The possibility of impossible cultures

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Insights from evolutionary developmental biology and the mind sciences could change our understanding of the human capacity to think and the ways in which the human mind constrains cultural expressions.

The mental abilities of humans and other animals seem to have far greater similarities than differences. In the past 20 years or so, there have been reports of animals acquiring language, producing music, feeling empathy and teaching, leading to the conclusion that the differences between human and animal thought are just matters of degree. Such a continuum also seems to apply to cultural forms, such as language, music and morality. Humans generate an extraordinary range of cultural expressions and seem to have an almost unbounded capacity to do so. Just think of the differences between musical styles — for example between baroque, bhangra, gamelan and hip hop — the variation seems to be limitless.

The idea that such variation is continuous implies that there are no meaningful attributes common to all mental abilities or all cultural forms, as well as no limits to the abilities or forms that are possible. From this viewpoint, there are no gaps in the distribution of mental capacities across species or in the distribution of potential cultural forms.

But if these commonly held ideas are approached from another perspective, the opposite conclusions can be drawn. On the basis of recent developments in evolutionary developmental biology and the mind sciences, especially linguistics, I propose that there are two crucial gaps within the range of variation: one representing psychological discontinuity between humans and all other animals, and the other representing cultural discontinuities within the range of possible cultural forms.

Contemplating the possibility of cultural discontinuities forces a further consideration: some cultural forms will never be considered or, if they are, will prove problematic to acquire and sustain — these can be thought of as impossible cultures.

Impossible morphologies

Nature provides a bewildering and seemingly unbounded variety of animal forms, from the microscopic (such as insects) to the macroscopic (such as dinosaurs), and from the pointy and spherical (blowfish) to the smooth and cylindrical (snakes). Until recently, the dominant idea was that variation emerged from random processes, with adaptations sculpted by the blind process of natural selection.

New molecular approaches have now sharpened our understanding of the sources of variation and of how developmental programs interact with and constrain evolutionary processes, leading to a restricted range of adaptations. Much of this work was inspired by the rich description of the Cambrian period (about 500 million years ago), in which there was a rapid and unprecedented explosion of new life forms.

The fact that such variation appeared within a short time span, and that simple organisms such as worms and insects were equipped with genomes almost as large as that of humans, leads to two conclusions and raises one substantive challenge.

First, given the rapid emergence of different life forms, the cellular machinery that evolved before and during the Cambrian was highly generative. That is, it provided a massive suite of options for organisms that were confronting different ecological circumstances and challenges. Second, although the genes encoding this machinery were in place, they were often hidden from view, their presence not evident at the level of anatomy or behaviour. This fact highlights the importance of documenting not only which regions of a genome can be expressed but also which regions can, but might not, be expressed.

Although the diversity of animal forms is proof of the range of variation that has evolved, it raises a question. Do animal forms fill up the space of possible forms, or, more generally, does the genome have the potential to create an unbounded range of variation with no gaps? Answers to this question are only beginning to emerge, but they suggest that there are at least three factors that constrain the range of potential forms, creating gaps that have never been filled and may never be filled. Specifically, it may be highly improbable that animals evolve a particular form or class of forms — impossible morphologies — because of phylogenetic inertia (the tendency for a trait to remain stable in a variety of species because it was previously successful in a common ancestor), lack of relevant environmental pressures that result in selection among the biologically given options, and physical design constraints.

To illustrate these issues, consider two examples, one from molluscs and another from birds. Ammonoids are extinct cephalopod molluscs with a shell that spirals out from the centre before opening up. Studying the structure of their shells reveals two relevant dimensions that, when quantified, account for the observed variation (Fig. 1): the rate at which the spiral opens out, and the distance between the centre of this spiral and the opening.

If spiral rate is plotted against distance to the opening for the theoretically possible space of ammonoid species, as well as the actual space, there is a density of forms in a few areas and then gaps. The occupied spaces in this ‘map’ show the forms that evolved, whereas the vacant spaces suggest either possible morphologies that have not yet evolved or impossible morphologies.

