultural trait, while environmental inheritance is more influential for touch-typing.

It is important to note that only *culturally relevant* aspects of the structure of an action need to be causally and informationally linked between the original and the copied token actions [252,91]. What is culturally relevant can be defined a posteriori: it is what remains the same over generations, what distinguishes members of a lineage of traits. Word-forms can be thousands of years old [210]. Different tokens, or individual productions, of a word (e.g. 'cat') are unique in many respects including loudness, pitch, voice timbre and duration. Acoustically, the word-form 'cat' will be very different when produced by speakers who have different accents, ages, genders or who lived 200 years apart. Yet most productions of 'cat' have something in common that allows an English speaker to recognize them as tokens of the same type. Instances of the way a couple embraces while dancing *canyengue*-style Argentine tango are also unique – affected, for instance, by the body size and shape of the two dancers. Nevertheless, they are recognized by dancers and are classified by dance scholars as tokens of the same type. The same applies to all observable actions that can be classified along social-cultural dimensions, such as meal times; attendance to religious services (whether one attends, the structure of the rituals); what you have for breakfast; family structure (members of a household); and who you vote for. In short, culturally relevant aspects of replicated actions are those that persist across individuals and generations, and they can only persist if they are adapted to the replication mechanism.

For cultural transmission to be replicative in the sense described here, the criteria for replication related to longevity, fecundity, similarity, causation and information transfer only need to be met during inheritance; that is, when a naive learner is copying the actions – and only the actions, not the intended functions, or goals – of an expert model. These criteria do not need to be met during usage, when the user may innovate, or modify her behaviour in order, for instance, to adapt to current contingencies such as a flaw in the material, or by mistake or accident, or intentionally. In those cases we can speak of innovation or mutation, which is also an essential ingredient of a full explanation of cultural evolution. The attested longevity of idiosyncratic, even arbitrary cultural variants for the same function, which may reach millennia, is evidence that replicative inheritance can be overwhelmingly greater than mutation.

The last criterion under 3.1, proposed by Millikan's [192], required an attested mechanism for transmission. This topic is developed in depth in the next section.

3.3. *The mechanisms of replication in human cultural inheritance*

The 'replication and emergence' model requires mechanisms for action replication that achieve the above criteria (longevity, fecundity, similarity, causation and information transfer). In addition, the mechanisms must support *content-indifferent copying* (to use Nettle, [197] phrase) of actions. This kind of copying meets the following three criteria: first, it must not be motivated by achieving the action's functional or conventional goal (e.g. the main goal of infant saying "hello" on a phone must not be to greet the person at the other end of the line). Second, it must be mediated by observational learning mechanisms (e.g. imitation). Third, it may benefit from teaching processes that do not require the learner to have full knowledge of the action's intended goal or normal function (e.g. helping a young

infant to learn how to say ‘mamma’). The reasons for copying actions must therefore be found not in functionality, but elsewhere. The remainder of this section proposes a series of mechanisms that may enable human action replication and carefully addresses how each of those mechanism supports content-indifferent copying of actions.

A mechanism that is obviously involved in action copying is motor, observational social learning. We saw in 1.3 that imitation, which is present in many species, results in the faithful reproduction of actions. Vocal learning, for example, underlies faithful copying of observable behaviour, irrespective of an immediate function in many species. Moreover, motor control in vocal learning species extends beyond the vocal modality (e.g. several vocal learning birds are able to ‘dance’, or entrain to musical beat, [211]). Compared to non-vocal learners (such as our evolutionary cousins, the other great apes), vocal learners have much more accurate and fine-grained motor control [220]. If ‘vocal’ learning in humans similarly extends beyond the vocal modality to any motor output (perhaps, notably, actions produced with the hands), then motor learning – the internal processes that permanently change the capacity for skilled motor performance [238,172,99] and that enables us to copy observed behaviour – is a good candidate mechanism for action replication. The exhaustive trial and error motor learning process that infants undergo during early enculturation allows them to copy actions very faithfully and consistently (even if tokens of the same action are flexible in the sense that they may result from different patterns of muscle activation, unique, and modifiable, [244]).

In her model of cumulative cultural transmission, Legare proposes the ‘copy when uncertain’ principle [161,265] to denote that children, in particular, tend to copy actions faithfully when they are unsure about their causes. This principle explains why conventional skills and actions that do not have an obvious functional goal, such as ceremonial dances or rituals, are copied faithfully [160]. In a more cognitive-mechanistic account, Heyes [115] appeals to Dual-systems theory’s [134] System 1 and System 2 to explain different types of copying in cultural transmission. System 1 – fast, implicit, automatic, unconscious thinking –, would underlie replication, or the automatic high-fidelity mapping between observed and produced actions. System 2 – slow, explicit, controlled, conscious thinking – would support reconstruction, or copying that is lower-fidelity, deliberate, and informed by previous knowledge. Action replication, like many other human cognitive traits, may be the result of general associative learning or specifically evolved cognitive mechanisms (see [31] for review). Heyes [116] defends that imitation requires associative learning, complemented by a precisely scaffolded cultural environment that includes artefacts such as mirrors, and culturally evolved “cognitive gadgets” such as social cues – e.g. parents imitating infants –, social tools – e.g. coordination, cooperative games –, and cognitive skills – e.g. imitation, normative thinking, shared intentionality. In Heyes’ [116] framework, therefore, we find a suitable mechanism – System 1 thinking plus a suite of cognitive gadgets – able to support content-indifferent action replication.

