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'Lamarckian' mechanisms in darwinian evolution

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Since the Modern Synthesis, evolutionary biologists have assumed that the genetic system is the sole provider of heritable variation, and that the generation of heritable variation is largely independent of environmental changes. However, adaptive mutation, epigenetic inheritance, behavioural inheritance through social learning, and language-based information transmission have properties that allow the inheritance of induced or learnt characters. The role of induced heritable variation in evolution therefore needs to be reconsidered, and the evolution of the systems that produce induced variation needs to be studied.

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'Lamarckism' and 'darwinism' are traditionally seen as alternative theories trying to account for evolutionary change (Box 1). The verdict of history is that Lamarck got it wrong – evolutionary change does not occur through the inheritance of acquired characters. Acquired characters are the outcome of *instructive processes*, such as those seen in embryonic induction, transcriptional regulation, and learning, all of which involve highly specific and usually adaptive responses to factors external to the responding system. The inheritance of the outcomes of instructive processes is deemed to be impossible. Adaptive evolutionary change is assumed to be based on darwinian (or more accurately neo-darwinian) evolution in which guidance comes exclusively from selective processes. The production and nature of heritable variation is assumed to be uninformed by the environment or by previous history. The future is open-ended, determined solely by the contingencies of life. It is neither foretold nor intimated.

General selection theory makes no assumptions about the origin of heritable variation. It maintains that evolution by natural selection will occur in any system with entities manifesting the properties of multiplication, heredity and heritable variation affecting reproductive success¹. In the current version of biological darwinism, it is assumed that information is digital and encoded in DNA base sequences, that multiplication of information occurs through DNA replication, and that variation, which is generated by mutation and recombination, is random with respect to the selecting environment and the developmental history of the organism and the lineage. However, this version of evolution – 'genic neodarwinism' – is incomplete: it gives natural selection an exclusive deterministic role in the evolution of all conceivable complex adaptations, but until recently it has had rather little to say about the evolution of new systems for acquiring, storing and transferring information, and even less about the evolutionary effects

of such systems once they are in place. Natural selection leads not only to the evolution of eyes, wings, and sonars, but also to the evolution of new evolutionary rules. Many of these rules undermine the assumption that variation is random. Mechanisms allowing the inheritance of acquired characters have evolved several times during the history of life, and understanding their evolution is crucial to understanding the transitions to new levels of individuality^{2–4}.

Evolved 'lamarckian' heredity systems

The heredity systems that we consider here are all complex mechanisms for the acquisition, storage and transfer of information. All evolved through natural selection, but they differ from each other in the type of information they transmit, in their evolutionary history, and in their evolutionary effects. They include adaptive mutational systems involving non-random changes in DNA, cellular heredity systems in which information is acquired and transmitted through intracellular structures and biochemical mechanisms, the transfer of patterns of behaviour through social learning coupled with certain types of social organization, and the transmission of information using symbolic languages. All of these systems allow certain outcomes of the interaction between the organism and its environment to be incorporated into and maintained within the information-carrying system, and the information to be transmitted to future generations. All therefore allow the inheritance of acquired or learnt characters.

Adaptive mutational systems: the intelligent genome

In the genetic inheritance system, information for making RNA and proteins is stored in DNA base sequences; an elaborate enzyme system enables this information to be replicated and transmitted to the next generation. Physico-chemical damage to the DNA and errors occurring during its replication can be removed by a battery of repair processes. Errors that remain, and sequence changes that are

created during repair, or result from the movements of genomic parasites, provide the raw material on which selection ultimately acts. Since replication and repair are enzyme-dependent processes, genetic variation in the enzyme-coding genes can affect their efficiency. In addition, base sequences differ in the likelihood that they will be damaged, replicated inaccurately, or be invaded by parasitic elements. Consequently, the type of DNA variation generated, the rate at which it is generated, and when and where it is generated, can all be selectively modified. Systems that were presumably selected to maintain the fidelity of the genetic inheritance system can, once they are in place, be modified and used in ways that lead to the generation of mutations at particular sites, or of a particular type, or at a particular time.