The second example comes from the Galapagos finches (or Darwin’s finches), 13 related species present on the Galapagos Islands. Observations from the time of Charles Darwin to the present show that inter-specific differences in beak morphology among these finches evolved as a result of selective pressures from differences in seed morphology and availability. Like ammonoid shells, however, not all theoretically possible variants evolved, and nor would they be expected to, given various physical constraints, including those that involve maintaining head position during flight and producing song. Molecular studies have now uncovered the machinery that facilitated this variation. Specifically, two genetic mechanisms control the length and height of the beak during ontogeny, by guiding the expression of genes that influence...
bone growth. For large-beaked finches, one of these proteins — known as bone morphogenetic protein (BMP [BMP4]) — is associated with bone growth earlier in development and is present at higher concentrations than in smaller-beaked finches. When the gene encoding BMP [BMP4] is inserted into a chicken embryo, the developmental outcome is a chick with a large, broad beak, instead of the small beak that is typical of this species. Importantly, this experimentally induced, unnatural anatomical variant develops seamlessly, appearing much like the large-beaked Galapagos finch. This observation suggests that developmental programs are set up as ‘engines of variation,’ providing a range of potential options for targeted selection. It also shows why cataloguing variation in living animals is insufficient for understanding both the range of variation and its potential constraints [all the studies were of living animals though, so are you referring to the transgenic chicken?].

The challenge in this research is to understand what causes gaps in form, harnessing the tools and theories of molecular biology, mathematics, physics, ecology, anatomy and behaviour. Why, specifically, have certain species never taken over a particular swath of morphological turf? What is it about this space that leaves it vacant? Some of the causes will be intrinsic to the organism (such as the absence of genetic material or developmental programs for building square ammonoids); some will be extrinsic (such as a lack of relevant ecological pressure that would favour hooked beaks); and some will arise due to historical constraints [what do you mean by a historical constraint (it would help if you could give an example as you have done for the other two)].

Two central ideas emerge from studies of animal form. First, the observed differences, although adaptive, arise from a core set of cellular mechanisms that generate a massive range of possible variation. Second, as generative as these mechanisms are, there are constraints, which arise from developmental factors, physics, history and ecology. As a result, to understand what a genome is capable of building, it is important not only to look to the fossil record or the extant animals but also to experimental manipulations that attempt to push nature beyond its visible bounds. Doing so will enable the causes of gaps in the range of potential animal forms to be better understood. Strikingly, this line of reasoning has direct parallels in the generative tradition of linguistics.

Gaps in linguistic form

Natural languages, both extant and extinct, are remarkably variable, seemingly boundless in terms of their variation in sound structures, lexicons and organizational principles. Inspired by early work in cellular biology, several linguists working in the generative tradition that Noam Chomsky initiated started challenging the idea that there is unbounded variation in linguistic form. In particular, the earliest challenges suggested that the observed variation was highly constrained and mediated by a set of universal computations that enabled every developing human infant, but no other animal, to acquire a range of possible languages. More specifically, the human brain has a uniquely evolved language capacity that links grammatical rules (syntax) with systems of meaning (semantics) and externalized expression in sound or sign (phonology) to provide a family of developmental options for building different languages.

Crucially, this perspective raised the idea of impossible languages: that is, linguistic structures that would either never be contemplated or, if contemplated and expressed, could not be learned. For example, no language has a rule that mandates placing a particular word (for example, ‘no’) in a fixed position (for example, the fourth position) in a linear sequence. And no language stipulates that a question must be asked backwards [please rephrase. backwards and forwards could be relative depending on what you’re used to]. Although there are controversies concerning the limits of linguistic variation, and the details of its universal structure, here I reveal three points of contact between work in the generative tradition of linguistics and evolutionary developmental biology research on animal forms.

