

Area review

Innateness and the sciences

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Abstract. The concept of innateness is a part of folk wisdom but is also used by biologists and cognitive scientists. This concept has a legitimate role to play in science only if the colloquial usage relates to a coherent body of evidence. We examine many different candidates for the post of scientific successor of the folk concept of innateness. We argue that none of these candidates is entirely satisfactory. Some of the candidates are more interesting and useful than others, but the interesting candidates are not equivalent to each other and the empirical and evidential relations between them are far from clear. Researchers have treated the various scientific notions that capture some aspect of the folk concept of innateness as equivalent to each other or at least as tracking properties that are strongly correlated with each other. But whether these correlations exist is an empirical issue. This empirical issue has not been thoroughly investigated because in the attempt to create a bridge between the folk view and their theories, researchers have often assumed that the properties must somehow cluster. Rather than making further attempts to import the folk concept of innateness into the sciences, efforts should now be made to focus on the empirical questions raised by the debates and pave the way to a better way of studying the development of living organisms. Such empirical questions must be answered before it can be decided whether a good scientific successor – in the form of a concept that refers to a collection of biologically significant properties that tend to co-occur – can be identified or whether the concept of innateness deserves no place in science.

Introduction

The concept of innateness is a part of folk wisdom. The commonsense view is that some traits of an organism are due (either entirely or to a large extent) to the organism's inborn nature and others are not. This distinction appears (in some form or another) in many different human cultures and possibly in all of them. The psychological mechanisms and biases that underlie the acquisition, deployment, and pancultural robustness of the distinction are being studied by cognitive psychologists and anthropologists (Carey 1985; Carey and Gelman 1991; Atran 1990, 1998; Medin and Atran 1999; Atran et al. 2001). Innateness is also a notion that biologists and cognitive scientists use. For example, some of the very people studying the psychology of the folk innate/non-innate distinction argue that the distinction is itself innate. Suppose that strong psychological biases really do cause human beings to think in terms of an

innate/non-innate distinction. If so, the scientists may be in the grip of this folk distinction. This would explain why they keep using it, even if the distinction tracks no interesting phenomena.

The innate/non-innate distinction has a legitimate role to play in science only if it relates to a coherent body of evidence and is able to play an important and positive role in the development of scientific theories. Consider, by analogy, the folk concept of force. This concept was imported into the physical sciences and it was gradually changed so as to fit the purposes of these sciences. Can something similar be done with the folk concept of innateness? In this paper, we examine many different candidates for the post of scientific successor of the folk concept of innateness, i.e. candidates for a theoretical reduction. We argue that none of these candidates are entirely satisfactory. In some cases, this is because the proposals to which the candidates make reference are inchoate, empty, or refer to other controversial notions. In other cases, it is because the overlap between the folk concept and the candidate successor is, at best, only partial. We believe, therefore, that no simple correspondence between the folk concept and a scientifically useful definition can be found.

Many important debates have been framed in terms of some version of the innate/non-innate distinction. Nevertheless, we think these debates can be improved by examining critically the various roles that the distinction has played and the ways these roles relate to each other. Researchers have treated the various scientific notions that capture some aspect of the folk concept as equivalent to each other or at least as tracking properties that are strongly correlated with each other. We argue, however, that the existence of these correlations should not be taken for granted. Whether these properties are strongly correlated or not is an important empirical issue. This empirical issue has not been thoroughly investigated because in the attempt to create a bridge between the folk view and their theories, researchers have assumed (implicitly or explicitly) that the properties must somehow cluster. It is wise not to bundle these different scientifically useful notions together under the label ‘innateness’ unless and until strong evidence is provided for the thesis that the properties referred to by these different notions are strongly correlated.

Methodology

We have not conducted any rigorous empirical investigations on the folk concept of innateness. In the absence of such investigations, we shall rely on what seem to be widespread intuitions and beliefs about which traits count as innate and which traits do not. These intuitions and beliefs are encapsulated in dictionary definitions such as this: “Innate: existing in a person (or organism) from birth; belonging to the original or essential constitution (of body or mind); inborn, native, natural; of qualities, principles, etc. (esp. mental); opposed to *acquired*, esp. in *innate ideas*” (from the Oxford English Dictionary). Widespread intuitions and beliefs generated by the concept of

innateness give us a way of identifying how the folk concept is deployed and thereby what kind of phenomenon it is supposed to track. In the paper, we shall often use them to point out the mismatch – both in terms of actual extensions and in terms of possible cases – between the folk concept and some proposed scientific definition of innateness. In some cases, the mismatch is great. In other cases, it is slighter but still significant.

In which circumstances, under what conditions, and in which ways can a folk concept be imported into the sciences? What are the conditions for a successful theoretical reduction? This is a difficult question. A proper answer would require a theory of concepts, of the way concepts can be more or less similar to each other, of the way they change over time, of the psychological rules that govern such changes, of the normative rules that ought to govern such changes, of the relation between the psychological rules and norms, etc. These issues are all controversial and we are not going to discuss them here. We shall only appeal to two kinds of considerations. First, there are considerations having to do with the scientific usefulness of the reducing concept. Very simply, if a candidate for scientific successor to a folk concept is not scientifically useful, then it is not a good candidate. Second, there are considerations regarding the overlap between the folk concept and some candidate scientific successor – and this explains the way we use commonsense intuitions and beliefs. While most authors agree that a complete overlap – in terms of actual extensions and possible cases – between a folk notion and its scientific successor is not necessary, everyone must agree that the smaller the overlap between a folk concept and a possible scientific successor, the harder it is to make the argument that the scientific concept is a concept of (roughly) the same phenomenon as the folk concept. That is, the bigger the mismatch, the more problematic is the alleged theoretical reduction.

How small does the mismatch have to be for the theoretical reduction to be possible at all? We don't have an answer to this question. We shall show, nevertheless, that a number of different scientifically useful concepts partially overlap in a significant way with the folk concept of innateness and that it is not possible to choose among such concepts on the basis of theoretical considerations.

Non-acquisition and regularities in development

'Innate' and 'acquired' are usually taken to be antonyms. This suggests the following proposition:

- (1) A trait is innate if and only if it is not acquired.

This proposal is unhelpful in discovering a scientific successor to the folk concept of innateness. On a minimal understanding of acquisition, a trait is acquired by an organism if at first the organism doesn't have the trait and then, at some subsequent time, the organism comes to have the trait (Samuels 2002). But on this minimal understanding all phenotypes are acquired. The only

non-acquired traits would be those that the organism has from the very beginning of its existence, such as the nuclear genes and the cytoplasmic factors present in its zygote. We need a non-minimal way of thinking about acquisition, such as ‘acquisition due to learning’, ‘acquisition due to the interaction with the environment’, etc. These notions do play a role in attempts to find a scientifically useful way of defining innateness and we shall examine them in the course of the paper. One way of thinking about acquisition in this context is in terms of post-natal processes. According to this line of thought, a trait is acquired in the sense of non-innate if it is acquired after birth. In other words:

(2) A trait is innate if and only if it is present at birth.

Clearly, this is not a good candidate as scientific successor to the folk concept of innateness. Prenatal learning occurs (DeCasper and Spence 1986; Spence and DeCasper 1987; Gottlieb 1992, 1997, 2003a) and learned traits are paradigmatic examples of lack of innateness according to the folk view. Moreover, many traits that are not present at birth are classified as innate by folk intuitions, as in the case of much sexual and parental behaviour that appears only in adulthood. The following proposal allows for the intuition that innate traits can appear long after birth:

(3) A trait is innate if and only if it reliably appears during a particular and relatively well-defined stage of the life cycle (e.g. at the onset of sexual maturity, immediately after the birth of the first child, etc.).

But the fact that a trait reliably appears during a particular developmental stage is compatible with the trait being a learned trait. Details of sexual and parental behaviour may well be affected by childhood experiences. Furthermore, some authors argue that despite the regularities in developmental timing, many human traits – e.g. basic folk-psychological skills – may be due to learning (Sterelny 2003).

Genetic influence

Most authors writing today suppose that innateness has something to do with genes: Pinker (1998, 2002, 2004), Tooby and Cosmides (1990a, 1990b, 1992), Plotkin (1997), Chomsky (1993, 2000), Marcus (2003), Fodor (2001), Baron-Cohen (2003), Miller (2000), Buss (2003), Wright (1997), Marler (2004), etc. But is it possible to provide a scientifically useful definition of ‘innate’ in terms of genetic phenomena? We shall consider the various options. One option is this:

(4) A trait is innate if and only if it is genetically determined.

