



## Why Pigs Don't Have Wings

Jerry Fodor

*Die Meistersinger* is, by Wagner's standards, quite a cheerful opera. The action turns on comedy's staple, the marriage plot: get the hero and the heroine safely and truly wed with at least a presumption of happiness ever after. There are cross-currents and undercurrents that make *Meistersinger's* libretto subtle in ways that the librettos of operas usually aren't. But for once Nietzsche is nowhere in sight and nobody dies; the territory is closer to *The Barber of Seville* than to *The Ring*. Yet, in the first scene of Act 3, the avuncular Hans Sachs, whose benevolent interventions smooth the lovers' course, delivers an aria of bitter reflection on the human condition. It comes as rather a shock:

Madness, Madness!  
Madness everywhere.  
Wherever I look . . .  
People torment and flay each other  
In useless, foolish anger  
Till they draw blood.  
Driven to flight,  
They think they are hunting.  
They don't hear their own cry of pain . . .  
When he digs into his own flesh,  
Each thinks he is giving himself pleasure.

So 'what got into Sachs?' is a well-known crux for Wagner fans, and one the opera doesn't resolve. (By Scene 2 of Act 3 Sachs is back on the job, arranging for Walther to get his Eva

and vice versa.) Sachs isn't, of course, the first to wonder why we are so prone to making ourselves miserable, and the question continues to be pertinent. We have just seen the last of a terrible century with, quite possibly, worse to come. Why is it so hard for us to be good? Why is it so hard for us to be happy?

One thing, at least, has been pretty widely agreed: we can't expect much help from science. Science is about facts, not norms; it might tell us how we are, but it couldn't tell us what is wrong with how we are. There couldn't be a science of the human condition. Thus the received view ever since Hume taught that *ought* doesn't come from *is*. Of late, however, this Humean axiom has come under attack, and a new consensus appears to be emerging: Sachs was right to be worried; we are all a little crazy, and for reasons that Darwin's theory of evolution is alleged to reveal. What's wrong with us is that the kind of mind we have wasn't evolved to cope with the kind of world that we live in. Our kind of mind was selected to solve the sorts of problems that confronted our hunter-gatherer forebears thirty thousand years or so ago; problems that arise for small populations trying to make a living and to reproduce in an ecology of scarce resources. But, arguably, that kind of mind doesn't work very well in third millennium Lower Manhattan, where there's population to spare and a Starbucks on every block, but survival depends on dodging the traffic, finding a reliable investment broker and not having more children than you can afford to send to university. It's not that our problems are harder than our ancestors' were; by what measure, after all? It's rather that the mental equipment we've inherited from them isn't appropriate to what we're trying to do with it. No wonder it's driving us nuts.

This picture – that our minds were formed by processes of evolutionary adaptation, and that the environment they are adapted to isn't the one that we now inhabit – has had, of late,

an extraordinarily favourable press. Darwinism has always been good copy because it has seemed closer to our core than most other branches of science: botany, say, or astronomy or hydrodynamics. But if this new line of thought is anywhere near right, it is closer than we had realised. What used to rile Darwin's critics most was his account of the phylogeny of our species. They didn't like our being just one branch among many in the evolutionary tree; and they liked still less having baboons among their family relations. The story of the consequent fracas is legendary, but that argument is over now. Except, perhaps, in remote backwaters of the American Midwest, the Darwinian account of our species' history is common ground in all civilised discussions, and so it should be. The evidence really is overwhelming.

But Darwin's theory of evolution has two parts. One is its familiar historical account of our phylogeny; the other is the theory of natural selection, which purports to characterise the mechanism not just of the formation of species, but of all evolutionary changes in the innate properties of organisms. According to selection theory, a creature's 'phenotype' – the inventory of its heritable traits, including, notably, its heritable mental traits – is an adaptation to the demands of its ecological situation. Adaptation is a name for the process by which environmental variables select among the creatures in a population the ones whose heritable properties are most fit for survival and reproduction. So environmental selection for fitness is (perhaps plus or minus a bit) the process par excellence that prunes the evolutionary tree.

More often than not, both halves of the Darwinian synthesis are uttered in the same breath; but it's important to see that the phylogeny could be true even if the adaptationism isn't. In principle at least, it could turn out that there are indeed baboons in our family tree, but that natural selection isn't how they got there. It's the adaptationism rather than the

phylogeny that the Darwinist account of what ails us depends on. Our problem is said to be that the kind of mind we have is an anachronism; it was selected for by an ecology that no longer exists. Accordingly, if the theory of natural selection turned out not to be true, that would cut the ground from under the Darwinist diagnosis of our malaise. If phenotypes aren't selected at all, then there is, in particular, nothing that they are selected for. That applies to psychological phenotypes *inter alia*.