Some pathogenic bacteria are able to adapt to ever-changing conditions because genes that are likely to provide the means of surviving are hypermutable. Moxon and his colleagues have shown that the pathogen *Haemophilus influenzae* can adapt to the changing conditions experienced in its host because genes influencing its antigenicity and other features are highly mutable⁵. These genes are characterized by tandem repeats of short DNA sequences which make them prone to genetic change through homologous recombination and strand slippage. Through selection, the genome of *H. influenzae* has evolved features that result in high rates of variation in the relevant genes. Similar highly targeted, locus-specific DNA changes are found in trypanosomes and other microbial pathogens.

Bacteria are able to generate variation not only at sites, but also at *times* when it is likely to be selectively useful. During starvation, some mutations arise at a higher rate than in non-starving cells. This could simply be because starved cells cannot carry out normal repair. However, it is increasingly clear that bacteria have evolved mechanisms enabling them to actively generate new variation in conditions where survival depends on genetic change. Shapiro found that one type of mutation in *Escherichia coli*, *araB-lacZ* fusions, involves a multi-step process that is physiologically regulated⁶. Recently, Wright has shown that amino acid starvation of *E. coli* increases transcription of a specific set of genes that enable them to survive, and these genes have enhanced mutation rates⁷. Genetic changes induced by altered environments have also been found in cultured plant and animal cells, and germline-transmissible changes have been well characterized in flax⁸ and mustard⁹.

Shapiro suggests that organisms respond to stress by activating their 'natural genetic engineering systems'⁶. There is biological and environmental feedback into

Box 1. Lamarckism and darwinism

The terms 'darwinism' and 'lamarckism' mean different things to different people¹⁶. Nowadays, they are rarely used in a historically correct way. Lamarck's theory of evolution was wide-ranging and included continual spontaneous generation of simple forms of life, progressive change caused by the inherent tendency of living matter to become more complex, modifications brought about by the increased use and disuse of parts in response to environmental conditions, and the inheritance of such modifications. In Darwin's theory the key mechanism leading to evolutionary change was natural selection of heritable variations, and Darwin put forward his pangenesis theory to explain the origin and behaviour of inherited variation. He accepted that when characters change through use or disuse the changes are inherited, and argued that new environments increase the rate at which variation is generated.

By the end of the 19th century, thanks largely to the efforts of Weismann, neodarwinians had purged darwinian evolution of pangenesis and the inheritance of acquired characters. Following the synthesis of genetics and darwinian ideas in the 1930s and 1940s, darwinism came to mean the theory that evolutionary change results from natural selection of the random genetic variations generated by mutation and recombination. The neolamarckians of the late 19th and early 20th centuries emphasized various parts of Lamarck's theory, but in modern biology lamarckism is usually equated with the inheritance of acquired characters. Other parts of the Darwin's and Lamarck's theories are usually ignored. In this article we use the terms darwinism and lamarckism in the familiar colloquial sense, rather than in a historically precise way.

the genome. This means that evolutionary change may be very rapid because mutation rates can be increased, and coordinated changes may occur at many sites within a single genome. Furthermore, although the induced genetic changes may not be specifically those that solve the organism's immediate survival problem, if similar stress episodes have been frequent in the past, the genome and genetic machinery may have been modified to target variation to a subset of sites or to be of a type that is likely to provide useful variation. Whether or not mutation is 'directed' in the sense that environmental factors induce exclusively those mutations that are beneficial is still highly debatable. However, given the well-known ability of natural selection to take two or more old functions and cobble them together to construct something new, it would not be surprising if the mechanisms that enable selective control of transcription have been coupled with those that maintain (or fail to maintain) genetic fidelity. The result would be that the inducible systems that turn genes on and off could then also turn the production of genetic change on and off.

We know that in some organisms the genetic system has been modified in ways that make the genome change in a directed way: in ciliates, formation of the macronucleus involves a complex, regulated series of sequence deletions, duplications and rearrangements; in amphibian oogenesis, rRNA genes are selectively amplified; in *Ascaris* development, large parts of the genome are deleted in somatic cells; in *Drosophila*, chorion genes are amplified in follicle cells; in the mammalian immune system, complex developmentally regulated DNA rearrangements followed by hypermutation underlie the production of antibody diversity¹⁰. The programmed generation of variation seen in these organisms shows that the genetic inheritance system can take part in instructive processes.

Cellular heredity: epigenetic inheritance systems

From what we know at present, it seems that only rarely is DNA sequence information changed during determination and differentiation. Most organisms have different ways of generating and transmitting cellular phenotypes – they use epigenetic inheritance systems (EISs). Three classes of EIS have been recognized: steady-state, structural, and chromatin-marking systems¹¹.

