Reconstructing Human Nature[1]

Paul E. Griffiths*

Introduction

The humanities and social sciences can hardly avoid making claims about human nature. The biological sciences are an obvious source of evidence to underpin or to undermine such claims. But attempts to access this evidence remain controversial. To some 'the biological basis of human nature' is the sound of science being mobilised behind a social agenda.[2] In its turn, this scepticism is frequently condemned as ideologically motivated.[3]

In this lecture I assume that there is a human nature, in the straightforward sense that it is possible to generalise about human beings. If this were not possible the humanities and social sciences would be restricted to the study of individuals and particular social groups. But many disciplines aim at knowledge of human beings in general and of human society in general. I will assume that they are right to do so. I will also assume that the biological sciences can help them to achieve their aims. My aim will be to show that this descriptive understanding of 'human nature' can be dissociated from some other connotations of the phrase. First, human nature is commonly thought of not merely as a description of what humans are like, but as the reason we are like that. I will argue that insofar as human nature can be conceived as an underlying cause of widespread human characteristics, it involves the whole organism-environment system that supports human development. There is no special part of

---

* *Paul E. Griffith is a Professorial Fellow in the Philosophy Department, University of Sydney. This inaugural lecture was given to the Arts Association on 11 August 2009.*

human beings such as our blood or our genes where human nature resides. Second, the generality of human nature stems from our ability to discern structure in the patterns of human similarity and difference, not merely from the existence of human universals.

Taken together these two themes weaken the association between the idea that something is part of human nature and the idea that it is inevitable. It is surely this association that has made many in the humanities and social sciences suspicious of biological accounts of human nature. However, overcoming the presumption that something cannot be changed does not imply that it can be changed, let alone that it can be easily changed. Perhaps the most important conclusion of this lecture is that the plasticity of human nature is a very specific research question and that it has traditionally been conflated with several other issues, issues which have as a result become unnecessarily controversial.

Before examining how the various connotations of the idea of human nature come apart, I will try to explain how they came to be put together. I will suggest that the presumption that the several connotations of the 'human nature' form a single package is part of an intuitive understanding of animals and their development that owes little if anything to the biological sciences.

Human nature as folkbiology

People do not need a scientific education to believe that plants and animals come in different kinds, and that each of those kinds has a nature shared by the individuals of that kind. Extra-scientific ideas about plants and animals are referred to as 'folkbiology', a term also used for the field which studies these ideas and is part of the broader field of cognitive anthropology.[4–6] Folkbiology research suggests that people everywhere identify at least three general levels of biological classification: a 'generic species' category (e.g., wombats and bluegums), a super-ordinate category of biological domains (e.g., animals and plants), and a subordinate category of species varieties (e.g., particular breeds or strains, such as the mountain brush-tailed possum). The generic species level is of particular importance. Membership in a generic species is associated with 'psychological essentialism'.[7] This is the belief that members of a species share an essence or inner nature which causes them to share the typical properties of that kind.[4, 8, 9] Human nature is simply the application of psychological essentialism to human beings. Psychological essentialism has been used to explain two findings about folkbiology. First, adults believe that membership in a species is inherited by descent and is not changed if someone or something changes the observable properties of an individual, even if this change makes the individual more similar to members of another generic species than to members of its original generic species. Second, adults believe that the development of species-typical traits does not depend on environmental influences. If asked to imagine a cow that has been raised by a family of pigs, adults assume that the cow will display the normal bovine trait of mooing instead of oinking like the pigs.[10, 11] Scott Atran has proposed that folkbiology has another core feature: the tendency to explain traits teleologically.[12] That is, people tend to explain the traits possessed by animals and plants by asserting that these traits have a purpose, but this additional proposal remains controversial.[13–15]

I have argued elsewhere that terms like 'innate', 'instinctive' and 'human nature' are expressions of this kind of psychological essentialism.[16] They express aspects of a folkbiological (implicit) theory of 'animal natures'.[17] Animal natures are transmitted from parent to offspring. When an individual develops, some of its traits are expressions of this inner nature, whilst others are imposed by the environment. The idea of human nature is simply an instance of this way of thinking.

Folkbiological classifications of plants and animals have an important practical role. They provide a framework for inductive inference. Generalisations from one organism to another are made in proportion to the distance of those organisms in the folk taxonomy. If you have never grown runner beans, you will place more confidence in your experience with french beans as a basis for doing so than in your experience with eucalypt saplings. The folkbiological distinction between traits that are expressions of an animal's nature and those that are imposed by the environment has a related role. It specifies the range of traits for which inductive inference within a species or larger folk classification is supposed to be reliable. If a trait is an expression of an animal's nature, then it make sense to expect other members of the species to share it. It also provides a source of expectations about heredity. If I wanted to breed a more aggressive brush-tailed possum in my locality I might try to do so by crossing local possums with the notoriously aggressive mountain sub-species, on the assumption that aggressiveness is part of their nature, along with differences in size and colour. But I would not expect the offspring of these matings to share their other parent's preference for my verandah over neighbouring verandahs, on the assumption that that is not part of their nature.

Bringing out the role of folkbiology in practical inferences of this kind helps to clarify what is meant by talk of an 'implicit theory' of animal natures. The mental representations which people use to think about animals produce characteristic patterns of inferential behavior. We can infer something about the structure of those representations from these patterns. This inferred structure is the 'folk theory' of this particular cognitive domain.

The folkbiology of animal natures

If 'animal natures' are to play their role in folkbiology, there must be some way to tell that a trait is an expression of an animal's nature. In earlier work, I suggested that three features are particularly associated with traits that are expressions of the inner nature that organisms inherit from their parents.[16, 17] These features are:

1. Fixity – the trait is hard to change; its development is insensitive to environmental inputs in development; its development appears goal-directed, or resistant to perturbation.
2. Typicality – the trait is part of what it is to be an organism *of that kind;* every individual has it, or every individual that is not malformed, or every individual of a certain age, sex or other natural subcategory.
3. Teleology – this is how the organism is *meant* to develop; to lack

> the innate trait is to be malformed; environments that disrupt the development of this trait are themselves abnormal.

Whether a trait has these three features will influence whether it is thought to stem from an animal's inner nature. Conversely, if a trait is thought to stem from an animal's inner nature it will be expected to have these three features. At a practical level, this means that evidence that a trait has one of the three features will lead to the expectation that it has the others.

