The Innate and the Acquired: Useful Clusters or a Residual Distinction From Folk Biology?

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ABSTRACT: The idea of the innate and the acquired is a part of folk-biology but is also used by biologists, psychologists and cognitive scientists in their disciplines. Are they right to do so? Innateness is often defined by appealing to the role of genes in development, to the role of Darwinian evolution in shaping developmental processes, to the non-involvement of learning during development, to developmental robustness, and to modularity. We argue that all such definitions are unsatisfactory. Some are unsatisfactory because they are based on simplistic and empirically outmoded views of development. Others are empirically defensible but are unsatisfactory because they do not capture the full breadth of the use of the term “innate” and, due to this restriction, they can easily lead to inferential mistakes. The definition of acquired behavior has been used with greater sophistication and is generally regarded as being heterogeneous. Nevertheless, in as much as the overall category has been seen in opposition to the innate, it has been an obstacle to a thorough investigation of how behavior develops. We suggest that a useful way forward is to examine whether or not the empirically well-established properties often associated with the concept of innate and the concept of acquired form theoretically useful clusters. This path leads to a much fuller appreciation of the view favored by Gilbert Gottlieb, according to which development involves the continuous interplay of the organism (and its genes) with its environment.


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INTRODUCTION

Despite many critiques of the practice of dividing up behavior into the innate and the acquired, the habit dies hard. In an earlier paper we examined the large number of different meanings of innateness and concluded that some were incoherent, having no place in science, or when their meanings were clear and empirical evidence was obtained, these characteristics did not necessarily correlate with each other (Mameli & Bateson, 2006). We argued that scientists often relied on the folk biology which cognitive scientists and anthropologists have started to study (Astuti, 2000; Atran, 1990; Atran et al., 2001; Carey & Gelman, 1991; Medin & Atran, 1999).

The vernacular usage is reflected in dictionary definitions. These typically refer to innate characters as being present at birth (inborn or congenital), part of the essence of an individual, or not learned. If “acquired” is taken as being the opposite of “innate,” folk understanding would have it that acquired characteristics are not present at birth (neither congenital nor inborn), not part of the essence of an individual, and (typically, at least in the case of cognitive and behavioral traits) learned.

Gilbert Gottlieb was a life-long opponent of the innate/acquired dichotomy and showed in his own empirical work how behavior is influenced by experience received before birth (or hatching in the case of the birds on which he worked) and that experience, on which acquired behavior depends, has many different facets to it. In this tribute to him, we argue that the way the innate/acquired distinction is currently used in biology and psychology raises problems because the various properties that biologists and psychologists take to be constitutive or indicative of innateness may not form coherent clusters.
The same applies to the category of “the acquired.” The realization that these various properties may not form coherent clusters is crucial in order to make progress in biology and cognitive science. The innate/acquired distinction may or may not have played a positive heuristic role in science in the past but, in the current state of knowledge, the distinction hinders the scientific understanding of behavioral and cognitive development. The use of the distinction generates in researchers the illusion that certain important empirical questions have already been answered, while in reality they have not.

USAGES BASED ON GENETIC ORIGINS

Many authors writing today suppose that innateness has something to do with genes (e.g., Baron-Cohen, 2003; Buss, 2003; Chomsky, 2000; Fodor, 2001; Marcus, 2003; Marler, 2004; Miller, 2000; Pinker, 1997, 2002; Plotkin, 1997; Tooby & Cosmides, 1992). In some cases, this supposition is based on imprecise ways of thinking about the role of genes in development. To argue, for instance, that a phenotype is innate if and only if genes and nothing but genes are required for its development is too simplistic. No phenotype is such that only genes are needed for its development, since an interplay between the organism and its environment is required at all stages of development. An alternative formulation that a trait is innate if and only if it is genetically influenced is equally naïve, but for the opposite reason. All phenotypes are genetically influenced because genes participate (one way or another) in the development of all phenotypes. A more satisfactory formulation would be 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 might be, and it is not trivial. Part of this difficulty is that environmental factors that are constant in a given set of conditions may nonetheless be very important in determining the precise characteristics of a phenotype. Microgravity studies, for example, suggest that the value of gravitational acceleration can make a difference with respect to musculoskeletal structure (Klein-Nulend, Bacabac, Veldhuijzen, & van Loon, 2003). If a man grew up on a planet with moon-like acceleration of gravity, he would not necessarily die, but his muscles and bones would not be the species-typical ones observed on Earth. It is likely that, for every phenotype, some environmental factor can be found such that changes in this factor produce changes in the phenotype (rather than just the death of the organism). In fact, this would be expected on the view that the environment does not 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 cellular transcription and translation are processed and used. This view was first shown to be correct by Jacob and Monod (1961) in their work on the lac operon genes. But only a small number of authors seem to have grasped the full implications of this phenomenon and the problems it creates for any gene-based understanding of the innate/non-innate distinction (e.g., Gilbert, 2001; Gottlieb, 2003; Lewontin, 2000; Meaney, 2003; Moore, 2001).