A first point of contact is the fact that children are born with the capacity to acquire a wide range of possible languages, as opposed to specific languages such as English, Korean or French. This implies that a child is equipped with an abstract acquisition device, allowing the ‘growth’ of many different languages. Further, as the child’s acquisition device generates a space of possible languages, something internal or external to the device thereby creates a space of impossible languages — forms that are never entertained by the child because they are poorly designed for acquisition and externalization in linguistic communication.

In cases in which languages, such as Esperanto, are invented, they are acquired in a different way (for example, by relying on rote learning and teaching as opposed to spontaneous acquisition), and they prove unstable over the long term, dying out like the extinction of a species.

The beauty of thinking about the child’s linguistic endowment as a system for building a space of languages is that it maps onto work in functional morphology described in the previous section. Thus, in the same way that biologists speak of morphospaces — n-dimensional volumes that define the range of existing and potential morphological variation — linguists can speak of ‘linguaspaces.’ These are n-dimensional environments that constrain the set of possible languages and therefore, by definition, establish the set of impossible languages. What is necessary, therefore, is to establish the set of parameters that allow the range of variation and place constraints on its overall form. An elegant example, with direct parallels to language, comes from analyses of the design space of skeletal morphology. On the basis of a functional library of only seven parameters, each with a few options, it is possible to account for approximately 80% of the skeletal variation observed since the Middle Cambrian (Fig 2). When environmental conditions favour selection of a particular option for one parameter, this imposes constraints on the selection of options for other parameters.

Although it is not yet possible to define the dimensions that constrain the range of possible languages (and thus establish the features of [ok?] impossible languages), adopting this perspective establishes an important methodological point. Akin to work in theoretical morphology, in order to understand the languaspace, it is important to go beyond the extinct and extant languages — languages that have been generated — to languages that could be generated, acquired and maintained.
over time. Given human creativity, a group of people could create a novel language that violates many of the universally shared features of language (for example, massive embedding, no constraints on word order and unpredictable relationship between syntactic categories). Experimental study of this point might entail creating artificial languages that eliminate, or modify in significant ways, the set of linguistic universals that have been catalogued by linguists\textsuperscript{[8]}. Given such modifications, would individuals acquire this system as human children acquire known languages? And after the language has been acquired, would it remain stable, lasting across generations of users? And would such systems be represented in the same neural circuits that mediate natural languages? If the ideas laid out thus far are broadly correct, the answer to all three of these questions will be no.

A second point of contact concerns the nature of the input and the timing of growth and development. When a child grows its native language, the appearance of certain structures is constrained by the appearance of others, as well as by the timing and magnitude of the input (that is, how much linguistic experience, at which time points, and from what sources). Some of these constraints are specific to language, and some result from the interaction between language-specific operations and processes that are more domain-general, including memory and learning. For example, recursive computations such as ‘merge’ (which, loosely defined, is an iterative operation that takes two elements and combines them into a set to create new expressions) are unlimited with respect to the number of iterated computations, but they are constrained by language-external processes of memory and comprehension, as well as by properties of the motor system that enable externalization, forced through a process of linearization (that is, each sound or sign has to emerge in communication in a linear sequence). By analogy, much of the work in evolutionary developmental biology suggests that the growth and development of different animal forms arises as a result of core molecular operations for generating variation (for example, rearrangement, repetition, magnification and division), with each of these processes further modified and constrained by the magnitude of experience.

A third point of contact concerns how the internal language system ultimately forms an acquired and externalizable language. If, as discussed earlier, the acquisition device constrains the range of possible languages by providing a set of options, then the role of environmental input is to favour, and thus select, certain options over others. This selective perspective, although uncommon in much [many?] of the mind sciences, aligns more closely with other work in biology, including studies of the immune system\textsuperscript{[1]}, the development of animal forms, the wiring of neurons\textsuperscript{[2,3]} and the acquisition of bird song\textsuperscript{[4]}. For example, songbirds have evolved brains with a set of developmental options for creating variation in song-relevant acoustic forms. Depending on the environment, certain note types are selected and are then reproduced in particular orders to create population-specific dialects — and so it is for language acquisition by humans. When a child is exposed to a particular linguistic environment, the relevant linguistic input or experience fixes the available options to create an externalizable language that is comprehensible to those who will care for and compete with the child.