In fact, an appreciable number of perfectly reasonable biologists are coming to think that the theory of natural selection can no longer be taken for granted. This is, so far, mostly straws in the wind; but it's not out of the question that a scientific revolution – no less than a major revision of evolutionary theory – is in the offing. Unlike the story about our minds being anachronistic adaptations, this new twist doesn't seem to have been widely noticed outside professional circles. The ironic upshot is that at a time when the theory of natural selection has become an article of pop culture, it is faced with what may be the most serious challenge it has had so far. Darwinists have been known to say that adaptationism is the best idea that anybody has ever had. It would be a good joke if the best idea that anybody has ever had turned out not to be true. A lot of the history of science consists of the world playing that sort of joke on our most cherished theories.

Two kinds of consideration now threaten to displace natural selection from its position at the centre of evolutionary theory; one is more or less conceptual, the other is more or less empirical.

*The conceptual issue.* There is, arguably, an equivocation at the heart of selection theory; and slippage along the consequent faultline threatens to bring down the whole structure. Here's the problem: you can read adaptationism as saying that environments select creatures for their fitness; or

you can read it as saying that environments select traits for their fitness. It looks like the theory must be read both ways if it's to do the work that it's intended to: on the one hand, forces of selection must act on individual creatures since it is individual creatures that live, struggle, reproduce and die. On the other hand, forces of selection must act on traits since it is phenotypes – bundles of heritable traits – whose evolution selection theory purports to explain. It isn't obvious, however, that the theory of selection can sustain both readings at once. Perhaps the consensus view among Darwinists is that phenotypes evolve because fit individuals are selected for the traits that make them fit. This way of putting it avoids the ambiguity, but whether it's viable depends on whether adaptationism is able to provide the required notion of 'selection for'; and it seems, on reflection, that maybe it can't. Hence the current perplexity.

History might reasonably credit Stephen J. Gould and Richard Lewontin as the first to notice that something may be seriously wrong in this part of the wood. Their 1979 paper, 'The Spandrels of S. Marco and The Panglossian Paradigm: A Critique of the Adaptationist Programme', ignited an argument about the foundations of selection theory that still shows no signs of quieting. A spandrel is one of those more-or-less triangular spaces that you find at the junctures of the arches that hold up a dome. They are often highly decorated; painters competed in devising designs to fit them. Indeed (and this is Gould and Lewontin's main point), casual inspection might suggest that the spandrels are there because they provide the opportunity for decoration; that, an adaptationist might say, is what spandrels were selected for. But actually, according to Gould and Lewontin, that gets things backwards. In fact, spandrels are a by-product of an arch-and-dome architecture; decide on the latter and you get the former for better or worse. Arches were selected for holding up domes;

spandrels just came along for the ride.

I assume that Gould and Lewontin got their architectural history right, but it doesn't really matter for the purposes at hand. What matters is that though spandrels survived and flourished, nothing at all follows about what, if anything, they were selected for. To a first approximation, you have spandrels if and only if you have a dome that's supported by arches; the two are, as logicians say, coextensive. Is it, then, that selection for arches explains why there are spandrels? Or is it that selection for spandrels explains why there are arches? It looks, so far, as though the story could go either way; so what tips the balance? Surely it's that domes and arches are designed objects. Somebody actually thought about, and decided on, the architecture of San Marco; and what he had in mind when he did so was that the arches should support the dome, not that they should form spandrels at their junctures. So that settles it: the spandrels weren't selected for anything at all; they're just part of the package. The question, however, is whether the same sort of reasoning can apply to the natural selection of the phenotypic traits of organisms, where there is, by assumption, no architect to do the deciding. If cathedrals weren't designed but grew in the wild, would the right evolutionary story be that they have arches because they were selected for having spandrels? Or would it be that they have spandrels because they were selected for having arches? Or neither? Or both?