The three features are described in very general terms, because they are supposed to be broad themes that will be interpreted and expressed differently in different cultures. For example, consider Teleology. The sense that interfering with an animal's nature leads to deformity or monstrosity, rather than simply something different, can be found in contemporary discussion of genetic engineering in the idea of 'genomic integrity'. H. G Wells's 1896 novel *The Island of Dr Moreau* shares this sense that no good can come of interfering, but in his case it is interference with the 'laws of growth', a concept derived from contemporary embryology. In a religious context these same normative overtones might be understood in terms of interfering with the divine order of things. A medieval or renaissance author would most naturally reach for the Aristotelian idea that form may fail to properly manifest itself in a particular sample of matter. For our purposes what is of interest is not the many ways in which people have thought that development is a normative process, but the broad existence of a sense that development is a normative process. It is this that I have labelled 'Teleology'.

The philosophical literature on the distinction between innate and acquired characteristics contains numerous proposed analyses of the concept of innateness.[18] There is an obvious overlap between the idea of innateness and the idea that animals have an inner nature, and so these analyses are potentially in competition with the three-feature model just outlined. But the three-feature model differs from traditional 'conceptual analyses' in some important ways. First, it is not intended to capture the meaning of a particular word, or a concept expressed by that word. Instead, it is an analysis of conceptual structure at a molar level: it purports to describe a model which people use to conceptualize a domain of phenomena, and which might be reflected in the use of several different terms when people are describing those phenomena. Second, the elements of the analysis are not supposed to constitute the concept under analysis in the way that truth, belief and justification are supposed to constitute knowledge in perhaps the most famous conceptual analysis of them all.[19] Instead the three features function as evidence for the presence of something else – an inner nature – and conversely as inferences that can be made from the presence of such a nature.

This model of the folkbiology of animal natures was tested by Machery, Linquist and myself by examining the effect of the three features on naïve subjects' application of the distinction between innate and acquired characteristics.[17] We argued that subjects will label a trait as innate to the extent that they take it to stem from the animal's inner nature, rather than being imposed on the animal by its environment. In that case, the three-feature model predicts that judgments of innateness will be influenced by all three features, and that they will influence those judgments independently, since each of the three features is evidence for a further, underlying property, not for one another.

To test these predictions, the three features were systematically co-varied in eight vignettes describing the development of birdsong. Birdsong was chosen because there are around nine thousand species of birds, with diverse methods of developing song, and the study of this diversity has been a major field of biological research for the past fifty years. Hence it was possible to provide realistic examples of birdsong development manifesting every possible combination of the three features. An example of one of the eight vignettes is:

> Birdsong is one of the most intensively studied aspects of animal behaviour. Since the 1950s scientists have used recordings and sound spectograms to uncover the structure and function of birdsong. Neuroscientists have investigated in great detail the areas of the brain that allow birds to develop and produce their songs. Other scientists have done ecological fieldwork to study what role song plays in the lives of different birds.
>
> The Alder Flycatcher (*Empidonax alnorum*) is a migratory neo-tropical bird which breeds in southern Canada and the northern USA. Studies on the

> Alder Flycatcher show that the song an adult male produces does not depend on which songs they hear when they are young. Studies also show that different males in this species sing different songs. Furthermore, close observations of these birds reveal that the males' song attracts mates and helps to defend their territory. Scientists therefore agree that the bird's song has a real function, like the heart in humans.
>
> On a 7-point scale, 1 meaning strongly disagree and 7 meaning strongly agree, how would you respond to the following statement?
>
> 'The song of the male Alder Flycatcher is innate.'

The first paragraph was the same for all the vignettes. The first sentence of the second paragraph introduced the bird by naming it and giving some irrelevant facts about it. The rest of the paragraph contained three 'information items' relevant to the three features, each in either a negative and positive version. Fixity was represented by whether or not the bird acquires its song by hearing it when it is young. Typicality was represented by whether or not song differs between individuals. Teleology was represented by whether or not the song has a 'function'. The order of these items was, of course, randomised to avoid order effects.

A fuller account of the experimental designs and data analysis can be found in the original publication.[17] The results were broadly supportive of the three-factor theory. In a between-subject study, in which each subject saw only one vignette, the three information items explained 22 per cent of the variance in their responses. This is quite a small proportion. However, we suspected this was merely because, in a between-subject design, any differences between subjects in background beliefs about the topic would show up as unexplained variance. This suspicion was borne out by the results of a within-subject study in which each subject responded to all eight vignettes. In this version, the three features accounted for 70 per cent of the variance. The greatest portion of variance was explained by Fixity, a slightly smaller amount by Typicality, and a very small amount by Teleology. Most significantly, there was no interaction between the three features. Each had an independent effect on whether the song was judged to be an innate trait.

In recent research currently under review we have developed new versions of the vignettes which we believe address some deficiencies in the original versions.[20] Unfortunately the conditions of acceptance forbid prior publication of the main findings of this paper, so they can only be described here in very general terms. A replication of the original study with these new vignettes confirms our previous results, with the exception that the effect of Teleology was not significant. This, together with the small size of the effect in the original study, suggests that Teleology is marginally relevant if at all to the application of the term 'innate'. However, as mentioned above, the three-feature model purports to describe how people conceptualize a domain of phenomena and this conceptualisation could be reflected in the use of several different terms when people are describing those phenomena. Our recent studies have shown that replacing the term 'innate' with other terms commonly used to discuss the issue of innate versus acquired alters the relative significance of the three features. With one particularly prominent term all three features explain a substantial proportion of the variance, with Teleology the second largest factor.

The folkbiology of animal natures is undoubtedly complex, and it may vary significantly between individuals and between groups. Nevertheless, the three-feature model does seem to capture something of how biologically naïve subjects understand animal natures and, by extension, human nature.

Folkbiology is false

It seems that people without a formal biology education manifest an implicit belief that an animal has an inner nature which makes it the kind of animal that it is, and which explains why the animal has certain traits that typify that kind. People judge that a trait stems from an animal's nature using evidence about Fixity, Typicality and Teleology. They also expect that traits which stem from an animal's nature will be Fixed, Typical, and Teleological. The problem is that this picture of the living world is not borne out by biology.

