Genotype-environment interactions and our understanding of the biological bases of human cognitive abilities[i]

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Abstract

The debate on the biological bases of human characteristics, and especially of cognitive abilities, has been raging in philosophy and biology essentially forever. The two extreme positions maintain that either a) the genes of an individual causally explain most of her characteristics, with the environment playing a modifier role, or b) the environments (physical but especially cultural) to which an individual is exposed during her life are the major determinants of her behavior, with the genes playing a secondary role. There is indeed convincing evidence to support both positions, but that does not mean that the truth lies somewhere "in the middle". Where would this middle be? Surely nobody think it possible to Solomonically divide an individual's intelligence or creativity in percentages due to the environment experienced by or to the genetic makeup of that individual. I will submit that the conceptual solution to the conundrum has already been provided by the study of genotype-environment interactions as understood in the context of the modern theory of reaction norms and phenotypic plasticity. However, no relevant data of this type can be obtained for humans because of ethical considerations as well as technical difficulties. While interesting conclusions can be derived for other mammals, and possibly even for some primates, the study of nature vs. nurture in humans is indeed very limited, and it is about time that the scientific community refrains itself from making grand statements that cannot be reasonably substantiated by the available evidence. This especially in light of the obvious implications of such studies for social and educational policies.

> Men have an extraordinarily erroneous opinion of their position in nature; and the error is ineradicable.
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> **W. Somerset Maugham** (1874–1966), British author. *A Writer's Notebook* (1949), 1896 entry.

Science or ideology?

The debate on the relative importance of nature (genetics) and nurture (environment) in determining human traits has been prolonged, acrimonious, and largely pointless. Great minds have engaged in it during the last 300 years, from philosophers of the like of John Locke and Thomas Hobbes, to scientists of the caliber of Stephen J. Gould, Richard Lewontin, and Edward O. Wilson, to social scientists like Arthur Jensen, R.J. Herrnstein and C. Murray. A great number of books and an even greater number of book reviews, articles, and media appearances have been devoted to the problem. Gould's "The Mismeasure of Man" (1996) echoed Lewontin and colleagues' "Not in Our Genes" (1984), while Wilson had previously published "On Human Nature" (1978), and Herrnstein & Murray subsequently produced "The Bell Curve" (1994). They are all largely unfounded on scientific grounds and at best provide interesting speculations. By and large, they all simply reflect the (respectable, yet largely groundless) opinions of their authors. More precisely, they all represent the hopes and ideological agendas of their esteemed proponents[ii].

This claim of mine may seem excessive, or even suicidal in view of the fame, scientific expertise, and political spectrum of the people I have mentioned. Yet, anyone familiar with the field of phenotypic plasticity (i.e., the way in which a genotype

responds to the environment Schlichting and Pigliucci 1998) in modern evolutionary biology will know that such a conclusion must follow from what we know of genotype-environment interactions in other organisms. My claim is not that we cannot (in principle) know anything about reaction norms (the function describing genotype-environment interactions) in humans, or that we do not know anything about genetic or environmental effects on human characteristics. But I submit that we currently do not know much that is pertinent to the discussions that these and other authors have been engaging in, and especially that we know very little that can sensibly inform our social policies. When eminent scientists in a field can draw such diametrically opposite conclusions about a given subject matter as Gould and Wilson do, it is a good bet that they are engaging in an intellectual exercise that is groundless enough from an empirical standpoint to allow for such latitude of positions. In this essay I will lay out my argument of why this is precisely the situation of our current knowledge of the biological basis of human nature. The reader should be warned that the following is as much a scientific discussion as it is one about philosophy, ethics, and politics. As such, and unlike the case of scientific controversies, the backgrounds and personalities of the characters involved are as relevant a consideration as their arguments.

Nature vs. Nurture

While it is safe to say that humans have always investigated into their own nature, and certainly since the onset of Greek philosophy, modern positions on the matter may more or less arbitrarily been traced to the works of two English philosophers, John Locke

and Thomas Hobbes. Locke (1632-1704) was the founder of the school known as empiricism, whereby knowledge can be gained only through the use of the senses, as opposed to rationalism, according to which the mind can derive knowledge solely on logical grounds. Locke became famous (and controversial) for his political ideas, questioning the divine authority of kings and affirming that the state has rights only when these are derived from a social contract with the people. In fact, many of his ideas where later adopted in the wording of the US constitution, and are therefore familiar to anyone living in a modern democracy. On the question of human nature, Locke thought of the human mind as a *tabula rasa* (literally, a blank slate). On it, experience writes and molds the individual throughout her life. Innate thoughts do not enter the picture, according to this view. Interestingly, Locke's theory of human nature – like the ones espoused by biologists such as Gould and Lewontin in modern times – was strictly coupled with his social theories. Locke thought that people are born essentially good and with equal rights, and that a good society should reflect these fundamental assumptions.

Thomas Hobbes (1588-1679) thought differently. In his books, and particularly in the famous "Leviathan; or, the Matter, Form, and Power of a Commonwealth Ecclesiastical and Civil", he proposed that human actions are controlled by mechanical processes, and that they are innately fearful and violent. Consequently, the only hope for humans is to submit entirely to an organized state (and religious authority), so to be forced to live in a reasonable way. This is not a far cry from the right-wing politics implicitly or explicitly adopted by fellows of the like of Jensen, Herrnstein, and Murray[iii].

Of course, the current version of the debate is – on the surface – far more sophisticated than the arguments advanced by Locke and Hobbes. In particular, it is

(supposedly) based on almost a century and a half of evolutionary biology, and almost a hundred years of genetics. These two being among the most successful intellectual enterprises in human history, and being based on facts rather than speculations, one might be justified in harboring some optimism that the debate is finally about to be solved. Alas, this is not the case just yet.

First of all, is there really a debate between opposite camps anymore, or are we simply dealing with a sliding scale along a continuum, with people disagreeing on where human attributes fall onto that continuum? Let us make no mistake about it. While both sides pay lip service to the idea that the solution to the riddle falls somewhere in the middle, this is by and large rhetoric. Furthermore, what does it *mean* to be in the middle in this context? Are we in the middle if we say that 50% of intelligence is determined by genes and 50% by the environment? What about 70% and 30%? Or is it more reasonable to propose that intelligence (or any other complex human trait) is the result of a vague and unspecified "interaction" (or an "emergent property") between nature and nurture?