While learners do observational learning, experts can contribute to action replication with teaching. Teaching-mediated enhancement of learning acts as an adaptive catalyst that ensures the faithful replication of opaque traits. In cumulative culture, opaque traits in which the relationship between an action and its function is not obvious, sometimes even to experts, are very common. In knitting, for example, the exact trajectory of the thread is crucial to obtain the desired outcome, but this may not be immediately obvious, as the effects are often only apparent after knitting many rows. Teaching ensures the trajectory is learned faithfully, even if learners (and even teachers) do not understand why it must be done in that particular way. Humans often learn that things are done in a certain way, and are ready to assume this is the correct way and any other way is wrong [139,140].

The dissociation between action and function during learning cannot be taken for granted. The functional fixedness effect for tool use predicts precisely the opposite, namely a strong fixation of a particular tool with a particular function, which may inhibit the of new functions for the tool (by abduction), and indeed, “may be suboptimal for flexible problem solving” [89]. Human adults and children over six years old display functional fixedness, and solving a task by using a tool for a novel function is slower if they had already associated the tool with its known utility function [55,88]. Chimpanzees also show extreme functional fixedness, as the experiments by Hanus et al. [100] demonstrate. In these experiments, chimpanzees were presented with a task whose solution involved spitting water in a tube in order to retrieve a peanut (by making it float closer to the end of the tube). It never occurred to the chimpanzees that they could use their own drinking water dispenser to get water for the task. However, if a new dispenser was installed in the experiment room, around 20% of the chimpanzees solved the task. They behaved as if they could only conceive that the water in their original dispenser was ‘for drinking’ and not ‘for retrieving peanuts’, while the water in a new dispenser was free to be associated with a new function. Crucially, human children under the age of six are happy to assign new functions to old tools that they already have functions for [100]. Younger children are still gathering

information that allows them to decide what the typical function of the tool is. The late onset of functional fixedness in humans permits the early replication of motor routines independently of their conventional function.

Action replication as defined in this paper, while not motivated by the action's *normal* function, is not functionless. In naive learners, the motivation to copy others may originate in a desire to promote social affiliation with the observed models [279,213,199,201,293,208,163,170]. In the case of infants and young children, those models are likely to be close family; model-based bias has little chance to operate at this early stage, since infants have no choice as to whom they copy – but the models available may inform the acquisition of the criteria for future model-based discrimination. Copying may also have intrinsic motivation [187]; or be favoured by normativity, the above-mentioned belief that our way to do things is the correct one [139,140].

Action replication is not the direct, automatic transfer from observed to produced behaviour. As mentioned in 1.3, it involves inferential learning, but of a very specific type of hypothesis: what is inferred is the motor activation pattern that will reproduce the observed action. We can say that the world around a social learner can be divided, in this respect, into two types of actions: those that can only be observed (e.g. a bird flying), and those that can be observed *and reproduced* (e.g. many everyday actions performed by fellow humans). Only the latter can become cultural replicators.

An illustrative example of action replication is the acquisition of the sounds of a language. During early language learning, infants learn accurately to reproduce the forms of their language before they start to learn the conventional ways of using them. At the babbling stage, from 5 to 7 months of age, infants' vocalizations come to resemble the native sounds of the ambient language, while the infants lose the capacity to produce and perceive non-native sound contrasts [282,151,278]. This process moulds perceptual-motor brain structures with long-term consequences – it is very difficult to master the distinction and pronunciation of the sounds of a language learned in adulthood. At around their first birthday, children start producing words and constructions in their language. Perfecting the production of these linguistic forms takes one to three more years, but most forms can soon be recognized as tokens of adult word-forms and constructions. Children often produce unanalysed chunks of speech larger than words [268,294]. These 'frozen phrases' may constitute up to 60% of 1-3 year olds' speech [217,167]. Importantly, however, at this age, children have not yet developed the conventional meanings for those forms [269,192]. In experiments, children may produce forms even if they cannot form rules about when they should be used based on semantic clues [240]. Early learning of linguistic actions – such as sounds, word-forms, phrases, and intonation patterns – may therefore happen independently of their function.