The idea is that a phenotype is innate if and only if genes and nothing but genes are required for its development. This idea is too simplistic because no phenotype is such that only genes are needed for its development. Genes by themselves don’t do anything. They require other developmental resources for phenotype production. Another possible definition is this:

(5) A trait is innate if and only if it is genetically influenced.

The problem with this proposal is the opposite. All phenotypes are genetically influenced because genes participate (one way or another) to the development of all phenotypes. So, again, this proposal is unable to provide a scientifically useful distinction that matches roughly with the folk distinction between innate and non-innate traits.

All traits are genetically influenced in some way but it might be argued that innate traits are influenced *distinctively* by genes, in ways that non-innate traits are not. The problem is then to specify what this distinctive way could possibly be. The most popular account of the (alleged) distinctive way in which genes affect the development of innate phenotypes appeals to the (alleged) informational properties of genes:

(6) A trait is innate if and only if it is genetically encoded.

That is, a trait is innate if and only if all of the information required for its development is contained in the genomic sequence. This proposal distinguishes between factors that provide developmental information and factors that don't. Environmental factors are always involved in the development of phenotypes but, in the case of innate phenotypes, the assumption is that environmental factors only play a non-informational role.

In order to evaluate this proposal, the notion of genetic information must be examined. Two attempts have been made to make sense of this notion. One states that genes represent the phenotypes to which they causally contribute and with which they are statistically correlated (Dawkins 1982; Sterelny and Kitcher 1988). The other states that genes represent the phenotypes for which they have been selected (Dawkins 1996; Sterelny et al. 1996; Maynard Smith 2000; Sterelny 2000, 2001, 2004). Both attempts face problems (Gray 1992, 2001; Griffiths and Gray 1994, 1997, 2001; Griffiths 2001, forthcoming; Godfrey-Smith 1999, 2000). Both accounts are unsatisfactory. The main problem for the correlational view is that many nongenetic factors are correlated with phenotypes but these nongenetic factors are not seen as representing those phenotypes. The selectional view has problems making sense of cases such as genetic disorders and the developmental information provided by new genetic mutations. Moreover, though the notion of genetic coding is perfectly legitimate when referring to the mapping between nucleotide sequences and proteins (or more strictly poly-peptides), no one has been able to show that the notion can be legitimately applied to the mapping between genes and phenotypes in general. In the absence of a good account of the general notion of genetic information, identifying innateness with the genetic coding of phenotypes is trading one confused notion for another and is therefore no progress at all. Another proposal is the following:

(7) A trait is innate if and only if its development doesn't involve the extraction of information from the environment.

This proposal dispenses with the notion of genetic information and only talks about environmental information. The proposal seems to capture at least some aspects of the notion of innateness behind Chomsky's influential use of poverty of the stimulus arguments. Human children cannot extract information about what are the 'permissible' syntactic rules from their environment and thereby knowledge of which syntactic rules are 'permissible' must be innate (Chomsky 1959, 1965, 1972, 1975, 1980, 1982, 1986, 1988, 1993, 2000; Fodor 2000; Cowie 1999; Khalidi 2002). Chomsky often mentions 'genetic determination' and 'genetic endowment' when talking about the innateness of the language faculty (e.g. Chomsky 1993, 2000). The assumption is that if the information about syntactic structures is not extracted from the linguistic stimulus, then it must be extracted from the genome. But none of his arguments depends on such an account that equates innateness with genetic determination or genetic information. Given the actual nature of his arguments, it seems more accurate to reconstruct Chomsky's account of innateness in terms of what knowledge can and cannot be acquired by interacting with the environment.

This proposal also captures some aspects of the notion of innateness defended by Lorenz (1965). One of the famous examples of innate behaviour used by Lorenz is the disposition of male sticklebacks to attack objects that are red below. The adaptive function of this trait is to chase away rivals and the trait achieves this function because male sticklebacks have a red area on their belly. The information that rivals have a red belly (or, more precisely, the information that red-bellied organisms are to be attacked) is not acquired by learning, as shown – according to Lorenz – by the fact that the sticklebacks attack objects that are red underneath even when they have had no interaction at all with other males. Hence, on Lorenz's view, the stickleback's disposition to attack objects that are red underneath is innate. The information that rivals are red underneath cannot be extracted from oxygen, water, nutrition, or from non-specific visual experience; hence it must be innate (Lorenz 1965, pp. 37 and 106).¹

One problem though is that some traits – such as scars and calluses – don't seem to involve anything that could be labelled 'information extraction from the environment' and yet they don't count as innate on the folk view. Even when this proposal is restricted to psychological traits, an important problem remains. The difficulty of finding a principled way to distinguish 'experiences' that provide mere developmental support from 'experiences' that provide information was stressed by Lehrman (1970) in his reply to Lorenz. Lehrman focused on the many different ways in which 'experiences' can affect development. In some cases specific experiences are required, in other cases non-specific experiences are required, and many cases fall in between these two

¹ It is worth noting that the famous experiment (due to Tinbergen) on the response of male sticklebacks to red underbellies that Lorenz used in his book has not been replicated (Rowland and Sevenster 1985).

extremes. It is a continuum and, for this reason, the dichotomous distinction of environment-as-information vs. environment-as-support cannot adequately capture the reality of biological phenomena (Bateson 1976, 1983, 1985). One interesting example of this is provided by Gottlieb's studies of the mallard ducklings (Gottlieb 1992, 1997). The studies show that the mallard ducklings' ability to recognise the species-specific call produced by adults is facilitated by the ducklings' auditory exposure to the call that they themselves produce while inside the egg. The call the ducklings produce and listen to before hatching is in many ways different from the adult species-specific call. The ducklings are better able to recognize the species-specific call by hearing the call that they produced before hatching. However, the experiential input is neither 'instructive' nor 'merely supportive'.

A related idea consists in explaining the distinctive way in which genes affect the development of innate traits by appealing to the concept of *developmental induction*. The underlying assumption is that it is possible to distinguish between factors that merely provide *support* to the development of a phenotype and factors that *induce* the development of the phenotype (Gilbert 2003b, c). Each gene and each environmental factor involved in the development of a given phenotype can – relative to that phenotype – have either an inductive function or a supportive function. Environmental factors are involved in the development of all phenotypes, but, according to this proposal, in the case of innate traits only genes play an inductive role:

- (8) A trait is innate if and only if it is not environmentally induced.

The notion of developmental induction needs clarification. Let us consider some examples. Whether a turtle develops into a male or a female depends on the incubation temperature of the eggs during the first trimester of development. In some species, eggs incubated above a temperature of about 30 °C develop into females and eggs incubated below about 30 °C develop into males (Janzen and Paukstis 1991; Yntema and Mrosovsky 1982; Crews 1996). In this case, temperature doesn't just generically support development but – by turning on and off certain sets of genes – it produces specific (and incompatible) changes in phenotypic structures. In contrast, the amount of nutrients present in each egg doesn't produce specific (and incompatible) changes in phenotypic structures. Without sufficient nutrients, the turtle will die, but the amount of nutrients doesn't cause the turtle to develop into a male rather than a female. With respect to sex determination, food is a merely supportive developmental factor, but temperature isn't. Accordingly, on this proposal, the sex of a turtle isn't innate.

Consider also the case of caste determination in social insects. Whether a bee becomes a worker or a queen depends on the amount and quality of nutrients the bee receives as a larva. These environmental factors induce a series of changes that – by turning on and off certain sets of genes – result in either the queen phenotype or the worker phenotype (Rachinsky and Hartfelder 1990; Evans and Wheeler 1999). Food doesn't just generically support development

but produces specific (and incompatible) changes in phenotypic structures. In contrast, the amount of oxygen available to a bee doesn't produce specific (and incompatible) changes in phenotypic structures. Without enough oxygen, the larva will die, but the amount of oxygen doesn't cause the larva to develop into a queen rather than a worker or vice versa. With respect to caste determination oxygen is a merely supportive developmental factor, but received food is an inductive developmental factor. The queen phenotype of a bee is thus not innate.

