The Human Genome, Human Evolution, and Gender

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Introduction

Two central views about biology remain deeply entrenched in popular thought. The first is a picture of evolution. This is a set of ideas that reached their canonical form in the mid-twentieth century, as the so-called New Synthesis of Darwinism and Mendelism, and a version of which has become widely known due to the exceptional popularising talents of Richard Dawkins. This is the view that evolution largely consists in small changes to genes, or to the human genome, which because of a small but incrementally advantageous change that they produce in the organism, gradually spread through the population. Large scale evolution is just the accumulation of these small genetic changes over very long periods of time. The second view concerns the centrality of the gene, or the genome. Often referred to as genetic determinism, this is the view that sees the fundamental nature of organisms as inscribed in their genomes.

These two doctrines fit together in an obvious way, and lead to the conclusion that if we can understand sufficiently well the evolutionary process that led to the particular genome of a particular organism, we will understand the essential nature of that organism. And these views also underlie a great deal of popular writing claiming to derive gender roles from biological theory, with the regrettable implication that gender is somehow inscribed in our genes and that changes in gender roles will, therefore, be difficult or impossible to bring about. The central point of the present paper will be to explain how contemporary biological thought has in fact moved far beyond these familiar theses, and that more up to date understandings provide no support for such genetic deterministic perspectives on human behaviour in general, or gendered differences in behaviour in particular.

Are the differences between men and women to be explained by biology or by society? Just about everything is wrong with this question. Most obviously, it presupposes that there is a reasonably reliable and well-defined set of differences between the human sexes in the first place, which is at least a central point at issue; and second it assumes, if not that any human feature is either biologically or socially caused, at least that we can partition causes between factors of these sorts. Both these assumptions are, at best, controversial. My positive thesis, an increasingly uncontroversial one among those who have familiarised themselves with the theoretical background, is that every human feature develops through an interaction between biological and environmental, often social, causes, so that both biology and the environment, again typically the social environment, are involved in almost all human traits of interest (see, e.g., Lewontin 2000). This does not show that any desired change in behaviour can be brought about at will, a view sometimes attributed to critics of biological determinism (Pinker, 2002) but, as I shall explain, it shows that we should be highly sceptical about suggestions that limits to human behavioural possibility are deeply engrained in our biology. A fortiori, we should be sceptical of such claims as applied to gender-related differences.

The most widely disseminated contemporary attempt to ground human sex differences, and thereby gender differences, in biology is Evolutionary Psychology. Following a growing convention, I capitalise Evolutionary Psychology to refer to a particular set of views on the evolution of human psychology associated particularly with writers such as Leda Cosmides and John Tooby, Steven Pinker, and David Buss. In criticising these views I do not, of course, mean to deny that our psychology evolved, since I assume that we evolved, and therefore our psychology did too. Evolutionary Psychologists, in this narrower sense, offer an atavistic view of human psychology, in which contemporary human behaviour is to be explained by appeal to its aptness for reproductive success in the Pleistocene, or late Stone Age. The means by which Stone Age traits are supposed to have descended to modern humans is that they were carried here in our genes. Hence this school of thought presupposes and lends credence to the idea that sexual dimorphism of behaviour is genetically caused.

A quite different line of investigation about which I shall say much less is behavioural genetics. Behavioural geneticists investigate contemporary humans and typically attempt to measure the heritability of behavioural traits. ‘Heritability’ is a highly technical term, generally taken to be a statistical measure of the extent to which the explanation of the variation in a trait is to be attributed to differences in genes, and is expressed as a number in the range 0-1. The interpretation of heritability is highly controversial. A sense of the difficulty the concept presents can be gained by noting that the heritability of a trait is necessarily zero for a genetically homogeneous population and necessarily 1 for a population in a uniform environment. Hence the impression too frequently given when heritabilities are reported, that they measure some intrinsic feature of the aetiology of a trait, is clearly mistaken. Of course this hardly constitutes an argument that the concept is misguided, and in fact it is a perfectly respectable and useful concept, for example in fields such as crop breeding. It does, however, point to the potential for the concept to mislead, and to the fact that it most certainly does not provide the identification of the causation of behavioural traits sometimes misattributed to it. For a properly detailed critique of human behavioural genetics, see Kaplan (2000).

Although human development, the process through which mature human traits emerge, is a very complex causal process, certainly some of the causal factors involved are properly described as biological. I shall begin the substantive discussion of this paper, therefore, by saying something about biological causes and more specifically genetic causes. I want here to highlight the diversity and complexity of even purely biological causes, and the divergence between contemporary biology and the way genetic causation is often thought of outside professional biological circles. This will prepare the way for seeing how the basic argumentative strategy of Evolutionary Psychology, and specifically its application to gender difference, is entirely out of touch with contemporary biology.

