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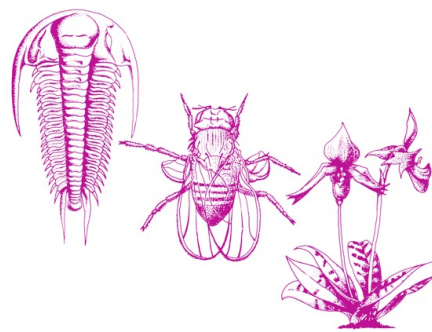
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Murder on the development express: who killed nature/nurture?

Evelyn Fox Keller: The mirage of a space between nature and nurture. Duke University Press, 2010

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Abstract Keller explains the persistence of the nature/nurture debate by a chronic ambiguity in language derived from classical and behavioral genetics. She suggests that the more precise vocabulary of modern molecular genetics may be used to rephrase the underlying questions and hence provide a way out of this controversy. I show that her proposal fits into a long tradition in which other authors have wrestled with the same problem and come to similar conclusions.

Keywords Nature/nurture controversy · Gene concept · Developmental niche · Interactionism · Developmental system · Behavior genetics · Developmental psychobiology

Introduction

In ‘Murder on the Orient Express’ Hercule Poirot confronts a baffling case: each clue Poirot is able to uncover points to a different suspect. The solution, famously, is that all the passengers have contributed to the murder: all the suspects are guilty. Evelyn Fox Keller’s book presents us with a similarly baffling case: if it were Keller alone who gave the fatal blow to the nature-nurture controversy, why can we, after scrutinizing the available evidence, find so many clues that point to other suspects?

Keller’s stated aim seems less “to crush” (p. 1) the debate than to locate the source for its persistence and our trouble with it; although that distinction becomes somewhat blurred in her concluding chapter. She concerns herself with “the particular form in which we today tend to frame discussions of the roles that nature and nurture play in development... with the tendency to think of nature and nurture

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as separable and hence as comparable, as forces to which relative strength can be assigned, as suggesting opposability and, accordingly, as inviting debate ... I am interested in the ways in which that framing is sustained by a particular set of scientific discourses” (p. 15f). In Chapter One, Keller locates the origin of nature/nurture with Galton and the new conception of heredity which developed in his day as “the transmission of something biological”, the hard inheritance of “fixed entities” rather than “malleable (or soft) particles” (p. 21f). One source of confusion in the nature/nurture debate, according to Keller, lies in the problematic language of (classical) genetics, with its multiply ambiguous central concept of the gene: “We might say, then, that a certain confounding of traits and trait differences was built into the science of genetics from the very beginning” (p. 43). Griffiths and Tabery (2008) have argued that the disagreement between behavior geneticists and their critics originated in part in their miscommunication about their different underlying concepts of gene action, one being the statistical difference maker, the other a hypothetical developmental gene. The second scientific usage causing, in her eyes, considerable confusion is the technical meaning of ‘heritability’, so easily confused with its vernacular meaning (p. 55ff). The former’s relationship to the innate/acquired distinction remains highly controversial. This point is not, nor does the author claim it to be, original, but she provides a valuable analysis of this linguistic practice in Chapter three.

There is of course no general agreement if the ‘crime’ in question should be regarded as a (repeatedly re-opened) ‘cold case’, or a case that has been solved a long time ago. Keller herself points out:

One of the most striking features of the nature-nurture debate is the frequency with which it leads to two apparently contradictory results: the claim that the debate has finally been resolved (...), and the debate’s refusal to die. As with the Lernian Hydra, each beheading seems to spur the growth of new heads. (p. 1)

Her sentiment is reminiscent of Susan Oyama’s often-cited passage:

“But wait”, the exasperated reader cries, “everyone nowadays knows that development is a matter of interaction. You’re beating a dead horse.” I reply, “I would like nothing better than to stop beating him, but every time I think I am free of him he kicks me and does rude things to the intellectual and political environment. He seems to be a phantom horse with a thousand incarnations, and he gets more and more subtle each time around. ... What we need here, to switch metaphors in midstream, is the stake-in-the-heart move, and the heart is the notion that some influences are more equal than others ...”. (Oyama 1985, pp. 26–27)

Keller goes on to ask what the nature/nurture debate is about. Of the questions formulated under its guise only *some* “express legitimate and meaningful concerns that can be addressed scientifically”. Others are either meaningless or unanswerable. For most of the book the reader is left with the impression that there is indeed only *one* question that makes sense in the context of the nature-nurture controversy. This question, which is usually asked by behavioral geneticists, “is statistical. It

asks about the percentage of variation in, say, IQ, that arises from inherited differences among individuals (so some parents pass on smart genes to their kids?) versus the percentage that arises from environmental differences (do some parents pass on books to their children?). This is the right question to ask, while the wrong question to ask is “mechanistic. It asks about how genes behave within individuals ... The fact that genes respond to experience is ... the wrong kind of fact to settle the nature-nurture debate” (Orr 2003, cited in Keller p. 3).