Another proposal about how to conceive of the distinctive role that genes play in the development of innate phenotypes appeals to the alleged informational properties of genes. The innate phenotype is supposedly encoded in the genes in the sense that all the information required for its development is contained in genomic sequences. This proposal distinguishes between factors that provide developmental information and factors that do not. Environmental factors are always involved (one way or another) in the development of phenotypes but, in the case of innate phenotypes, environmental factors only play a non-informational role. This is, for example, the way in which Jacob and Monod re-drew the innate/non-innate distinction in light of their discovery of environmentally sensitive genomic regions (Fox-Keller, 2000). The problems faced by these kinds of proposals are well known. The notion of genetic coding is perfectly legitimate when referring to the mapping between nucleotide sequences and proteins (or more strictly polypeptides), because in this case it is easy to identify the code-like relation. It is much more difficult to substantiate the claim that the mapping between genes and phenotypes in general is informational (Godfrey-Smith, 2000). The image of the coding of polypeptides in nucleotide sequences came from good science, but it is often overextended in references to the supposed one-for-one relation between genotype and phenotype.

Genes might be seen either as representing the phenotypes to which they causally contribute and with which they are statistically correlated (Dawkins, 1982; Sterelny & Kitcher, 1988). Or they might be seen as representing those phenotypes for the development of which they were required and increased in frequency in the course of biological evolution (Dawkins, 1996; Maynard Smith, 2000; Sterelny et al., 1996). The first view sidesteps the issue of the many non-genetic differences that cause and are correlated with phenotypic differences. The second view sidesteps the issue of the many non-genetic factors that were required for the development of phenotypes (Gray, 2001; Griffiths, 2001; Griffiths & Gray, 2001). In the absence of a good account of the general notion of genetic information, identifying innateness with the genetic coding of phenotypes is unlikely to succeed.
A related proposal is that a trait is innate if and only if its development does not involve the extraction of information from the environment. This proposal replaces the notion of genetic information with one of environmental information. The proposal provides one plausible interpretation of the notion of innateness implicit in Chomsky’s use of poverty of the stimulus arguments (Chomsky, 1959, 1975, 1980, 1986, 1987, 2000). Chomsky’s influential work is arguably the most important factor responsible for the current popularity of the innate/non-innate distinction in cognitive psychology. Thus, an understanding of the way Chomsky draws this distinction is important in order to establish whether the scientific use of the distinction is helpful or not. On Chomsky’s account, human children cannot extract information about what are the “permissible” syntactic rules (in terms of human natural languages) from their linguistic environment, and thereby syntactic knowledge must be innate (Cowie, 1999; Fodor, 2000; Khalidi, 2002). Chomsky often mentions “genetic determination” and “genetic endowment” when writing about the innateness of the language faculty (e.g., Chomsky, 2000). The assumption seems to be 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 useful to reconstruct Chomsky’s view of innateness in terms of what knowledge can and cannot be acquired by interacting with the environment.

In spite of this clarification, this proposal remains problematic for two reasons. First, just as with the notion of genetic information, no one has been able to provide a good explicit account of the notion of environmental information (Oyama, 1985). Second, even if the claim for such a thing as extractable environmental information is accepted, it is not easy to draw a sharp distinction between acquisition processes that involve informational extraction from the environment and acquisition processes that do not (Bateson, 1976). Thus, the notion of information extraction from the environment is unlikely to provide the basis for a useful scientific distinction between innate and non-innate traits. Of course, much depends on how the relations between environmental information, learning, and adaptability are conceived (Mameli & Papineau, 2006). We shall deal with some aspects of this complex issue in the following sections. We shall also see that Chomsky’s claims on innateness can be interpreted in ways that differ significantly from the interpretation just given.

We conclude this section by looking at yet another approach to making scientific sense of innateness in genetic terms. This proposal appeals to the intuitive connection between the idea that a trait is innate and the idea that the same trait is “hereditary” and suggests that a trait is innate if and only if it is highly heritable (Jacobs, 1981). In scientific parlance, heritability is a family of statistical concepts that apply to the variation for a phenotypic trait existing in a given population at a given time (Falconer & Mackay, 1996; Mameli, 2004). For purposes of present discussion, we shall focus on broad heritability, defined as the ratio of the variance of the phenotype due to genetic variation to the total variance of the phenotype in the population, since this is the notion of heritability usually associated with innateness.

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 equivalent to high broad heritability, invariant phenotypes cannot be innate. So, on this proposal, in a human population where all individuals are capable of acquiring language, being able to acquire language is not innate. The view that innateness is high broad heritability requires not only that some variation exists, but also that this variation is due almost entirely to genetic differences. So, on this proposal, in a human population where all individuals are able to acquire language except for those individuals affected by some non-genetic disease (such as brain damage generated by a viral infection), the ability to acquire language is not innate.

More generally, the problem with the proposal that innateness is equivalent to high heritability is that it makes the innateness of a trait of a particular organism dependent on the composition of the population to which that organism belongs. Changes in the population can change the heritability (and, thereby, on this view, the innateness) of the traits of an organism, despite the fact that all the phenotypic characteristics of the organism and the way such characteristics develop are the same.

Another consideration is that it is perfectly possible for a trait to be highly heritable in a population but also learned by each individual within the population, and it is perfectly possible for a trait to be highly heritable in a population but also not developmentally robust. For example, among people brought up in Sweden the ability to distinguish between different uses of the “a” vowel might be highly heritable. However those people who are not brought up in Sweden have great difficulty in detecting the different uses of the vowel. This indicates that early exposure to the sounds is important in this form of speech perception (Gponik et al., 1999; Kuhl, Williams, Lacerda, Stevens, & Lindlam, 1992; and for other examples see Bateson & Martin, 1999). If high heritability were taken as a definition of innateness, then innateness would not indicate developmental robustness or the
non-involvement of learning, which are often seen as characteristic features of innate traits (see the discussion below). In general, heritability estimates provide by themselves only population-specific indicators of sources of variation in developmental processes (Bateson & Martin, 1999; Gottlieb, 2003; Lehrman, 1970; Lewontin, 1974; Meaney, 2003).