Another example of action replication is pretend or imitative play. Play is "activity done for its own sake, characterized by means rather than goals" [245]. For example, around 12 months, a child engaging in pretend play "may use a brush or comb on their hair (...) or hold a telephone to their ear" [82]. She is merely copying behaviour, but not for the same goal as adults: she does not actually comb her hair or talk to anyone on the telephone; she may not even know what those goals are. Play is pedagogical and allows children to practice actions that will be important in adult life [117], but it should be uncontroversial that, when performed by a young child, the actions often do not achieve – and are not intended to achieve – their normal or conventional adult function. Between 2 and 5 years of age, "children take great pleasure in imitating the ordered doings of their elders, but in practice they know nothing of their *raison d'être*" [213].

Further to these examples, classic studies showing that aggressive [9] or sharing [101,221] behaviour is strongly influenced by imitation learning and social approval. In those experiments, after seeing a model act with different levels of aggression or generosity, children's behaviour matches the observed levels. These effects are confirmed outside the laboratory, with criminality [6] and child abuse [136] being transmitted cross-generationally. Verbal instruction or persuasion alone, however, does not have the same results as observational learning of behaviour [32,226,233]. Henrich [106] suggests this is because actions are more costly than speech, and therefore should have stronger evolutionary purchase. Alternatively, verbal induction, explanations, preaching, pleas or orders may not lead to production of the desired actions because cultural inheritance requires observation and production of the actions. The present model of action replication predicts that verbal input – which is composed, effectively, of motor actions – should also be copied, perhaps when instructing someone else. Moreover, linguistic actions could be replicated even if they are at odds with related but nonlinguistic actions, and this might be a factor behind cognitive dissonance [70]. Consider a child who replicates her family's actions of never giving money when asked at a charity appeal, and also the family's verbal actions claiming to be very generous. When the child eventually understands the implications of those two actions, cognitive dissonance may ensue.

Although much cultural inheritance takes place early in life, it also occurs when naive adults observe others' actions – either in a novel situation, or when producing an outcome for which they do not possess an associated cultural trait. Adults over-imitate in experimental situations [183,289], in other words, they do copy actions regardless of the actions' normal function. Arguably, this also bears out in real life situations. When receiving instruction for a new skill, such as playing an instrument or working a piece of machinery, naive adults learn and adopt the methods they are taught, rather than attempt to figure out their own methods. The copying fidelity attained by adults may not be as high as that attained by children. Adults learning a second language rarely achieve a perfect native accent, and other skills that require great motor accuracy such as skiing and tai chi (see [80]) may be more difficult to acquire and require much more time, effort or instruction, when learned as an adult than as a child. This difficulty experienced by adults could be related to sensitive periods for very early motor learning, when the machinery for replication is developing, or to the interference of already-learned actions. Perhaps once we have acquired certain early bodily habits (e.g. the sounds of the ambient language before we start to speak or the postures and stances observed if skiing or tai chi are present in our early ambient), we are not truly naive learners, as action copying is biased by prior learning, and therefore action replication cannot take place (see section 3). Another case in which adults may do content-indifferent action replication is when they learn rituals. Rituals have rules that can evolve independently of any function [250]. The extremely ancient and complex traditional Vedic rituals, for instance, are performed for their own sake and have no symbolic meaning or communicative function [249].

Infants and children do not copy any and all of the actions they see to the same extent. Reasons for copying certain actions more than others include those actions being perceived as intentional [39]; being construed as ostensive-communicative and therefore goal-directed [143]; being favoured by the above-mentioned transmission biases [24] or by other forces, such as pattern completion biases [256]. All of these reasons can be related to Heyes' [116] cognitive gadgets. The extent to which these factors are learned or innate is largely unknown and probably varies between cultural domains and traits. Early in development, the probability that an action is copied may be related to perceptual, processing or production biases, such as the developmental cognitive restrictions in Elman's [64] 'starting small' model or Newport's [198] 'less is more' idea. But even if actions are observed and replicated in a content-indifferent way, learners soon have the opportunity to observe and experience the actions' outcomes, and associations between the actions and their outcomes and contexts begin to emerge in the learners' minds. The outcomes of an action may include: the causal effects of the action itself (e.g. the changes produced when using a tool); expressions of intention, approval, disapproval, recognition; and even being copied back from others. These outcomes, in turn, may modulate the probability of production of the action in the future. In some cases this modulation may happen vicariously – e.g. if a naive learner witnesses someone stealing and then being punished for it, she may never steal at all. There is a theoretical boundary between an early production of an action as a direct consequence of unbiased observational copying on one hand, and subsequent productions, in which associations between the actions and their outcomes are observed. The former constitutes replicative inheritance of actions and is subject to selection for fidelity; the latter inform the development of mental culture, which is the site of selection for function. The following section describes mental culture development as a process of emergence of associations between actions and their outcomes and contexts, during usage.