Keller accuses those who address nature/nurture without a focus on her ‘single, well-defined and meaningful question’ of “confounding statistics and mechanisms” (p. 3). Perhaps that is the reason why there are few references in Kellers book to the many other authors who have undertaken similar projects. Keller does give examples of the easy slippage from trait to trait difference and from population to individuals by philosophers of biology like Elliot Sober, Kenneth Waters, and Neven Sesardic (p. 36ff), and by behavior geneticists (p. 65ff). But there is little discussion of the many previous authors who have debated the virtues of causal analysis versus statistical correlations, or attempted to reconceptualise the nature/nurture debate (for some citations see below). Amongst the points they have raised are points that have been taken up more or less explicitly by the author as well: (a) answers in terms of heritability would defy any meaningful or unambiguous interpretation; (b) “the interdependence of genes and environment in development necessarily undermines any measurement involved in the effort of partition the statistical variance” (p. 34); (c) behavior genetics’ attempts of formulating meaningful questions and providing scientific answers rests on unquestioned assumptions about the nature of ‘nature’ and ‘nurture’, gene and environment, and their interaction; and d) it is these assumptions that make the question meaningful by cementing the dichotomy in the first place.

The following sections will introduce a list of ‘suspects’ and their motives for harming the victim, who should receive partial responsibility in the unlikely event that the body of the victim is ever found.

Changing the debate and the question

The nature/nurture debate assumes nature and nurture to be separate, but developmentally interactive causes, embodied by genes and environment, respectively. Questions about their relative contribution are questions about the causes of phenotypic *differences* rather than phenotypic *traits*. Answers concern *how much*, rather than *how*, each cause contributed to the total phenotypic variation of the trait in a population. Behavior genetics inherited this reformulation of Galton’s traditional ‘how much’ question from R. A. Fisher, one of the founders of quantitative genetics. However, presenting the question of trait differences in a population as the only feasible one depends, first, on accepting that this is the only question we can answer scientifically. It depends, second, on accepting the distinction between nature and nurture, and their respective quantification through a ‘how much’ question as meaningful or important.

With respect to the first point, this question was indeed the only one answerable through the techniques of classical Mendelian genetics, with its conception of genetic factors—phenotypic difference makers—as the units of inheritance. This classical gene was a hypothetical unit of function, inferred from observed changes between phenotypes. Keller goes to some length in pointing out that the methodology of classical genetics only gave geneticists access to phenotypic differences, which they correlated with underlying hypothetical factors, the alleles of the wild-type gene associated with the trait in question (e.g. p. 43). Classical genetics couldn't say anything more about the causes of trait differences (red versus yellow flowers), let alone the origin of traits (flower color): “[The] theory of the gene is justified without attempting to explain the nature of the causal processes that connect the gene and the characters” (Morgan 1926, p. 26, cited in (Amundson 2005, p. 150).

With the advent of molecular genetics and molecular developmental biology, however, it became feasible to answer a different question, namely *how*, rather than merely how much, genes and environment causally contribute to the phenotype of an organism. But as Keller points out, both laypeople and scientists are often interested in explaining the difference between two outcomes. This, however, would not exclude seeking a mechanistic rather than a statistical explanation. Individual differences are produced by the operation of mechanisms (“difference mechanisms”) just as much as a singular phenotypic outcome (Tabery 2009).

In one well-studied example of a difference mechanism, epigenetics has been shown to mediate the transgenerational effect of maternal care behavior in rats. Natural variation in maternal care, elicited by experiences of the mother, influences the development of stress responses and of exploratory and maternal care behavior in the offspring. Low maternal licking and grooming behavior, a reaction to adverse environmental conditions, results in a cascade of neuro-endocrine and epigenetic mechanisms. One pertinent effect is the permanent down-regulation in the expression of the glucocorticoid receptor gene in the pup's hippocampus via the methylation of its promoters. This in turn leads to high stress-reactivity in the pup. Hence stressed, alert mothers produce stressed, alert daughters who develop into stressed mothers. Conversely, relaxed mothers that show a high level of licking and grooming produce relaxed offspring that turn into high licking mothers. In other words, maternal behavior establishes stable patterns of gene expression in the pups that affect brain development and the behavior of the next generation of mother rats. The behavior of these second-generation mothers reestablishes the patterns of methylation in their pups (Meaney 2001; Weaver et al. 2004).