The position of Gould, Lewontin and others is that the environment is the major determinant of human nature. Their creed could hardly be summarized more concisely than by the title of one of their books, the above mentioned "Not in Our Genes". If the cause of intelligence, aggression, or whatever other aspect of our behavior is not in our genes, it must surely be found in the environment. Now, these scientists are certainly not simpletons, and they understand perfectly well the fundamentals of biology and of genetics (Lewontin is arguably one of the foremost geneticists of the second half of the 20th century). So, how can they claim that genes do not have anything to do with the human condition? Technically, they don't. The modern nurture school acknowledges that

genes influence human behavior, but they haste to add that whatever such influence may be, it can be overridden by the comparatively much larger effect of environmental conditions, chiefly education and socioeconomic status. How do they know this? They do not. For example, Gould (in the revised edition of "The Mismeasure of Man", p. 355) says that "the *biological* basis of human uniqueness leads us to reject biological determinism" (his emphasis). Gould is here implying that what we know of the biology of humans negates a major role of genes in shaping our characteristics. Simply put, this is a grand statement for which there is no convincing empirical evidence, either in favor or against. We don't know much about the biological basis of human nature; so, to use whatever scant knowledge is available to reach general conclusions about entire research programs is simply unwarranted. A few pages later (p. 363), Gould continues: "most of the behavioral 'traits' that sociobiologists try to explain may never have been subject to direct natural selection at all – and may therefore exhibit a flexibility that features crucial to survival can never display". Notice the repeated use of "may". He himself recognizes that we do not know. If it is true that lack of relevant information is a valid objection to a particular theory (sociobiology) – as Gould suggests – it is equally true that the same dearth of information is a problem for the opposite theory (nurturism). The problem is that the nurturists seem to advocate the notion that their theory is the default, which should be embraced if there is no evidence to the contrary. This is a peculiar behavior, akin to the reasoning of creationists who maintain that any gap in the fossil record must be taken as prima facie evidence of divine creation (Johnson 1997).

On the other side of the divide, Jensen, Herrnstein, Murray, Wilson (albeit in a category of his own) and many others are convinced that genetics and natural selection

have shaped the physical as well as mental characteristics of all living beings, including humans. When Murray (1998) suggests (in the title of one of his articles) that "IQ will put you in your place" he is assuming that IQ is written in stone in the DNA of each one of us. He, like the nurturists, also bows to a formal acknowledgment of the opposite camp by saying that an optimal environment may have "some" effect. But the role of the genes is so powerful that he and Jensen go on to suggest that governments should not waste too much time and money in improving education and economic conditions, because that will not alter one's place in society as determined by her IQ. The bright people are going to stay that way regardless of the conditions, and the morons (a technical term in early social science studies to indicate people with low IQ) are going to be morons no matter what.

How do these researchers know that the balance between the two forces is so much in favor of genetics? Again, they don't. For example, Murray (1998) affirms that "the research bears out what parents of children with unequal abilities already know – that try as they might to make Johnny as bright as Sarah, it is difficult, and even impossible, to close the gap between them." This is a very specific conclusion about the shape of human reaction norms for IQ (see below), a conclusion that simply is *not* supported by any published research and only represents Murray's twisted wishful thinking. On his part, Rushton (1998), in an essay amusingly entitled "The Mismeasure of Gould", discusses the evidence favoring a link between characteristics of the human brain and human behavior. He cites: "Adrian Raine … tentatively concluded that frontal-lobe dysfunction was associated with violent behavior, including rape." Is this supposed to be compelling evidence? And of what, exactly? Of course damaged brains will cause

altered behaviors, this is a finding that has been a persistent result of neurophysiology for over a century (Ramachandran and Blakeslee 1998; Damasio 1999). But this does not tell us anything about the flexibility (plasticity) of such behaviors and how they respond to environmental change. Without this knowledge, any statement to the effect that genetics is more important than nurture is empty rhetoric.

Evolutionary psychology, the more recent incarnation of human sociobiology, does not make things that much better. Despite cautionary statements by some of its luminaries, such as Steven Pinker (1997), most of that discipline's literature is littered with the same kind of wild guesses and unsubstantiated just-so stories that plagued sociobiology to begin with (for a critical assessment of questions and methodologies, see: Daly and Wilson 1999).

As it is easy to imagine, the debate goes far beyond academia. In fact, most of the discussion has raged outside proper academic channels, with vitriolic attacks and counter-attacks published in outlets such as the *New York Times Book Review* or on the World Wide Web. At times, the confrontation has gotten physical, as in the infamous instance of a scientific meeting at which an opponent of his sociobiological ideas treated Wilson to a downpour of ice water on his head. Gould has used the unorthodox stratagem of reviewing the same book ("The Bell Curve") twice, to make sure that his invectives will reach the largest possible audience. On the other hand, Rushton complains of Gould's unfair "character assassination" in "The Mismeasure of Man", while starting one of his own articles with the following sentence (quoting from one of Gould's archrivals, John Maynard Smith):

> Gould occupies a rather curious position, particularly on his side of the Atlantic. Because of the excellence of his essays, he has come to be seen by non-biologists as the pre-eminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see

> him as a man whose ideas are so confused as to be hardly worth bothering with, but as one who should not be publicly criticized because he is at least on our side against the creationists.

If that is not character assassination, it is hard to see what qualifies. So much for fair play and scientific integrity[iv], but as I mentioned at the beginning, this is not really a scientific debate, and the reader can and should appreciate the contrasting personalities involved in it as well as their philosophies and motives. The point I am trying to make here is not simply to indulge in a demonstration of how ugly things can get when science has direct social implications; rather, this is a salutary exercise in the psychology and sociology of science itself.

One thing is clear: each side has done a marvelous job at poking large holes in the flanks of the other, of which peculiar situation I am clearly taking advantage here. Let me briefly discuss how some of the apparently sound arguments used by each camp can in fact been dismissed quite easily, and how the insistence upon such arguments on the part of either nurturists or naturists indicates poor understanding, less than objective analysis, or both.

One of Gould's major attacks against genetic determinism is based on what he calls the "reification" fallacy. Simply put, the fact that a statistical correlation exists among two or more variables does not imply that that correlation corresponds to a physical entity or demonstrates the existence of a real phenomenon underlying the correlations. So, for example, genetic determinists interpret the fact that the scores from different types of intelligence tests correlate in multivariate space as an indication of the existence of an underlying factor describing general intelligence, which they call "g". g, Gould objects, is simply a statistical artifact of the fact that the different tests are designed in a similar way, so that of course individuals who score high on one test will

score high on another, while individuals who don't do as well on one test will fail another one too. This may be true, except that Gould then does not apply his preaching to his own scientific research. He published several papers (Gould 1984; Gould 1989) describing the (statistical) covariation among morphological traits measured in land snails of the genus *Cerion*. In that body of work, he argues that these correlations show the *existence* of several "constraints," i.e. limitations on the future evolutionary trajectories of these populations of snails. Furthermore, he goes on to *name* such constraints! Is that not a perfect example of "reification"? Obviously, the practice is either acceptable or questionable to an equal measure in *both* cases, not just when it is not convenient for Gould's position.