4. Mental culture is emergent

The goal of much work on cultural evolution is to highlight the role of culture in explanations of human diversity. Richerson and Boyd [227] cite Nisbett and Cohen's [202] claim that “the South is more violent than the North because southern people have culturally acquired beliefs about personal honor that are different from their northern counterparts” [227]. For them, behaviour depends on mental culture. The same conclusion emanates from Tomasello et al.'s [275] claim that intention-reading (a cognitive, mental skill) guides imitation of behaviour. I will argue that causality flows in both directions, and that mental culture is also dependent on behavioural actions.

There is substantial debate about the nature of mental representations (e.g. [263,173]), but for the purposes of this argument, 'mental culture' or 'mental cultural traits' refers to what Boyd and Richerson [24] and Richerson and Boyd [227] call culture: that is, socially learned information residing in the mind, including knowledge, skills, beliefs and values. The following sections contend, specifically, that mental culture is emergent. Section 4.1 defines emergence and its properties, 4.2 argues that mental culture is not replicated and 4.3 defends that that mental culture qualifies as emergent (see Fig. 1).

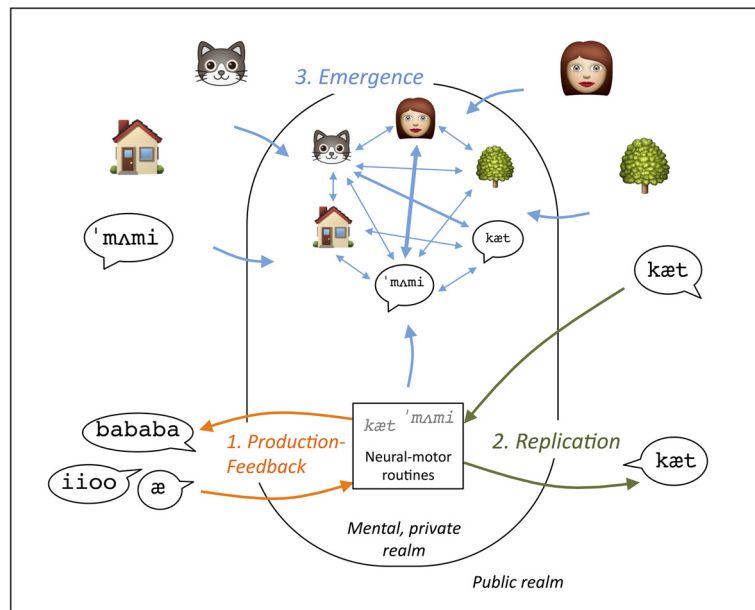


Fig. 1. Mechanisms involved in replication and emergence. A naive learner (whose mind is represented by the oval in the figure) observes items in the public realm, the world (outside the oval, in the figure). Some of the items – the actions – can be not only perceived in others, but also produced by oneself. The first stage of cultural transmission in an individual involves production-feedback loops (1, orange arrows) of actions: the child learns to control her movements, to match neural-motor routines to motor-behavioural outcomes and, eventually, to achieve her motor goals. The second stage involves the replication of actions produced by others and observed by the learner (2, green arrows). The third stage, the emergence of mental culture (3, blue arrows), is mediated by inference and by associations between one's own and others' actions, the outcomes of those actions, and the contexts in which they occur.

4.1. Emergence

Emergence [165] happens in complex systems when multiple interactions at a local level give rise to new phenomena at higher hierarchical levels. The central tenet of emergentism says that when a certain level of complexity is attained, novel properties appear. Emergent properties are irreducible; that is, they cannot be derived, explained or predicted by the properties of the system's component elements [180,141]. Emergence involves downward (or top-down) causation [142], meaning that the emergent higher-level entities have causal effects on lower-level components. Emergent outcomes are highly sensitive to initial conditions [169] and are usually based on many strongly interdependent variables. For these reasons, it is very difficult to predict the behaviour of an emergent system with accuracy. Examples of emergent phenomena include phase transitions (e.g. from solid to liquid, [14]), the weather [169], organismal development [179,93,263,209], and human behaviour and cognition [137,176,262]. The laws governing those phenomena are not reducible or predictable from the laws governing the molecules, the information in the genes and the environment, or interactions between cells or neurons.

By way of illustration, I will elaborate on the development of organisms as an instance of emergence. Organisms emerge from many complex, interrelated interactions between genes and the environment. This involves, first, the interactions between DNA and the intra-cellular environment, which provides a medium in which the molecules are stable as well as the necessary chemical factors – both those required for DNA replication, transcription and translation, and those required for cell metabolism, such as catalysts and nutrients. A second set of interactions exists within the organism (e.g. differentiation of tissues and organs). A third set of interactions are those between the organism and its external environment, including other organisms of the same and other species, and factors in the physical environment, such as gravity, the climate, etc. The final state of the phenotype cannot be reduced to, or fully explained or predicted by the properties of the genes and the environment. Top-down causation processes during development are found at all levels, from the expression of genes being triggered by mechanical forces produced when the gastrula – an early stage of the embryo – changes shape [246] to psychological effects on physiological processes.