As well as questioning whether mechanistic explanations are really irrelevant to settling the nature/nurture debate, we may, secondly, question whether the debate needs ‘settling’ in the first place. With respect to the second point, ‘Settling the nature-nurture debate’ suggests that the debate has at its core a valid question. Laying the debate to rest, however, could also mean revealing the question as ill-formulated, one with no unambiguous or easily interpretable answer, or one not based on a meaningful distinction. While for eugenicists like Galton or Fisher that question may indeed have been deeply meaningful, this is much less clear for scientists without such a political inclination. The authors who Keller never cites but

likely regards as having asked the 'wrong question' never claimed to 'settle' the nature/nurture debate, at least not in her preferred sense of assessing relative contribution. On the contrary, most were interested in the nature of the interaction between genes, organism and environment that undermines the opposition between nature and nurture. However, at least in the first chapter of her book Keller seems to adopt a well-known move in behavior genetics which James Tabery has called the 'defense-by-distinction'. The standard response of behavioral geneticists to their critics has been to accuse them of failing to distinguish between causes of individual development and causes of differences in a population (Tabery 2007).

One of the harshest critics of behavior genetics was the late developmental psychobiologist Gilbert Gottlieb. It would be quite misguided to accuse Gottlieb of conflating questions at the statistical population level with causal-mechanistic questions leveled at individual organisms. Hardly anyone was clearer about the distinction, and more adamant about the inadequacy of the former versus the latter in understanding the causes of behavioral development (Gottlieb 1995; Turkheimer et al. 1995; Turkheimer 2000; Griffiths and Tabery 2008). According to Gottlieb it was the behavior geneticists who engaged in conflation and slippage:

The population view of behavioral genetics ... is based on the erroneous assumption that a quantitative analysis of the genetic and environmental contributions to individual differences sheds light on the developmental process of individuals ... While such a finding [that the heritability of personality traits increases over the lifespan] cannot validly be applied to individual development, most people take this conclusion to mean that, over the course of individual development, the genetic influence on behavioral and psychological outcomes increases with age, in comparison to environmental influences. (Gottlieb 2003, 338)

Interestingly, not even all behavior geneticists agree with Orr or Keller on the one 'single, well-defined and meaningful question'. Turkheimer, one of Gottlieb's main adversaries, admits that the comparison with causal-mechanistic studies in animal behavior genetics shows statistical behavior genetics in an unfavorable light. Behaviour geneticists did not eschew causal analysis from choice, they were forced to do so by the ethical restrictions on investigating human subjects (Turkheimer 2000; see also Griffiths and Tabery 2008, 334).

Beyond interactionism and dichotomous thinking

Everybody knows that all traits are essentially dependent on both genes and environment. Keller goes so far as to claim that we would have known that even without any scientific insight from genetics, genomics or epigenetics. This idea has indeed been around for as long as the gene itself. It was at the heart of Wilhelm Johannsen's original 'genotype conception of heredity' (Johannsen 1909). Lancelot Hogben, J. B. S. Haldane and others reiterated the point in response to Fisher's invention of the analysis of variance (Tabery 2008), and Conrad Waddington spared no effort to place the 'epigenotype' (Waddington 1942) and the 'developmental

system' (Waddington 1952) at the heart of biology. But these authors could say little about the underlying mechanisms of interaction. Their efforts certainly did not prevent equally influential biologists drawing a sharp distinction between innate and acquired features of the phenotype (Lorenz 1957, (1937); Tinbergen 1951). Even today Jason Scott Robert has concluded from an analysis of the prevalence of genetic determinism among molecular biologists that the idea is more than just a straw man (Robert 2001). So why does Keller claim that input from the relatively new field of molecular epigenetics would, instead of helping the debate, rather alleviate the conceptual muddle the debate has found itself? Keller herself admits at one point that the truism of interaction does little to stop laymen and scientific authors alike regarding nature and nurture as "clearly distinguishable causes of development" (p. 30).