Research in the generative tradition of linguistics suggests therefore that, like the variety of animal forms, the sense of unbounded variation in linguistic form is illusory, concealing a suite of universally held, biologically instantiated mechanisms for generating variation, allowing acquisition and constraining the space of possible languages. Although biologists have long sensed the close connection between the generative properties of language and generative biological systems [ok?], including the immune system, microbial diversity and proteonomics [please briefly define proteonomics]\textsuperscript{[5,6]}, relatively few students of the mind sciences have acknowledged such connections with other domains of human knowledge\textsuperscript{[7,8]}.

Phylogenetic mind gaps

[This section is v long -- it help to add another crossheading after the subheadings for the 4 capacities] It has been argued that the history of life on Earth presents eight main evolutionary transitions, beginning with the replication of molecules to form populations of compartmentalized molecules and ending with the change from primate societies to human societies with language\textsuperscript{[9]}. From this viewpoint, the birth of language caused a transition from non-human animals to humans. There are two problems with this view, however. First, it assumes, as Darwin did, that there is mental continuity among humans and other animals, while nonetheless acknowledging that language had a role in making humans different. Second, it treats language as a monolithic part of our psychology (as opposed to a capacity with a suite of distinctive computations), and it fails to recognize other, more distinctive, properties of brain function that facilitate the seemingly limitless variation in cultural expression and modes of thought. By contrast, I propose [ok?] that humans evolved unique neural capacities after divergence from the last common ancestor with other animals some 6 to 7 million years ago, and these capacities created a fundamental, and unprecedented, gap in the evolution of animal minds\textsuperscript{[10,8]}. It created what I call our humaniqueness. Specifically, humans alone evolved four distinctive computational capacities.

Generative computation

Recursive and combinatorial operations provide the only known mechanisms for generating an almost limitless variety of meaningful expressions, whether

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**Figure 2: The parametric space of skeletal variation.** There are seven core properties or parameters (coloured boxes), each with two to four possible states (each labelled with a capital letter), making a total of 21 variables. Situation indicates the location of skeleton: internal (A) or external (B). Material indicates the composition of the skeletal elements: rigid (C) or flexible (D). Number refers to the number of skeletal elements: one (T), two (V) or three or more (W). Shape indicates the shape of these elements: rods (G), plates (H), cones (J) or solids (K) [Solids does not seem to fit with the rest -- please check.] Growth indicates the way the elements are put together: by accretion (L), as branching serial units [ok?] (M), by replacement or moulting (Z), or by remodelling (N). Assembly indicates where the elements are assembled: growth in place (X) or prefabrication (Y). And interplay indicates how the elements interact: no contact (P), jointed (Q), sutured or fused (R) or imbricate (S; that is, folded over or overlapping). A human finger is designed on the basis of one state (red circle) from each of the seven properties, specifically ACWGNXQ. (Modified, with permission, from ref. 29.) [The figure has been redrawn by our artists. Please check carefully. (2) It’s unclear why the options are not labelled in alphabetical order. It seems a little odd to go from D to G, for example. Because we’ve redrawn this, we can relabel each option if you would like. (3) It’s unclear what N is depicting. If you can explain this, then we might be able to alter the diagram to make it more obvious.]
mathematical, linguistic, musical or moral. Recursion is an iterative operation, in which a rule is called up repeatedly to create new expressions, be they embedded phrases within a sentence, new musical scores with repeating themes, or tools within tools (for example, a Swiss army knife). Each expression has a unique interpretation or function depending on the arrangement of the elements. By contrast, combinatorial operations allow discrete elements to be unified and ordered, thus creating new ideas, which could be expressed as novel words (walkman from walk and man) or novel musical forms [edits ok?].