It's a commonplace that Darwin constructed the theory of natural selection with an eye to what breeders do when they choose which creatures to encourage to reproduce. This reading of Darwin is by no means idiosyncratic. Darwin 'argues by example, not analogy,' Adam Gopnik wrote in the *New Yorker* in October last year. 'The point of the opening of "The Origin" isn't that something similar happens with domesticated breeds and natural species; the point is that the very same thing happens, albeit unplanned and over a much

longer period.' It's true, of course, that breeding, like evolution, can alter phenotypes over time, with consequent effects on phylogenetic relations. But, on the face of it, the mechanisms by which breeding and evolution operate could hardly be more different. How could a studied decision to breed for one trait or another be 'the very same thing' as the adventitious culling of a population? Gopnik doesn't say.

The present worry is that the explication of natural selection by appeal to selective breeding is seriously misleading, and that it thoroughly misled Darwin. Because breeders have minds, there's a fact of the matter about what traits they breed for; if you want to know, just ask them. Natural selection, by contrast, is mindless; it acts without malice aforethought. That strains the analogy between natural selection and breeding, perhaps to the breaking point. What, then, is the intended interpretation when one speaks of natural selection? The question is wide open as of this writing.

The answers that have been suggested so far have not been convincing. In particular, though there is no end of it in popular accounts of adaptationism, it is a Very Bad Idea to try and save the bacon by indulging in metaphorical anthropomorphisms. It couldn't, for example, be literally true that the traits selected for are the ones Mother Nature has in mind when she does the selecting; nor can it be literally true that they are the traits one's selfish genes have in mind when they undertake to reproduce themselves. There is, after all, no Mother Nature, and genes don't have, or lack, personality defects. Metaphors are fine things; science probably couldn't be done without them. But they are supposed to be the sort of things that can, in a pinch, be cashed. Lacking a serious and literal construal of 'selection for', adaptationism founders on this methodological truism.

There are delicious ironies here. Getting minds in general, and God's mind in particular, out of biological explanations is a

main goal of the adaptationist programme. I am, myself, all in favour of that; since I'm pretty sure that neither exists, I see nothing much to choose between God and Mother Nature. Maybe one can, after all, make sense of mindless environmental variables selecting for phenotypic traits. That is, maybe one can get away with claiming that phenotypes are like arches in that both are designed objects. The crucial test is whether one's pet theory can distinguish between selection for trait A and selection for trait B when A and B are coextensive: were polar bears selected for being white or for matching their environment? Search me; and search any kind of adaptationism I've heard of. Nor am I holding my breath till one comes along.

*The empirical issue.* It wouldn't be unreasonable for a biologist of the Darwinist persuasion to argue like this: 'Bother conceptual issues and bother those who raise them. We can't do without biology and biology can't do without Darwinism. So Darwinism must be true.' Darwinists do often argue this way; and the fear of hyperbole seems not to inhibit them. The biologist Theodosius Dobzhansky said that nothing in biology makes sense without Darwinism, and he is widely paraphrased. The philosopher Daniel Dennett says that 'in a single stroke, the idea of evolution by natural selection unifies the realm of life, meaning and purpose with the realm of space and time, cause and effect, mechanism and physical law.' (Phew!) Richard Dawkins says, 'If superior creatures from space ever visit earth, the first question they will ask, in order to assess the level of our civilisation, is: "Have they discovered evolution yet?"' Shake a stick at a Darwinist treatise and you're sure to find, usually in the first chapter, claims for the indispensability of adaptationism. Well, if adaptationism really is the only game in town, if the rest of biology really does presuppose it, we had better cleave to it warts and all. What is indispensable therefore cannot be dispensed with, as



Wittgenstein might have said. The breaking news, however, is that serious alternatives to adaptationism have begun to emerge; ones that preserve the essential claim that phenotypes evolve, but depart to one degree or other from Darwin's theory that natural selection is the mechanism by which they do. There is now far more of this sort of thing around than I am able to survey. But an example or two may give the feel of it.

Adaptationism is a species of what one might call 'environmentalism' in biology. (It's not, by any means, the only species; Skinnerian learning theory is another prime example.) The basic idea is that where you find phenotypic structure, you can generally find corresponding structure in the environment that caused it. Phylogeny tells us that phenotypes don't occur at random; they form a more or less orderly taxonomic tree. Very well then, there must be nonrandomness in the environmental variables by which the taxonomic tree is shaped. Dennett has put this idea very nicely: 'Functioning structure carries implicit information about the environment in which its function "works". The wings of a seagull . . . imply that the creature whose wings they are is excellently adapted for flight in a medium having the specific density and viscosity of the atmosphere within a thousand metres or so of the surface of the Earth.' So, phenotypes carry information about the environment in which they evolved in something like the way that the size, shape, whatever, of a crater carries information about the size, shape, whatever, of the meteor that made it. Phenotypes aren't, in short, random collections of traits, and nonrandomness doesn't occur at random; the more nonrandomness there is, the less likely it is to have been brought about by chance. That's a tautology. So, if the nonrandomness of phenotypes isn't a reflection of the orderliness of God's mind, perhaps it is a reflection of the orderliness of the environments in which the phenotypes evolved. That's the theory of natural selection in a nutshell.