The examples suggest that changes in inductive factors generate changes in which phenotypes develop, while changes in supportive factors result at most in the death of the organism. Given this, (8) can be interpreted as follows: let T be a trait of an organism; consider all the environmental factors that are required for T's development; if by changing one or more of these environmental factors it is possible to produce a trait qualitatively different from T without killing the organism, T is not innate; otherwise T is innate. More concisely:

(9) A trait is innate if and only if it is not possible to produce an alternative trait by means of environmental manipulations.²

This proposal has obvious problems. Consider, for example, the case of the development of normal species-typical human limbs. According to folk intuitions, this trait is innate. The maternal womb is one of the environmental factors required for the development of this phenotype. Hence, the maternal womb should be a mere supportive factor for the development of species-typical human limbs. But changes in the maternal womb affect the structure of the developing limbs. For example, a thalidomide-bathed womb generates the development of limbs that differ markedly from the species-typical limbs that develop in thalidomide-free wombs. So, on this proposal, the structure of the limbs of a person with species-typical limbs is not an innate trait of that person because, had that person developed into a thalidomide-bathed womb, she wouldn't have had species-typical limbs.

According to folk intuitions, the structure of species-typical human muscles and bones is innate. But microgravity studies suggest that the value of the acceleration of gravity can make a difference with respect to musculoskeletal structure. If a woman grew up on Mars, she wouldn't necessarily die, but her muscles and bones wouldn't be the species-typical ones. Does this show that the species-typical structure of muscles and bones is not innate? More generally, it is likely that for every phenotype some environmental factor can be

² This idea is sometimes expressed in terms of an innate trait being "a phenotypic difference due to a genetic difference" (Tinbergen 1955; Jensen 1961; Cassidy 1979; Jacobs 1981; Pinker 2004). One way of interpreting this definition is in terms of existing differences at the population level. When interpreted in this way, it is equivalent to defining innateness as high broad heritability (see the next section). Another way of interpreting the definition is in terms of 'virtual differences': an innate trait is such that, were some of the genes involved in the development of the trait changed, a trait with a different structure would develop, while changes in environmental factor would result either in the death of the organism or in no significant phenotypic change at all.

found such that changes in this environmental factor produce changes in the phenotype (rather than just the death of the organism). In fact, this would be expected on the assumption that the environment doesn't just provide the energy and matter required by developmental processes but is also partly responsible for which nuclear genes are switched on and off and for the way the products of transcription and translation are processed and used. In an effort to avoid such problems, the proposal might be rephrased as follows:

(10) A trait is innate if and only if all environmental manipulations capable of producing an alternative trait are abnormal.

Thalidomide-bathed wombs are abnormal environments for humans and this is why human species-typical limbs are innate even though they don't develop in thalidomide-bathed wombs. Temperatures below 30 °C are normal for turtles and, in some species, femaleness doesn't develop at such temperatures. This is why femaleness in these species isn't innate. But in order to assess this reformulation, it is necessary to know what counts as a normal change in environmental circumstances and what doesn't. And it is important to make sure that this distinction is not merely driven by pre-theoretic intuitions about what should and shouldn't count as innate. One possibility is to define abnormality in statistical terms:

(11) A trait is innate if and only if all environmental manipulations capable of producing an alternative trait are statistically abnormal.

One suggestion is that an environmental factor is to be considered normal – with respect to the development of a phenotype in the organisms of a given species – if all or most of the organisms in the species share that environmental factor. This is obviously too strong: an incubation temperature above 30 °C is clearly a normal environmental factor for turtles (otherwise being a male would be a developmental abnormality) but it is not true that all or most turtles share this factor (otherwise few if any females would exist). Another suggestion is that an environmental factor is normal if, say, at least 10% of the organisms share the environmental factor. This doesn't work either. The nutritive regime that leads to the queen phenotype is shared by less than 10% of bees, and yet it clearly is a normal environmental factor (otherwise being a queen would be a developmental abnormality). Moreover, suppose the use of Prozac becomes culturally universal in the human species. In these circumstances, a Prozac-free diet would become abnormal and, on the current proposal, Prozac-induced euphoria would become innate.

Another way to distinguish between normal and abnormal environmental factors is to appeal to evolutionary history. An environmental factor is to be regarded abnormal – with respect to the development of a phenotype in the organisms of a given species – if and only if it is not one of those environmental factors that organisms of this species are adapted to. We can call such factors *evolutionarily abnormal*. Humans are not adapted to thalidomide-bathed wombs and to Martian gravity. Such environmental circumstances are

evolutionarily abnormal for the human species. Thus, environmental manipulations of this kind should not be considered in determining whether species-typical human limbs, muscles, and bones are innate, despite the fact that such manipulations make a difference with respect to the development of these body structures. In contrast, turtles are adapted to incubation temperatures both above and below 30 °C. Both kinds of temperatures are evolutionarily normal. So, manipulations in incubation temperatures should be considered in the question of whether sex is innate in turtles.

(12) A trait is innate if and only if all environmental manipulations capable of producing an alternative trait are evolutionarily abnormal.

This proposal is still unsatisfactory because it allows many learned traits to be classified as innate. Human children acquire the belief that water exists in liquid form by interacting with samples of water and by learning the properties of this substance. As such, according to folk intuitions, this belief is not innate. But the only way to have a child who doesn't believe that water is a liquid is to put the child in an evolutionarily abnormal environment, such as an environment where no water in liquid form is available. So, according to this proposal, the belief that water exists in liquid form is innate. To avoid problems of this sort, one might attempt to exclude all learned traits from the category of innate. We turn to this strategy in the section after next. In the following section, we consider whether there is some concept of heritability that can function as a scientific successor to the folk concept of innateness.

Heritability

The concept of heritability is often mentioned in connection with the concept of innateness. Moreover, there is an intuitive connection between the idea that a trait is innate and the idea that the same trait is 'hereditary'. This suggests the adoption of the following proposal:

(13) A trait is innate if and only if it is highly heritable.

Heritability is a statistical concept that applies to the variation for a phenotype existing in a population at a given time. In fact, heritability is not a single concept but a family of concepts. *Broad heritability* is defined as the ratio of the variance of the phenotype due to genetic variation to the total variance of the phenotype in the population. That is, a trait has high broad heritability in a population to the extent that the existing variation for that trait in the population is due to genetic variation. *Narrow heritability* gives the extent that the existing variation for the phenotype is due to variation in genes considered independently of their interactions with other genes at the same or at different loci. *Selectional heritability* measures the phenotype's response to selection relative to the intensity of the selection pressure. *Covariational heritability* measures the strength of the correlation between close relatives for the

phenotype in the population under study. Many textbooks (e.g. Futuyma 1997; Ridley 2003) claim that narrow heritability, selectional heritability and co-variational heritability are effectively equivalent. This is an oversimplification that can lead to the ignoring of important biological phenomena (Falconer and Mackay 1996; Lynch and Walsh 1997; Mamei 2004). For purposes of present discussion, we shall focus on broad heritability, but the arguments we present can be easily generalised to the other notions of heritability.

If variance in a trait is entirely due to genetic variance, broad heritability is 1.0; if it is entirely due to variance in non-genetic factors, broad heritability is 0.0. Many problems exist with the view that innateness can be identified with high broad heritability. If innateness is high heritability, invariant phenotypes cannot be innate. So, in a population where all organisms have two legs, the trait 'having two legs' cannot be innate. The view that innateness is the same as high heritability requires not only that some variation exists, but also that this variation is due to genetic differences. So, in a population where all organisms have two legs except for those that have lost the one leg in some accident, the trait 'having two legs' cannot be innate. More generally, the problem with this attempt to find a scientific successor to the concept of innateness is that it makes the innateness of a trait of a particular organism depend on the composition of the population to which that organism belongs. Changes in the population to which an organism belongs can change the heritability (and, thereby, on this view, the innateness) of the traits of an organism, despite the fact that all the intrinsic properties of the organism remain the same. This is incompatible with the folk view.

It must also be noted that it is perfectly possible for a trait to be highly heritable in the population but also learned by each individual within it. If high heritability is compatible with learning then high heritability cannot be a good scientific successor to the folk concept of innateness. In general, heritability estimates provide only extremely poor information about developmental processes (Lehrman 1970; Lewontin 1974, 2000; Bateson and Martin 1999; Bateson 2001; Gottlieb 2003b; Meaney 2003). This by itself should make us suspicious of any attempt to try to use the notion of heritability to clarify innateness, which is supposed to be a developmental phenomenon. For example, contrary to some common misinterpretations of heritability estimates (Jensen 1969; Herrnstein and Murray 1994), the high heritability of a trait doesn't support the hypothesis that the trait is developmentally robust. As we shall explain in a later section, some attempts to find a scientific successor to the concept of innateness focus on that part of the folk view according to which an innate trait has low malleability. But high heritability says little about how difficult it is to change a trait in circumstances other than those in which it was measured (Lewontin 1974, 2000; Bateson and Martin 1999; Bateson 2001; Moore 2001).