4.2. *Mental culture does not replicate*

Global, emergent properties can emanate from local rules, but even if the local rules are identical, there is no guarantee of similarity, no information transfer, and no causality between successive emergent entities – for example, in the realm of the weather, between one storm and the next; in development, between two identical twins; and in cognition, between “the same” idea in different minds.

Focusing on culture, a mental cultural trait may be similar between individuals in the same lineage, such as an expert model and her learner, and it may show longevity and fecundity (persist for many generations and be present in many individuals). However, there is no information transfer or causality between copies of the trait across the two minds. A cultural trait in the learner’s mind cannot be directly caused by a trait in the teacher’s mind, if only because the former does not have direct access to the latter. Any causation must be mediated by observable, public proxies of the mental trait such as observed actions in the physical environment. Mental traits are underspecified by their public manifestations; that is, an action contains only a fraction of the information of the corresponding mental trait. For instance, word-forms underspecify their meaning [19,21,77]. Consequently, the structure of the learner’s mental trait cannot be explained by the structure of the teacher’s mental trait, and not even by the structure of the mediating public actions alone.

This brings us back to similarity. In biology, a consequence of the replication of genes and emergent development is that, over cross-generational transmission, similarities between a parent’s phenotype and her offspring’s are due to similarities in the environment and the genes. In culture, similarity between the mental traits of teacher and learner must be caused by environmental factors, and by the fact that they are informed by the same (replicated) actions.

As far as transmission mechanisms are concerned, in contrast to her claim of faithful copying of conventional actions such as rituals, Legare [160] proposes that instrumental or technological skills, which require an understanding of the relationship between action and function, are copied with low fidelity because this understanding may promote innovation. The present model would contend that instrumental skills are initially copied in a content-indifferent way and only later, through repeated production and observation of the outcomes (and also through teaching) is their function understood. Innovation happens after a goal is intended and, therefore, after the threshold between inheritance and usage has been crossed. Similarly, the conscious, deliberate kind of learning that happens under System 2 in Heyes [116] cognitive account of cultural transmission, forms novel, experience-dependent associations between the actions produced and observed by a learner and their outcomes. Unlike System 1, System 2 may be modulated by teaching, which enhances the inductive learning of functions and goals.

4.3. *Mental cultural traits are emergent*

During the development of an organism, phenotypic traits emerge from the interaction between genes and the environment. Analogously, mental cultural traits emerge from interactions between replicated cultural actions on one hand and the environment on the other (the environment comprising both the material environment and the environment of cultural transmission mechanisms – that is, human minds, cognitive skills and biases, Fig. 2). As reviewed in 1.1, the animal and comparative culture literature emphasizes the role of socially learned cultural actions, while cultural attraction theorists focus on the contribution of cognitive and ecological factors to the emergence of mental culture.

The proposal that mental traits are emergent is at the core of connectionism [181] and the dynamic systems approach to development [263]. Emergence starts very early on, when infants learn to control their behaviour, and continues throughout life: “just as hand trajectories are not computed, but discovered and assembled within the act of reaching, so too does *thinking* arise within the contextual, historical, and time-dependent activity of the moment” ([262], emphasis added). Emergence entails associative learning. Going back to language learning, as replicated linguistic actions are produced repeatedly, their social and grammatical use becomes increasingly adult-like: conventional, culture-specific and context-appropriate. The repeated production and perception of the sounds in the ambient language (local interactions) result in the emergence of (mental) phonological categories [168,264]. Repeated observation and production of a sound sequence across contexts informs the emergence of word meaning. Usage-based accounts of language learning show how young children acquire grammatical categories and rules from regularities in their linguistic and non-linguistic input (e.g. [232,157,158,235,177,92]). And over repeated usage, word-forms that are initially observed and produced in specific contexts (e.g. the word-form ‘puppy’ refers to a specific puppy) start to be generalised to different communicative situations (‘puppy’ extends to refer to any puppy). Along the process,

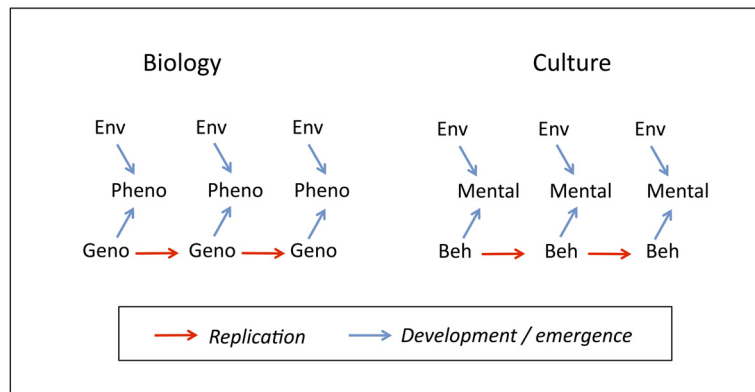


Fig. 2. Replication and emergence in biology and culture. In genetic inheritance, genes are replicated, and the phenotype emerges from the interaction between genes and the environment. Phenotypic traits can be inherited in the sense that they may persist crossgenerationally (I inherited my father's nose), but they are not replicated. In culture, actions can be replicated, and an individual's mental culture emerges from the interaction between observed and produced actions and their environment (e.g. their function, context, consequences, outcomes, the materials available). Mental cultural traits may be similar across generations only to the extent that they are informed by the same (replicated) behaviours and/or by the same – persistent, environmentally inherited – environment.

through cognitive mechanisms such as category induction and associative learning, children eventually home in on adult word meanings [85,94,45,269,2].