Mental symbols Humans readily, without instruction, convert sensory experiences and abstract thoughts into externalized symbols, either as words or images. This capacity cuts across domains of knowledge and sensory experience, enabling humans to express beliefs in sentences, to depict particular melodies with explicit notations, and to provide logos indicating when to turn off the highway for a hamburger or a coffee.

Promiscuous interfaces Humans have unique creative capacities and problem-solving abilities, which stem from the capacity to combine representations promiscuously from different domains of knowledge. For instance, humans can combine the concepts of number, belief, causality and harm in deciding that it is sometimes morally obligatory to harm one person to save the lives of many.

Abstract thought Some thoughts derive from direct sensory experiences: for example, thinking of red items such as cherries and blood requires experience with these, as opposed to non-red objects such as celery and bone. But many human thoughts are abstract, with no explicit or even necessary sensory connection. These include concepts such as infinity, grammatical categories such as nouns and verbs, and ethical judgments such as permissible and forbidden.

The proposal that our humaniqueness, and these four properties in particular, finds almost no parallels in any other animal suggests that there were fundamental changes in genomic and neurobiological function during a relatively recent period of human evolutionary history. These changes provided humans with an unprecedented capacity to generate variation in culturally meaningful forms, albeit constrained in important ways.

Although anthropologists disagree about the timing of the human cultural revolution, many researchers [ok?] point to fundamental changes starting some 800,000 years ago in the Early Palaeolithic, with a crescendo of change at around 45,000–40,000 years ago in the Late Palaeolithic. This period is associated with the generation of symbols (mathematical, artistic and ritualistic), controlled fire for use in cooking and other forms of environmental transformation, and tools with multiple components and functions (for example, tools used for expressing both aggression and music [ok?]). Given that this 5,000-year interval [ok?] is barely noticeable on an evolutionary timescale, and that such cultural expression emerged rapidly, the parallel with the Cambrian is striking: that is, something similar to a genetic revolution must have occurred during this period, providing humans with an unprecedented set of capacities for generating novel cultural expressions in language, morality, music and technology. Specifically, at some point before or during the Paleolithic, the human brain was transformed from a system with a high degree of modularity with few interfaces to a system of modules with numerous promiscuous and combinatorially creative interfaces. This system provided a universal framework on which cultural options could be realized.

To enrich these ideas, I next discuss comparative evidence that supports the evolutionary uniqueness of these four essential properties of human brain function and reveals the discontinuity — the gap — between human and animal minds.

Recursive and combinatorial operations are ubiquitous (and therefore domain-independent) in human mental life, operating in language, music, morality, technology and mathematics. A simple example, in the case of language, is creating a list, which has the recursive rule AND X+, where X is the name of a person. Thus, one list could be Sally AND Bill AND Sam AND Jane, and so on. This example, which every child immediately understands, illustrates the almost limitless capacity of humans to create linguistic expressions (that is, the property of discrete infinity), as well as the fact that the child's starting state is not blank but prepared with a competence that readily and implicitly understands recursive operations. In the example above, there is simply no experience that informs the child about the iterative and limitless power of list building. [Long paragraph broken into 2] Iterating a rule such as AND X+ is a type of looping operation in which the same computation is returned to repeatedly until some other function terminates the operation. Although many vertebrates have evolved brains with reciprocal connections or loops between different cortical areas (for example, basal ganglia [of the brain?] to the cortex and back), these loops are restricted to particular functions. At the most general level, it is clear that the motor systems of all animals must involve recursive operations to allow organisms to take a discrete set of motor options and generate a vast range of functionally meaningful motor acts or sequences in novel environments. For example, whether an organism flies or runs, its legs must repeatedly lift and fall or its wings must repeatedly beat. However, because an organism's habitat and climate is constantly changing, the iterative or recursive rule of cycling through leg lifts or beating the wings must be flexible so that the animal's response can vary in response to environmental change.