The most obvious way in which the folkbiological picture fails to mesh with biology is that neo-Darwinism denies that members of a species share some common underlying property – presumably a genetic property – which makes them members of that species'.[16, 21, 22] Instead, Darwinian species are collections of organisms united by a pattern of ancestry and descent. There is no particular stretch of DNA that an organism needs to possess to belong to a species. An organism can even be more genetically similar overall to some members of another species than to some members of its own species. Membership of a species is like membership of a family, not like being a sample of a chemical element.[23–25] But this criticism does very little to destabilise folkbiology. It seems clear that most biologically naïve people today believe that it is an animal's DNA which makes it the kind of animal that it is. This is true however little they know about DNA. They may also believe that human beings are humans and cats are cats because of some special genes found in all and only humans and all and only cats respectively. But this second belief can be dropped while leaving the first belief intact, and the conceptual scheme of folkbiology can allow that there are differences between the natures of one animal and the next, as long as the members of a species have natures that are very similar to one another, and the fact that something is part of an animal's nature implies that it will be shared by almost all individuals of the same species.

A more significant way in which folkbiology is not borne out by biological science is that when the three features of Fixity, Typicality and Teleology are given a contemporary biological interpretation, they turn out not to be strongly associated with one another.

What I mean by a 'biological interpretation' of a feature is some property which manifests the basic conceptual themes of that feature, but which also makes sense in terms of current biology. For example, the Aristotelian idea of formal causation would not be a good biological interpretation of Teleology, because contemporary biology does not recognise formal causation. Instead, the obvious biological interpretation of Teleology is Darwinian adaptation. Normativity is accommodated in the conceptual framework of neo-Darwinism by appealing to design by natural selection.[26, 27] An organism is malformed if it fails to develop the phenotype which it was designed to develop by natural selection.

The obvious biological interpretation of Fixity is 'canalisation'.[28]

A trait is *environmentally* canalised if its development is relatively insensitive to the manipulation of environmental parameters. A trait is *genetically* canalised if its development is relatively insensitive to the manipulation of genetic parameters. The philosopher André Ariew has argued that the concept of innateness should be redefined to mean simply environmental canalisation. A trait is more innate the more environmental parameters its development is unaffected by, and the wider the range of variation in those parameters which fail to affect it.[29, 30]

The obvious biological interpretation of Typicality is being a species-typical characteristic. A trait is species-typical if a scientific description of the species would have no reason to mention variation in that trait. This does not mean that no variation exists, but rather that it can be safely regarded as pathological, or too rare to be of any biological significance.

It is worth noting that versions of these three biological properties appear, along with several others, in Matteo Mameli and Patrick Bateson's review of the many definitions of the term 'innate' that have been proposed in biology.[31]

Given these biological interpretations of the three features I will now argue that:

1. Adaptation (Teleology) does not imply developmental canalisation (Fixity);
2. Typicality does not imply environmental canalisation (Fixity);
3. Adaptation (Teleology) does not imply Typicality.

1. **Adaptation does not imply developmental canalisation**

It is easy to suppose that traits which have evolved by natural selection must develop independently of the specifics of the developmental environment. If a trait plays a role in promoting survival and reproduction, surely its development cannot be left to chance? But this thought overlooks an alternative source of stability. Rather than making development independent of environmental parameters, evolution can make development reliable by stabilizing environmental parameters at the right value or by exploiting preexisting environmental regularities. The birdsong researchers Meredith West and Andrew King have described development as occurring in an 'ontogenetic niche'. West and King and their collaborators have conducted a long term study of the ontogenetic niche of the Brown-headed Cowbird *Molothrus Ater* which exemplifies this concept.[32–34] Cowbirds are obligate nest parasites (like cuckoos) and do not hear their parents sing as they grow up. It was therefore assumed that they sing 'innately'. West and King showed that amongst other processes, male song is shaped by feedback from female cowbirds, whose wing stroking and gaping displays in response to the songs are strong reinforcers for males. Female song preferences are themselves socially transmitted. As a result of these and other processes cowbirds reliably transmit not only species-typical song, but also regional song dialects.

In many species, the stabilization of the parameters of the ontogenetic niche is achieved through parental care. The developmental psychobiologist Celia Moore has shown how the sexual development of male rats depends on maternal care.[35, 36] The spinal cord nuclei of male rats differ from those of female rats in ways that allow the male to use his penis during copulation. These neural differences result from differences in gene expression in the developing spinal cord of the rat pup, which in turn result from differences in the amount of licking of the genital area by the mother, which in turn results from greater expression in male pups of a chemical that elicits maternal licking. This kind of research – the experimental study of how the structure of the organism at any one stage in its development, starting with the fertilised egg, interacts with the developmental niche to give rise to the next stage – is typical of the field of developmental psychobiology.[37]

There is a strong evolutionary rationale for the existence of the 'ontogenetic niche'. Natural selection does not select for mechanisms which buffer traits against variation in the environment unless variation of that kind regularly occurs in the environments in which the species lives. There is no evolutionary advantage in a mechanism to allow cowbirds to develop song in environments in which they do not associate with members of their own species after fledging, or rats to develop normal sexual behaviour in environments in which they are not cared for by their mothers. In fact, any buffering mechanism which is not regularly used will tend to decay by mutation. One famous example is the inability of humans and their relatives to synthesise ascorbic acid (vitamin C). The ascorbic acid synthesis pathway was disabled by mutation during the long period in which our fruit-eating ancestors had no chance of developing vitamin C deficiences.[38] As Terence Deacon has put it, organisms are 'addicted' to innumerable aspects of their environments, from ascorbic acid, to gravity, to social interactions.[39]

2. Typicality does not imply environmental canalisation

This follows more or less directly from the considerations just given. One of the functions of the ontogenetic niche is to ensure the reliable development of species-typical traits (the other, complimentary function will be discussed in the next section). The ontogenetic niche is precisely a way of ensuring the trans-generational stability of adaptations without environmental canalisation.

Another way to look at the concept of the ontogenetic niche is to consider the organism as a 'developmental system', which includes both the traditional starting point of an organism – the egg – and those aspects of what would traditionally be described as the environment which make up the ontogenetic niche for that egg.[40–43] If we consider the whole system, then many adaptations are, indeed, canalised against perturbations in developmental parameters – both genetic and environmental. The mechanisms that create this canalisation extend far beyond the contents of the fertilised egg, let alone the genetic material which it contains. In the case of the cowbird discussed above, the reliability with which cowbirds develop species-typical song is ensured by mechanisms that include a flock of cowbirds. The burgeoning study of these distributed mechanisms for canalising normal development has been termed 'ecological developmental biology'.[44]

The concepts of ontogenetic niche and developmental system run counter to a widely shared intuition that the true nature of something is best revealed by removing exogenous influences and allowing it to develop under the influence of endogenous factors alone. When applied to organisms, that intuition is simply wrong.[41, 45] You cannot find out what an ant is 'really like' by removing the influence of the rest of the ant colony. These 'external influences' are an essential part of the biological nature of the ant. It is these 'environmental' factors that will determine whether it develops into a queen, a worker or some other caste, to mention only the grossest aspects of its phenotype. It is equally absurd to suppose that the 'biological' aspects of human beings can be revealed by removing the perturbing influence of society or culture.[46]

3. Adaptation does not imply Typicality

The process of evolution by natural selection has no intrinsic tendency to produce species-typical traits. Some adaptations are monomorphic – all human beings have lost the ability to synthesise vitamin C. Other adaptations are polymorphic – some human beings can metabolise lactose as adults and others cannot.