In the opposite camp, naturists have always argued that their incontrovertible evidence is based on rigorous studies of twins reared together or apart. The statistical arguments are quite complex, but they boil down to the fact that twins have a high degree of genetic similarity, compared, for example, to fraternal siblings, or to unrelated individuals – such as adopted children. If twins show a higher correlation of their IQ scores than the control groups, this is taken as prima facie evidence for genetic determination of intelligence. Not so easily. First of all, this approach ignores the fact that the real problem is how to determine human reaction norms (see below), not to simply estimate heritabilities. Second, it is an astoundingly naïve reading of the data themselves. For example, it underestimates the fact that the environment in which twins or other siblings are raised can play a major role. If twins are reared together, their environments are also going to be very similar. In statistical terms, this causes a complete confounding effect of genetics and environment. Furthermore, even if the twins are separated at birth,

this does not guarantee that their environments will be dissimilar, thereby allowing a statistical decomposition of nature and nurture effects. Indeed, most adoption agencies take great care in assigning children to families of social, economic, and cultural status similar to the ones characterizing the biological family (Levins and Lewontin 1985; Lewontin 1992). Attempts at counteracting this problem by using some measures of the environment as "covariates" in the analyses are technically sound, but again rather simplistic. Does anyone really believe for a moment that just measuring income is going to take a great portion of the environmental differences away (Murray 1998)? Twin studies are not very useful for the simple reason that they control for only one of the two factors, the genetics but not the environmental. Thus, while yielding evidence of *some* sort of genetic basis to human behavior, they provide us with no information on the all-important genotype-environment interactions. A technical paper written on similar grounds but dealing with plants or animals would be mercilessly rejected by any journal editor worth her salt as the unacceptable work of a dilettante.

A perfect example of how unreasonable and unscientific *both* parties are in this controversy is given by their arguing over the relationship between intelligence and brain size. As you would expect, the nurturist camp claims that there is no relevant connection between the two, while the genetic determinists insist that brain size has a lot to do with intelligence (both camps admit that the brain's fine structure is more important than simple size). The latter position is backed by the now incontrovertible correlation between brain size and IQ: about 0.44. This sounds impressive, but it is much less so once one realizes that a correlation of 0.44 between two variables means that one explains only 21% (0.44^2) of the variance of the other. That is, while brain size is indeed

associated with intelligence (or at least that component of intelligence measured by IQ tests – and that is an entirely different controversy which I will not even attempt to touch here), about 80% of the variation in IQ scores in the population does *not* depend on brain size. It seems to me that there is ample space in that 80% for environmental effects, but of course this finding is trumpeted by Rushton (1998) as a decisive blow to the nurturists. It does not come even close to that effect.

Back on the other side of the fence, Gould (in "The Mismeasure of Man") takes the preposterous position of flatly denying even the existence of such correlation. He builds implausible scenarios of respected scientists of the 19th and 20th century "leaning" on their balances, or stuffing just the right amount of measuring pallets in skulls to come up with the "right" results. Even if we conceive that as a possibility, Gould himself acknowledges that the correlation would not disappear, but encourages us to ignore such a "minor" detail. Gould goes even so far as to make the argument that since clearly intelligent individuals, such as the French anatomist Cuvier and Nobel Prize novelist Anatole France, had brains that span almost the whole gamut of human values (1830 and 1017 grams respectively), brain size doesn't have anything to do with intelligence. This is such a ridiculous claim that, made in a different context, would undermine a scientist's credibility. The fact that two variables are correlated, and even causally connected, does not imply that you cannot pick two arbitrary data points and use them to contradict the general trend. Since the brain size-IQ correlation explains only about 20% of the variance, it is no surprise that some very small brains belong to intelligent people (or vice versa, some very large brains to particularly dumb subjects). This does not negate the validity of the correlation by any stretch of the imagination. For example, historian and

social scientist Frank Sulloway (1997) demonstrated quite clearly a very strong statistical relationship between mental attitudes and birth order. First-born individuals tend to be much more conservative and refractory to innovations than later born ones. Sulloway also advanced good arguments for why this link is probably causal, and not just statistical. The explanation may have to do with the idea of family niches: first and later born siblings literally fill different niches in the eyes of their parents, and the resulting family dynamics mold much of their character and actions. Sulloway noted that this effect is more important (statistically, that is it explains more variance) than other traditional explanations such as social or economic status, or gender. Sulloway's data, however, are perfectly consistent with a large role of these other factors, as well as with a role played by innate (genetic) determinants, simply because birth order does not explain the whole variance in behavioral responses. It should be clear to every graduate student that biological and social studies can only thrive on the understanding of general trends, and that there are exceptions to be found everywhere. However, these exceptions do not negate the rules. Biology is not pure mathematics and to pretend otherwise, as Gould selectively does in the case of the nature-nurture debate, is questionable to say the least.

What do we actually know about the biological basis of human characteristics?

The discussion in this essay does not have to be taken as a nihilistic statement on the state of our knowledge of genetic and environmental effects on human characteristics.

We do indeed know a lot about it, but we do not know even close to as much as the nurturists and the genetic determinists actually claim or imply.

On the genetic front, there is little doubt that genes control (affect would be a better term) the development of the brain. Since the brain and the peripheral nervous system determine human behavior, then in some sense it is undeniable that we behave because of our genes. Indeed, it would be foolish to deny this possibility where humans are concerned, since it has been ascertained for every other animal that has been sufficiently studied. A large and fascinating literature on brain damage provides direct and incontrovertible evidence that alterations in the physical structure of the brain (which can be brought about by accident or by mutations) directly affect all sorts of human behaviors, including subtle personality traits (Gazzaniga 1998; Ramachandran and Blakeslee 1998; Damasio 1999). Nurturists routinely make fun of the idea of genes affecting homosexuality or religious beliefs. But there is no doubt that both homosexuality and religious beliefs do have a physical basis in the brain (and how could it be otherwise, since they are human behaviors?), and are therefore alterable by genetic mutations, at least in principle.

The topic of homosexuality is exceedingly controversial and emotional, but it does represent a great example of why the nature-nurture controversy is important, and at the same time of why neither camp is “right”. It is quite clear that homosexual behavior can be acquired or lost, so in some sense there must be environmental components to it. At the same time, the level of exposure to male or female hormones in the womb also very significantly affects gender preferences and sexual behavior of the adult individual (for a lively tour of the implications and references see: Moir and Jessel 1992). While

hormonal levels can be considered an environmental factor, the way in which the brain responds to them is definitely genetically hardwired (because it depends on the presence and expression of hormonal receptors).