Therefore I believe that the insights of molecular genetics, postgenomics and (environmental) epigenetics have filled, and continue to fill, a very important knowledge gap by elucidating the *exact mechanism* by which environmental factors are involved in the regulation of gene expression. Some authors eager to denounce the distinction between nature and nurture call the 'environmental programming' of behavior through DNA methylation "life at the interface between a dynamic environment and a fixed genome" (Meaney and Szyf 2005). For some people who have been involved in the nature/nurture debate for a long time, notably Susan Oyama, one of the biggest challenges was to go beyond an interactionist consensus. To her a superficially 'democratic' (Kitcher 2001) interactionism can cover an underlying belief in the inequality of developmental resources. The concept of a 'developmental system', comprised of the organism in its developmental environment, was designed to promote a more genuine 'causal parity' between genetic and non-genetic developmental resources that play analogous roles (Oyama 1985, 2000, 2001). Gilbert Gottlieb's term of a 'developmental manifold' was introduced for a similar reason some 40 years ago (e.g. Gottlieb 2003). Meredith West and Andrew King, influenced by Daniel Lehrman and T. C. Schneirla's fight against the simplistic instinctive/learned behavior distinction (Lehrman 1970; Schneirla 1957), followed up by "settling nature and nurture into an ontogenetic niche" (West and King 1987, see below). These ideas are all ways to emphasise that non-genetic developmental resources, often lumped together under 'the environment', are not merely permissive background factors, but can be instructive causes of development (Stotz 2006b).

Another 'suspect' who early on criticised the term 'interaction' is Richard Lewontin. He has promoted an active conception of the organism: neither genes nor the environment, but the organism makes the trait. More importantly he argued vehemently against the idea that the organism has to adapt to a preformed environment that poses problems for the organism. In its place he suggested that organisms actively construct their environments, which in turn influence the evolution of organisms (Lewontin 1982, 2000).

Questioning the innate-acquired distinction

Keller is concerned with the 'mirage of space' that somehow developed between the terms nature and nurture, and how this mirage is maintained and reinforced. She

repeatedly admits that it is not that clear what exactly is meant by 'nature' and 'nurture'. Answers such as inborn/innate/inherited versus acquired/learned, or gene versus environment, are in themselves ambiguous, given how hard it is to pin down concepts such as genetic causation (Gannett 1999; Smith 2000) or innateness (Linguist et al. 2011; Mameli and Bateson 2006).

In light of this it is perplexing when Keller states that: "Examples of epigenetic inheritance ... are of immense importance to development; they radically change our understanding of inheritance; and they can also have a profound effect on evolution. The important point here, however, is that in themselves, such effects have little if anything to do with the nature-nurture debate as formulated in the examples I cite" (p. 5). In Keller's own analysis, the origin of the separation between nature and nurture lied in the reconceptualisation of heredity in terms of internal, biological entities, a shift from soft, or plastic, to hard, or fixed, inheritance. So one might assume that another reconceptualisation of inheritance to include extended inheritance systems should matter a great deal. Particularly if these inheritance systems include the inheritance of environmentally induced and developmentally regulated variation, the very 'soft inheritance' whose abandonment was, according to Keller, the reason why nature and nurture became opposites. The whole edifice of the distinction between malleable and unchangeable may come down, and with it, if Keller is to be believed, the rationale for quantifying the relative contributions of nature and nurture to development (p. 74f).

This of course assumes that resolving the nature/nurture debate demands more than a final assignment of relative importance to either factor. The resolution will not be something like this:

The nature-nurture debate is over. The bottom line is that everything is heritable, an outcome that has taken all sides of the nature nurture debate by surprise. (Turkheimer 2000, 160)

Instead, the resolution may look something like this:

Trying to resolve the dichotomy of nature and nurture by putting more weight on one or the other leaves the nature of both "nature" and "nurture" untouched. Instead, we must recast these terms, so that they are no longer seen as candidates for combination or compromise. The reconceptualization of development and evolution that is necessary for this recasting is what the developmental systems approach is about. (Oyama 2002, 163)

Many aspects of the environment and its experience by a developing organism are there by design: "genes inherit a rich and supportive environment, a fact few dispute but few discuss with any urgency" (West and King 1987, 552). West and King define the ontogenetic niche as the set of ecological and social circumstances inherited by organisms (West and King 1987, 550). The developing organism can expect to encounter this niche in development as reliably as it does its genome: "It's the dependability of the niche in delivering certain resources to the young that makes it a legacy" (West, King, and Arberg 1988, 46). I would add epigenetic, epistemic, cultural, and symbolic legacies to this list and would point to Jablonka and Lamb's 'dimensions' of heredity as a thorough and principled effort to

taxonomize the contents of the developmental niche (Jablonka and Lamb 2005). Together, these legacies are designed to provide the developmental resources needed to reconstruct the life cycle in each generation.