Lack of learning and adaptive plasticity

It is central to the folk view of innateness that learned traits are not innate and innate traits are not learned. One may exploit this intuitive connection between

innateness and lack of learning and propose that in scientific contexts ‘innate’ should be taken to be equivalent to ‘not learned’:

(14) A trait is innate if and only if it is not learned.

One problem with this proposal is that learning is itself a theoretically controversial notion, variously regarded as hypothesis testing, conditioning (classical or operant), synaptic pruning or some other kind of selective process that operates on neural structures, any change in a brain network due to stimuli generated in the sensory apparatus by the interaction between the external environment and the sensory organs, etc. The relations between these views of learning are far from clear, and often display inconsistencies. For example, Quartz and Sejnowski (1997; Quartz 1999; Elman et al. 1996) argue that many characteristics of neural structures count as not learned on the view that learning is hypothesis testing and count as learned on the view that learning is a change in neural structures due to perceptual processing. Which version of ‘not learned’ gets the status of scientific successor of the folk concept of innateness?

Samuels (1998, 2002, 2004) believes that the connection between ‘innate’ and ‘not learned’ is fundamental and should be at the centre of a scientifically useful notion. But he believes that defining ‘innate’ as ‘not learned’ is too simplistic and makes the following proposal:

(15) A trait is innate if and only if (i) the trait is psychologically primitive and (ii) the trait results from normal development.

A trait is psychologically primitive if and only if a psychological explanation of its development doesn’t exist (in principle and not just in this specific historical moment). The trait may be explainable in biological or chemical or physical terms, but if it is not explainable in psychological terms, then – provided that it is not due to abnormal development – it counts as innate.

Let us examine clause (i). Learning is a psychological process. An explanation of the development of a trait in terms of learning is therefore a psychological explanation. So, if a trait is learned, it is not psychologically primitive. Clause (i) preserves the intuition that learned traits are not innate, but it does so without having to choose among the various accounts of learning. Moreover, it generalises the intuition that learned traits are not innate to other kinds of psychological processes (Cowie 1999).

The motivation for (ii) is the desire to avoid certain kinds of counterexamples. Consider, for example, what Damasio (1994) calls “acquired sociopathy”. Acquired sociopathy is a particular set of cognitive/emotional dispositions that people acquire when damage to the ventromedial prefrontal cortex occurs as a result of accident, tumour, or brain surgery. This set of cognitive/emotional dispositions is psychologically primitive. Its emergence is not explained in psychological terms because the emergence of these dispositions is due to brain damage and not to psychological processes such as learning. But despite it being psychologically primitive, acquired sociopathy is innate according to folk intuitions.

A difficulty with this account is one that Samuels himself recognizes: the account is incomplete in so far as no explanation of what counts as normal development is given. Defining innateness in terms of normal development without a clear view about normal development may turn out, once again, to be the trading of one inchoate notion for another. But apart from this, we have two serious concerns with Samuels's account.

The first has to do with the notion of psychological primitiveness, which we believe to be problematic. The distinction between psychological explanations and non-psychological explanations is fuzzy and it seems to depend more on arbitrary disciplinary boundaries than on matters of fact. For example, Fodor (1981) believes that the developmental triggering of cognitive structures is not a psychological process because it is not a rational-causal process but rather a brute-causal process (and on these grounds he claims that triggered cognitive traits are innate). In contrast, many behavioural biologists believe that triggering is one of the many processes involved in psychobiological development and as such it counts as a psychological process. Who is right? And why should it matter? Important empirical differences exist between, say, songbirds that need to learn their species-specific song from their conspecifics and songbirds that only need to be exposed to some song or other (not necessarily the species-specific one) in order to acquire the species-specific song. But nothing important seems to be at issue in the choice between saying that both processes are psychological and saying that the first (learning) is psychological and the second (triggering) is not.

The second concern we have with Samuels's proposal is that it works only for cognitive traits. Temperature-dependent sex determination in turtles is not learning or any other process that could plausibly be classified as psychological. So, the femaleness and the maleness of turtles are psychologically primitive. Moreover, these maleness and femaleness are certainly not due to abnormal development. Therefore, they count as innate on Samuels's account, but they are not innate on folk intuitions. In order to deal with these cases, Samuels restricts his account to cognitive traits. But, for our purposes, this restriction is unsatisfactory.

Can we find an alternative account that avoids these problems? One obvious thought is that learning is only one of a larger class of mechanisms that have evolved to produce adaptive plasticity. That is, learning is only one of a larger class of mechanisms that have evolved to produce different phenotypes in response to different environmental circumstances. The reason why temperature affects sex determination in turtles is because turtle eggs have an evolved developmental mechanism with the function to give rise to maleness at certain temperatures and femaleness at other temperatures. Intuitively, traits produced by mechanisms adapted to map different environments onto different phenotypes ought not count as innate. This suggests the following proposal:

(16) A trait is innate if and only if it is *not* produced by developmental mechanisms adapted to produce different traits in response to different environmental conditions.

This proposal guarantees that learned traits and traits such as the sex of turtles don't count as innate. But, if we leave this proposal as it is, the limbs that develop in thalidomide-bathed wombs and the acquired sociopathy due to brain injury are classified as innate. Such traits are not due to mechanisms adapted to map environmental differences onto phenotypic differences. No mechanism evolved to map the presence of thalidomide in the womb onto the production of abnormal limbs and no mechanism evolved to map brain injury onto abnormal cognitive/emotional dispositions. In order to avoid classifying these traits as innate, one needs to modify the proposal. One possibility is to appeal to normal development. The proposal would then be the following:

(17) A trait is innate if and only if (i) it is not produced by a mechanism evolved to map different environmental conditions onto different phenotypes and (ii) it results from normal development.

Just like Samuels's proposal, this proposal is incomplete if no account of normal development is given. What account of normal development should we adopt? We don't have room to explore all the available options and so we shall only present what we think is the most interesting option, namely, an appeal to the distinction – mentioned in a previous section – between evolutionarily normal and evolutionarily abnormal developmental factors. For a given phenotype of a given organism with a given genotype, development is normal if and only if it is not affected by evolutionarily abnormal environmental factors, that is, environmental factors that were not present during the evolution of the trait and to which the organism isn't adapted. Given this view of normal development, the definition of innateness becomes the following:

(18) A trait is innate if and only if (i) it is not produced by a mechanism adapted to map different environmental conditions onto different phenotypes and (ii) it doesn't result from the impact on development of evolutionarily abnormal environmental factors.

Clause (i) guarantees that learned traits and traits such as the femaleness of turtles don't count as innate. Clause (ii) guarantees that traits like acquired sociopathy and limbs whose development has been affected by thalidomide-bathed wombs don't count as innate. The conjunction of the two clauses guarantees that traits like species-typical limbs count as innate despite the fact that differences in the concentration of thalidomide in the womb can induce differences in the phenotype. This proposal is superior to Samuels's in that it applies to both cognitive traits and non-cognitive traits, it doesn't appeal to an unclear and perhaps spurious distinction between psychological and non-psychological explanations, and the unexplained distinction between normal and abnormal development has been replaced by the more precise distinction between environmental influences to which the organism is adapted and environmental influences to which the organism isn't adapted.

How does this account of innateness match with the folk view? Consider an evolutionary scenario in which a Prozac-free diet becomes evolutionarily

abnormal for human beings. In that situation, Prozac-induced euphoria would become innate according to the current account, while on the folk view it wouldn't. Another important difference between the folk view and the current proposal can be seen by focusing once again on the turtles. On the folk view, being a male and being a female are not innate traits in the turtles. But now consider the species-typical reproductive behaviour of male and female turtles. According to folk intuitions, these behaviours are innate despite the fact that sex determination itself is not innate. The intuitive picture seems to be one where every turtle is seen as 'containing within itself' two different and incompatible ways of living, the male way of living and the female way of living (Bateson 1983, 2001; Bateson and Martin 1999; van der Weele 1999; Gilbert 2001, 2003a; West-Eberhard 2003). Which way of living is 'activated' or 'switched on' depends on incubation temperature and thereby is not innate. But both ways of living are present (in their potential rather than actual form) within each turtle. This explains why people have the intuition that the species-typical reproductive behaviour is innate, despite the fact that the expression of such behaviour depends on an environmental switch. This intuition is not captured by the current proposal about what the scientific successor of the folk concept should be.