Perhaps one of the most emotionally charged (and actively avoided by most scientists) areas of inquiry concerns religion (Larson and Witham 1997; 1998; Pigliucci 1998). It would be foolish to claim that the environment, given all we know about the psychology of individual humans and the sociology of human societies, does not preponderantly affect religious beliefs. Nevertheless, Ramachandran (1998) reports that micro-seizures in the temporal lobes are associated with unusually vivid religious experiences, often complete with sounds, visual stimuli, and a sense of sudden cosmic "understanding". It is easy enough to imagine genetic mutations making some individuals more prone to such seizures, and therefore genetically affecting their propensity for religious beliefs. In both the cases of homosexuality and of religious beliefs, it doesn't make any sense to take an ideological posture and defend it regardless of the evidence. However, the data also do not allow us to disentangle the relative contributions of nature and nurture in a neat and simple way, they only lead us to conclude that both components must be there.

A recent example of a scientifically sound investigation of the biological basis of complex human behaviors is the study of the peculiarities of Einstein's brain when compared to appropriate controls from the general population (Witelson et al. 1999). As it is well known, Einstein was gifted with an unusual mathematical ability; it is also well known that in humans increased mathematical ability is associated with an expansion of the inferior parietal region of the brain. Witelson and colleagues found that Einstein's

brain was about 15% larger than the controls precisely in that region and therefore concluded that they may have pinpointed at least part of the biological basis of the great physicist's rare ability. This, of course, is not to say that Einstein's mathematical genius was written in his genes: a change in brain structure can be brought about by mutations or by environmental influences (or both). Yet, it is uncanny to see how several immediate reactions in the mass media were along the lines of "reductionist" science attempting to "diminish" the contribution of Einstein to human thought. How would the demonstration that such contributions came from his brain in any way diminish Einstein's figure? Where *else* could his genius have been coming from? Along similar lines, Tang and coworkers (1999) genetically engineered mice to overexpress the NMDA (N-methyl-D-aspartate) receptor 2B in their forebrains. NMDA receptors are synaptic coincidence receptors that are known to play a fundamental role in memory formation and learning. Not surprisingly, the transgenic mice showed enhanced cognitive abilities, perhaps opening an important window toward both the understanding of the complex phenomena of learning and memory and the treatment of debilitating human diseases affecting them. Since a gene codes the NMDA 2B receptor, this is a pretty clear demonstration that higher cognitive abilities in humans are indeed under genetic control. It does not follow, however, that this single gene (or any other gene, for that matter) is all there is to know in order to understand cognition.

A clear, simple, and largely unemotional example of why both nurturists and genetic determinists are partially right, but neither can address the most important questions, is given by the environmentally curable genetic disease known as Phenilketonuria (PKU). PKU is caused by a simple "inborn metabolic error", i.e. a

mutation that does not allow the formation or proper functioning of an enzyme that metabolizes the amino acid phenylalanine. Often (though not always)[v] this results in accumulation of the amino acid in the brain during development, which in turn causes a host of phenotypic and behavioral effects, including severe mental retardation. The link between the genetic level (the mutation and consequent enzymatic defect) and the phenotype/behavior is unusually straightforward, and therefore offers an ideal example of how genes can affect behaviors, although no genetic determinist would go so far as to say that this is a gene *for* normal intellectual development. On the other hand, a very simple dietary change (i.e., a change in behavior) can completely neutralize the genetic effect: an individual can grow up normally by carefully avoiding phenylalanine, which is why many soda cans carry a warning label for PKU patients. This is the most extreme and one of the few clear cases of plasticity one can document in humans. So, one has to conclude that PKU is *both* genetically determined and environmentally plastic. The crucial question, however, still remains: what are the reaction norms of PKU genotypes? There surely are several PKU genotypes, not only because the mutation can be caused by different alleles at the main locus, but also because the effects of the mutation depend on the other genes that interact with that locus. Furthermore, there may be plenty of other environmental circumstances that affect the degree of occurrence and gravity of PKU symptoms. We simply do not know, and we will not know any time soon given the obvious limitations on experimental research in human genetics.

Summarizing, we *can* (and in many instances we do) know that a trait is affected by changes in the genetic makeup of a person. Similarly, we can and do know that a given characteristic or behavior can be altered by changes in the environment. What we

do not know is if and how these two effects interact with each other. Unfortunately, this is the single most crucial thing there is to know about the nature-nurture controversy.

Why we don't know what really matters

The fact that the quantitative genetics of human behavior is far less advanced than most "experts" would like the public to think is a logical consequence of what we have been discussing in this book about genotypes, environments, and phenotypic plasticity. It can be summarized in a few simple, yet apparently incredibly difficult to sink in, sentences.

First of all, what we would really like to know is how genes and environments interact to produce a certain phenotype or behavior *in an individual*. Given that this has so far proven to be a very difficult and elusive goal, human quantitative geneticists have shifted the target to a general (statistical) understanding of *variation within and among human populations*. Enter the venerable concept of heritability, i.e., the ratio between the genetic and the phenotypic variance for a particular trait, measured by a variety of breeding designs. The result of this shift is that, assuming a given trait turns out to have a heritability of 70%, one cannot in any meaningful way say that 70% of that trait in a particular individual is due to her genes and the remaining 30% to the environment. All one can say – under ideal circumstances – is that 70% of the phenotypic variation in the population is associated to differences in the genetic constitution of its individuals. The problem is that for humans the circumstances are never "ideal," since measurements cannot be taken under the same set of environmental conditions. This is Lewontin's

mantra: heritability is only a local measure; it estimates the amount of genetic variation for a quantitative trait *only* within a particular population (set of genes) and in a particular environment (Lewontin 1974, Figure 1). It cannot be reasonably extrapolated either to other populations or to other environments without further empirical research.