It is hard to see why the prejudice that adaptations will be species-typical persists, given the obvious evolutionary rationales for these alternative outcomes. Natural selection will favour monomorphic traits when the relevant ecological factors are temporally stable and spatially uniform, and when there is a single winning strategy in evolutionary competition. When the success of a strategy depends on which strategy other organisms adopt (frequency-dependent selection), selection will often favour polymorphic outcomes. When ecological factors fluctuate over time, selection may maintain a variety of types, or favour the emergence of 'phenotypic plasticity'.[47–49] When ecological factors fluctuate across space, selection will favour the emergence of a range of 'ecotypes', or the evolution of phenotypic plasticity.

The second function of the ontogenetic niche is to provide the input to mechanisms of phenotypic plasticity, the phenomena in which organisms develop differently depending on the environment in which they find themselves. The classical example of phenotypic plasticity is the water flea *Daphnia pulex*, which invests resources in growing a defensive 'helmet' if it is exposed to chemical traces of predators, or if its mother has been exposed to those traces.[50] The first of these triggers is an example of intra-generational phenotypic plasticity, and the second of trans-generational phenotypic plasticity, also known as a 'parental effect' on the phenotype.[51, 52]

I discussed above how parental care can be used to stabilize the parameters of the ontogenetic niche. But parental care can also be used as a mechanism of adaptive phenotypic plasticity. A 'parental effect' is a correlation between the phenotype of the parent and the phenotype of the offspring over and above any correlation due to the genes passed from parent to offspring. The account by Michael Meaney and collaborators of the role of parental care in the development of temperament in mice and rats is a good example of this phenomenon. The BALBc strain of laboratory mouse is

> highly fearful, and maze dull ... these animals show increased endocrine and behavioral responses to stress, they are hyperactive and show profound learning and memory deficits that are associated with, among things, impaired hippocampal development.[53, 57]

Cross-fostering BALBc pups to mothers of the more laid-back C57 strain removes the differences between the two strains. Working with individual differences in a population of laboratory rats, rather than the difference between two strains of mice, Meaney and collaborators showed how the amount of licking and arched-back nursing which pups receive from their mother regulates gene expression so as to direct the development of the pup's brain.[54] It is plausible that in wild rats maternal behaviour reflects the mother's stress levels. It may convey information to the pup about the likely quality of its environment and 'preset' stress metabolism to match that environment.

Peter Gluckman and collaborators have applied a similar approach to human health.[55–57] They argue that the prevalence of many common 'lifestyle diseases' has a significant component that is due to the malfunctioning of mechanisms of phenotypic plasticity. In 'predictive adaptive responses' the developing foetus uses cues from the metabolism of the mother to set a developmental trajectory that will be adaptive in environments predicted by those cues. When the relationship between cue and environment has changed, as they argue it has in many cases today, these mechanisms produce maladaptive outcomes.

Human nature and developmental systems

I have given some examples of ways in which Fixity, Typicality and Teleology can become dissociated. In the light of this it becomes possible to get to the heart of what is wrong with the folkbiological conception of 'animal natures'. When William Johanssen introduced the terms 'gene', 'genotype' and 'phenotype',[58] he did so by contrasting the 'genotype conception of heredity' with the earlier conception of heredity derived from human cultural practices of inheritance. When I inherit a house, it is the very house that my parents lived in. The house reflects the cultural environment of the generation who built it – parents or grandparents – not the cultural environment of the person who inherits it. But genetic inheritance is not like this. In genetic inheritance I inherit a developmental factor – a gene – which interacts with *my* environment to produce a phenotypic outcome. This is why Johanssen needed to introduce the distinction between genotype and phenotype, to make clear that no-one literally inherits blue eyes or coronary heart disease. Earlier theories of biological heredity had concentrated on the correlation between parent and offspring, as if it were the parent's phenotype that produced the offspring's phenotype. But correlations between parent and offspring phenotypes are only indirectly related to the mechanisms of biological heredity. If I and my father both have coronary heart disease it is not because I have inherited my father's coronary heart disease, but because I have inherited genes that produce coronary heart disease in certain environments, and my father and I both live in those kinds of environment.

In his 1911 paper Johanssen explained the relationship between genotype and phenotype using the 'norm of reaction' – a graphical representations of a phenotypic variable as a function of genotypic and environmental variables.[59] The norm of reaction concept makes clear that all traits depend upon both genes and environment, even those which are, in the clearest sense of the phrase, genetically determined. A trait can be said to be genetically determined if with respect to some environmental variable (E) an organism with a given genotype (G1) will develop the same phenotype (P) way, no matter what value the environmental variable takes [*Figure 1*]. For example, a disease caused by the loss of one or both normal copies of a gene might develop in *every* environment except those specifically structured as clinical interventions to cure the disease. Nevertheless, if we wanted to understand how this disease develops, we would need to understand both genetic and environmental factors, and how they interact. The reverse applies, of course, to traits which are completely 'environmental' – to understand how these traits develop it is necessary to understand how the environments which 'determine' them regulate gene expression!

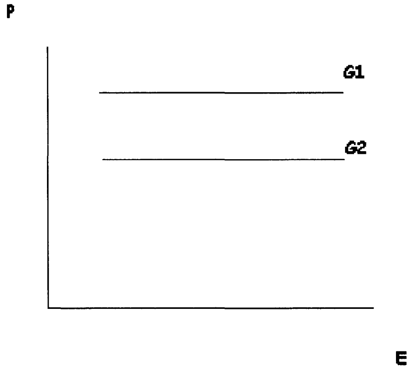

Figure 1: A norm of reaction in which the phenotype P is 'genetically determined'.