Non-malleability

Innateness is often associated with non-malleability. On the folk view, the innateness of a trait implies that the trait is robust with respect both to its development and to its continuance. An innate phenotype is generally supposed to be a phenotype produced by a process that is difficult to disrupt (developmental non-malleability) and a phenotype that is difficult to modify once it has developed (post-developmental non-malleability). The first thing to notice for the view that innateness can be identified with developmental robustness is that developmental robustness is a matter of degree. On the folk view, the distinction between innate and non-innate traits is often seen as a sharp dichotomy. The second thing to notice is that developmental and post-developmental robustness do not necessarily go together. Developmental malleability may be followed by non-malleability, as in many examples of human food preferences that, once established, are hard to modify. And developmental non-malleability may be followed by considerable malleability, as in the case of the human smile, which reliably appears in infants during the fifth or sixth week after birth and is successively greatly modified by social interactions and cultural influences. In spite of all this, is it possible to use the intuitive connection between innateness and non-malleability to ground a scientific successor to the folk concept? Wimsatt (1986, 1999) tries to do this by using the notion of 'generative entrenchment'. His proposal is this:

(19) A trait is innate to if and only if it is generatively entrenched in the design of an adaptive feature.

A feature *F* of an organism *O* is generatively entrenched to the extent that the development and the functioning of other features of *O* causally depend on *F*. If *F* is a feature such that the development and proper functioning of many adaptive features depend on it, then strong stabilizing selection for *F* is likely to have taken place during evolution. This stabilizing selection is likely to have resulted in *F*'s developmental processes becoming more and more robust and in mechanisms ensuring that, after it has developed, *F* remains in place and unmodified for as long as it is needed for the development and operation of the adaptive features that depend on it. So, innate learning mechanisms are generatively entrenched in that they underwrite the development and proper functioning of important cognitive and behavioural skills. In the same way, what immunologists call the 'innate components of the immune system' are generatively entrenched in that they underwrite the development and proper functioning of important immunological abilities. But many features count as innate on the folk view and yet are not entrenched: e.g. eye colour and genetic diseases. And many features that are generatively entrenched are intuitively not innate. For example, in literate societies reading skills are generatively entrenched in that many of the cognitive skills people acquire in these societies depend on the prior acquisition of reading skills. But reading skills are not innate on the folk view: reading requires intense training. Cases like these show that generative entrenchment cannot provide a smooth transition from an intuitive to a scientifically useful characterization of the innate/non-innate distinction.

A different account is given by Ariew (1996, 1999, manuscript) in terms of the notion of canalization. Waddington defined canalization as "the capacity [of development] to produce a particular definite end-result in spite of a certain variability both in the initial situation from which development starts and in the conditions met during its course" (Waddington 1975, p. 99, 1957). Ariew interprets canalization as a trait's insensitivity to variation in developmental factors, both genetic and environmental. Consider the species-typical structure of human limbs. If silencing gene *G* has no effect on the development of normal human limbs, then one can say that normal human limbs are genetically canalized with respect to variation in *G*. Similarly, if the development of a phenotype *P* is insensitive to variation in environmental factor *E*, then *P* is environmentally canalized with respect to *E*. So, if sex assignment in birds is insensitive to variation in incubation temperature, avian sex assignment is environmentally canalized with respect to incubation temperature. According to Ariew, this notion of environmental canalization can serve as the scientific successor to the commonsense concept of innateness:

(20) A trait is innate if and only if it is environmentally canalized, in the sense that it is insensitive to some range of environmental variation.

However, every phenotype is insensitive to variation in some environmental conditions and sensitive to variation in some other environmental conditions. This seems to commit Ariew to the view that every phenotype can be said to be

innate with respect to some ranges of environmental variation and non-innate with respect to other ranges of environmental variation. Every phenotype is both innate and non-innate! For example, species-typical human limbs are sensitive to variation in the amount of thalidomide that is found in the maternal womb but insensitive (as far as we know) to variation in how much TV the mother watches during pregnancy. So, on this view, normal human limbs are innate with respect to amount of TV watched and non-innate with respect to the amount of thalidomide.

Ariew is aware that all phenotypes are sensitive to some ranges of environmental variation and insensitive to others. In order to deal with this problem, he suggests that only some ranges of environmental variation are to be considered in order to establish whether a trait is innate or not. Ariew would presumably want to say that sensitivity to variation in amount of thalidomide is not relevant to establishing the innateness of species-typical human limbs and that, if one restricts one's attention to the 'permissible' environmental ranges, species-typical human limbs will be classified as innate by his definition. This move is similar to a move we have considered in a previous section. And the problem is exactly the same. How does one distinguish in a principled way the ranges of variation that are relevant to assess the innateness of a trait and the ranges that are not? How can we make sure that our intuitions about what counts as a permissible range are not just driven by our pre-theoretic intuitions about what should be classified as innate?

The problems faced by Ariew's account may be avoided by adopting a more scientifically useful notion of canalization (Bateson 1985; Gilbert 2002; Hallgrímsson 2002; West-Eberhard 2003; Wilkins 2003). The central idea is that canalization entails the existence of evolved "buffering" mechanisms. Distinguishing between developmental canalization and post-developmental canalization, we suggest: a phenotype *P* is *developmentally canalized* if an evolved mechanism *M* exists to ensure that *P* develops in the face of certain perturbations, and *post-developmentally canalized* if an evolved mechanism *M* exists to ensure that *P* is not modified by the occurrence of certain events after its development is complete. The larger is the range of events that *M* is adapted to deal with, the more canalized is *P* (either developmentally or post-developmentally). These notions provide a way to make more precise the intuitive notions of, respectively, developmental robustness and post-developmental non-malleability. Still more precision is achieved by distinguishing between environmental and genetic versions of developmental and post-developmental canalization. If, in the case of developmental canalization, *M* is adapted to deal with a specific range of genetic variability, then *P* can be said to be *genetically* developmentally canalized. If *M* is adapted to deal with a specific range of *environmental* variability, then *P* can be said to be *environmentally* developmentally canalized. The same applies – *mutatis mutandis* – to post-developmental canalization.

Having made the notion of canalization more precise by appealing to evolved mechanisms and to the ranges of variability that these mechanisms are adapted to

deal with, we need to ask whether this notion can give us a scientific successor to the folk concept of innateness. A positive answer would justify the strong connection between innateness and developmental and post-developmental robustness in the writings of Evolutionary Psychologists (Barkow et al. 1992; Tooby and Cosmides 1992; Plotkin 1997; Wright 1997; Atran 1998; Pinker 1998, 2002; Buss 2003, etc.).³ Consider the following proposal:

(21) A trait is innate if and only if it is developmentally environmentally canalized, or (for brevity) DEC.

Species-typical human limbs are DEC. Mechanisms have evolved to buffer the development of human limbs against many environmental factors, even though such mechanisms have not evolved to deal with exposure to thalidomide during development. So, on this account, species-typical human limbs count as innate. The reproductive behaviour of a queen bee is DEC too, despite the fact that this behaviour is switched on by a specific nutritional regime at the larval stage. So, this trait also counts as innate. But the problem with this proposal is that many learned traits count as DEC too. For example, Sterelny (2003) argues that folk-biological taxonomical abilities are DEC *and* culturally acquired. Similar problems apply to the following proposal:

(22) A trait is innate if and only if it is post-developmentally environmentally canalized (PEC).

Consider behavioural imprinting by which many birds learn to recognize their parents (Bateson 2000a). On the folk view, recognition of parents is not innate in these organisms. But the system has evolved to ensure that once the ability to recognize the parents has developed, such ability remains relatively immune to the effects of further experience. That is, this ability is PEC.

Yet another problem for this approach arises with genetic disorders. Genetic disorders are not canalized in the sense that we have defined. No mechanisms are adapted to buffer the development of, say, phenylketonuria (PKU), even though the development of the syndrome can be prevented by appropriate diet. The developmental and post-developmental robustness of this disease is due to the disruption that given genetic mutation produces on species-typical developmental and physiological processes. So, PKU would not be classified as innate by an account that identifies innateness with evolved buffering.