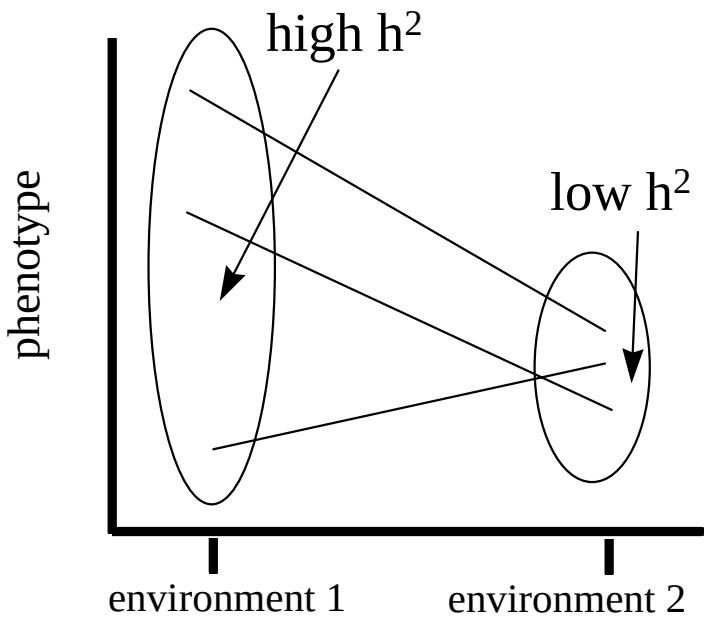

Figure 1. A hypothetical population with three genotypes characterized by distinct reaction norms along an environmental gradient. Where the reaction norms converge, the heritability of the trait is low; where they diverge, the heritability is high. Heritability, therefore, is a complex function of the environment and of the genetic constitution of the population.

Using again the concept of reaction norms, it is rather easy to understand where the problem lies. The extreme genetic determinist position (which, of course, nobody really espouses, but which provides a convenient conceptual endpoint) can be visualized as in Figure 2. The three reaction norms are flat, indicating that there is no effect of the environment whatsoever. They are also widely spaced apart, suggesting that genetic differences do result in major phenotypic/behavioral differences. If this were indeed the case, no social program of any kind would be worth a dime. However, we know that this is not the real scenario, because we have plenty of evidence supporting the existence of *some* significant environmental effect on human behavior.

The extreme nurturist hypothesis is instead the one depicted in Figure 3. Here the reaction norms are all sloped, indicating a dramatic effect of the environment. They are also so close together in a bundle that there basically are no differences among genotypes. I hope that even the staunchest supporter of humane social policies, however, will admit that this scenario is as unlikely and inconsistent with the scant data we have as the previous one.

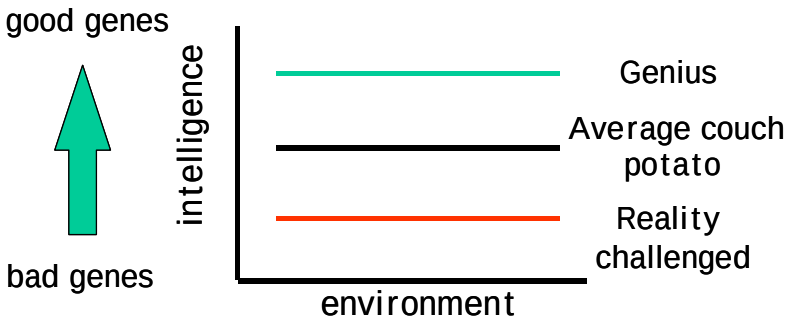

Figure 2. A reaction norm depiction of the extreme genetic determinism model.

What is the real shape of human reaction norms? I would *guess* something approaching Figure 4: some genotypes are almost not responsive to environmental changes, others respond significantly, and still others are dramatically affected by the environment. Furthermore, the differences among genotypes are large in some environments (e.g. at the left and right extremes of the graph), but small in others (e.g. in the center of the hypothetical environmental range). If this were the case, the truth would indeed lie somewhere in the middle, though such middle would not be a simple average of genetic and environmental effects. However, the fact of the matter is that, again, we do not know. While we can confidently exclude both extreme scenaria, there are an infinite number of potential configurations in the middle. Since we cannot ethically grow genetic replicates of human beings under controlled and diverse environmental conditions, we simply do not know what the patterns of plasticity for human cognitive

traits are. Scientists should acknowledge this and move on. But the temptation is apparently too great for us not to sin.

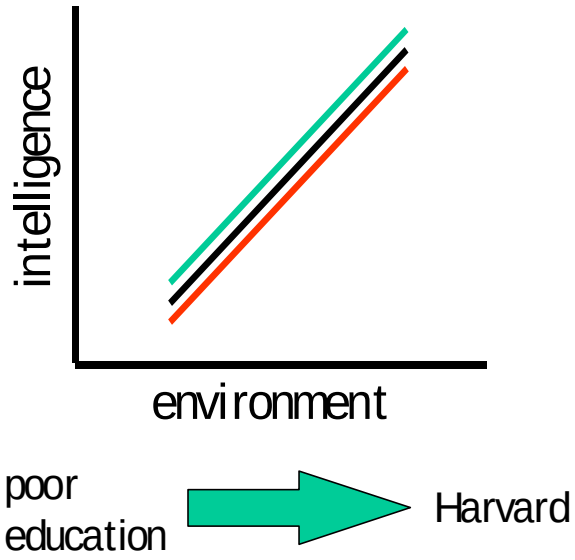

Figure 3. A reaction norm depiction of the extreme nurturist position.

A characteristic example of how difficult it is even for renowned biologists to get over what Feldman and Lewontin (1990) called "the heritability hang-up" can be found in works by sociobiologist Edward O. Wilson. In his "Consilience: the Unity of Knowledge" (1998) he explains his theory of gene-culture evolution, i.e., how genes and environments co-evolve to shape species' destiny, humanity in particular. The chapter entitled "From Genes to Culture" is an odd mix of an enlightened vision of the problem and a stubbornly orthodox one, as if Wilson couldn't make up his mind. After admitting that "all biologists speak of the interaction between heredity and environment", he goes on to introduce the concept of reaction norm. He correctly points out that:

> Redefined with the more precise concepts of genetics, nurturists can now be seen to believe that human behavioral genes have very broad norms of reaction, while hereditarians think the norms are relatively narrow. In this sense the difference between the two opinions is thus one of degree, not of kind. It becomes a matter that can be settled and agreed upon empirically.

Wilson must know that the empirical way to settle this matter would be to selectively breed humans and raise them under controlled conditions, an ethical impossibility. Nevertheless, he expresses some optimism that the matter will eventually be settled

through the accumulation of data while not providing a clue as to how this would be done.

Wilson also brings up the concept of heritability. Even though he expressly admits that there is a genotype-environment correlation that makes the use of heritability measures inadequate, and that heritability is 'flexible' (i.e., it depends on the environment), he calls these "peculiar twists". While coming so close to destroying (or at least greatly reducing) the very meaning and usefulness of heritability, he still affirms that "the measure has considerable merit, and in fact is the backbone of human behavioral genetics". He proceeds by imagining a series of scenaria in which we would be able to measure heritability in different cultural (and therefore environmental) contexts, predicting that in some cases heritability would increase, in other it would decrease. Let me be clear on this point: such predictions have no foundations whatsoever given current procedures in empirical quantitative genetics. The only way to make them in a reliable way is either to do the experiment, which is both ethically impossible and technically extremely difficult, or to understand exactly how genes and environments interact from a mechanistic standpoint. The latter objective is not as of now even within the range of the most powerful telescope that any scientist may hope to use to divine the future.