A norm of reaction figure makes it obvious that genetic (or environmental) determinism is *special case. If genetic and environmental factors interact 'additively'* [*Figure* 2] then the phenotypic value depends on both genetics and environment. But in this case, genotype makes a *constant difference* across some range of environments. While the genetic variable does not determine the actual value of the phenotypic trait in each individual, it does determine the differences between individuals. Some authors have suggested that genetics and IQ are related in this way.[60] If correct, this would mean that educational enrichment would cause everyone to get higher test scores, but would not change the ordering of their scores.

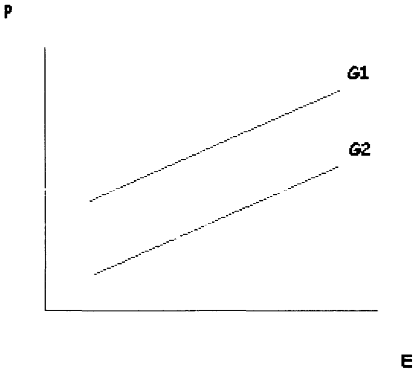

Figure 2: Purely additive interaction between genotype and environment.

A third possibility is that genotype and environment interact non-additively [*Figure 3*]. In that case they *jointly* determine the outcome in a very strong sense: the effect of each factor on the outcome is a function of the particular value taken by the other factor. Thus, for example, an animal with genotype 1 might grow larger than an animal with genotype 2 in one environment but not in another. Sophisticated, scientific critiques of 'genetic determinism' are not attempts to elevate the environment at the expense of the genes. They argue that development typically resembles this third picture.[61, 62]

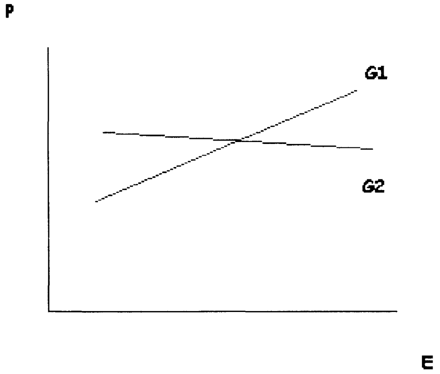

Figure 3: Non-additive interaction between genotype and environment.

The error at the heart of folkbiology is the idea that some traits are expressions of an internal factor – the nature of the animal – whilst others result from the action of the environment. If the best biological interpretation of an animal's inner nature is its genetic endowment, then this is false. Both 'innate' and 'acquired' traits result from the interaction of genes and environment – a truism sometimes known as the 'interactionist consensus'.[63] The difference between innate and acquired traits is a matter of the shape of the norm of reaction, which is a property of the whole developmental system. Most importantly, 'innate' and 'acquired' are simply two amongst the many patterns of interaction between genes and environment. Once we consider two variables, that is, more than one genetic and one environmental parameter, it is not even clear that innate and acquired can be interpreted as two ends of a spectrum .[64]

At a still deeper level, the folkbiological conception of the organism is inadequate. It conceives of an animal as having a finished, adult form. Development is a goal directed process directed towards that end, and senescence is a decline from that finished state. But, as the developmental biologist Conrad Waddington noted:

> An animal is, in fact, a developmental system, and it is these systems, not the mere static adult forms which we conventionally take as typical of the species, which become modified in the course of evolution.[40]

From an evolutionary point of view an organism is a process from conception to death. This process is the implementation of a life-history strategy – a series of decisions to allocate resources to growth, reproduction and other activities.[65] The real product of evolution is not an adult phenotype, but a developmental system that gives rise to a life-history.

'But only genes are inherited...'

DNA or 'the genes' have become popular culture signifiers for the true nature of each animal or even, in some recent advertisements, the true nature of each brand of car.[66, 67] This identification is reinforced by the idea that genes are the only thing an animal genuinely inherits from its parents, or at least that the only alternative to genetic heredity is a special phenomenon called 'cultural heredity' found in humans and in a minimal form in a few other species. The environment may be essential for the genes to produce an organism, but the environment cannot be part of the nature of the organism because it is not inherited.

But it is simply not true that biological systems reproduce themselves by tossing strands of DNA into the world to meet their fate. Instead, natural selection has created many ways in which parents can influence the form of their offspring in addition to providing their genome. These mechanisms are commonly referred to as mechanisms of 'epigenetic inheritance'.[68–71] The term 'epigenesis' has a long and distinguished history in biological thought, stretching back far beyond the discovery of genetics. In current usage, however, 'epigenetic inheritance' has two senses, one rather specific and one more general. In the strictest sense, epigenetic inheritance refers to the transmission of material in the fertilised egg in addition to the DNA and which acts to modify gene expression in the next generation. The best studied of these mechanisms is DNA methylation, a process by which organisms can attach additional chemical groups to some of the nucleotides that make up the DNA sequence so as to render certain genes more or less active in their offspring. Male and female parents often apply different methylation patterns, giving rise to the phenomenon of 'parental imprinting' in which a genetic variant only produces a phenotypic effect if it is inherited from a parent of one sex. Methylation underlies many of the 'parental effects' mentioned above. Other important mechanisms of epigenetic inheritance include modifications of the structural components of chromosomes – histones – and the inheritance of small RNAs in the cytoplasm of the egg.

In a broader sense, epigenetic inheritance refers to any mechanisms creating parent-offspring correlation independent of correlations in genotype. For example, the inheritance of temperament in rats and mice described above depends on methylation to stabilise gene expression patterns in the lifetime of an individual rodent, but those methylation patterns are not passed on directly to offspring. Instead, they are re-established in response to maternal behaviour. This is 'behavioural' inheritance rather than 'epigenetic' inheritance in the strict sense.[69]

The 'nature' of an animal is supposed to be something it inherits from its parents, which explains why it has the properties which are typical of its species, and whose manifestation counts as normal development. In the folkbiological picture an animal's nature is to be contrasted with the influence of the animal's environment. I have argued that the apparent continuity between this picture and the idea that animals inherit a genome which interacts with the environment is specious. First, as shown in the previous section, every trait depends on the interaction of genes and environment, and the patterns of interaction between them cannot be reduced to two types corresponding to 'innate' and 'acquired'. Second, as shown in this section, inheritance is not restricted to the genetic elements of the developmental matrix. If an animal's nature is what explains normal development, then its nature includes many of the environmental influences with which 'nature' has traditionally been contrasted.

The examples considered so far have also highlighted the phenomenon of phenotypic plasticity. Evolution designs mechanisms for producing diversity as well as uniformity. An animal's nature is thus relevant to explaining why it differs from others of the same kind, as well as why it resembles them. Human nature includes human diversity.