All this of course does not mean that the discovery of strong correlations within particular populations between specific genetic differences and specific phenotypic differences is of little value for developmental biology and psychology. On the contrary, when interpreted properly such correlations may be very useful. Thus, for example, the discovery that the presence of a specific genetic mutation is correlated in a small population with a specific case of linguistic impairment might suggest that the mutation (or some nearby region of the genome) is causally involved in the impairment. But, again, the correlation by itself does not tell us whether (and in what way) that region of the genome plays a role in normal linguistic development, whether (and to what extent) learning is involved in normal or abnormal linguistic development, or whether (and to what extent) normal and abnormal linguistic development are developmentally robust.

Even if it does not (at least not by itself) provide a useful way to make scientific sense of the innate/non-innate distinction, the language that associates a genetic difference with a phenotypic difference is an important way of operationalizing the link between genes and behavior (Hinde, 1969; Jacobs, 1981; Jensen, 1961) and, apart from its utility in developmental studies, it is central in debates about biological evolution and in particular about the role of Darwinian evolution. The question that we now address is whether it is possible to justify the utility of the innate/acquired distinction on the basis of Darwinian theory.

**USAGES BASED ON EVOLUTIONARY ORIGINS**

The idea that Darwinian evolution and innateness are somehow related is a popular and powerful idea (Johnston, 2001). Attempts to relate innateness to survival and reproductive success go back to Darwin himself. He used the word “innate” as synonymous with “inherited” and he used “instinct” as synonymous with “inherited behavior” (Darwin, 1859, 1871, 1872). What does “inherited” mean in this context? The view implicit in Darwin’s writings is that some privileged material that determines the development of certain traits—including behavioral 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 was not just Darwin’s view. It was the received view in the nineteenth century (Mameli, 2005). What Darwin famously and importantly added was the proposal that inherited traits can evolve by a process of differential survival and reproduction. When the results of Mendel’s breeding experiments were rediscovered and the science of genetics started in earnest, genes were identified with those entities that are transmitted from parents to offspring at conception and are exclusively responsible for the development of the inherited traits. This account of the trans-generational stability of phenotypic form was and still is extremely popular, but is undermined by developmental studies showing the highly interactive nature of developmental processes, including the development of those traits that exhibit Mendelian inheritance (Bateson, 1983).

Attempts have been made to relate innateness to Darwinian evolution without making an appeal to genetic determinist views of trans-generational stability implicit in the twentieth century Modern Synthesis of Darwinism. The most common proposal is that a trait is to be counted as innate if and only if it is a direct product of Darwinian evolution. Symons (1992, p. 141) states: “The question whether a trait is ‘in our genes’ can be construed as a question about whether the trait is a Darwinian adaptation.” One famous version of this proposal can be found in Lorenz (1965). Lorenz, whose earlier views about instinct had been sharply and influentially criticized by Lehrman (1953), reformulated the innate/acquired distinction in terms of adaptive information stored in the genome by the process of Darwinian evolution and adaptive information extracted from the environment. He wrote:

“No biologist in his right senses will forget that the blueprint contained in the genome requires innumerable environmental factors in order to be realized in the phenogeny of structures and functions. During his individual growth, the male stickleback may need water of sufficient oxygen content, copepods for food, light, detailed pictures on his retina, and millions of other conditions in order to enable him, as an adult, to respond selectively to the red belly of a rival. Whatever wonders phenogeny may perform, however, it cannot extract from these factors information which simply is not contained in them, namely, the information that a rival is red underneath.” (Lorenz, 1965, p.37)

One thing to notice is the similarity between Lorenz’s views and Chomsky’s views about the contrast between genetic and environmental sources of information. The difference between the two authors lies mainly in the fact that Lorenz formulated his account by appealing to the
Darwin’s theory of evolution, while Chomsky did not. Both Lorenz and Chomsky saw a clear-cut distinction between experiences that produce their effects on behavior through learning and experiences that are required for normal development and, when withheld, damage the animal in some way. We shall discuss the supposed sharpness of this distinction when we consider the category of the acquired below.

A different point is that if innateness is equivalent with being a Darwinian adaptation then the by-products of Darwinian adaptations (the evolutionary spandrels of Gould & Lewontin, 1979), genetic diseases, and the phenotypic effects of new genetic mutations (whether they are adaptive or not) and some examples of epigenetic activation or silencing of genes cannot be classified as innate.