Steady-state systems are based on positive feedback loops. At its simplest, a gene produces a product that stimulates further activity of the gene and hence further synthesis of the product. Once switched on by physiological or developmental events, the cell lineage continues transcription unless the concentration of the product falls. In structural inheritance systems, cell structures are used to template the formation of new similar structures. For example, genetically identical ciliates can have different patterns of cilia on their cell surface which are inherited; even experimentally altered patterns can sometimes be transmitted to daughter cells¹². Recent studies of prions provide further examples of structural inheritance¹³. In the third type of EIS, chromatin-marking, states of chromatin that affect gene expression are clonally inherited. The textbook example is the transmission of the inactive X chromosome in female mammals: once one of the two X chromosomes in a cell has been inactivated, all of the descendants of that cell normally have the same X inactive. Information about gene and chromosome activity is contained in what have been called chromatin marks, i.e. in the proteins associated with DNA and the distribution of DNA modifications such as cytosine methylation¹⁴.

We can only guess at the evolutionary origins of the various EISs. Simple feedback and structural inheritance systems probably evolved very early in evolutionary

Box 2. Genetic assimilation through the culturally-driven Baldwin effect

The transformation, through darwinian selection, of a learnt response into a fixed or 'instinctive' response is known as the 'Baldwin effect', although two other late nineteenth-century scientists, Lloyd Morgan and Fairfield Osborne, suggested a similar mechanism. The basic idea is clearly expressed by Morgan: '... any hereditary variations which coincide in direction with modifications of behaviour due to acquired habit would be favoured and fostered; while such variations as occurred on other and divergent lines would tend to be weeded out. ... We may look upon some habits as the acquired modifications which foster those variations which are coincident in direction, and which go to the making of instinct.' (cited by Hardy²⁷, p. 197).

The British embryologist and geneticist, C.H. Waddington, suggested a similar process, genetic assimilation, for the evolutionary acquisition of some physiological and developmental adaptations. Using *Drosophila*, Waddington showed that a character whose development originally depended on an environmental stimulus became, through selection in the inducing environment, genetically fixed and began to appear in the normal non-inducing environment. This happened through the sexual reshuffling of genes and selection of those combinations that produced progressively more rapid and efficient responses to the stimulus⁴².

Social learning may augment the probability of genetic assimilation of behaviour patterns. Tradition makes selection more directional and more persistent because it leads to the transmission of the same selective regime. A behaviour pattern that becomes traditional through social learning is often more enduring than that acquired by individual learning because it results from the self-perpetuating social structure, and may continue even when the environmental conditions that first initiated it in a particular individual have changed.

history, but chromatin-marking systems depend upon DNA and its orderly replication, so they must have followed the evolution of DNA-based inheritance. DNA methylation and heterochromatinization are both ways of inactivating repeated DNA sequences such as those that arise from viral invasion, so the chromatin-marking EISs may have originated as defence mechanisms against genomic parasites which were later modified by selection to fulfil additional roles in gene regulation and cell memory^{15,16}.

Whatever the origins of the various EISs, they were probably selectively refined in early unicells living in environments that fluctuated in a regular way (e.g. between summer and winter)^{11,17}. When environmental fluctuations are short relative to the lifespan, selection favours adjustment through physiological change (for example, turning genes on and off); when they are long, so that many generations are spent in each phase of the cycle, adaptation through the selection of genetic variation is possible. However, in cycles of intermediate length, where adaptation through selection of genetic variations is usually too slow (although hypermutable loci may evolve), the ability to transmit functional states (for example, whether a gene is on or off) should be strongly selected. Any genetic changes that link epigenetic switching to the environmental change would have obvious selective advantages.

The outcome of this type of selection was systems through which alternative cellular phenotypes, including induced phenotypes, could be transmitted in cell lineages with various degrees of fidelity. Such systems opened up new evolutionary possibilities. EISs were probably important in the transition to multicellularity^{2,18}, because the phenotypic uniformity they gave to a clonal group of cells made the variation within groups less than variation

between groups. Certainly, complex ontogenies would have been unlikely without EISs, since the ability of cells to transmit their induced epigenetic states to daughter cells is fundamental to development. In organisms that reproduce by budding or fragmentation, induced changes in epigenetic states can readily be transmitted to further generations. In such organisms inherited epigenetic variations may be able to 'hold' an adapted state for long enough to allow similar genetic variations to catch up. Theoretically, transmitting induced phenotypes, even if only for a few generations, can have considerable advantages in some environments¹⁹.