In pretend play, as a child produces successive tokens of actions or rituals, these become associated in his or her mind with the effects, responses and reactions they obtain, including feedback and teaching from others, and with aspects of the context such as location, materials and social environment. These learned associations are, like Piaget's [214] *schemata*, incipient knowledge about the meanings, values and functions associated with the actions (e.g. to comb one's hair to make it neat, to talk on the phone to communicate with someone), and about the reactions they elicit (e.g. a smile or a frown from a parent).

Thelen and Smith [263] claim that “higher order mental activities, including categorization, concept formation, and language, must arise in a self-organized manner from the recurrent *real time* activities of the child” ([262], emphasis added). Counting is a case in point: initially, children learn to produce behaviourally (orally, using the fingers) the number sequence without relation to quantity [78]; later, they develop an understanding of quantities in specific contexts (for specific objects) and finally, through association and comparison, the abstract number and counting concepts emerge [193]. Piaget [213] sees a causal continuity between motor rituals at 10-12 months of age, symbolic pretend play, rules, and finally moral reasoning by preadolescence. Once self-generated and socially imitated behaviour is ritualised, schemas are constructed as those rituals interact with the children's reasoning capacities. Social cognitive theory [10,11] similarly proposes that knowledge and attitudes (e.g. about aggression or gender-linked behaviour) emerge from social interaction. In early childhood, the reactions the child expects from others regulate child behaviour; later on, through imitation, pedagogy and observation of social reactions, children construct their own values and attitudes, which become the major regulator of behaviour [12]. Consider a child who observes her family avoid or react in a nervous way when they see the police in the street, and another child whose family reacts in a calm way and approach the police. The children are likely to replicate the observed behaviours and, partly as a consequence of that, they will develop distinct mental attitudes towards the police. In the context of congruent behaviours within each family, additional different attitudes, values and identities will emerge in the two children. This supports the idea that sustained, consistent modelling provided by parents and others in the social group should have a strong causal impact on a child's developing mental culture, and therefore on his or her identity – if you observe yourself behaving like this, then you infer that you must have this attitude and therefore you must be this kind of person. Insofar as your actions are replicas of the actions of your social group, your inference can be phrased as ‘we have this attitude and we are this kind of people’ and your identity acquires a social dimension. Indeed, identity, the mind itself, and consciousness and the self have been defined as emergent [8,102,181,242]. (Note, however, that, evidently, not all emergent mental traits have a uniquely cultural, social origin. Individually learned behaviour and other asocial experience also shape the mind.)

actions	ideas, beliefs, attitudes
behavioural	mental
public	private
inheritance	usage
replication	emergence
selection for fidelity	development
unbiased copying	selection for function
	epicultural factors

Fig. 3. Key concepts in the two proposed realms in cultural evolution: replication on the left and emergence on the right.

Throughout our lives, an increasingly intricate body of emergent cultural mental traits shapes our *enculturated* minds and bodies, which, in turn, constrain further learning. This is downward causation, one of the key processes that characterise emergence. Possessing certain knowledge, values, skills or attitudes may facilitate or hinder the adoption of novel actions and play a role in the emergence of further mental traits. It additionally conditions the production of actions during usage, and therefore the availability of variants of actions to be replicated by learners.

Language has an interesting status in culture. On one hand, it is a mechanism for cultural transmission [53,153]; and on the other, it is a culturally transmitted trait itself [145]. The cultural inheritance of language has been discussed above: from the point of view of inheritance, linguistic behaviour is composed of observable, replicable actions. In its role as a mechanism for transmission, however, language plays a unique catalyzing role in the emergence of mental traits because it is symbolic; that is, its function is to activate existing mental traits in the hearer [60]. Linguistic actions can therefore contribute to the emergence of new mental traits from the combination of existing ones. Many of these existing mental traits (the meanings activated by linguistic replicators), circularly, emerged from action replication and experience with usage.