But as soon as it's put that way, it's seen not to be the only possibility. External environments are structured in all sorts of ways, but so, too, are the insides of the creatures that inhabit them. So, in principle at least, there's an alternative to Darwin's idea that phenotypes 'carry implicit information about' the environments in which they evolve: namely, that they carry implicit information about the endogenous structure of the creatures whose phenotypes they are. This idea currently goes by the unfortunate soubriquet 'Evo-Devo' (short for 'evolutionary-developmental theory'). Everybody thinks evo-devo must be at least part of the truth, since nobody thinks that phenotypes are shaped directly by environmental variables. Even the hardest core Darwinists agree that environmental effects on a creature's phenotype are mediated by their effects on the creature's genes: its 'genome'. Indeed, in the typical case, the environment selects a phenotype by selecting a genome that the phenotype expresses. Once in place, this sort of reasoning spreads to other endogenous factors. Phenotypic structure carries information about genetic structure. And genotypic structure carries information about the biochemistry of genes. And the biochemical structure of genes carries information about their physical structure. And so on down to quantum mechanics for all I know. It is, in short, an entirely empirical question to what extent exogenous variables are what shape phenotypes; and it's entirely possible that adaptationism is the wrong answer.

One can think of the Darwinian account of evolution as prompted by the question: why are some phenotypes more similar than others? Darwin's answer was that phenotypic similarity is, pretty generally, explained by common ancestry; and the more similar two creature's phenotypes, the less remote is the nearest ancestor that they share. There are isolated examples to the contrary, but there's no serious doubt

that this account is basically correct. And, if it's not the best idea anybody ever had, it's pretty good by any of the local standards. When you ask Darwin's question – why are phenotypes often similar? – you do indeed get Darwin's answer. But if you ask instead why it is that some phenotypes don't occur, an adaptationist explanation often sounds somewhere between implausible and preposterous. For example, nobody, not even the most ravening of adaptationists, would seek to explain the absence of winged pigs by claiming that, though there used to be some, the wings proved to be a liability so nature selected against them.

Nobody expects to find fossils of a species of winged pig that has now gone extinct. Rather, pigs lack wings because there's no place on pigs to put them. To add wings to a pig, you'd also have to tinker with lots of other things. In fact, you'd have to rebuild the pig whole hog: less weight, appropriate musculature, an appropriate metabolism, an apparatus for navigating in three dimensions, a streamlined silhouette and god only knows what else; not to mention feathers. The moral is that if you want them to have wings, you will have to redesign pigs radically. But natural selection, since it is incremental and cumulative, can't do that sort of thing.

Evolution by natural selection is inherently a conservative process, and once you're well along the evolutionary route to being a pig, your further options are considerably constrained; you can't, for example, go back and retrofit feathers.

That all seems reasonable on the face of it; but notice that this sort of 'channelling' imposes kinds of constraint on what phenotypes can evolve that aren't explained by natural selection. Winged pigs were never on the cards, so nature never had to select against them. How many such cases are there? How often does a phenotype carry information not about a creature's environment but about aspects of its endogenous structure? Nobody knows.

But it bears emphasis that, on this way of thinking about evolution, the mechanisms by which phenotypes are constructed may very well be numerous and heterogeneous. This is one of the important ways in which evo-devo differs from adaptationism. Darwinists generally hold that natural selection, even if it isn't all there is to evolution, is vastly the most important part. By contrast, channelling couldn't conceivably explain the structure of phenotypes all by itself. But that leaves it open that channelling might be one among many mechanisms by which phenotypes express endogenous structure, and which, taken together, account for (some? many? all of?) the facts of evolution. If, as I suggested, the notion of natural selection is conceptually flawed, such alternatives would be distinctly welcome.