That said, the recursive properties of the motor system seem to be locked into motor function in all animals but humans. For example, in striking contrast to the recursive operations in human language, with its unrestricted use of different content or classes of words, the looping circuitry that is necessary for song acquisition in songbirds only supports singing and, in some cases, mimicry of other biological and non-biological sounds. This circuitry is not, however, used when they acquire the calls that constitute their repertoire more generally, including the sounds used in social interactions, food discovery and alarm calls.

A second example [is the motor system example the first example?] of generative computation comes from the domain of artefacts, in particular the creation and diversity of human tools. Unlike many of our simplest tools, such as the pencil, animal tools consist of only a single material, never include more than one functional component, are typically dispensed after their first use and are never used for functions other than the original one. The first two features reveal that, unlike human tools, the representation of animal tools is not combinatorial. A pencil can combine four materials (graphite, wood, metal and rubber) to create four functions (graphite for writing, wood for holding the graphite, metal for attaching the rubber to the wood, and rubber for erasing). Moreover, each material can be used for a variety of other functions: for example, rubber can be a component of chewing gum. As experiments reveal, if a young child is asked what she can do with a pencil other than write, she will immediately offer such functions as holding up her hair, puncturing a plastic cover and poking a friend. Only humans think of artefacts as being designed for a particular function but, as a result of promiscuous interfaces, entertain many other possible functions.

The generative mechanisms that underpin so much of human mental life acquire their expressive power because the recursive and combinatorial operations can functionally ‘grab’ the outputs of different modular systems or domains of knowledge. This capacity for promiscuously creating interfaces between domains is almost absent in animals. Thus, although both human and animal brains are characterized by modular functions and mechanisms, the modular outputs are typically restricted to a single functional problem in animals but are broadly accessible in humans. Non-human animals therefore show a form of myopic intelligence, designed to solve one problem with exquisite efficiency. For example, although honeybees have a symbolic dance that indicates the distance, direction and quantity of food, this communication system is largely restricted to food despite the intricate social lives of bees. Although meerkat adults teach their pups how to kill scorpion prey by providing them with age-appropriate
opportunities for handling and dismembering, teaching does not occur in any other context\textsuperscript{5}. Although plovers use a deceptive display to lure predators away from their nest of eggs, they do not deceive in any other situation\textsuperscript{4}. And although chimpanzees use the direction of another's eyes to guide strategic competition, they are far less skilled at using another's eyes to guide cooperation\textsuperscript{25}. By contrast, in humans, neither language, teaching, deception, or the use of seeing to infer knowing are restricted to a single context.

Generative mechanisms in human cognition are further enhanced by the fact that they operate over mental symbols, reducing memory load over non-symbolic representations. Further, because symbols can be attached to any concept — whether real or imagined, abstract or anchored in sensory experience — they allow great flexibility in our modes of thought and communication. Although 40 years of research has been invested in the capacity of animals to produce or comprehend externalized symbols, the relevant evidence that they do so\textsuperscript{ok?} is, at best, weak, including findings from studies of natural communication or artificial acquisition of human-created signs or symbols\textsuperscript{1,2,4,18}. Thus, even in cases in which animals spontaneously produce signals that seem to convey information about an external object (such as a predator or food) or event (such as movement of a group or submission to a dominant member\textsuperscript{ok?}), the number of different signals with such semantic properties is exceedingly small. The same limitations apply to studies of captive animals that have been trained to acquire a symbolic system\textsuperscript{19}. These repertoires pale in comparison to even a human toddler, who can use hundreds of words and will soon have a repertoire of thousands.