The emergence of mental cultural traits can be an extremely complex process, involving the interplay of observable factors (including multiple actions associated with their contexts, outcomes, models and responses) and non-observable factors (including pre-existing culturally and individually acquired – and perhaps also innate – mental traits and biases, as well as individual cognitive and perceptual traits such as personality or biases on salience). The pathways from culturally inherited actions (plus social learning mechanisms, plus environment) to a person's mental culture are likely to be as complex as the pathways from genes (plus cellular and external environments) to organism. Supra-individual or distributed cultural institutions including technology, the economy, languages, politics or science are likely to be several levels of emergence away from the processes proposed here, namely the replication of actions and the emergence of mental culture in individuals; but the latter processes are necessary for the former to exist.

5. Discussion

The replication and emergence model (see Fig. 3) recasts the central tenets of Dual Inheritance Theory (e.g. [24,227]) and Cultural Attraction Theory (e.g. [247,195]) in a new light, and integrates those theories with empirical work on comparative and human social learning (e.g. [81,223,289,153,283,160]). By including the concepts of replication, variation, selection and adaptation, environmental feedback and emergence, this model of cultural transmission supports the view that culture is a Complex Adaptive System [104,73,15,16], a Darwinian system [188,190] or an instantiation of a selection system [37,122]. It incorporates social cognitive theory (e.g. [10]), dynamic systems approach to cognitive development [263], cognitive science of cultural evolution [115,116] and usage-based theories of language [48,269] to link the evolutionary processes of inheritance, variation and selection with social-cognitive mechanisms.

The present model of cultural transmission does not (yet) fully cover all of cultural transmission. For example, it does not elaborate on the degree to which inheritance, usage and ecological inheritance shape different cultural domains or cultural traits. Nor does it explain in detail language-mediated transmission, or the transmission of artefacts

and the rest of the material culture. In the present outline of the replication and emergence model, language-mediated transmission would be classed as teaching. However, the complexities introduced by the fact that language is simultaneously culturally transmitted and a mechanism for cultural transmission are only briefly outlined (in section 4.3). The material culture constitutes the culturally constructed ecological niche that may pose selection pressures on the transmission and innovation of action variants, but how it is transmitted – is it replicated, or emergent? Or something else? – is also not addressed here in any depth. Nevertheless, the model is intended to be flexible enough to integrate future explanations for these and other aspects of culture.

The replication and emergence model supports a definition of culture that must incorporate public behavioural, as well as mental traits. In fact, it places the onus of explanation for culture on public actions, since mental cultural traits that are never manifested as behaviour cannot be said to be cultural, as they cannot be inherited, but arbitrary actions that are not necessarily connected to a mental trait (e.g. those that are not fully intended, understood or even realized by those who produce them) can nevertheless be culturally inherited, and persist for long periods (e.g. pause fillers in speech, such as English ‘erm’ or ‘you know?’, or gestures and mannerisms that characterize a population, such as the typical interpersonal distance). The model also highlights that causality in cultural transmission flows bidirectionally – if asymmetrically – between public actions and mental traits, with actions informing the emergence of mental cultural traits, and the enculturated mind modulating the production of actions.

Application of the replication and emergence hypotheses leads to a re-classification of transmission biases and factors of attraction. Boyd and Richerson’s [24] direct, or content-based bias, is a property of humans – a learner’s preference for cultural variants that are genetically adaptive; that is, that are likely to increase the learners’ biological fitness. Content-based bias can now be recast as a property of cultural traits, and then we can speak of *intrinsic properties* of a trait that affect its likelihood of being adopted. Since adoption of a trait by a new learner constitutes replication, increasing the likelihood of adoption equals increasing the fitness of the trait. And increases in fitness involve one of two processes: either selection, if the trait is heritable, or guided variation/directed mutation, if the trait is favoured during innovation. Content-based biases equal, therefore, selection pressures. If the intrinsic properties of the trait tend to increase the fidelity with which it is transmitted, then content-based bias poses selection for fidelity (e.g. experimental, miniature languages that evolve to be simpler and more compressible and thus can be copied with higher fidelity, [146]); if they tend to increase its efficiency or efficacy, then content-based bias poses selection for function (e.g. languages that evolve to be expressive, and thus effective for communication, [147]). In contrast, model- and frequency-based biases do not involve intrinsic, heritable properties of traits. The fact that a celebrity drinks coffee brand X in an advertisement makes the trait ‘drinking brand X’ culturally fit in the sense that it is more likely to be adopted by observers. However, when a non-celebrity learner buys and drinks coffee X, the trait has lost the property that made it culturally fit (it is not drunk by a celebrity any more). Frequency is, similarly, not intrinsically heritable. Interestingly, model-based bias in favour of a particular variant may become sensitive to selection because it is pseudo-inherited in parent-transmitted traits – I saw my parents produce a behavioural variant and I will produce it for my children, so over generations, the behaviour consistently has the non-intrinsic feature ‘being produced by parents’. Frequency bias can also be pseudo-inherited when the majority or minority variants are consistently preferred, but not in cases of frequency-dependent selection in which very frequent traits tend not to be adopted and vice versa (e.g. when we want to be original or exclusive). Model- and frequency-based biases may be seen as ‘epicultural’ factors (homologous to epigenetic factors, [129]) that modulate the cognitive salience, and therefore the cultural fitness of traits, but are only heritable in the short or medium term. Finally, factors of attraction, posited by a model of culture that emphasizes reconstruction and transformation (and therefore downplays the heritability of cultural trait properties), are characterized within the replication and emergence model of cultural transmission as factors of guided variation, which operate only during usage, not during inheritance.