We conclude, then, that while an appropriately defined notion of canalization captures an important aspect of the folk concept of innateness, canalization cannot provide an entirely satisfactory scientific successor to the folk concept.

³ We believe that psychological understanding is helped by evolutionary considerations (see also Heyes 2000, 2003). But the label 'Evolutionary Psychology' is used for a specific way of applying evolutionary considerations to the study of psychological phenomenon, i.e. the way defended – most prominently – by Tooby and Cosmides (1992) and by Pinker (1998).

Species typicality and adaptation during evolution

According to the folk view, an innate trait is a trait that is part of the nature of the organism. The nature of the organism is something that ‘drives’ the development of the organism ‘from inside’. An altogether different way of making scientific sense of this part of the folk view exploits the notion of species-specificity, that is, of traits that are typically present:

(23) A trait is innate if and only if it is species-typical.

This seems to be the view of innateness that motivates talk about ‘universal human nature’ or ‘the psychic unity of humankind’ (Tooby and Cosmides 1990a, 1990b, 1992; Barkow et al. 1992; Pinker 1998, 2002; Buss 2003; Gander 2003, etc.). What does ‘typical member of the species’ mean? If ‘typical’ means ‘statistically normal’, then worker bees are typical and queen bees are atypical. Hence, on this proposal, being a worker is an innate trait of bees and being a queen isn’t. Similarly, on this account, genetic diseases are not innate, since they affect only a small number of individuals in the species. Moreover, in many species, learned traits are shared by all statistically normal members. In many species of birds, all normal members learn the species-specific song by listening to other members, but according to folk intuitions the learned song is not innate. Perhaps the idea is that species-typical features are those that result from the operation of natural selection.

This thought leads us to yet another way that scientists have sought to make sense of biological natures. According to Symons, the question whether a trait is ‘in our genes’ is best construed as a question about whether the trait is a Darwinian adaptation (Symons 1992, p. 141). On this view:

(24) A trait is innate if and only if it is a Darwinian adaptation.

This seems to be the view of innateness that motivates talk about ‘evolved human nature’ (Tooby and Cosmides 1990a, 1990b, 1992; Barkow et al. 1992; Plotkin 1997; Wright 1997; Pinker 1998; Buss 2003, etc.). But not all Darwinian adaptations are genetically based. Natural selection acts upon selectionally heritable variation in fitness, but selectionally heritable variation need not be of genetic origin (Griffiths and Gray 1994; Sterelny et al. 1996; Sterelny 2001, 2004; Mameli 2004). A Darwinian adaptation is simply a phenotype that has spread (has increased in frequency) in a population because of Darwinian selection *for* this phenotype (Sober 1984, 2001; Futuyma 1997), and this can occur by natural selection operating on genetic variation, on non-genetic variation, or on both. We shall call a *standard* Darwinian adaptation any Darwinian adaptation that has been selected for *in virtue of the existence of additive genetic variation for this phenotype*. The proposal would then be the following:

(25) A trait is innate if and only if it is a *standard* Darwinian adaptation.

This view entails that genetic disorders as well as the phenotypic effects of new genetic mutations are not innate, while on the folk view they are.

Furthermore, on this definition, evolutionary spandrels don't count as innate either. If the human preference for rhythmic noises and sounds is a by-product of the way natural selection has shaped the human auditory system, then such preference isn't innate on this proposal, despite being the by-product of an innate feature. Yet another problem arises from the fact that additive genetic variation for fitness can affect learned traits. This means that learned traits can and often are standard Darwinian adaptations. As Lehrman put it, 'nature selects for outcomes' (1970, p. 28), and nature can select for an outcome that either requires or doesn't require learning (Griffiths and Gray 1994; West-Eberhard 2003; Bateson 2004a).

Genetically based heritable variation in fitness is present both in learned traits and in non-learned traits and the crucial difference between a learned trait and a non-learned trait could be a genetic difference. Hence, both learned traits and non-learned traits can spread because of genetically based Darwinian selection for them. Fish-catching is a species-typical behaviour pattern of the osprey, an eagle that uniquely snatches with its talons healthy fish from the water's surface. This skill emerges in ospreys as a result of a long and complicated learning process. Is this behaviour a Darwinian adaptation? Suppose that at some stage the ospreys didn't exhibit this behaviour at all. Then a genetic mutation *G* that allows or motivates ospreys to learn to catch fish from the water appeared in some individual. Fish-catching was fitness enhancing: fish-catchers had higher fitness (on average) than non-catchers. Fish-catching was heritable because *G* was genetically transmissible, and natural selection increased the frequency of fish-catchers and decreased the frequency of non-catchers. On this scenario, fish-catching is a standard Darwinian adaptation of the ospreys, despite being a learned trait.

Natural selection can also distinguish among different genetically caused variants of a learned trait, thereby creating cumulative improvements in learned traits. Consider the ospreys again. Some are better at fish-catching than others. Some of these differences may be due to genetic differences that affect the way ospreys learn how to catch fish and they may lead to an evolutionary change in the population. The variants that spread are standard Darwinian adaptations, despite the fact that they are learned. Since, on the folk view of innateness, learned traits are not innate traits, 'genetically based Darwinian adaptation' cannot be a good successor to the folk concept.

The idea that natural selection and innateness are somehow related is a popular and powerful idea (Johnston 2001; Griffiths 2004). Attempts to relate innateness to natural selection go back to Darwin himself. Darwin used the word 'innate' as synonymous with 'inherited' and 'instinct' as synonymous with 'inherited behaviour' (Darwin 1859, 1871, 1872). According to this view, some developmentally privileged material that determines the development of certain traits – including behavioural traits – is transferred from parents to offspring at the moment of conception. These traits are the biologically inherited or instinctive ones; all other traits are 'acquired'. This wasn't just Darwin's view; it was the received view (Mameli 2005). What Darwin – famously and

importantly – added was the thought that inherited traits can evolve by a process of differential survival and reproduction. When Mendel's results were rediscovered, genes were identified with those entities that are transmitted from parents to offspring at conception and that are responsible for the development of the inherited traits. So, 'inherited' (and thereby 'innate') became synonymous with 'genetically determined', and 'instinct' became synonymous with 'genetically determined behaviour'. A version of this view can be found in Lorenz's writings in the 1930s. According to Lorenz (1937, 1939), all basic units of behaviour are either instinctive (genetically determined) or acquired (determined by experience). Lorenz thought that innate/inherited/genetically-determined traits can only be explained evolutionarily but not developmentally and that acquired traits can only be explained developmentally but not evolutionarily.

Unsurprisingly, embryologists and developmental biologists reacted sharply. The most important reaction was Lehrman's (1953). Lehrman stressed the often non-obvious role that experiences of various kinds play in development and pointed out – among other things – that, independently of their phylogenetic origins, all phenotypes are amenable to developmental analysis because all phenotypes are the result of developmental processes. In response to Lehrman's and other authors' critiques of the notion of innateness (Hebb 1953; Schneirla 1956), Tinbergen (1955, 1963) – who had adopted and advanced Lorenz's research program (Tinbergen 1951) – conceded that the innate/non-innate distinction was not a good tool for studying behaviour. Hinde (1966) embraced Lehrman's approach and proposed to dispense with any attempt to draw a sharp distinction between innate and non-innate behaviours. But many others refused to give up (Eibl-Eibesfeldt 1961). In his 1965 book, Lorenz conceded that all phenotypes require environmental factors in order to develop, that many behavioural phenotypes require non-obvious experiences of some kind or another for their development or for their expression, and that all traits are amenable to developmental explanation. But he claimed that these concessions are no threat to a scientifically useful innate/non-innate distinction (Marler 2004). He argued that the only way to study properly behaviour patterns and phenotypes in general is by thinking about the sources of their adaptedness. Adaptedness refers to the organism's ability to survive and reproduce in the environment in which it evolved. Lorenz insisted that only two sources of adaptedness exist: Darwinian natural selection and ontogenetic adjustment, of which learning is just one case. Innate traits are those that derive their adaptedness from the genome and, ultimately, from the process of natural selection that has moulded the genome. Non-innate traits are those that derive their adaptedness from interactions with the environment.