Genes as Causes of Behaviour.

A simple picture, widely promoted and perhaps widely believed, sees genes as the causes of features of the human brain which, in turn, cause people to behave in certain ways. Of course, a sufficiently rarified sense of 'cause' may very well make this true. No doubt genetic factors play an essential part in human development: if there were no genes there would certainly be no brain. But equally if there were no food, or too many tigers, or countless other internal and external contributors, positive and negative, to development, there would be no brain. This is hardly enough to capture what the proponent of genetic causation has in mind.

So what is the genetic contribution to development that some see as so special? The biological function for which genes are best known is the provision of templates for the production of proteins. Proteins are the most important structural molecules in humans as in other organisms, and many proteins are essential to the structure and function of the brain. So it is at once easy to see the necessity of genes in the development of the brain. However, we should also note that this is a surprisingly low level function to be taken as the most important in determining the fine structure of the brain that, in turn, determines the specifics of behaviour. This is especially so when we realise that the full set of genes does not determine precisely which proteins are produced in any particular cell, something that is obvious when we consider the great diversity of structure and function found in the many different cell types in the human body—liver cells, muscle cells, blood cells, nerve cells, and so on—all of which share, more or less, exactly the same complement of genes. As a matter of fact it is increasingly clear that the genome has the potential to produce a vast diversity of different sets of proteins (and of RNAs, the molecules that are intermediaries in the process of protein production). A variety of quite well understood mechanisms are now recognised that enable a particular gene to produce a whole range of different protein products[1].

It was once thought, and perhaps still is by some, that an additional function of the genome was the regulation of the activities of the genome so that as well as providing the templates for proteins the genome also somehow determined which proteins were produced and where. This is the idea encapsulated in the idea of a genetic programme, an idea that maintains a vision of the entire organism somehow encoded in the genome. However, it is now recognised that the factors that determine the activity of the genome are much more varied than this picture proposes. The genome is a dynamic entity, in constant interaction with other chemical constituents in the cell. Other molecules bind to the genome, changing its physical configuration, and influencing which parts of the sequence are transcribed at any moment. It might be

[1] An elementary survey of these mechanisms, as well as of much of the biological material sketched in this paper, can be found in Barnes and Dupré 2008.

imagined that the presence of these other molecules, mainly RNAs and proteins, was itself determined by the genome, and therefore that they were merely part of the system by which the genome regulates itself. There are two reasons for rejecting this view, both of which are fundamental in providing a more defensible view of the role of the genome in biology.

First, there is no point in the life cycle at which the DNA starts de novo to populate the cell. DNA is always found in complex cellular environments with which it is in dynamic interaction. It is sometimes suggested that multicellular organisms reach a bottleneck in the production of the fertilised egg, or zygote, at which there is nothing but DNA to carry developmental information to the next generation. Thus evolution is seen as a long sequence of genomes, each of which tests the organism for which it is a blueprint against the demands of natural selection. But the reality is that evolution consists of a sequence of cell divisions, and the full chemical complement of the cell is involved in the process of cell division. The evolutionary history which informs the development of the organism is not merely the static information deposited in DNA sequence, but the dynamic chemistry of a sequence of cells stretching back into deep pre-history. The (relative) stability of biological forms has been maintained by a continuously dynamic sequence of molecular equilibria, not by a static object somehow embodying all the information necessary to recreate such forms.

Second, the chemistry of the cell can be affected, all the way to the genome, by environmental influences on the organism. Cellular influences on the genome are studied generally in the burgeoning field of epigenetics. The epigenetic phenomenon which has been most thoroughly studied in this context, though it is by no means the only one, is methylation. This is a modification of one of the bases in the DNA sequence, cytosine, in which a hydrogen atom is replaced by a methyl group (CH_3), and converted to 5-methyl-cytosine. This can either suppress or enhance the expression of the gene in which the modification occurs. It used to be thought that this process was always reversed during the formation of sex cells, so that these effects were limited to the lifetime of an organism. But it is now clear that this is not the case, and that not only is the methylation state of the genome influenced by environmental effects up to and including the interaction of the whole organism with its environment, but that these can be passed on to offspring, so that the environment can affect the evolution of a lineage through this mechanism. (If anyone suspects that the bogey of Lamarckism is here rearing its ugly head, they are quite right.) However, direct reproductive transmission of methylation patterns is not essential for these to be stabilised in a lineage. A famous example is the effect on infant rats of maternal care including especially genital licking. This has a range of effects on the behavioural development of the rat pups, some at least of which have been shown to be mediated by methylation of genes in brain cells. Rat pups deprived of proper genital licking become more generally fearful and maladjusted in various aspects of sexual and maternal behaviour (Weaver et al. 2004). One likely consequence is that female rats so deprived will be less likely to provide proper genital licking to their pups, so that this genetic, or technically epigenetic, change, could be transmitted by a mechanism that passes through the maternal behaviour.