Rethinking human diversity

Both folkbiology and traditional academic approaches to human diversity have an unfortunate tendency to contrast the universal, biological traits of human beings with their diverse, cultural traits. But evolution creates systems designed to function in a developmental context. In a species like ours that developmental context includes socialisation and exposure to all those factors that make up a culture. So this contrast is not well drawn. The ideas advocated in this lecture suggest an entirely different approach to human diversity, but one with strong precedents elsewhere in biology.

I touched above on the fact that Darwinian species are collections of populations of varying individuals. There is no essential property or cluster of properties that makes an organism a member of a species, except perhaps the historical property of being united in a particular kind of genealogical network. The same is true of the higher taxonomic groups which unite several species. But this does not mean that the intrinsic properties of individuals are irrelevant for taxonomy. The pattern of similarities and differences between organisms provides evidence of their evolutionary relationships. These inferred relationships are the justification for grouping them into species and higher taxa.

The same, evolutionary, principles are used by biologists to classify the parts of organisms. The bones in a vertebrate skeleton are not classified in terms of their shape or position, but their shape and position is used as evidence of their evolutionary relationships, and they are classified in terms of those relationships. For example, the tiny bone supporting the equally tiny 'bastard wing' that disrupts the flow of air over a bird's wing is the same bone that is found in one of my fingers (there is some remaining controversy as to *which* finger), and that bone in my finger is the same bone as a long, thin bone that supports the wing-membrane of a bat. Despite the enormous differences in the shape and position of these bones, their shape and position provides solid evidence that these three are 'homologues' of one another. Classification by homology is the basis of anatomy, physiology, and neuroanatomy. The same fundamental principles underlie the classification of genes and of molecular-level structures in the cell. The classification of behaviour by homology poses special difficulties, but is a familiar part of behavioural biology. Yet, surprisingly, classification by homology has been neglected as an approach to human cultural diversity.[72]

Homology has two particular strengths as a way of conceptualising human diversity. First, homology is a principle of identity through difference. Human facial expressions of emotion are homologous to certain facial expressions in chimpanzees, as was first pointed out by Darwin. But the homologous pairs of expression differ substantially in both form and function. Homology is not a matter of similarity, but of identifying the *corresponding* components of two systems. One important use of homology is as a principled way to use one system as a model for investigating another system. The best model for a human emotion in chimpanzees is the homologous emotion, and this conclusion does not depend on any particular degree of similarity between the two. Hence, homology allows us to appreciate human diversity whilst still seeking to illuminate that diversity in terms of our common evolutionary origins.

Second, recent developments in biology have reinterpreted the relationship between homology and genetics in a way that can act as a model for solving the problematic issue of the biological basis of novel human behaviours. Since the 1980s there have been major advances in molecular developmental biology – the field which relates developmental biology to the regulated expression of genes and the interaction of gene products. These advances include the realisation that the identity (homology) of parts at one level of biological organization is independent of the identity (homology) of their constituent parts at a lower level of organization. This came about primarily through the discovery of highly conserved gene control circuits underlying traits that are not homologous. Thus, for example, the paired appendages of vertebrates and arthropods share ancient genetic mechanisms that are hypothesized to have been in place controlling outgrowths of some sort from the bodies of the most ancient animals. Those mechanisms are homologous to one another.[73] But the appendages they produce – the legs and arms of vertebrates and the legs of insects – are not homologous to one another. Conversely, the cascade of gene expression that induces masculinisation of the foetus in *Ellobius* rodents and the male sexual characteristics that result from that process are homologous to those seen in other mammalian species, despite the fact that some *Ellobius* species have lost the Y chromosome and the homologue of SRY, the 'sex determining' gene.[74] The lesson of these examples is that evolution can preserve a trait whilst transforming the molecular mechanism that produces it and, conversely, that evolution can redeploy an existing mechanism to underpin the development of a novel trait.

These principles have important applications to the biological basis of human diversity. Human diversity results mainly from the fact that human development is an interaction between the evolved developmental system and a wide range of environments, including novel environments. Exploring this micro-diversity in the way that biologists explore the diversity of living forms would mean replacing the question 'is this the same?' with the question 'is this homologous, and at what level of analysis?' For example, the question of whether certain emotions are found in all human cultures has been addressed by asking how similar they are, or by identifying some aspect of similarity and arguing that it is (or is not) essential to the identity of that emotion.[75] It would be both more meaningful and more tractable to seek to identify the corresponding (homologous) elements of the emotional repertoire of the two cultures, and to determine at what level of analysis claims of homology can be defended. For example, it need not be whole emotions that are homologous. A behavioural expression might be homologous although it has now been recruited for a very different function. Or an early phase in the development of two very different emotions might be homologous, reflecting their diversification from some shared precursor.

Comparative biology provides sophisticated ways to think about the commonalities that underlie biological diversity. Bringing order to that diversity is not about identifying universal elements, but about finding order in the pattern of similarity and difference. This order reflects the fact that diverse organisms descend from a common ancestor and also the fact that many developmental mechanisms are shared amongst organisms and are reused in new contexts. Hence corresponding parts can be identified in different organisms at various levels of analysis. Taking a biological perspective on human nature can mean treating human diversity in much the same way. It need not be restricted to demonstrating or refuting the existence of human universals.

Conclusion

In this lecture I have tried to sketch a conception of human nature and its biological basis that can be welcomed by the humanities and social sciences. In doing so, I have had to argue against a highly intuitive picture of human nature which derives from 'folkbiology'. In place of this, I have tried to put a picture of human nature in which development is central. I have suggested that the primary sense which should be attached to the term 'human nature' is simply what human beings are like, not some cause that makes them that way. As such, human nature is primarily the pattern of similarity and difference amongst human beings. This pattern results from the operation of the evolved human developmental system in a wide variety of environments, some of them novel. Human nature in the other sense – the cause of this pattern – is the human developmental system. This is distributed far beyond the traditional boundaries of the organism in the whole matrix of resources that previous generations bring into existence through multiple mechanisms of heredity.

Notes

1 This research was supported under Australian Research Council's Discovery Projects funding scheme DP0878650.

2 Hilary Rose and Steven Rose, *Alas Poor Darwin: Arguments Against Evolutionary Psychology*, New York, 2000.

3 Steven Pinker, *The Blank Slate: The Modern Denial of Human Nature*, New York, 2002.

4 Scott Atran, *Cognitive Foundations of Natural History: Towards an Anthropology of Science*, Cambridge and New York, 1990.