A more general issue in relation to the attempt of equating innateness with Darwinian adaptation is that whether or not a character evolves depends upon heritable variation in fitness, but the heritable variation need not be of genetic origin (Griffiths & Gray, 1994; Mameli, 2004). A Darwinian adaptation is simply a phenotype that has increased in frequency within a population because of the benefits for survival and reproductive success of this phenotype (Sober, 1984). This means that a Darwinian adaptation can be generated by phenotypic differences deriving from genetic variation, from non-genetic variation, or from both (Mameli, 2004). Moreover, as Lehrman (1970) put it, “nature selects for outcomes” (p. 28), and—in those cases where learning reoccurs reliably—the character that is most likely to increase survival and reproductive successes might or might not require learning, and this is true even in those cases in which the underlying variation is entirely genetic in origin. Thus, a Darwinian adaptation, even one derived from genetic variation, can be a learned trait, and learning is usually considered to be incompatible with innateness. One example is the social attachment that many birds and mammals have for their own kind (Bateson, 2000). All normal individuals have such an attachment, but they all acquire this attachment through their social experience, despite attachment being a Darwinian adaptation. Other examples are provided by the acquisition in birds and mammals of hunting and migratory skills both of which may be crucial for survival (Mameli & Bateson, 2006).

A different approach is one with which Lorenz himself was very much involved, namely the comparative approach to behavior and the emphasis on similarities in behavior of members of the same taxonomic group. Behavioral similarities and differences could, Lorenz (1941) argued, be used to classify species. The same approach is implicit when modern writers examine patterns of behavior that are characteristic of a species. This seems to be the view of innateness that motivates talk about “universal human nature” or “the psychic unity of humankind” (e.g., Buss, 2003; Gander, 2003; Pinker, 2002; Tooby & Cosmides, 1992). Species-typical features, it is argued, usually result from the operation of Darwinian evolution and, as such, are usually innate. The same argument is often applied to some genetically-defined sub-population, such as one of the sexes or all the individuals that possess an abnormal genetic element (e.g., Baron-Cohen, 2003). However, traits that are typical in a species can obviously be learned. For example, as already mentioned, the social attachment of many birds and mammals for their own kind is species-typical and at the same time the result of social experience.

When a trait is common in a given species (or in a genetically defined sub-population within a species), it may in some circumstances be a symptom of lack of learning. But the association between typicality and lack of learning is context-specific and should not thereby be taken for granted. The same applies to the association between species-typicality and developmental robustness. As with the heritability data, the discovery that a trait is typical within a species (or in a genetically defined sub-population) may certainly help to understand the way the trait develops. But by itself such discovery does not entail any specific hypothesis about the development of the trait.

**USAGES BASED ON DEVELOPMENTAL ROBUSTNESS**

Innateness is often associated with non-malleability (e.g., Pinker, 2002). Waddington recognized that many characteristics of organisms are buffered against perturbation during development. In his terms, they are developmentally “canalized” and he 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, 1957).

Cassidy (1979) and Ariew (1999) have suggested that the concept of canalization—in so far as it can serve as a scientifically useful way of capturing the notion of developmental robustness—can be used as an adequate scientific definition of innateness (see also Sober, 1998). Wimsatt (1999) used the notion of ‘generative entrenchment’ to make much the same point. His proposal is that a feature of an organism is generatively entrenched to the extent that the development and the functioning of other features of the organism causally depend on that feature. Canalization and generative entrenchment are related properties. If the development and proper functioning of many adaptive characteristics depend on a given feature, then the developmental processes required for the feature
are likely (for evolutionary reasons) to be robust and highly canalized.

It is interesting to note that canalization offers yet another way of interpreting Chomsky’s claims about the development of linguistic abilities. Chomsky’s arguments for the innateness of Universal Grammar amount to arguments for the existence of certain features of linguistic competence (i.e., deep generative-grammatical features) whose development in every normal human child is buffered against variation in the linguistic environment in which the child happens to grow up.

An innate phenotype is often supposed to be one produced by a process that is difficult to disrupt (developmental non-malleability), and one that is difficult to modify once it has developed (post-developmental non-malleability). However, it is important to realize that developmental and post-developmental robustness do not necessarily go together. A trait that is robust with respect to its development may not also be robust with respect to its continuance, and vice versa. Developmental malleability may be followed by non-malleability, as in many examples of alternative phenotypes found throughout the animal kingdom, including humans (Bateson et al., 2004). Conversely, 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 (Bateson & Martin, 1999).

A potentially interesting claim is that a trait is innate if and only if it is regularly expressed at a given stage of development. Etymology suggests that innate means “present at birth.” However, since colloquial usage also suggests that innate means “not learned” and prenatal learning is known to occur (DeCasper & Fifer, 1980; Gottlieb, 1997), presence at birth is an unsatisfactory criterion. More plausibly, innateness could be applied to traits that are regularly expressed at a given stage of development. For instance, migratory birds that have been hand-reared start showing migratory restlessness at the times of year when they would naturally start to move away from their breeding grounds or return to them (Gwinner, 1996). Humans start to walk at about the age of one, talk at about the age of two and express many new features of the environment. Indeed, despite the regularities in developmental timing, many human traits may be due to learning (including, e.g., basic folk-biological competence: Sterelny, 2003). This shows, more generally, that developmental stability is compatible with (and sometimes is generated by) learning. As such, develop-

mental stability—and thereby canalization—is not plausibly equated with innateness. The same applies to generative entrenchment. For example, in literate societies reading skills are generatively entrenched in the sense that many of the cognitive skills people acquire in these societies depend on the prior acquisition of reading skills, but the acquisition of these skills requires intense training.

We emphasize that, whatever way “robustness” is used, it is a relative term. Behavior may be more or less canalized by development and the use of the robustness concept as though it were a synonym for innateness does not result in a dichotomy. The insinuation of the folk biological distinction into an empirically strong body of evidence is clearly unjustified.