Humans, of course, are subject to similar processes. These have been extensively studied by Marcus Pembrey and his colleagues in the longitudinal ALSPAC study at Bristol University, who have discovered various transgenerational effects of maternal nutrition on several generations of offspring. This has long been suspected in the case of the wartime famine in the Netherlands, which appears to have produced not only low birth-weight babies for the generation that experienced the famine, but also for their well-nourished children. One important recent result, extending the phenomenon to paternal as well as maternal influences, has been a report of the effect of very early onset of smoking (up to 11 years of age) by fathers, which tends to produce obesity in male, but not female, children (Pembrey et al., 2005). Induced changes in methylation patterns appear to be involved in these effects.

The point of all this is not to suggest that behaviour determined by epigenetics is somehow undisturbing in a way that genetically determined behaviour is not. The point is rather to revise the ideas about genetics which, together with the view of evolution to which I shall next turn, have been central to the tradition of simplistic biological explanations of behaviour, of which Evolutionary Psychology is merely the latest example. The assumption of the centrality of the genome mentioned at the beginning of this paper is well summarised by the so-called Central Dogma of Molecular Biology, a thesis first expounded by Francis Crick (1958). Whether or not this was intended with a measure of irony, as the selection of the term ‘dogma’ might suggest, it has been taken very seriously by many later commentators. What the Central Dogma asserts is that information flows in one direction only, from DNA to RNA to proteins. The epigenetic phenomena that I have just mentioned are just one central respect in which this dogma can now be seen wholly misguided. As I have said, the genome, and the DNA it contains is in constant interaction with other molecules and structures in the cell, and the cell is in interaction with other components of the organism. Causal influences run up and down between structures at all levels of the hierarchy that composes the organism.

Evolution

The other idea mentioned at the beginning of this paper is a view of evolution. As presented and widely popularised by Richard Dawkins (1976, and numerous later works) this is a vision of evolution as fundamentally consisting of a long sequence of genomes stretching into the deepest past. This fits perfectly with the second idea, the centrality of the genome, as each of these genomes is seen as carrying the information necessary to construct the organism that will actually confront the world of natural selection. The failure of the Central Dogma to survive recent scientific insights should already raise suspicions about the viability of this picture of evolution, but in this section I shall confront it more directly.

It has frequently been noted that the view of evolution to which I have just alluded, as a sequence of genomes each providing the blueprint or code for an organism, makes possible the complete exclusion from evolutionary theory of the process of development, the process through which the fertilised egg becomes a mature adult. This omission has been the central concern of one important counter-trend in evolutionary biology, evolutionary developmental biology, or evo-devo (see, e.g. Raff 1996; Carroll 2005). Evo-devo has stressed that what most fundamentally evolves in multicellular organisms such as ourselves is the developmental process itself, and this, as I have been stressing is something that involves much more than a set of information encoded in the genome. Complementary to evo-devo, though occasionally accused of being a ‘merely’ philosophical critique of orthodox evolutionary theory, is developmental systems theory (DST) (Oyama et al. 2001).

DST sees the fundamental units of evolution as life cycles, and looks at the reproduction of life cycles as involving a whole nexus of developmental resources that are provided by ancestral organisms to promote the development of descendant organisms. Such resources include, of course, the genome and its enclosing cell and epigenetic inheritance, but also parental behaviour, and a wide range of environmental modifications that organisms make to provide circumstances that favour the successful development of their offspring.

Here I should also mention another very important though more orthodox enhancement of evolutionary theory in recent years, which has obvious affinities with DST, the idea of niche construction (Odling-Smee et al. 2003). The phenomenon was beautifully documented by Charles Darwin (1882), in his classic investigation of the way that earthworms transform the soil in which they live, and do so in ways that produce an environment in which they thrive. Everyone is familiar with the construction of dams by beavers, nests by many species of birds, and complex hives or mounds by the social Hymenoptera or by termites. It is obvious in all these cases that organisms modify their environments in complex ways that are essential features of the processes through which they survive and reproduce, and it is increasingly recognised that this is a quite typical aspect of biological evolution. From the perspective of DST, such modifications of the environment contribute important parts of the developmental nexus that facilitates the replication of life cycles.