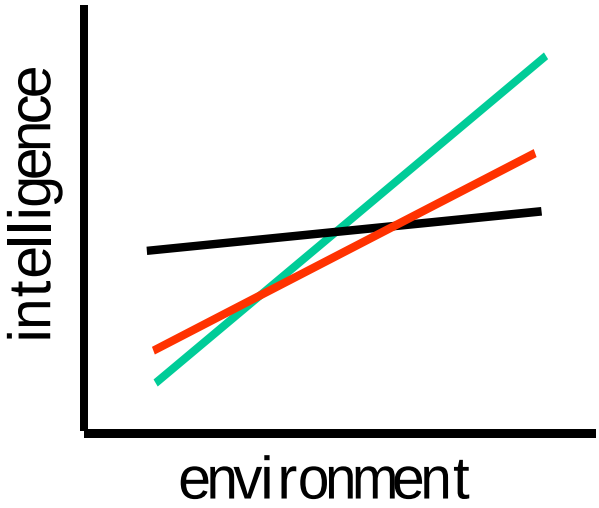

Figure 4. Do actual human reaction norms for intelligence look like these? Perhaps, perhaps not.

Worse, immediately after

providing the reasons for being extremely cautious about heritability measures, Wilson says:

> Nurturists have also traditionally thought that the heritability of intelligence and personality traits is low, while hereditarians have considered it to be high. That disagreement has largely been solved. In contemporary Caucasians of Europe and the Unites States at least, heritability is usually in midrange, with its exact value varying from one trait to another.

It is astounding to see this kind of reasoning on the part of a biologist who demonstrably knows better. Unfortunately, he is not alone. I think it would be of great interest to psychologists and sociologists to try to explain how one can have all the pieces of the puzzle in mind, even put them together in almost the right way, and still fail to perceive the emerging picture. As it is clear when one considers the environmental plasticity of heritability measures (see below; and as Wilson himself freely acknowledges), it just does not make any sense to use heritability across environments. Since the Caucasians to whom Wilson is referring were raised under different environments, the resulting estimates of heritability of IQ are a hopelessly confounded hodge-podge of nature and nurture. They emerge from genotype-environment interactions during the entire lives of the organisms concerned, not just from the genetic component as it is simplistically assumed. The only confidence limits that can be reasonably put around such “estimates” are zero to one hundred percent, not exactly an example of good empirical science.

The environmental dependence of heritability is by no means a mere theoretical possibility. In many organisms in which the experiment can and has been done, a strong dependence of heritability on the environment has been found for many (albeit not all) traits. For example, the work of Mazer and Schick on wild radish (Figure 5) clearly shows that the heritabilities of three traits (flowering time, petal area, and pollen volume) are highly dependent on the density of conspecifics, a crucial environmental parameter in

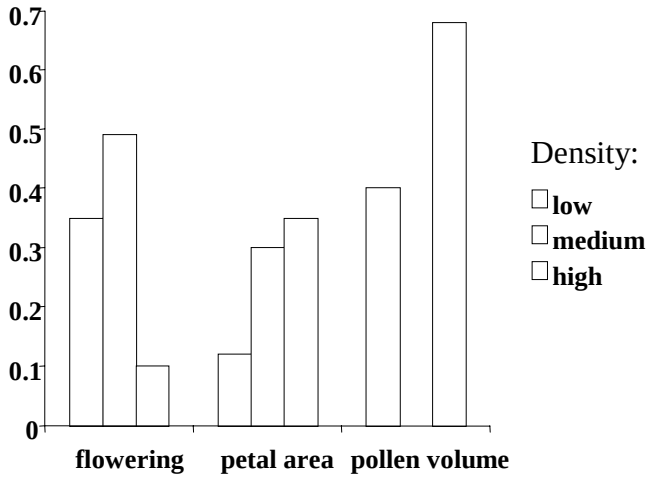

Figure 5. Changes of heritability of different traits with the environment in wild radish. Notice how the heritability of the same trait (flowering time, petal area, or pollen volume) dramatically depends on the environment (low, medium, or high density of conspecifics). Also, the pattern of variation of heritability with the environment is not the same for different traits. (From data in Mazer and Schick 1991)

plants. More importantly, there is no regular pattern describing such interdependence: heritability is lowest under high density for flowering time, but under low density for petal area, and under medium density for pollen volume. Therefore, one cannot even say that a particular environmental range is likely to yield high heritabilities while another is associated with low heritabilities. It depends on the character (and, probably, on the population in which the study is conducted). This may be a frustrating aspect of biological reality, but ignoring it does not help, and – in the case of humans – may lead to disastrous social policies.

What are we to do?

What kind of evidence would settle once and for all the nature-nurture debate on the biological basis of human behavior? The answer is in fact very simple, and such an experiment has already been done, for example, by Cooper and Zubek (1958)[vi]. On rats, that is. They compared “intelligence”, as measured by the ability to avoid mistakes in running through a maze, in two inbred, genetically distinct lines of rats. One line had been selected for high performance in the maze (“bright” line), the other for particularly

low performance ("dull" line). When reared under a standard environment, comparable to the one in which the selection process occurred, the two lines showed a highly significant difference in their abilities. Cooper and Zubek, however, also reared individuals of the two lines in two other environments: a situation in which the cage was entirely devoid of visual and tactile stimuli ("poor" environment), and one in which the developing animals were exposed to brightly colored walls and toys ("enriched" environment). The results are simply stunning (Figure 6). Under the poor conditions, the bright rats performed as badly as the dull ones; furthermore, under the enriched environment the dull rats did as well as the bright ones! This translates into a high heritability and marked genetic differences in the standard environment, but no heritability under either extreme environment. The inescapable conclusion is that maze- running ability in rats has a very plastic reaction norm, and that different genotypes converge onto similar phenotypes at extreme environmental conditions. I am not suggesting here that this particular experiment is flawless. For one thing, only two genotypes were tested,