The concept of a developmental niche provides a genuine alternative to the nature/nurture dichotomy (West and King 2008; Stotz 2008; Stotz and Allen 2008). The niche equals nurture insofar as it nurtures the developing organism, and it equals nature insofar as it is part of the organism's endowment (see also Oyama 2002). It undermines the traditional dichotomy between heredity and individual experience, since it highlights how experience, including in some taxa learning, are involved in the development of species-typical behavior. Aspects of experience are part of the mechanism of heredity.

Conclusions

Keller's concludes her detailed analysis and critique of behavior genetics in Chapters 2 and 3 with a beautiful passage:

... I would argue that many behavioral and quantitative geneticists actually mean that a high measure of a trait's heritability, while clearly referring to a population, also has implications for the causal dynamics of individual traits. Precisely because the meaning of the term is uncontrollable, the dual implication of heritability—of transmission from generation to generation both of genes and of genetic variance—is almost impossible to avoid. Moreover, I suggest more generally that much of our interest in heritability—as well as many of the arguments put forth on behalf of the importance of measuring such a quantity—rests deeply and inextricably on the unspoken ambiguity of the terms, and on the slippage that ambiguity invites. It rests, in short, on the informal fallacy that formal logic calls equivocation. (p. 71)

What needs to be done? Keller's recommendation echoes that of many if not all the suspects introduced in the preceding sections, including some that she had earlier accused of conflating mechanism and statistics:

If we want to know what makes us what we are, what we need to understand is how these various systems of heredity interact to shape our development, both ontogenetically and phylogenetically. If we want to know what makes us different from one another, then here too the complexities of development must be taken into account. (p. 72)

Lets quickly summarize the puzzling argumentation laid out by Keller. The first chapter suggests that the muddle of the nature/nurture controversy exists because too many scientists cannot escape a slippage from trait difference to trait, and from population to individual. The debate can only be regarded in terms of the *relative contribution of genes and environment*, not the *developmental interaction* between them. Chapter two and three, in contrast, exposes the language of (classical) genetics and heritability studies in behavior genetics as the main culprit of the conflation between trait and trait difference. It is also in Chapter three where Keller

reveals how much behavior geneticists themselves have to gain from the persistence of such conflation. We must deduce here that it is actually the supposedly only meaningful question introduced by Fisher and adopted by behavior genetics that keeps the debate alive. In Chapter four Keller uses some of the best arguments from those scientists I have introduced as primary suspects for rephrasing the original questions, but without acknowledging that they have made these same arguments.

There can never be too many books criticising the nature/nurture divide. Biological thought is haunted by the many incarnations of this dichotomy and the assumptions it creates about the structure of biological systems and the nature of explanation in the biological sciences. The successes of genetics and molecular biology are often seen as a triumph of nature over nurture. But a survey of those developments reveals that this is a mistake (Griffiths and Stotz 2013). In an attempt to uncover the underlying 'nature' of organisms, molecular biology has revealed the interdependence of organism and environment. The regulatory architecture of the genome reaches outside the genome itself, outside the cell, and outside the organism. Factors outside the gene not only activate, they differentially select and they create biological information. The basis of biological specificity is distributed between coding sequences, regulatory machinery, and the broader developmental niche. Many of the factors involved in genome regulation are highly context-sensitive, which allows them to relay environmental information to a reactive genome which has evolved to let environmental inputs play an instructive role in the determination of phenotypes. The overall picture is one of 'molecular epigenesis' (Stotz 2006a).

Meanwhile, new perspectives have developed on nurture. Some of these focus on developmental plasticity—the ability of organisms to modify physiological, morphological or behavioral phenotypes in response to their environments. Others focus on the role of exogenetic processes in biological heredity. Much of this effort has been directed at cellular epigenetic heredity systems, but others have started to investigate inheritance at the behavioral/psychological, ecological, linguistic/symbolic, socio-cultural and cognitive-epistemic levels. Much of the new science of nurture adopts a reductionistic research strategy, tracking both the process of nurture and its effects down to the molecular level.

A more epigenetic understanding of nature together with a more mechanistic understanding of nurture renders many of the old dichotomies blurred or entirely incoherent. Genes, in some of their guises, are defined by their broader context. The environmental is an essential component of the evolved developmental system. Heredity is a mechanism for plasticity as well as fixity. If the nature/nurture dichotomy is still alive, it is in very poor health.

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