5 Brent Berlin, *Ethnobiological Classification*, Princeton, NJ, 1992.

6 Brent Berlin, Dennis Breedlove and Peter Raven, 'General principles of classification and nomenclature in folk biology', *American Anthropologist* 74 (1973): 214–42.

7 Douglas Medin and Scott Atran, 'The native mind: Biological categorization and reasoning in development and across cultures', *Psychological Review* 111 (2004): 960–83.

8 Susan Gelman, *The Essential Child: Origins of Essentialism in Everyday Thought*, New York, 2003.

9 Douglas Medin and Anthony Ortony, 'Psychological essentialism', in Stella Vosniadou and Anthony Ortony, eds, *Similarity and Analogical Reasoning*, Cambridge, 1989, 175–95.

10 Scott Atran, Douglas Medin, Elizabeth Lynch, Valentina Vaparansky, Ucan Ek' Edilberto and Paulo Sousa, 'Folkbiology doesn't Come from Folkpsychology: Evidence from Yukatek Maya in Cross-Cultural Perspective', *Journal of Cognition and Culture* 1 (2001): 3–42.

11 Paolo Sousa, Scott Atran and Douglas L. Medin, 'Essentialism and folkbiology: Further evidence from Brazil', *Journal of Cognition and Culture* 2 (2002): 195–223.

12 Scott Atran, 'Causal constraints on categories', in D. Sperber, D. Premack and A. J. Premack, eds, *Causal Cognition: A Multi-Disciplinary Debate*, Oxford, 1995, 263–65.

13 Susan A. Gelman and Lawrence A. Hirschfeld, 'How Biological is Essentialism?', in Douglas L. Medin and Scott Atran, eds, *Folkbiology*, Cambridge, MA, 1999, 403–46.

14 Deborah Kelemen, 'Functions, goals and intentions: Children's teleological reasoning about objects', *Trends in Cognitive Sciences* 12 (1999): 461–68.

15 Deborah Kelemen, 'Are children "intuitive theists"? Reasoning about purpose and design in nature', *Psychological Science* 15 (2004): 295–301.

16 Paul E. Griffiths, 'What is Innateness?' *The Monist* 85.1 (2002): 70–85.

17 Paul E. Griffiths, Edouard Machery and Stefan Linquist, 'The Vernacular Concept of Innateness', *Mind and Language* 24.5 (2009): 605–30.

18 Paul E. Griffiths, 'The Distinction Between Innate and Acquired Characteristics', in Edward N. Zalta, ed., *Stanford Encyclopedia of Philosophy*, Stanford, CA, 2009.

19 Edmund L. Gettier, 'Is Justified True Belief Knowledge?', *Analysis* 23 (1963): 121–23.

20 Stefan Linquist, Edouard Machery, Paul E. Griffiths and Karola Stotz, 'Exploring the Folkbiological Conception of Behavioral Development', *Philosophical Transactions of the Royal Society B*. Under consideration.

21 Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, Inheritance*, Cambridge, MA, 1982.

22 Elliot Sober, 'Evolution, Population Thinking and Essentialism', *Philosophy of Science* 47.3 (1980): 350–83.

23 David L. Hull, 'Are species really individuals?', *Systematic Zoology* 25 (1976): 174–91.

24 Michael T. Ghiselin, 'A radical solution to the species problem', *Systematic Zoology* 23 (1974): 536–44.

25 Paul E Griffiths, 'Squaring the circle: Natural kinds with historical essences', in Robert A. Wilson, ed., *Species: New Interdisciplinary Essays*, Cambridge, MA, 1999, 208–28.

26 Colin S. Pittendrigh, 'Adaptation, natural selection and behavior', in Anne Roe and George Gaylord Simpson, eds, *Behavior and Evolution*, New Haven, 1958, 390–416.

27 Ruth G. Millikan, *Language, Thought & Other Biological Categories*, Cambridge, MA, 1984.

28 Conrad H. Waddington, 'Canalisation of development and the inheritance of acquired characters', *Nature* 150 (1942): 563–65.

29 André Ariew, 'Innateness and Canalization', *Philosophy of Science* 63.3 (1996): S19–S27.

30 André Ariew, 'Innateness', in Mohan Matthen and Christopher Stevens, eds, *Handbook of the Philosophy of Science*, Amsterdam and Oxford, 2006, 567–84.

31 Matteo Mameli and Patrick P. G. Bateson, 'Innateness and the sciences', *Biology and Philosophy* 22.2 (2006): 155–88.

32 Meredith J. West and Andrew P. King, 'Settling nature and nurture into an ontogenetic niche', *Developmental Psychobiology* 20 (1987): 549–62.

33 Meredith J. West and Andrew P. King, 'Female visual displays affect the development of male song in the cowbird', *Nature* 334 (1988): 244–46

34 Meredith J. West, Andrew P. King, David J. White, Julie Gros-Louis and Grace Freed-Brown, 'The development of local song preferences in female cowbirds (*Molothrus ater*): Flock living stimulates learning', *Ethology* 112 (2006): 1095–107.

35 Celia L. Moore, 'The role of maternal stimulation in the development of sexual behavior and its neural basis', *Annals of the New York Academy of Sciences* 662 (1992): 160–77.

36 Celia L. Moore, 'Maternal contributions to the development of masculine sexual behavior in laboratory rats', *Developmental Psychobiology* 17 (1984): 346–56.

37 George F. Michel and Celia L. Moore, *Developmental Psychobiology: An interdisciplinary science*, Cambridge, MA, 1995.

38 Thomas H. Jukes and Jack Lester King, 'Evolutionary loss of ascorbic acid synthesizing ability', *Journal of Human Evolution* 4 (1975): 85–88.

39 Terence W. Deacon, *The Symbolic Species: The Coevolution of Language and the Brain*, New York, 1997.

40 Conrad H. Waddington, 'The evolution of developmental systems', in D. A. Herbert, ed., *Twenty-eighth Meeting of the Australian and New Zealand Association for the Advancement of Science*, Brisbane, 1952, 155–59.

41 Susan Oyama, *The Ontogeny of Information Developmental systems and evolution*, Cambridge, 1985.

42 Susan Oyama, Paul E. Griffiths and Russell D. Gray, eds, *Cycles of Contingency: Developmental Systems and Evolution*, Cambridge, MA, 2001.