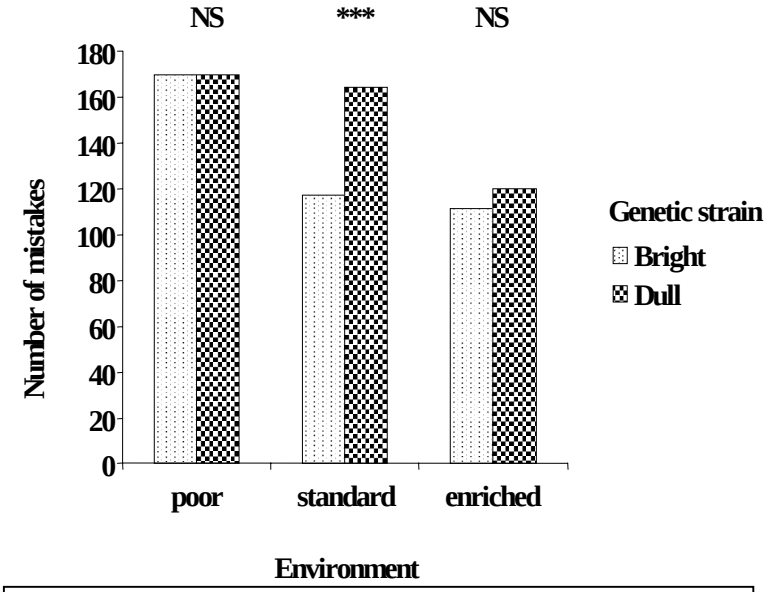

Figure 6. Effect of nurture (quality and stimulation properties of the environment) on "intelligence" (ability to avoid mistakes in mazes) in genetically distinct laboratory lines of rats. Notice how the genetic differences are significant (i.e., there is a significant heritability) only in the environment in which the lines were selected, but they disappear in the other two environments. (After data from Cooper and Zubek 1958)

and they were certainly not a representative sample of natural populations. Furthermore, the cognitive ability being tested was a relatively specific one, and its correlation to generalized intelligence (if there is such thing) remains to be ascertained. Finally, one could easily conceive of other (and more naturalistic) kinds of environments that may yield very different results. However, all these problems are also common to any human study published so far. The point I want to make is that this is the kind of data that would go a long way toward empirically answer the question of heritability and plasticity of human behaviors, as invoked by E.O. Wilson. For obvious reasons, we cannot expect this kind of data to appear any time soon in the scientific literature about humans, but similar experiments in other vertebrates would go much further than any piece of rhetoric or speculation.

So, how should scientists answer pressing requests from the public and policy makers when it comes down to our knowledge of intelligence and other behavioral traits in humans? I believe some answers and suggestions can be given, but only if accompanied by careful statements about the great limitations imposed by the impossibility of carrying out the proper experimental manipulations. While good science can be done by using only indirect and statistical approaches, we have to remember that the only way known so far to dissect the functionality of complex systems is by direct manipulation. It is therefore odd to witness grand statements about human nature being pronounced by quantitative geneticists (who can only use a statistical approach) or molecular biologists (who can only empirically investigate one component of the system, but cannot perform the required sophisticated experiments involving manipulations of environmental conditions as well as of genotypes).

The first and perhaps most important thing we can definitely conclude from what we know of the biological basis of human behavioral traits is that they tend to be plastic. Therefore, regardless of any politically motivated right-wing rhetoric, education programs do have a good chance to succeed. In fact, even if humans were genetically distinct in their abilities, and even if an improvement in environmental conditions will maintain such differences (a very unlikely scenario), it would still be worth funding educational programs. Such hypothetical situation is depicted in Figure 7. The reaction norms are widely spaced, indicating a high heritability of the trait being examined. Furthermore, the spacing remains constant across environments, suggesting that the heritability is high regardless of the environmental conditions.

Still, a better quality of the environment improves the performance of every genotype. I would argue that it is well worth spending our money to have a society in which the computer literacy, or the artistic inclination, of every human being is enhanced. We will still have Mozarts on one hand and mediocre musicians on the other, but everybody would be able to appreciate and even play music.

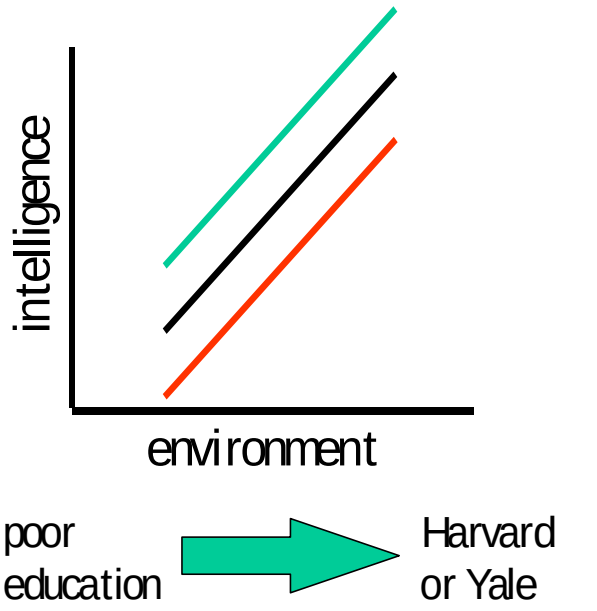

Figure 7. A hypothetical (unlikely and worst-case) scenario showing why educational programs should be implemented even if humans are characterized by marked and environmentally-invariant differences in behavioral traits.

The second fact that we can confidently state is that most human traits (including behavioral ones) do have a

genetic basis. It simply could not be otherwise, given that the structure of the brain is dictated in part by genes, and considering all we know about the effects on behavior of brain anomalies. This, I am sure, translates into a very politically incorrect position, in which genetic differences among races, genders, and individuals may indeed exist. I don't see, however, how this acknowledgment would necessarily translate into discrimination and abuse. The first is a fact of nature, completely impervious to our judgments and hopes. The second is a matter of attitudes and policies, both of which can be changed. To translate one into the other is to commit the naturalistic fallacy (Moore 1912)

What scientists cannot and should not venture to say, however, is how the two previous points can be combined in order to understand the interactions of genes and environments. This is indeed a crucial question, because some educational approaches, for example, may be more or less fruitful depending on the precise shape of human reaction norms. The same can be said for policies concerned with curbing crime, or for a host of other fundamental and difficult decisions we have to make in our societies. Unfortunately, it should be clear by now that this is where the line must be drawn and the only honest answer a scientist can give is: **I do not know**. It is astounding to see how difficult the utterance of these simple words can be, a side effect of which is the publication of scientifically largely useless volumes such as the "Bell Curve" and its many rebuttals. The reasons to yield to the temptation of saying more than your data and theories allow is, of course, relatively easy to understand. Sociologists, psychologists, and philosophers of science have long pointed out that personal egos, social prestige, financial rewards (personal or for research) all play into this in a remarkably complex

ensemble (Kuhn 1970). The fact remains, however, that there are – and always will be – some questions that science cannot answer (either at the moment, or in general). As Richard Lewontin put it in a similar context: “I must say that the best lesson our readers can learn is to give up the childish notion that everything that is interesting about nature can be understood. ... It might be interesting to know how cognition (whatever that is) arose and spread and changed, but we cannot know. Tough luck” (Lewontin 1998). Learning to live with this conclusion actually empowers the scientist, because by not pretending to be omniscient she can enjoy the fruits of the single most effective tool humans have ever devised to understand the world. It also is the only decent thing to do.