Most of the conceptual representations acquired by animals seem to be largely anchored by sensory experiences, lacking the abstractness that characterizes so much of human thought. One exception to this comparative claim comes from recent studies of mathematical knowledge in humans and animals, in particular the neurobiological and psychological mechanisms that support both non-linguistic and linguistic quantification\textsuperscript{4,6,10,21}. A wide range of animals are endowed with the capacity to quantify the number of individuals in an array not only spontaneously but also across modalities (for example, visual and acoustic), and even in cases in which they are required to integrate modalities.

Even with the abstractness of number representation in animals, however, there are important ways in which human thought, through its promiscuous interfaces, transforms this representation in unique ways. Consider, as an example, the distinction made in many human languages between singular and plural. At its core, this is a system of set-based discrimination that distinguishes between one and many but not between many and many. Thus, the morphological extension -s is used in English to count objects whether there are 2, 100 or 1 million cats, trees or pencils but not if there is only 1 of these objects. Studies of rhesus monkeys suggest that they share, with humans, an important aspect of this set-based quantification system\textsuperscript{25}. Specifically, in a foraging task in which sets of food items are presented and then concealed, rhesus monkeys preferentially pick a location with many pieces of food over one piece but not many pieces over many.

This non-linguistic, set-based system is present in human development but is then transformed as a result of an interface with the abstract properties of human syntax. Thus, although in English there are 2, 100 and 1 million cats, there are also –2, 0 and 1.0 cats. Consequently, when a neural connection was made between the evolutionarily ancient, set-based system and the evolutionarily recent syntactic system, a conceptual transformation emerged that was simple but abstract: anything that is not precisely 1 acquires the -s extension. This case study highlights both the limits of animal thought and the transformative effects on conceptual representation that emerge when abstract concepts from different domains of knowledge interface.

### Cultural gaps

Open a history book and explore the variation in visual arts, the changing attitudes about morally forbidden acts, the explosion of languages across the globe, and the endless gadgets that humans design to solve every problem from the most mundane (for example, an asparagus peeler) to the most profound (rockets to explore the solar system). This shows a spectacular diversity with all the signatures of a system capable of change. No other animal mind is comparably endowed.

Controversy arises, however, over which cognitive capacities were crucial for creating the mental gap. And when the distinctive cognitive architecture of humans was in place, there is controversy over whether it provided humans with an unbounded potential to create cultural variation. I propose\textsuperscript{ok?} that much of the variation observed in human culture is highly constrained, with the space of possible cultures only sparsely populated, leaving several gaps that constitute impossible cultural forms. This perspective, with its parallels to work in theoretical morphology and extension of the general approach that has motivated work in generative linguistics, implies that some cultural forms will never be entertained or, if they are, will rapidly die out because they are unlearnable or learned with great difficulty. This view has interesting implications for both the study of culture and the biology (the genes, neural circuits and cognitive processes) that facilitates and constrains cultural acquisition and transmission.

The idea that there are cultural gaps raises the same kinds of questions as the idea that there are gaps in animal form. That is, it is necessary to understand what generates variation in cultural forms and why certain theoretically possible forms are never realized. On the basis of what can be observed, humans are born with a mental tool kit for creating, and especially for understanding, cultural variation in linguistic, musical, artefactual and moral expression. This tool kit consists of a suite of developmental programs that generate variation, the raw material for a selective process that crystallizes a particular form of expression. When cultural forms crystallize, perhaps as a result of a process of cultural inertia, gaps may emerge, because it is not possible for the individuals within the culture to imagine alternatives — a poverty of the imagination. In other words, people may get stuck in a cultural rut because the human mind cannot move beyond the constraints imposed by history. The other main reasons for cultural gaps are the absence of relevant environmental triggers and the possibility that some ideas are never contemplated. These issues form the core of the argument for thinking about human cognition as massively generative but highly constrained. They also raise a serious methodological problem.