THE ACQUIRED: EXPERIENCE, LEARNING, AND PLASTICITY

Just as the concept of “the innate” grew out of folk biology, so did its nominal opposite, the concept of “the acquired.” However, while attributions of innateness are often used to avoid providing detailed developmental explanations, much attention has been paid to the many different facets of acquired behavior. Developmental processes involved in plasticity and the adult processes involved in learning have long been recognized as being heterogeneous and have been subject to considerable analysis. For example, W.H. Thorpe’s book “Learning and Instinct in Animals” (Thorpe, 1956) brought the insights of European ethology together with the vast corpus of work on the various mechanisms of learning obtained in American and Russian laboratories as well as those in psychology departments in many other parts of the world. Thorpe classified learning into five categories. He distinguished habituation, classical conditioning, instrumental conditioning, latent learning, and insight learning. Numerous splittings and lumpings have followed, and the cognitive revolution has greatly enriched our toolbox for understanding learning processes. The heterogeneity of learning is widely accepted in the modern literature.

Lehrman (1970) illustrated the conceptual problem facing anyone who wishes to neatly demarcate the effects of experience on general development from those that provide “information” through learning. A classification of the developmental determinants of behavior into those that have specific effects and those that have general effects is likely to be revised as fresh evidence is collected. Furthermore, it assumes a classification of behavioral units or types about which agreement may not be widespread. Finally, it cuts arbitrarily across a continuum.
None of these points render such a classification useless but they do mean that a sharp distinction between determinants with specific and general effects may create conceptual difficulties when attempts are made to unravel the processes involved in development. Certain types of evidence, such as that provided by the development of social preferences in young chicks and ducklings, do not fit easily into a framework in which experience is either “relevant” or “irrelevant” (Bateson, 1976). Therefore, when study moves from preliminary sorting of complex material to detailed and comprehensive analysis, the assumptions underlying a classification of behavior patterns in terms of origins must be recognized and, if needed, revised.

Even when considering experience that has a specific effect on behavior, it may be very difficult to know in advance when an animal is likely to generalize the effects of one kind of training to a novel situation or what might be equivalent types of experience for an animal. The potential importance of this issue, which was discussed in detail by Schneirla (1966) and Gottlieb (1973a), is easily underestimated. It is helpful to distinguish, as Gottlieb (1973b) has done, between “facilitative precursors” and “determinative precursors.” This is a distinction between factors in development that have quantitative effects and those that have qualitative effects. In the gray area between the two categories, it is probably difficult to decide whether a factor facilitates a process that has already been established or is responsible for the development of a new one. Later Gottlieb (1980) added to this classification by adding a third category of “maintenance.” In this case experience is required in order to keep a characteristic of the individual in functional order. The idea is expressed in the colloquial expression “use it or lose it” but is seen in many experimental studies of neural function such as the requirement for visual input to maintain connections from the eye to the visual cortex of mammals. Finally, one form of experience might enable other forms of experience to exert their effects on behavior and in that sense is necessary but not sufficient for the development of behavior (Bateson, 1983). These predisposing influences are seen most dramatically in those examples of developmental plasticity in which experience triggers the expression of a whole suite of characteristics that would otherwise not be seen in that individual.

Many animals and plants develop defensive structures if they are exposed to cues associated with predators early in life. The classic case is the small fresh water crustacean, *Daphnia*, that develops a defensive helmet and tail spike only if its mother is exposed to the kairomones of a predatory midge (e.g., Laforsch, Beccara, & Tollrian, 2006). The sexual behavior and secondary sexual characteristics of an adult male gelada baboon can develop along two or distinctly different tracks. Many males will defend and breed with a harem of females. After a relatively brief but active reproductive life, he is displaced by another male and never breeds again. To position himself so that he can acquire and defend a harem, the male must grow rapidly at puberty. He develops the distinctive golden mane of a male in his prime and becomes almost twice the size of the females (Dunbar, 1985). However, when many such males are present in the social group, an adolescent male may adopt a distinctly different morphology and style. He does not develop a mane or undergo a growth spurt. Instead, he remains similar in appearance and size to the females. These small males hang around the big males’ harems, sneakily mating with a female when the harem-holder is not paying attention. Since the small, sneaky male never has to fight for females, he is likely to have a longer, if less intense, reproductive life. If he lasts long enough he may even do better in terms of siring offspring than a male who pursues the alternative route of growing large and holding a harem. It is believed that these two different modes of breeding morphology and behavior represent two distinctly different developmental routes, and each male baboon must commit himself to one or other of them before puberty. Once the male’s adult phenotype has been determined, he will be predisposed to learn particular skills that enable him to breed most effectively.

In the cases of developmental plasticity that abound across the animal kingdom, the individual animal starts its life with the capacity to develop in a number of distinctly different ways. Like a jukebox, the individual has the potential to play a number of different developmental tunes. But during the course of its life it plays only one tune. The particular developmental tune it does play is triggered by a feature of the environment in which the individual is growing up—whether it is the odour of its predators, the available quality of food, or the presence of other males. Furthermore, the particular tune emanating from the developmental jukebox is adapted to the conditions in which it is played (Bateson, 1987; Bateson & Martin, 1999). The juke-box analogy has its drawbacks because it implies the tune is pre-formed somehow (Oyama, Griffiths, & Gray, 2001); like everything else, the expressed phenotype has to develop. The analogy with “programming” (e.g., Horton & Stetson, 1990; Whimbey & Denenberg, 1967) is even worse because it implies that the environmental trigger contains some of the instructions for the phenotype that will be expressed. Perhaps, the best general term for the processes is an old one used in development biology for many years, namely “induction.”