Introducing a mechanism for replication makes the model relevant to the study of cumulative cultural evolution. Faithful replication can support the cross-individual and therefore cross-generational transmission of modified actions and combinations of actions. The content-indifferent, unquestioning nature of action replication solves a particular learning problem: if learners reproduce actions without needing to understand how they are linked to outcomes and goals, they can reproduce opaque and complex traits, which are typical outcomes of cumulative evolution. Therefore, processes of variation able to achieve modification and recombination, plus content-indifferent action replication able to support the persistence of innovations, together, explain the *mechanism* of cumulative cultural evolution – how cultural traits are created and transmitted. The *outcomes* of cumulative culture – the distribution of traits – can be

explained by selection (for fidelity or for function), in what amounts to a characterization of cumulative cultural evolution as a Darwinian process.

A key prediction of the replication and emergence model is that the (genetic) adaptations of humans to culture must have involved a shift of focus from function (I see someone do some actions leading to e.g. obtaining food, and that prompts me to attempt to achieve the same goal) to actions (I see someone doing something that achieves a function such as obtaining food, and that prompts me to copy the actions) in social learning. This adaptation may have involved the inhibition of rationality, a positive bias for social affiliation, and it is likely to have coevolved with enhanced trust and social tolerance. Importantly, the shift from function to action is distinct from – and is not necessarily subsumed by – other social-cognitive adaptations often connected to cultural evolution such as theory of mind and shared intentionality [268].

Making a clear distinction between inheritance and usage also highlights a flaw in cultural attraction theory's minimization of the role of inheritance in cultural transmission. Consider the following examples of cultural transmission: correcting spelling mistakes when copying text [43], correcting deviations from the standard form when copying a defective five-point star [248] or letters [241]; an *experienced* cook adapting an existing recipe to his or her taste rather than copying it exactly [43]; and limited imitation of suicide or obesity [195]. All of those examples, which are presented as instances of transmission, involve enculturated individuals who had *previously* inherited the relevant action variants (how to write a word, the way to draw a 5-point star or a letter, culinary techniques, observation that most people do not commit suicide and do not behave in ways conducive to obesity). The situations described in the examples do not involve inheritance; instead, they require that inheritance has taken place beforehand. The replication and emergence model provides an explanation of how actions and the corresponding mental traits were inherited (by replication and emergence, respectively) and recasts the transmission examples above not as *inheritance*, but in terms of deployment of previously inherited traits during *usage*.

The model also has practical implications. Understanding the cognitive mechanisms underlying cultural transmission will inform interventions aimed at changing behaviour. A prediction stemming from the framework is that behavioural change (see e.g. [191]) should be more effectively achieved by modelling of actions than by means that target mental traits, such as verbal instruction (see also [115]). Another prediction is that in order to change people's attitudes, trying to change their actions when they are naive should be more effective than at a later stage. Testing these and further predictions would provide important insights into the nature of cultural transmission and the degree of heritability and pathways of inheritance followed by different cultural traits (following e.g. [41]) that could connect cultural evolutionary studies with education and social policy.

Finally, one last analogy between biological and cultural evolution. Before genes were discovered, evolutionary theory remained in the theoretical realm. Much was understood about species, variation and selection, but the ultimate mechanism of life was not known (see e.g. [239]). When the small (in fact, microscopic) mechanism of transmission of biological information, DNA replication, was discovered (even if still not fully understood, as lingering theoretical disputes attest, see [216] for review), whole areas of academic inquiry and practical application ensued. DNA is not the whole of biology. For those asking questions about anatomy, physiology, or ecology, genetics is largely irrelevant. But they know that anatomy, physiology, and ecology ultimately require DNA replication. Even in the process of development, the role of genes can be described as minuscule, since they intervene only at the very first, relatively simple step of extremely complex, long chains of causality, and interact with extremely varied environments. Despite being so small, however, no one would say the role of genes is insignificant.

High-fidelity, content-indifferent replication of actions by naive individuals may seem insignificant in the large scheme of human culture, especially when asking questions about complex cultural institutions such as technology, religion, art, literature or politics, or about abstract entities such as attitudes and values. A corollary of the model I have defended is that if actions are not replicated, then culture could not have evolved to produce technology, religion, art, attitudes etc. In the replication and emergence model, biases and transformations explain selection processes that affect variation and development; however, in order to explain inheritance across any domain that we want to call cultural, this model categorically requires (although it does not necessarily privilege) action replication.

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