Humans have developed this aspect of the developmental process to an extent unprecedented in animal evolution. Maternity wards in hospitals and schools are only the most obvious of the human institutions that provide essential aspects of the process by which humans are reproduced. And of course it is the unique complexity and diversity of human behaviour that makes such environmental resources essential to successful human development. No one, I suppose, imagines that there are genes that cause people to build schools. One reason (of many) why this is an absurd notion is that most people never show the slightest inclination to build a school. The serious point is that human societies exhibit an enormously elaborate division of labour. And this division of labour is one of the things that schools, and many other related institutions, make possible. Whereas the division of labour in insect colonies appears to be largely biologically determined, though the proportions of different types may be controlled by the present needs of the colony, nothing of the sort is true for humans. Adam Smith (1776), who most influentially theorised the idea of the division labour, makes the point vividly:

> The difference between the most dissimilar characters, between a philosopher and a common street porter, for example, seems to arise not so much from nature as from habit, custom, and education. When they came into the world, and for the first six or eight years of their existence, they were perhaps very much alike, and neither their parents nor playfellows could perceive any remarkable difference. About that age, or soon after, they come to be employed in very different occupations. The difference of talents comes then to be taken notice of, and widens by degrees, till at last the vanity of the philosopher is willing to acknowledge scarce any resemblance.

It is a prerequisite for the possibility of such divergence in development that human biology allows for a great deal of behavioural flexibility. In short, the transfer of developmental resources from internal to external is required by the complexity of human social arrangements. But it is important to realise that as with so many human traits taken to be the distinguishing human excellence, this externalisation of developmental resources, though taken to a much greater degree than in any other organism, is far from unique.

Evolutionary Psychology

Let me now return to Evolutionary Psychology. Evolutionary Psychologists suppose that the basic human psychological repertoire consists of a set of specialised modules evolved to deal with the problems that confronted our ancestors in the Stone Age. Why the Stone Age? The answer, at least in opposition to suggestions that much human behaviour is of more recent origin, is simply that they assume an antiquated model of evolutionary change according to which significant evolutionary change must take hundreds of thousands or millions of years. This is a model according to which evolutionary change requires the selection over many generations of a series of incremental changes to the genome, each of which provides an incremental improvement in the adaptedness of the organism. It is easy to see why this would be a slow process. Humans have long generation times, and the spread of a perhaps only slightly advantageous mutation through the population may take many generations. Indeed it is easy to doubt whether a million years or so would be long enough for the evolution of entirely new psychological mechanisms.

But, as I have very briefly explained, there is much more to evolution than this. And we should not see the genome, especially in an organism as complex as the human, as a blueprint, but rather as an extremely large and flexible set of chemical resources. Organisms can come to use these resources in quite different ways, and this use can be stabilised through the creation of reliable cues or further resources in the environment. Such a view of evolution has been developed in great detail and quite generally through the concept of phenotypic plasticity (West Eberhard 2003). In the first place, as the name suggests, this view emphasises the great flexibility with which phenotypes respond in their development to variation in the environment. It is also supposed that a repeatedly adaptive phenotypic response to the environment may be followed by a process of genetic accommodation, in which the adaptive response gradually comes to constitute the default output of the genome. This idea is generally known as the Baldwin Effect, having been proposed as early as 1896 by the American psychologist James Mark Baldwin. When these insights are combined with an awareness of the extent of external developmental resources constructed by contemporary humans, models of the spread of genetic variations derived from classical population genetics become wholly irrelevant to understanding contemporary human behaviour. The idea that humans are properly adapted to life in the Stone Age, but somehow survive in the very different environment of the modern city, seems rather remarkable given that we are surely the most successful large animals currently on the planet—indeed, we've killed off most of the others. Fortunately there is no reason whatever to believe it.

So what should we make of the conclusions about gendered difference so successfully disseminated by Evolutionary Psychologists (Buss 1994; Geary 1998) and earlier by Sociobiologists? As almost everyone knows, their central dogmas are based on an exploration of the differences in evolutionary costs and benefits deriving from different reproductive strategies for males and females. The core premise is that the possible reproductive success of males is much higher, sperm being cheap and plentiful, while eggs are larger and more expensive to produce. Added to the fact that females generally invest considerable resources in gestation and care of infants, the overall female contribution to the cooperative enterprise is much more significant and valuable than that of the male. On this basis, males are predicted to attempt to spread their seed as widely as possible, while females are predicted to try to get maximum value for their scarce resource, either by securing a male partner who will contribute to childcare, or by finding the male with the best possible genes. A more Machiavellian scenario suggests that with a bit of deceit they may manage both, which suggests in turn that the child-rearing male will be keeping a close eye on his partner and will have a low tolerance for any extramarital sex on her part.