The implication of many of the examples of developmental plasticity is that environmental induction provides a forecast about the conditions of the world that the
individual will subsequently inhabit. In mammals the best route for such a forecast may be via the mother. Vole pups born in the autumn have much thicker coats than those born in spring; the cue to produce a thicker coat is provided by the mother before birth (Lee & Zucker, 1988). The value of preparing in this way for colder weather is obvious. Maternal forecasting by induction is now thought to be very important in human biology and has important implications for adult health when, because of large changes in economic conditions, the maternal forecast is wrong (Bateson et al., 2004).

Apart from the generally adaptive consequences of developmental plasticity, the experience of the young individual may be such that the normal course of development is disrupted (Gluckman et al., 2005). The individual may not die and, as West-Eberhard (2003) has emphasized, it may be able to accommodate to its disabilities. Here is yet another form of plasticity, emphasizing once again how heterogeneous is the category of “the acquired.”

Another matter to keep in mind is that the term “experience” is extremely general and it covers both cases in which the environment impacts on the organism through some mechanism that might be classified as psychological—such as some kind of perceptual or learning process, as in the case of the gelada baboons—and cases in which the environment impacts on the organisms through mechanisms that are merely physiological and do not require any kind of psychological description—as in the case of fur-thickness determination in voles. Between the paradigmatic cases of plasticity through psychological mechanisms and the paradigmatic cases of plasticity without psychological mechanisms, a whole set of cases of plasticity exist for which it is not clear whether they should be seen as being brought about by psychological mechanisms or not. The processes by which organism/environment interactions produce interesting developmental outcomes are many and varied and difficult to categorize in terms of a learning/not-learning dichotomy.

Samuels (2004) believes that the connection between “innate” and “not learned” is fundamental but that defining “innate” as “not learned” is too simplistic. He suggests that a trait is innate if and only if (i) the development of the trait is not explainable in psychological (as opposed to neurological, chemical, or physical) terms and (ii) the trait results from normal development. Samuels intends this account to capture—among other things—Chomsky’s views on innateness. The account tries to cash out the Chomskian “does not require the extraction of information from the environment” in terms of the apparently less problematic “does not require psychological processes (and thereby cannot be explained in purely psychological terms).”

A first difficulty with this account is one that Samuels himself recognizes, namely that no explanation of what counts as normal development is given. Defining innateness in terms of normal development without a clear definition of normal development may turn out to be the trading of one inchoate notion for another. A second difficulty is that the distinction between psychological and non-psychological explanations is, as we have just suggested, 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. In contrast, many behavioral biologists believe that triggering involved in developmental plasticity is one of the many processes of psychobiological development and as such it counts as a psychological process. But it is hard to see how this debate (framed in this way) could amount to anything more than a terminological disagreement. A third difficulty with Samuels’ proposal is that it relates only to cognitive traits. Any other form of variable phenotype dependent on developmental plasticity (e.g., the case of sex in turtles) would be lumped in together with innate traits.

This difficulty could at first sight be avoided by replacing “learning” with a more general notion. Learning mechanisms are only a subset of a larger set of mechanisms evolved to map different environmental circumstances onto different phenotypes, be they morphological, physiological, or behavioral phenotypes. Thus, one proposal would be to regard a trait as acquired if and only if it is produced by developmental mechanisms that are adapted to produce different traits in response to different environments. On this basis, however, the limbs that develop in thalidomide-bathed wombs and acquired sociopathy due to brain injury (Damasio, 1994) would be classified as not acquired. 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 not acquired, an appeal has to be made to normal development. These traits can be discounted by saying that they are “abnormal.” But once again this proposal is incomplete if no account of normal development is given. The next step then would be to provide a theory of what counts as normal development and what does not. One view is that normal development has to be defined in terms of what is statistically normal in a given species at a given time. Another view is that normal development has to be defined in terms of what is evolutionarily normal for a given species. We have argued elsewhere (Mameli and Bateson, 2006; Mameli and Papineau, 2006) that neither of these two views provides a notion of
developmental normality that can be used in a scientifically unproblematic account of innate/acquired dichotomy.

MODULARITY

Gilbert Gottlieb was committed to understanding the processes of development. Our critique of the folk biological biases that still permeate so much of the thinking about development has a similar purpose. The processes involved in behavioral development may look forbiddingly complicated on the surface and one approach to development has been to suggest that everything interacts with everything else—which verges on the obscurantist. A challenge to such thinking is the evidence for the segregation of characteristics in closely related individuals. How is it that characteristics such as a big nose or a retiring disposition skip a generation? How is it that siblings are so different from each other at birth? How is rapid artificial selection for behavioral characteristics such as tameness possible? None of the evidence that leads to such questions implies any simple correspondence between an inherited factor and the development of a phenotypic characteristic. But the evidence does suggest that fractionation and “independent inheritance” of some of the factors necessary for development happens all the time.