References

Cooper, R.M. and Zubek, J.P. (1958) Effects of enriched and restricted early environments on the learning ability of bright and dull rats. Canadian Journal of Psychology 12:159-164.

Daly, M. and Wilson, M.I. (1999) Human evolutionary psychology and animal behaviour. Animal Behaviour 57:509-519.

Damasio, A. (1999) *The Feeling of What Happens: Body and Emotion in the Making of Consciousness*. Harcourt Brace & Co., New York, NY.

Feldman, M.W. and Lewontin, R.C. (1990) The heritability hang-up. Science 190:1163-1168.

Gazzaniga, M.S. (1998) The split brain revisited. Scientific American 279 1, July, pp. 50-55.

Gould, S.J. (1984) Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: a way of studying nonadaptation. Systematic Zoology 33:217-237.

Gould, S.J. (1989) A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. Evolution 43:516-539.

Gould, S.J. (1996) *The Mismeasure of Man*. W.W. Norton & Co., New York.

Herrnstein, R.J. and Murray, C. (1994) *The Bell Curve: Intelligence and Class Structure in American Life*. Free Press, New York, NY.

Johnson, P. (1997) *Defeating Darwinism by opening minds*. InterVarsity Press, Downers Grove, IL.

Kuhn, T. (1970) *The structure of scientific revolutions*. University of Chicago Press, Chicago.

Larson, E.J. and Witham, L. (1997) Scientists are still keeping the faith. Nature 386:435-436.
Larson, E.J. and Witham, L. (1998) Leading scientists still reject God. Nature 394:313.
Levins, R. and Lewontin, R.C. (1985) *The dialectical biologist*. Harvard University Press, Cambridge, MA.
Lewontin, R.C. (1974) The analysis of variance and the analysis of causes. American Journal of Human Genetics 26:400-411.
Lewontin, R.C. (1992) *Biology as ideology : the doctrine of DNA*. HarperPerennial, New York, NY.
Lewontin, R.C. (1998) The evolution of cognition: questions we will never answer. In: D. Scarborough and S. Sternberg (eds.) *Methods, Models, and Conceptual Issues. An Invitation to Cognitive Science*, pp. 107-132. MIT Press, Cambridge, MA.
Lewontin, R.C., Rose, S. and Kamin, L.J. (1984) *Not in Our Genes*. Pantheon, New York, NY.
Moir, A. and Jessel, D. (1992) *Brain Sex: the Real Difference Between Men and Women*. Delta, New York, NY.
Moore, G.E. (1912) *Ethics*. Oxford University Press, London, England.
Murray, C. (1998) IQ will put you in your place. accessed: ue255;}{\pard\plain11/7), web page, www.eugenics.net.
Pigliucci, M. (1998) A case against god: science and the falsifiability question in theology. Skeptic 6 2, pp. 66-73.
Pinker, S. (1997) *How the Mind Works*. W.W. Norton, New York, NY.
Ramachandran, V.S. and Blakeslee, S. (1998) *Phantoms in the Brain: Probing the Mysteries of the Human Mind*. William Morrow, New York, NY.
Rushton, J.P. (1998) The mismeasure of Gould. accessed: ue255;}{\pard\plain11/7), web page, www.eugenics.net.
Schlichting, C.D. and Pigliucci, M. (1998) *Phenotypic Evolution, a Reaction Norm Perspective*. Sinauer, Sunderland, MA.
Sulloway, F.J. (1997) *Born to rebel: birth order, family dynamics, and creative lives*. Vintage Books, New York, NY.
Tang, Y.-P., Shimizu, E., Dube, G.R., Rampon, C., Kerchner, G.A., Zhuo, M., Liu, G. and Tsien, J.Z. (1999) Genetic enhancement of learning and memory in mice. Nature 401:63-69.
Wilson, E.O. (1978) *On Human Nature*. Harvard University Press, Cambridge, MA.
Wilson, E.O. (1998) *Consilience: the unity of knowledge*. Knopf : Distributed by Random House, New York, NY.
Witelson, S.F., Kigar, D.L. and Harvey, T. (1999) The exceptional brain of Albert Einstein. Lancet 353:2149-2153.

[i] A sanitized version of this essay is currently in press as part of my book *Beyond Nature vs. Nurture: the Genetics, Ecology, and Evolution of Genotype-Environment Interactions* by Johns Hopkins University Press. The publisher has thought necessary to cut out all discussions of the sociology of the nature-nurture debate, because it is not "scientific". In my modest opinion, this fails to understand that science is, in part, a matter of sociology and psychology of the characters involved, especially when it comes to emotionally charged arguments such as the ones discussed here.

[ii] Notice, for example, that most of the works cited in this essay are popular books or articles, not academic publications which enforce peer review.

[iii] This neat classification of characters, scientific positions, and ideologies, breaks down when we consider E.O. Wilson. His biological theories emphasize a reductionist understanding of human nature, and the entire discipline of sociobiology – which he single handedly established – is based on the assumption that genes play the lion share in the game of life. On the other hand, his writings (Wilson, E.O. (1998) *Consilience: the unity of knowledge*. Knopf : Distributed by Random House, New York, NY.) reflect a remarkably progressive attitude toward human society, in line with the most optimistic philosophers of the Enlightenment. This just goes to show the complexity of human nature.

[iv] Incidentally, living on Gould's side of the Atlantic while originating on the other side, I really think that Maynard Smith's characterization is rather unfair *on scientific grounds*. Gould, while certainly controversial, is highly respected as a biologist, not just as an anti-creationist.

[v] I am in debt to my philosopher friend Jonathan Kaplan for pointing out to me that the literature on PKU is far from presenting the simple story found in textbooks. One of the reasons there is more variation in the phenotypic expression of the disease than it is commonly acknowledged may be that the effects of the mutation depend on the genetic background in which it occurs. Having the same gene for PKU can result in different levels of phenylalanine in the blood, and having the same level of phenylalanine in the blood can result in different levels of physical problems, depending on the individual. In other words, some combinations of other genes interacting with the focal one may greatly reduce, or entirely eliminate, the deleterious effects.

[vi] I am again in debt to Jonathan Kaplan for bringing this data set to my attention.