Lorenz formulates his view in terms of adaptive information stored in the genome by the process of natural selection and adaptive information extracted from the environment. As we have seen in a previous section, these notions are very problematic. And the discussion in this section has shown that the identification of innateness with Darwinian adaptation is unsatisfactory. A possible

reformulation of Lorenz's account is put forward by Hogan (1994, 2001). His suggestion is to replace the notion of innateness with the notion of *pre-functionality*:

(26) A trait is innate if and only if it is pre-functional.

A trait is pre-functional if it appears in development ready to serve its apparent adaptive function before it can do so or before having been tried and adjusted. The fish-catching behaviour of ospreys is not pre-functional since it doesn't achieve its function from the first moment it appears. On the contrary, it achieves its function only after a long process of adjustment and refinement due to the interaction between the osprey and its potential prey. Contrast this with a component of preening found in mallard ducklings. The component is identical to the behaviour of an adult mallard spreading the oil secreted by the preen gland above their tail onto its feathers. The difference is simply that the ducklings perform this behaviour weeks before their preen glands start to produce oil. This behaviour pattern is pre-functional.

One difficulty with this proposal is that, as Hogan himself points out, the same trait can have different functions and, thereby, it may count as pre-functional with respect to one function but not with respect to another. Another difficulty is that traits affected by perceptual or social learning can be pre-functional. For example, the mallard ducklings' preference for the maternal call depends on the pre-hatching auditory exposure to the ducklings' own vocalizations, but the trait is pre-functional in that, after hatching, it is ready to serve its function – help the ducklings recognize the species-specific call – without any need for trial and error learning.

Summary and implications for science

We have considered 26 different candidates for scientific successor to the folk concept of innateness (Table 1), and none is problem-free. Some proposals – such as innateness as (1) non-acquisition, (4) genetic determination, and (9) the impossibility of producing an alternative phenotype via environmental manipulations – are problematic because no phenotype can be classified as innate if these proposals are accepted. Other proposals – innateness as (5) genetic influence and (20) insensitivity to some range environmental variation or other – have the opposite problem: on these proposals, all phenotypes have to be classified as innate. Some proposals – (6), (7), (8), (10), (14), (15), and (17) – are unsatisfactory in that they appeal to unclear, unexplained, or controversial notions, such as 'genetic information', 'learning', 'developmental induction', and 'normal development'. Proposals (14) and (15) are unsatisfactory also because they can be applied to exclusively cognitive traits rather than all phenotypes. Definitions appealing to heritability – (13) – are to be rejected primarily because they make the innateness of a trait something that depends on the specific population where the trait is measured. Hogan's notion

Table 1. Twenty-six candidates for scientific successor to the folk concept of innateness.

A trait is innate if and only if:

- (1) It is not acquired.
 - (2) It is present at birth.
 - (3) It reliably appears during a particular stage of the life cycle.
 - (4) It is genetically determined.
 - (5) It is genetically influenced.
 - (6) It is genetically encoded.
 - (7) Its development does not involve the extraction of information from the environment.
 - (8) It is not environmentally induced.
 - (9) It is not possible to produce an alternative trait by means of environmental manipulations.
 - (10) All environmental manipulations capable of producing an alternative trait are abnormal.
 - (11) All environmental manipulations capable of producing an alternative trait are statistically abnormal.
 - (12) All environmental manipulations capable of producing an alternative trait are evolutionarily abnormal.
 - (13) It is highly heritable.
 - (14) It is not learned.
 - (15) (i) It is psychologically primitive and (ii) it results from normal development.
 - (16) It is not produced by developmental mechanisms adapted to produce different traits in response to different environmental conditions.
 - (17) (i) It is not produced by a mechanism evolved to map different environmental conditions onto different phenotypes and (ii) it results from normal development.
 - (18) (i) It is not produced by a mechanism adapted to map different environmental conditions onto different phenotypes and (ii) it does not result from the impact on development of evolutionarily abnormal environmental factors.
 - (19) It is generatively entrenched in the design of an adaptive feature.
 - (20) It is insensitive to some range of environmental variation.
 - (21) It is developmentally environmentally canalized, i.e. there exists an evolved mechanism adapted to ensure that the development of the trait is robust with respect to some environmental perturbations.
 - (22) It is post-developmentally environmentally canalized, i.e. there exists an evolved mechanism adapted to ensure that the continuance of the trait is robust with respect to some environmental perturbations.
 - (23) It is species-typical.
 - (24) It is a Darwinian adaptation.
 - (25) It is a standard Darwinian adaptation.
 - (26) It is prefunctional.
-

of pre-functionality – (26) – is unable to provide a good successor to the folk concept because the same trait may be pre-functional with respect to one adaptive function but not with respect to another. The statistical notion of abnormality is also unhelpful – as shown by the very counterintuitive results generated by proposal (11).

Some of the remaining proposals can be taken off the list by noticing that they constitute defective versions of other proposals: (2) is a defective version of (3), (16) is a defective version of (17), and (24) is a defective version of (25). We are therefore left with these eight proposals: (3), (12), (18), (19), (21), (22), (23), (25). Let us call these proposals *the finalists*. Each of the finalists identifies

innateness with a given property, respectively: (3) reliably appearing in a particular stage of the life cycle; (12) being such that environmental manipulations capable of producing an alternative trait are evolutionarily abnormal; (18) not produced by a mechanism adapted to map different environmental conditions onto different phenotypes and, at the same time, not produced by the impact of evolutionarily abnormal environmental factors; (19) generatively entrenched; (21) developmentally environmentally canalized; (22) post-developmentally environmentally canalized; (23) species-typical; (25) standard Darwinian adaptation. Let us call these properties *innateness properties* (i-properties).

In the course of the paper, we have argued that the overlap between the finalists and the folk concept is only partial. Because of this, none of the finalists can provide an entirely smooth transition from the folk view to a scientifically useful and precise definition. Can we find a definite winner among the finalists despite the fact that no finalist is perfect? Can we identify a proposal that provides the smoothest transition? If we focus on the issue of the overlap between the folk concept and the various finalists, we can certainly observe that the overlap is greater in some cases than in others. For example, the overlap between the folk view and proposal (18) seems to be greater than the overlap between the folk view and proposal (3). But in some cases, differences in overlap are extremely difficult to assess. Is the overlap between the folk view and (18) greater than the overlap between the folk view and (21)? Or is it the other way around? And even assuming that this question has a definite answer (which we doubt), is the difference between (18) and (21) enough to justify choosing one over the other as a definitive scientific definition of innateness? We think there is no principled theoretically-driven answer to questions of this kind.

Alternatively, one definition might be selected at random from the finalists' group. After all, anyone can stipulate 'innateness' to mean whatever he or she wants it to mean and all these proposals specify scientifically useful concepts. But a deeper problem concerns the relations among the finalists rather than the relations between the folk view and any of the finalists. It shouldn't be assumed that what counts as innate according to one finalist also counts as innate according to another finalist (Bateson 1985, 1991, 2000b, 2004b; Griffiths 1997, 2002; Mameli and Papineau 2005). The different proposals are non-equivalent. In fact, some of the examples we have presented during the examination of the candidates show clearly that – at least in some cases – what is classified as innate by one proposal is classified as not innate by some other proposal. This is shown in Table 2. It would be unwise, therefore, to choose, say, (18) over (21) as a scientific definition of innateness, because this could be easily taken to imply that the i-property specified by (18) is correlated with the i-property specified by (21) and with the properties specified by the other proposals in the finalists' group.

Whether the i-properties are strongly correlated or not is an empirical question, and an important one. If these correlations were known, a number of important questions could be answered:

- (a) How often and in what circumstances are species-typical traits developmentally and post-developmentally environmentally canalized?
- (b) How often and in what circumstances are species-typical traits generatively entrenched?
- (c) How often and in what circumstances are species-typical traits the result of stable developmental sequences?
- (d) How often and in what circumstances are developmental and post-developmental environmental canalization both present?
- (e) How often and in what circumstances does natural selection result in developmental or post-developmental canalization?
- (f) How often and in what circumstances does natural selection result in generative entrenchment?
- (g) How often and in what circumstances does natural selection result in stable developmental sequences?
- (h) How often and in what circumstances does natural selection result in adaptive plasticity?
- (i) How often and in what circumstances can the mechanisms responsible for adaptive plasticity result in developmental or post-developmental canalization?
- (j) How often and in what circumstances can the mechanisms responsible for adaptive plasticity result in generative entrenchment?
- (k) How often and in what circumstances can the mechanisms responsible for adaptive plasticity result in stable developmental sequences?
- (l) How often and in what circumstances are species-typical traits due to mechanisms for adaptive plasticity?
- (m) How often and in what circumstances are stable developmental sequences produced by evolved canalizing mechanisms (as opposed to, say, developmental constraints)?