This brings us to the issue of modularity. It is a much discussed topic in cognitive psychology and developmental biology (e.g., Barkow et al., 1992; Callebaut & Rasskin-Gutman, 2005; Fodor, 1983, 2000; Hirschfeld & Gelman, 1994; Pinker, 1994, 1997; Samuels, 2000, 2005; Schlosser & Wagner, 2002; Sperber, 1996, 2001, 2005). A system is modular if it is composed of quasi-independent parts each of which is tightly integrated within itself but operates with a certain degree of independence from the other parts. The quasi-independent parts are the modules, and the greater is their independence from each other, the more modular is the system. Modular systems can be hierarchically organized. This happens when a module is itself composed of subordinate modules (Schlosser & Wagner, 2002; Simon, 1962).

In cognitive science, modularity as quasi-independence is usually cached out in terms of informational encapsulation and domain specificity. A useful account of these two notions is given by Sperber. According to him, a cognitive device is domain-specific if its function is to process only inputs belonging to some delimited empirical domain, and a cognitive device is informationally encapsulated only if it is one that uses a limited database to process its inputs (e.g., Sperber, 2005). Domain specificity is quasi-independence in inputs, while encapsulation is quasi-independence in proprietary databases. These two kinds of quasi-independence can (and perhaps often do) go together. But this is not a necessity. As Sperber himself points out, working memory can be seen as a domain-general device which processes inputs whatever their contents, but is encapsulated in that some information is present in the brain that working memory cannot access when processing its inputs. On Sperber’s account, a cognitive device deserves to be classified as a cognitive module only if it is both domain-specific and informationally encapsulated. Sperber (1994) introduced the phrase “massive modularity” to refer to the view that the human mind contains many cognitive devices almost all of which are modules. In that paper and in subsequent writings, he presented many interesting (but far from conclusive) arguments in favor of this view. Sperber is careful in pointing out that it makes no sense to identify modularity with genetic influence, canalization, or lack of learning:

“Even though the existence and many characteristics of mental modules are explained by biological evolution, this does not imply that modules are simply phenotypic expressions of genes, or that the development of each and every module is strongly canalized. On the contrary, it would be in the nature of modules to vastly differ from one another in this as in other respects. For some of the problems cognitive modules handle, “pre-wiring” may be appropriate. For other problems, an effective modular solution may involve adding data to the proprietary database of an otherwise predetermined module. In other cases still, the development of a module may involve drawing on information picked up from the environment not just to enrich the database but also to shape procedures.” (Sperber, 2005)

Arguments that cognitive modules need not and often do not have the properties usually associated with innateness have often been presented by commentators who are skeptical about the usefulness of the notion of innateness in cognitive science (e.g. Elman et al., 1996; Johnson, 1997; Karmiloff-Smith, 1992; Sterelny, 2003). We agree with Sperber that cognitive modules need not be developmentally robust and that their development may involve learning. Domain-specificity and informational encapsulation are architectural properties of cognitive systems. Such architectural properties may result from many different kinds of developmental processes, including some which involve learning or which are not developmentally robust.

The same conclusion can also be reached from a different direction. Consider for example Fodor’s theory of cognitive architecture (Fodor, 1981, 1983, 2000). Fodor maintains that the cognitive devices responsible for belief-fixation and practical reasoning are not domain-specific or encapsulated. However, he also maintains that many components of such devices (many concepts, many
sections of the database, etc.) are not learned and are developmentally robust.

Domain specificity and informational encapsulation are not developmental properties. But what about ontogenetic modularity (which obviously is a developmental property)? A phenotypic trait is developmentally modular if the processes responsible for its development are quasi-independent—in the sense specified above—from the processes responsible for the development of other traits in the same organism. Developmental modularity is now being intensely studied by evolutionary and developmental biologists because, expanding upon a suggestion by Lewontin (1978), some authors have argued that developmental modularity is a very important condition for rapid and efficient evolvability (e.g., Wagner & Altenberg, 1996). In particular, one important focus of this research has been the relation between developmental modularity and what might be called “genetic modularity,” the degree to which different sections of the genome are quasi-independent in relation to their effects on developmental processes.

Some authors suggest that many cognitive competences are acquired by learning through the operation of domain-specific learning mechanisms (e.g., Gallistel, 1999). The domain specificity of the learning mechanisms makes the learning process responsible for the acquisition of these competences quasi-independent from other acquisition processes. Such phenomena might explain the reliability of the learning processes involved in the development of evolutionarily important competences (e.g., Pinker, 1997; Sterelny, 2003). In cases of this kind, the resulting competence is both developmentally modular and learned. These aspects of modern thought do not spring out of either folk psychology or folk biology and are likely to be highly productive in uncovering how behavior develops.

DO CLUSTERS EXIST?

We have considered many different properties of phenotypes that biologists and cognitive scientists take to be constitutive or strongly indicative of innateness and of its opposite. Some of the properties—such as those that appeal to unclear or confused notions of developmental information, normal development, or genetic influence—not only cannot provide the basis for an explicit definition of innateness, but are also of little utility from a theoretical point of view. In contrast, some of the other properties we have considered can and do play a very important role in the biological and cognitive sciences. Let us call “i-properties” (where “i” stands for “innate”) the scientifically useful properties that biologists and cognitive scientists tend to associate with innateness. The list of i-properties includes properties such as: being a Darwinian adaptation, not due to learning or more generally to developmental plasticity adapted to generate different phenotypes in different environments, being developmentally robust (generatively entrenched or canalized), being species-typical (or typical within a specific sub-population), being developmentally modular, etc. Let us call “a-properties” (where “a” stands for “acquired”) the properties that are the opposite of the various i-properties.