Social learning and the origin of traditions

Animals acquire information that affects the way they will behave in the future and store it in their nervous systems. In animals that show parental care and other forms of social interaction, patterns of behaviour can be transferred between individuals and across generations. New patterns of behaviour, first acquired either by accident or by individual learning in new conditions, can be transmitted transgenerationally through social learning²⁰. This inheritance system operates at the whole organism level, and the information encoded is analog in nature – as a rule, it is not readily dissociated into independently heritable parts, but is contained in the dynamics of the interactions between the organism and its social and ecological environment. It is this dynamic system that is reconstituted anew every generation.

In birds and mammals, social learning occurs when the presence of one relatively experienced individual increases the chances that a naive individual learns a similar behaviour pattern. A young male song-bird, hearing the song of his father, learns some of the idiosyncratic components of the song, and will later transmit

it to his sons²¹. Naive blackbirds, seeing the mobbing behaviour of conspecifics towards a particular target, learn to mob this type of object, even when it is harmless²². One of the best-studied cases of social learning in mammals is Aisner's and Terkel's study of cultural inheritance of a novel feeding habit in Israeli black rats (*Rattus rattus*)^{23,24}. These rats have recently extended their range to include the Jerusalem-pine forest, where the only source of food is the pine seeds enclosed within inedible pine cones. The rats reach the nutritious seeds by an elaborate cone-stripping technique. Results of cross-fostering experiments, where pups of stripping mothers were raised by non-strippers and vice versa, have shown that the ability to strip pine cones efficiently is learnt and not genetically determined.

Social learning can have important effects on the evolution of behaviour, and hence on our interpretation of evolutionary change. First, when we observe a new heritable pattern of behaviour in a population, its origin and maintenance cannot automatically be assumed to be due to genetic variations. The inheritance of purely 'cultural variations' has to be seriously considered. Second, taking behavioural inheritance into consideration leads to alternative or complementary interpretations of known patterns of behaviour. For example, it is possible to show that adoption can spread and be maintained within populations through the social learning of certain parenting styles²⁵. Third, the possibility that sexual imprinting and other mechanisms of social learning can initiate speciation must be considered²⁶.

New acquired habits and traditions, such as pine cone-stripping, often precede genetic adaptations, and exert persistent directional selection for genetic variations that are congruent with the new pattern of behaviour. For example, the continual use of pine seeds as a major source of food gives a selective advantage to any genetic variation that improves the finding, processing, and digestion of pine seeds. In addition, selection for the ability to learn this particular behaviour pattern ever more efficiently and rapidly may eventually lead to it becoming dependent on fewer learning trials, or even on no learning trials at all – in short, it may lead to partial or full genetic assimilation (Box 2)²⁷.

Symbolic languages

Language is part of the behavioural inheritance system. However, some properties of language make it qualitatively different from any other information storage and transmission system: language has a structure, or syntax, that allows generativity and creativity. Utterances are organized into sentences by applying rules for

the formation of hierarchical, recurring constructions of meaning-relations. This leads to the production and comprehension of an infinite number of meaningful sentences. Moreover, language increases the scope of transmissible information: the information is not only messages about the world, but also messages about beliefs, about past and future, and about things distant, abstract, and absent. Unlike other types of information transmitted through the nervous system, linguistic information is organized digitally, and is decomposable into semantic units. The differences between individuals in the ability to use a particular language, and the differences between languages, show how plastic the system is, notwithstanding the fact that language has an evolved genetic basis²⁸.

Reconstructing the evolution of language is extremely problematical, not only because we have to rely on very indirect evidence, but also because there is disagreement among linguists as to what qualifies as 'true' language. The ape-language controversy illustrates the problem: Kanzi, the language-instructed bonobo (*Pan paniscus*), can (arguably) understand some form of simple spoken English, and is able to converse, though with little syntactical regularity and with the aid of human-made visual symbols, about his desires and intentions²⁹. However, many linguists are adamant that the non-syntactical communication and representation system of Kanzi and other language-instructed higher apes are not a true language, but rather a 'proto-language'³⁰. The acquisition of syntax, which is unique to humans, is perceived by many linguists as a saltatory event. However, to most evolutionary biologists it seems more likely that the phonetic system, the ability to learn many lexical elements, and syntax must all have evolved through gradual cultural and genetical evolution. Eventually, from some form of proto-language, the mature language of *Homo sapiens* evolved.