43 Paul E. Griffiths and Russell D. Gray, 'Developmental Systems and Evolutionary Explanation', *Journal of Philosophy* 91 (1994): 277–304.

44 Scott F. Gilbert and David Epel, *Ecological Developmental Biology: Integrating Epigenetics, Medicine and Evolution*, Sunderland, MA, 2009.

45 Susan Oyama, *Evolution's eye: A systems view of the biology-culture divide*, Durham, NC, 2000.

46 One exciting application of this perspective is the proposal that the developmentally meaningful aspects of genome structure are themselves

not intrinsic, but dependent on the wider developmental context. See Karola Stotz, 'With genes like that who needs an environment: Postgenomics argument for the "ontogeny of information"', *Philosophy of Science* 73.5 (2006): 905–17, 47; 'Molecular epigenesis: Distributed specificity as a break in the central dogma', *History and Philosophy of the Life Sciences* 28.3–4 (2006): 527–44; 'The Ingredients for a Postgenomic Synthesis of Nature and Nurture', *Philosophical Psychology* 21.3 (2008): 359–81.

47 Paul M. Brakefield and Pieter J. Wijngaarden, 'Phenotypic Plasticity', in Brian K. Hall and Wendy M. Olson, eds, *Keywords and Concepts in Evolutionary Developmental Biology*, Cambridge, MA and London, 2003, 288–98.

48 Carl D. Schlichting, 'Environment', in Hall and Olson, eds, *Keywords and Concepts*, 108–14.

49 Sonia E. Sultan, 'Phenotypic plasticity for plant development, function and life history', *Trends in Plant Science* 5: 12 (2000): 537–42.

50 Julia Lüning, 'Phenotypic Plasticity of Daphnia pulex in the Presence of Invertebrate Predators: Morphological and Life History Responses', *Oecologia* 92.3 (1992): 383–90.

51 Timothy A. Mousseau and Charles W. Fox, eds, *Maternal Effects as Adaptations*, New York and Oxford, 1998.

52 Tobias Uller, 'Developmental plasticity and the evolution of parental effects', *Trends in Ecology and Evolution* 23.8 (2008): 432–38.

53 Michael J. Meaney, 'Nature, Nurture, and the Disunity of Knowledge', *Annals of the New York Academy of Sciences* 935 (2001) 50–61.

54 Ian C. G. Weaver, Nadia Cervoni, Frances A. Champagne, Ana C. D'Alessio, Shakti Sharma, Jonathan R. Seckl, Sergiy Dymov, Moshe Szyf and Michael J. Meaney, 'Epigenetic programming by maternal behavior', *Nature Neuroscience* 7.8 (2004): 847–54.

55 Peter Gluckman and Mark Hanson, *Mismatch: Why Our World No Longer Fits Our Bodies*, Oxford, 2006.

56 Peter D. Gluckman and Mark A. Hanson, 'Living with the Past: Evolution, Development, and Patterns of Disease', *Science* 305 (2004): 1733–36.

57 Peter D. Gluckman, Mark A. Hanson, Hamish G. Spencer and Patrick P. G. Bateson, 'Environmental influences during development and their later consequences for health and disease: implications for the interpretation of empirical studies', *Proceedings of the Royal Society B* 272 (2005): 671–77.

58 William Johannsen, 'The Genotype Conception of Heredity', *American Naturalist* 45 (1911): 129–59.

59 Richard Woltereck, 'Weitere Experimentelle Untersuchungen über Artveränderung, speziel über das Wesen Quantitativer Artunterschiede bei Daphnien', *Verhandlungen der deutschen zoologischen Gesellschaft* 19

(1909): 110–73.

60 Irving I. Gottesman, 'Genetic Aspects of Intelligent Behavior', in N. R. Ellis, ed., *Handbook of Mental Deficiency*, New York, 1963, 253–96.

61 James G. Tabery, 'Biometric and Developmental Gene-Environment Interactions: Looking Back, Moving Forward', *Development and Psychopathology* 19 (2007): 971–97.

62 Paul E. Griffiths and James G. Tabery, 'Behavioral Genetics and Development', *New Ideas in Psychology* 26.3 (2008): 332–52.

63 Philip J. Kitcher, 'Battling the undead: How (and how not) to resist genetic determinism', in R. Singh, K. Krimbas, D. Paul and J. Beatty, eds, *Thinking about Evolution: Historical, Philosophical and Political Perspectives (Festchrift for Richard Lewontin)*, Cambridge, 2001, 396–414.

64 Paul E. Griffiths and Edouard Machery, 'Innateness, canalisation and "biologicizing the mind"', *Philosophical Psychology* 21.2 (2008): 397–414.

65 Paul E. Griffiths, 'In what sense does "nothing in biology make sense except in the light of evolution"?', *Acta Biotheoretica* 57.1–2 (2009): 11–32.

66 Dorothy Nelkin, 'Molecular metaphors: the gene in popular discourse', *Nature Reviews: Genetics* 2 (2001): 555–59.

67 Dorothy Nelkin and M. Susan Lindee, *The DNA Mystique: The gene as a cultural icon*, New York, 1995.

68 Eva Jablonka and Marion J. Lamb, *Epigenetic Inheritance and Evolution: The Lamarkian Dimension*, Oxford, New York, Tokyo, 1995.

69 Eva Jablonka and Marion J. Lamb, *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*, Cambridge, MA, 2005.

70 Eva Jablonka and Gal Raz, 'Transgenerational Epigenetic Inheritance: Prevalence, Mechanisms, and Implications for the Study of Heredity and Evolution', *Quarterly Review of Biology* 84.2 (2009): 131–76.

71 Eva Jablonka and Eörs Szathmáry, 'The evolution of information storage and heredity', *Trends in Ecology and Evolution* 10.5 (1995): 206–11.

72 For a philosophical introduction to the concept of homology and its applications, see the Special Issue of *Biology and Philosophy* 22.5 (2009) edited by Ingo Brigandt and myself.

73 Neil Shubin, Cliff Tabin and Sean Carroll, 'Fossils, genes and the evolution of animal limbs', *Nature* 388 (1997): 639–48.

74 Walter Just, Wolfgang Rau, Walther Vogel, Mikhail Akhverdian, Karl Fredga, Jennifer A. Marshall Graves and Elena Lyapunova, 'Absence of Sry in species of the vole Ellobius', *Nature Genetics* 11.2 (1995): 117–18.

75 Paul E. Griffiths, *What Emotions Really Are: The Problem of Psychological Categories*, Chicago, 1997.