I have criticised the standard elaboration of these ideas for human evolution in detail elsewhere (2001a; 2001b), and I shall not repeat this exercise here. For now I want to make some more general points. First, the core argument that I have just sketched is a quite general one, applying to any sexual species in which a considerable amount of pre- or post-natal investment is required by the female for reproduction. I do not doubt that it has wide relevance for understanding a lot of natural history. There are many species in which the most successful males appear to monopolise much of the attention of the females; sometimes this can lead to otherwise maladaptive marks taken by females as measures of male fitness being hugely developed by processes of sexual selection. Highly ornate birds such as peacocks, and huge and aggressive elephant seals are standard exemplars of such sexual systems. The Irish Elk is hypothesised to have driven itself to extinction by excessive sexual selection of the massive antlers of the male, which eventually perhaps dragged it forever into the bog. Many more birds pursue cooperative child-rearing strategies, and here careful observation also suggests that females often pursue the Machiavellian strategy alluded to above, and males do indeed appear to spend a great deal of time spying on their mates in an attempt to prevent this.

So what does this tell us about humans? The Evolutionary Psychologists' project is to consider the so-called environment of evolutionary adaptation, the Pleistocene, and infer which variant of these familiar sexual mating systems is likely to have evolved for humans. Given the rather limited information we have about the environmental conditions that faced humans a million years ago, let alone about their social and sexual mores, this is a difficult task, but there is no shortage of theorists willing to imagine sometimes Flintstonian scenarios relevant to its solution. One might well wonder why it would not be more useful to investigate empirically the actual sexual behaviour exhibited by modern humans. It is true that having constructed their atavistic hypotheses, Evolutionary Psychologists do sometimes engage in such empirical work (e.g. Buss 1994). The problem is that they find that sexual behaviour is both interculturally and intraculturally highly variable. So, armed with their Stone Age hypotheses, the goal is to find the underlying universal tendencies somehow concealed by the vagaries of human history and culture. There is clearly a sense that this underlying biological reality, rather than mere empirical behaviour, is what is important.

We should remember that despite occasional impressions to the contrary that may be gleaned from Evolutionary Psychological writings, much of the behaviour we are considering is far more ancient than Stone Age humans. Female concerns with care of their young and male interests in contributing at least their genes to the reproductive process can certainly be traced to much more distant non-human ancestors. The point of recalling this point is to insist that, contrary to the suggestion most notoriously propagated by Steven Pinker, to reject of the Evolutionary Psychologists' world view is not to embrace the so-called Blank Slate view of human nature according to which culture can write whatever it chooses on an entirely formless human mind. Quite general evolutionary considerations may lead us to suspect that maternal care, a tendency to male promiscuity, and very likely a somewhat more focused female tendency to promiscuity, may be features of human development that will emerge under a wide range of circumstances.

The crucial point, however, is that whatever these deep tendencies, actual empirical observation of both our primate relatives and the diversity of human societies reveals enormous diversity in the relations between the sexes. And once we escape the outdated and limited view of evolution that precludes any real change except over aeons of time, this diversity can be taken at face value, and as clear evidence of the flexibility of human sex/gender systems. Among non-human primates we can find highly promiscuous species such as our own closest relatives the chimpanzees and even more strikingly the Bonobos; the Hamadryas Baboon lives in large groups characterised by moderate polygyny; many species of gibbon appear to be largely monogamous; and Capuchin monkeys live in large groups with a dominant male with pre-eminent sexual access to females; and so on. In the case of humans, numerous cultural anthropologists have documented the diversity of human sexual behaviour and human gender roles, and feminist historians have documented the changes in these aspects of human life in both recent and distant history. Human behaviour, including the behaviour that is differentiated by sex and gender, is extremely flexible and humans can develop in many different ways. As I mentioned earlier such flexibility is indeed a prerequisite for the complex and variable division of labour that is also a unique and distinctive feature of human life. To repeat, this does not mean that the human mind is a Blank Slate, nor that it is a trivial matter to shape human behaviour in particular desired directions. It does mean that there are no simple biological limits to human possibility, and that gender differences are much better studied by detailed exploration of their actual present and historical manifestations than by futile speculations about life in the Stone Age.

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