Does the impossibility to identify innateness with all of the scientifically useful properties that we have called “i-properties” mean that the concept of innateness is scientifically useless? Not necessarily. Let us suppose, for example, that the i-properties are strongly correlated with each other and that, thereby, (in general) when a phenotypic trait has one i-property it also tends to have most (even though not necessarily all) of the other i-properties. In this scenario—let us call it Scenario 1—the i-properties constitute a coherent cluster, that is, a set of properties that have a strong tendency to co-occur. In this scenario that a-properties also constitute a coherent cluster. Coherent clusters are useful for explanatory, classificatory, and inferential purposes (and some have argued that they are a form of natural kind, cf. Boyd, 1991). If the i-properties and a-properties form separate coherent clusters, then it is possible to identify the innate with one cluster and the acquired with the other cluster. In this case, the concepts of the innate and the acquired would be “cluster” concepts and would be important tools for making progress in biology and psychology. But the i-properties need not be strongly correlated with each other, nor need the a-properties—let us call this Scenario 2. In this scenario, the i-properties and a-properties do not form coherent clusters and the presence of an i-property in a trait provides only poor (and highly context-specific) information about the presence of other i-properties in the same trait. The same would be true for a-properties. In this case, given that the innate and the acquired can be identified neither with a scientifically useful property nor with a coherent cluster of scientifically useful properties, the concept of the innate and the concept of the acquired have no scientific utility.

If reality resembles Scenario 1, the concepts of innateness and its opposite have a legitimate role in science. In contrast, if reality resembles Scenario 2, innateness and its opposite do not have a legitimate role in science. Which of the two scenarios is the real one? Do the i-properties and a-properties form coherent clusters or not? In what way and to what extent are i-properties related to each other? These are difficult empirical questions. And they are empirical questions for which, by and large, no good answers have been found yet. Unfortunately, the use of the distinction between the innate and the acquired generates in researchers the
illusion that these empirical questions have already been properly answered, while in fact they have not. So, for example, some Evolutionary Psychologists assume that if a human cognitive structure is a Darwinian adaptation then it is also developmentally robust and, thereby, it develops reliably in the current environment, even though its fitness consequences in the current environment may be different from those the trait had in the environment in which it was advantageous. 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 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 (Buss, 2003; Pinker, 1997; Tooby and Cosmides, 1992; etc.). Many problems are associated with adaptive thinking and the assumptions behind it. Darwinian evolution operating on genetic variation may or may not generate developmental robustness and species-typicality. Moreover, Darwinian evolution 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, therefore, be treated with great caution.

More generally, many of the examples we have presented in the previous sections show that in many cases the presence of a given i-property does not guarantee that of other i-properties. Obviously, these are just isolated examples and, as such, they do not prove that the i-properties do not form a coherent cluster. But the examples we have discussed—and similar ones—show that the issue about whether the i-properties form a coherent cluster or not is an important and difficult one. The same is true for the a-properties. The use of the innate/non-innate distinction has hindered the ability of researchers to see the importance and the difficulty of this issue and, thereby, hinders progress in the biological and cognitive sciences. The very fact that, as we have seen, Chomsky’s views on innateness can be interpreted in many different and incompatible ways should make people alert to the dangers involved in using the innate/non-innate distinction.

Many important questions need to be asked about the various facets of the innateness concept. Which environmental conditions determine the evolution of which i-properties? How is developmental plasticity related to the various i-properties? What is the relation between developmental robustness and the non-involvement of learning? What is the relation between plasticity and robustness? In which cases are developmental and post-development robustness associated? In what circumstances are learning processes developmentally modular? In what circumstances do such processes generate entrenchment? When does learning (or developmental robustness) result in species-typicality? What exactly is the relation between entrenchment and robustness? Or between entrenchment and modularity? And so on. Only when satisfactory answers to questions like these are found it will be possible to say whether the i-properties and the a-properties form coherent clusters, and only then it will be possible to say whether the innate/non-innate distinction has any scientific utility.

For our part, we are sceptical whether a useful dichotomy between phenotypes that are innate and those that are not innate will be found. This scepticism is not based on the assumption that all behavioral and cognitive systems develop in the same way. Our point is simply that we do not think that there are just two different kinds of developmental processes. The triggering mechanisms involved in producing alternative phenotypes are unlikely to be similar to the many processes of learning which, in their turn, probably differ radically from each other. Furthermore, the processes involved in the development of some neurobiological systems are probably quite different from those that require plasticity and may be more akin to the development of an organ such as a kidney. Yet the outcome of development will often have involved interplay between these systems. This conclusion does not denigrate the value of identifying features that are important in development, such as robustness, nor attempts to discover how they have evolved. It merely asserts that features may be co-opted for use in different ways and in different combinations.

Over-used metaphors from engineering such as “hard-wiring” and “pre-programming” applied globally to the outcome of development fail to capture the character of the processes and once again invite the mistaken view that they can be contrasted with their opposites. We believe that a thorough investigation of developmental processes has been hindered by indiscriminate use of the labels “innate” and “acquired.” Their use encourages researchers to bundle together notions that should be distinguished from each other and to assume that important questions
Innate and Acquired

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REFERENCES


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