Certain basic preconditions for language evolution were presumably present in our ancestors, since they exist in the higher apes, and also in some monkeys. These include intense sociality with a highly evolved social intelligence involving some theory of mind (the ability to understand another individual's intentions), a sign system that functions to modulate social interactions, and increased voluntary motor control of hands, breathing, and the expression of emotions³¹. Dunbar has stressed the importance of social bonding among individuals for early proto-language evolution³². He argued that as human groups grew in size, grooming was no longer able to manage the intimate and complex social interactions within the group. Language evolved as a more

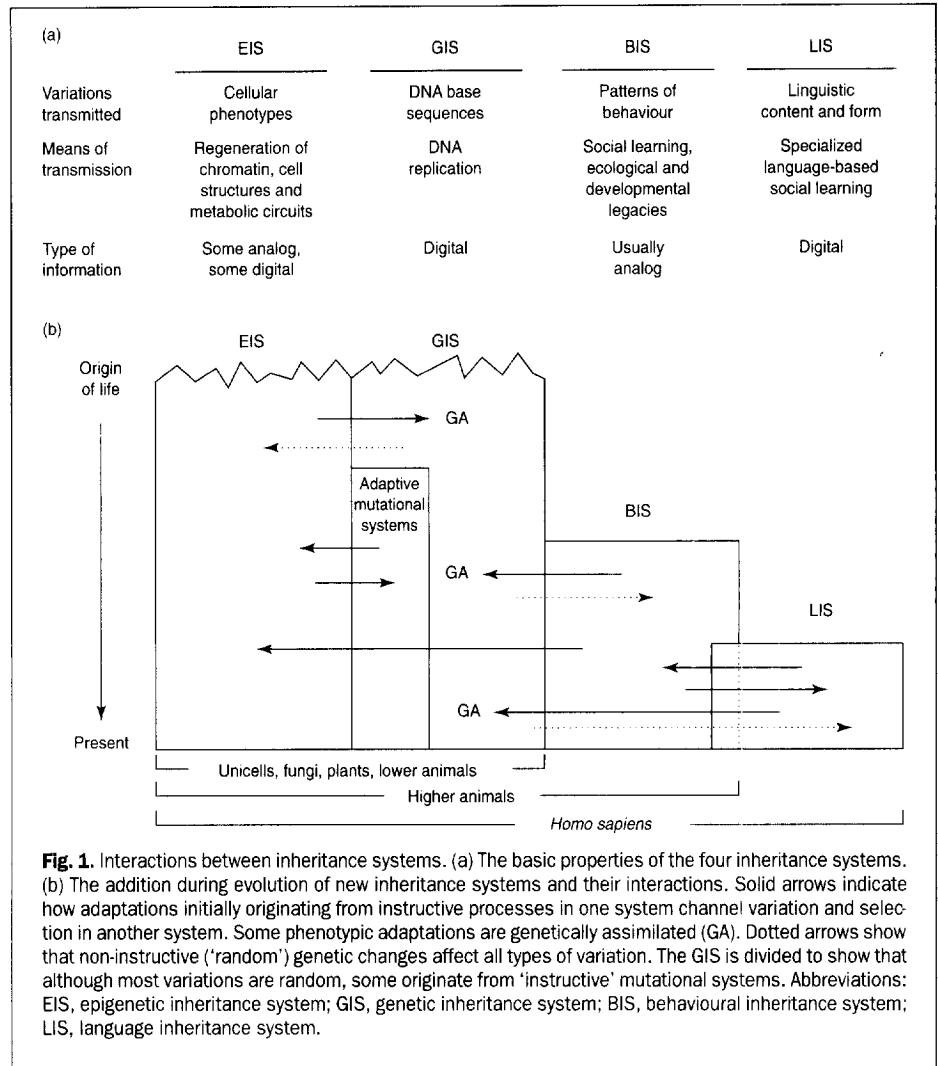


Fig. 1. Interactions between inheritance systems. (a) The basic properties of the four inheritance systems. (b) The addition during evolution of new inheritance systems and their interactions. Solid arrows indicate how adaptations initially originating from instructive processes in one system channel variation and selection in another system. Some phenotypic adaptations are genetically assimilated (GA). Dotted arrows show that non-instructive ('random') genetic changes affect all types of variation. The GIS is divided to show that although most variations are random, some originate from 'instructive' mutational systems. Abbreviations: EIS, epigenetic inheritance system; GIS, genetic inheritance system; BIS, behavioural inheritance system; LIS, language inheritance system.