A thorough investigation of such questions has been hindered by indiscriminate use of the label 'innate'. The vernacular concept of innateness seems to be a multifaceted or 'protean' concept (Bateson and Martin 1999). Because all finalists capture some aspect of the vernacular distinction between innate and non-innate traits, the use of the label 'innate' encourages researchers to think that such proposals are roughly equivalent to each other, to bundle together notions that should be distinguished from each other, and to assume that the questions just mentioned have already been fully answered, when in fact they haven't.

For example, Evolutionary Psychologists assume that if a human cognitive structure is a standard Darwinian adaptation then it is also a developmentally environmentally canalized trait and, thereby, it will develop reliably in the current environment, even though its fitness consequences may be different. This assumption is the basis for the application of what they call 'adaptive thinking'. Adaptive thinking (as applied to specifically human cognitive adaptations) works like this: (a) consider what the Pleistocene environment – the environment where the human lineage evolved – was like, (b) determine

Table 2. The i-properties are not necessarily co-occurrent.

	Grooming behaviour in rats	Smile in human infants	Reproductive behaviour of queen bees	Femaleness in turtles	PKU	Osprey's fish-snatching	Structure of normal human adult limbs	Belief that water is a liquid (in humans)	Belief that the Earth is round (in humans)
Proposal (3)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	To some extent	No
Proposal (12)	Yes	Yes	No	No	Yes	Yes	Yes	Yes	No
Proposal (18)	Yes	Yes	No	No	Yes	No	Yes	No	No
Proposal (19)	Yes	To some extent	Yes	Yes	To some extent	To some extent	Yes	Not really	No
Proposal (21)	Yes	Yes	To some extent	To some extent	No	To some extent	Yes	Not really	No
Proposal (22)	Yes	No	Yes	Yes	No	No	To some extent	Yes	No
Proposal (23)	Yes	Yes	No	No	No	Yes	Yes	Yes	No
Proposal (25)	Yes	Yes	Yes	Yes	No	Yes	Yes	Possibly	No

which cognitive structures had higher relative fitness in that environment, (c) conclude that such cognitive structures are now species-typical and develop in all normal human beings (Tooby and Cosmides 1990b, 1992; Pinker 1998, 2002; Buss 2003, etc.). Many problems are associated with adaptive thinking and the assumptions behind it. Natural selection operating on genetic variation may or may not generate developmental environmental canalization and species-typicality. Moreover, natural selection may or may not generate developmental buffering with respect solely to environmental variation similar to the environmental variation that affected fitness in a negative way when the trait in question was evolving. Consider the genes that in the Pleistocene contributed to the development of fitness-enhancing mental structures and that as a result have a high frequency in the human species. What is the reason to believe that such genes give rise today to the same mental structures to which they gave rise in the Pleistocene? The developmental environment of human cognitive structures has changed in many important and evolutionarily unpredictable ways. The assumption that cognitive adaptations evolved during the Pleistocene are developmentally canalized with respect to such changes in developmental environment should be treated with caution. One should not assume that adaptive thinking is going to work for such traits.

Labels like ‘innate’ and ‘human nature’ obscure the as yet unsolved empirical issues on which the assumptions like those used by Evolutionary Psychologist depend. In fact, it is probably because of the use of such labels that Evolutionary Psychologists have not felt the need to provide empirical evidence in support of the view – which is fundamental for their overall theory – that the property of being a standard Darwinian adaptation, the property of being strongly developmentally environmentally canalized, and the property of being species-typical are strongly correlated in the case of human cognitive structures.

The i-properties may be strongly correlated, statistically clustering as a group. They may actually *tend*, for each given trait, to be either all present or all absent, i.e. the presence of an i-property may increase the likelihood that other i-properties will be found in that trait. This tendency may be imperfect and yet real. While some of our examples seem to indicate that this is unlikely, we certainly don’t have any systematic body of evidence that shows that the i-properties don’t cluster. One thing to keep in mind is that the properties may cluster in some domains (e.g. morphological and behavioural traits in insects) but not in others (e.g. cognitive traits in humans). Consider Figure 1. The horizontal axis represents what we may call *innateness score*, that is, the number of i-properties possessed by each trait (from 0 to 9). The vertical axis represents the frequency of occurrence of traits with a given innateness score. If the real curve is flat then the i-properties don’t cluster. In contrast, if the real curve is bimodal, the i-properties do cluster, even though no strict dichotomy survives. The distribution of i-properties in different domains may give rise to different curves: the real curve may be flat in the case of cognitive human traits and it may be bimodal in the case of insect behaviour.

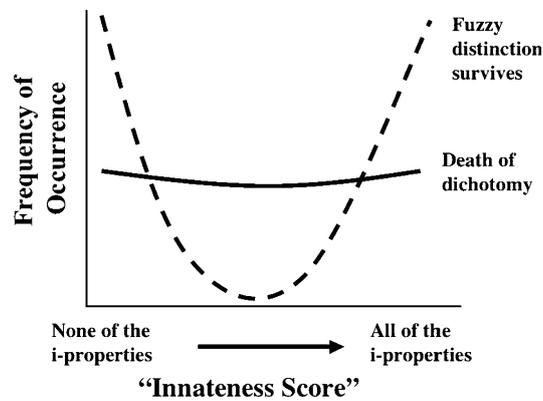


Figure 1. The horizontal axis represents the innateness score, the number of i-properties possessed by each trait. The vertical axis represents the frequency of occurrence of traits with a given innateness score. Two possible outcomes are shown. If the frequencies were bimodal as shown by the dashed line, then a fuzzy distinction between “innate” and “not innate” would survive. However, if the distribution were approximately flat, as shown by the solid line, the dichotomy should die.

Let us suppose that the i-properties are strongly correlated with each other, and that they are so not just in some particular domain but in general. What would then happen to the project of finding a legitimate place within science for the commonsense conception of innateness? If the i-properties cluster, then it is appropriate to say that the folk concept does track a real biological phenomenon: it tracks the clustering of the various i-properties, it tracks what we can call the ‘innateness syndrome’. So, if the i-properties cluster, the concept of innateness can be said to refer to traits on the right side of the bimodal curve in Figure 1, i.e. traits that have the innateness syndrome and tend to manifest a large number of the symptoms. In this case, the scientific successor of the folk concept of innateness would be a concept of the following form:

(27) *A trait is innate to the extent that it has a large number of i-properties.*

If the i-properties do cluster, this concept would be scientifically useful in that it could play a positive role in theory development and in the discovery of generalizations. Consider, by analogy, the case of biological species. Different scientific accounts of biological species exist. Some accounts define species in terms of the possibility of interbreeding and gene flow. Other accounts define species in terms of phenotypic or genetic similarity. Still other accounts define them in terms of cladistic relations or some other kind of genealogical relations (Wilson 2005). Despite the fact that these accounts are not equivalent, in many cases they give the same answer as to whether or not a particular group of organisms constitutes a biological species, especially when the accounts are restricted to multicellular sexually reproducing organisms. This means that – at least for multicellular organisms with sexual reproduction – the various properties specified by the different accounts of species cluster. Biodiversity is

clumped, and even if different ways of referring to the clumps exist and no single way captures all possible ways in which biodiversity is clumped, the clumps are a real phenomenon. The folk concept of species can thereby be seen as referring to the clumped structure of biodiversity and the concept can play a positive role in science (Brigandt 2003). If the *i*-properties really are strongly correlated, then something similar can be done with the folk concept of innateness.

This means that those who want to argue for a legitimate place for the folk concept of innateness within the sciences need to provide good evidence in favour of the thesis that the *i*-properties are strongly correlated. In the absence of such evidence, we shouldn't try to use the notion of innateness while doing science. In the absence of such evidence, the various debates that have been framed in terms of innateness are better dealt with by referring to each of the *i*-properties individually. This will help researchers to avoid making assumptions that are empirically ungrounded and it will encourage them to see what are the fundamental empirical issues that still remain to be addressed.

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