In many accounts of cross-cultural variation, there is a tendency to rely on ethnographies describing past and current cultures. But as in the case of animal forms, such descriptions only showcase what has been realized and not what could be realized in different circumstances or what might never be realized regardless of the circumstances. In particular, if humans are equipped with developmental programs that can generate a space of cultural expressions — a ‘culturespace’ — the observable cultures might occupy only a small fragment of the potential space. To uncover whether the currently empty space is within the range of theoretically possible cultures, experiments and computer simulations must be carried out to determine which of a range of possible cultural variants are evolvable, intelligible, acceptable, learnable and stable over time; work like this is well underway in the study of language, [\textquoteleft where researchers are? or do you mean that there are 4 study areas?\textquoteright implementing modelling, cognitive experiments and neuroimaging\textsuperscript{6,13–15}].

Some of these ideas have also begun to proliferate outside linguistics, in the less-studied domains of music\textsuperscript{6,16–18} and morality\textsuperscript{18}, with intriguing experimental evidence and novel theoretical insights. Both music and language share core resources, such as the use of combinatorial operations and the representation of hierarchical structure — an analysis that has been supported by neuroimaging studies revealing that both of these engage regions in the brain in common\textsuperscript{19}. An important aim of this work is to map the range of possible musical forms, together with the mechanisms that generate and constrain such forms\textsuperscript{25}. Significantly, this research refers not to what can be produced (as this is up to the whims of a composer and the quirksiness of people’s preferences) but rather to what can be perceived.
So are there musical forms that cannot be perceived or therefore represent impossible structures? The answer is, unambiguously, yes. For example, all music has a hierarchical structure in which there are groups of notes, phrases and sections. Therefore, a musical grammar that generates output in which grouping makes no difference represents a gap in the existing ‘musicspace’ and thus seems impossible. Further, and paralleling the previously mentioned case in language of a grammar with a fixed position for a word class, imagine a musical system in which meaning is derived not from hierarchically related pitches but strictly from a fixed permutation of the set of 12 tones of the chromatic scale and from transformations on the entire set. This is a kind of structure that cannot be perceived except through conscious decoding.

An analogy has also been drawn between language and morality. Evidence suggests that, like language, some of the computations underlying human moral judgments operate outside human awareness, are abstract, and show considerable similarity regardless of gender, age, religious belief or education. Although, at present, there is no understanding of the possible and impossible moral systems — the ‘moral space’ — the charting of this space is an inevitable outcome of the perspective taken here. For example, in several studies, including some cross-cultural work, individuals consistently judge that harming one individual as a means to some greater good (such as saving the lives of many) is worse than harming the one individual as a by-product or side effect. For example, if a toxic gas is about to be released through a vent into a room that contains ten people, it seems worse to push one person. From this work, it can be predicted that in a second room where there happens to be just one individual, a similar judgment would be expected. And like the study of side effects would be judged worse than means). If this prediction is correct, the reverse principle (that is, that side effects are worse than means) would be expected. And like the study of language, music, and combinatorial operations to generate hierarchical structures, there has been no progress in identifying the circuits that are responsible for this ubiquitous capacity, including the genetic changes that made such domain-independent generative computations possible in humans but no other species. One might wonder, nonetheless, whether it will one day be possible to take the kinds of reciprocal or looping circuits observed in non-human animals, especially those that appear in all motor systems, and re-engineer them (either genetically or through neurodevelopmental manipulations) to interface with the conceptual resources that these species have evolved, creating a songbird that can sing not only with passion but also with the richly thematic and meaningful expressions that characterize a Wagnerian leitmotif.

Regardless of how far these techniques can be taken in the future, they open up unprecedented possibilities for understanding questions of evolution and cognitive capacity. Consequently, they show how the theories, technologies and findings of molecular biology, evolutionary [“developmental”? biologists, neuroscience, cognitive psychology, linguistics and anthropology can be productively combined to understand one of the most profound problems of intellectual life: how humans evolved a uniquely generative brain that allows massive cultural expression, and why there are gaps in the cultural record — spaces that no human brain will ever fill with linguistic, musical, moral or technological forms.

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