effective grooming-system, because it involves several individuals at the same time. Other authors have stressed other features that have been important in the evolution of language, such as its prosodic and rhythmical aspects which lead to group-bonding³³, and its role in extending and allowing voluntary access to memories³⁴.

The reconstruction of the evolution of language involves reconstructing the evolution of a 'linguistic community', for language is a community activity. The gelada baboons (*Theropithecus gelada*), whose rhythmical and melodious vocalizations accompany every act of their busy social lives³⁵, might be a good model for such a community. If we add to the gelada 'vocal' community the more sophisticated intellectual capacity of higher apes, and the use of vocalization for the transfer of information about specific events, such as vervet monkeys' (*Cercopithecus aethiops*) predator-specific alarm calls³⁶, we have a preliminary linguistic community. The linguistic abilities of Kanzi give us some idea as to how much could have been achieved by cultural evolution without genetic changes. The transition from proto-language to a full syntactical system may

be especially difficult to reconstruct, but contrary to the opinions of those linguists who envisage the sudden emergence of mature syntactical language from proto-language³⁷, it is possible to construct a plausible detailed scenario of this transformation, as recently shown by Aitchison³⁸.

The evolution of language may have been driven by cultural evolution, followed by genetic assimilation. Genes and culture co-evolved, with the rare linguistic innovations of adults being quickly adopted and absorbed by the young children of the group, to become the behavioural norm and habit of the next generation³⁹. Cultural evolution for ever more efficient linguistic competence 'stretched' the linguistic abilities of the individuals and exerted stable and consistent directional selection on the underlying, genetically-encoded features of the nervous system that promote ever more effective language use⁴⁰.

Conclusions

All the inheritance systems that we have described have the properties necessary for darwinian evolution: the information (be it digital or non-digital) can

vary, and the variations can be transmitted across generations. Natural selection of the variations leads to adaptation and divergence. Although variations may result from random errors in maintenance and copying processes, heritable variations in these systems (1) are often induced or learnt, (2) are frequently adaptive, (3) can sometimes be generated at a very high rate and are often reversible, (4) may affect several characters in the same individual, and (5) may affect several individuals in a similar way. Rapid, reversible, co-ordinated, induced or learnt changes are not characteristics of the classical genetic system. Although the evolved systems allowing 'adaptive' mutation obviously depend on DNA variations, DNA base sequence changes are not required for the generation of epigenetic, behavioural, and language-based variations.

It is possible to study the effects of each inheritance system in isolation from the others for a limited number of generations, but the different systems clearly interact. One of the most neglected and challenging aspects of the study of evolutionary history is the investigation of these interactions. A simple schematic illustration of the interrelationships is shown in Fig. 1. Genetic adaptations may be guided by heritable induced or learnt phenotypic adaptations, usually through genetic assimilation. As additional inheritance systems evolved, the new systems began to guide the changes at the underlying levels. As the figure shows, the importance of the different systems is not the same in all groups. While EISs and genomic mutational systems have probably played a major role in the evolution of unicellular organisms, plants, fungi and lower animals, behavioural inheritance systems have attained prominence in higher animals, and language has a major directing role in human evolution.

Instructive (or 'lamarckian') inheritance systems are all adaptations that have evolved through darwinian natural selection, often through the selection of randomly generated variations. The kind of environment in which such systems have evolved is likely to have been one with some re-occurring features, but with enough temporal or spatial diversity to preclude a fixed genetic response on the one hand, yet on the other hand make an individual, physiological response too costly^{16,17,41}. Once present, these instructive inheritance systems constrain and channel evolution. Unlike other constraints on evolutionary change, such constraints do not merely define the range of the possible, they also, more positively, specify what is likely. The future may spring more directly from the present than we have been accustomed to believe.

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