Here's another kind of process that appears to explain some (very striking) facts about phenotype formation, but is quite different from either adaptation or channelling. In fact, it takes us back to spandrels. Gould and Lewontin say that spandrels are an artefact of selection for arches. Lacking arches, domes fall down; so arches are selected for supporting domes. But arches are linked to spandrels for reasons of geometry; so spandrels aren't selected for, they are 'free riders' on selection for arches. The moral is that phenotypic traits can carry information about linkages among the mechanisms that produce them. Free-riding is always suggestive of such linkages, and free-riding is ubiquitous in evolution.

There's a really lovely experiment that provides an example. The working hypothesis was succinctly summarised by Lyudmila Trut in *American Scientist* in 1999: 'Because behaviour is rooted in biology, selecting for tameness and against aggression means selecting for physiological changes in the systems that govern the body's hormones and neurochemicals. Those changes, in turn, could have had far-reaching effects on the development of the animals

themselves, effects that might well explain why different animals would respond in similar ways when subjected to the same kinds of selective pressures.’ In the vocabulary I’ve been using: one might expect a galaxy of other phenotypic traits to be endogenously linked to tameness, and hence to free-ride on selection for it. Such properties would co-evolve with tameness even if they have little or no systematic effect on fitness; in effect there would be evolution without adaptation. Moreover, insofar as the genetic and physiological mechanisms that link tameness to its free-riders hold across a range of species, one might expect that selecting for tameness will have similar phenotypic by-products in creatures of quite different kinds.

The experimental investigation of these hypotheses involved forty years of inbreeding for tameness in thirty or so generations of silver foxes. The results are impressive. On the one hand, foxes that were bred for tameness also tended to share a number of other phenotypic traits. Unlike their feral cousins, they tend to evolve floppy ears, brown moulting, grey hairs, short curly tails, short legs and piebald coloration (in particular, white flashes). Inbreeding for tameness also had characteristic effects on the reproductive cycles of the foxes and on the average size of their litters. And these are all traits that other domestic animals (dogs, cats, goats, cows) also tend to have. An adaptationist might well wonder what it is about dogs, cats etc that makes curly tails good for their fitness in an ecology of domestication. The answer, apparently, is ‘nothing’. Curly tails aren’t fitness enhancing, they just happen to be linked to tameness, so selection for the second willy-nilly selects the first.

This case is much like that of spandrels, but much worse from an adaptationist’s point of view. You can explain the linkage between domes, arches and spandrels; the geometry and mechanics of the situation demands it. But the ancillary phenotypic effects of selection for tameness seem to be

perfectly arbitrary. In particular, they apparently aren't adaptations; there isn't any teleological explanation – any explanation in terms of fitness – as to why domesticated animals tend to have floppy ears. They just do. It's possible, of course, that channelling and free-riding are just flukes and that most or all of the other evolutionary determinants of phenotypic structure are exogenous. It's also possible that palaeontologists will someday dig up fossilised pigs with wings. But don't bet on it.

So what's the moral of all this? Most immediately, it's that the classical Darwinist account of evolution as primarily driven by natural selection is in trouble on both conceptual and empirical grounds. Darwin was too much an environmentalist. He seems to have been seduced by an analogy to selective breeding, with natural selection operating in place of the breeder. But this analogy is patently flawed; selective breeding is performed only by creatures with minds, and natural selection doesn't have one of those. The alternative possibility to Darwin's is that the direction of phenotypic change is very largely determined by endogenous variables. The current literature suggests that alterations in the timing of genetically controlled developmental processes is often the endogenous variable of choice; hence the 'devo' in 'evo-devo'.

But I think there's also a moral about what attitude we should take towards our science. The years after Darwin witnessed a remarkable proliferation of other theories, each seeking to co-opt natural selection for purposes of its own. Evolutionary psychology is currently the salient instance, but examples have been legion. They're to be found in more or less all of the behavioural sciences, to say nothing of epistemology, semantics, theology, the philosophy of history, ethics, sociology, political theory, eugenics and even aesthetics. What they have in common is that they attempt to explain why we are so-and-so by reference to what being so-and-so buys for

us, or what it would have bought for our ancestors. 'We like telling stories because telling stories exercises the imagination and an imagination would have been a good thing for a hunter-gatherer to have.' 'We don't approve of eating grandmother because having her around to baby-sit was useful in the hunter-gatherer ecology.' 'We like music because singing together strengthened the bond between the hunters and the gatherers (and/or between the hunter-gatherer grownups and their hunter-gatherer offspring)'. 'We talk by making noises and not by waving our hands; that's because hunter-gatherers lived in the savannah and would have had trouble seeing one another in the tall grass.' 'We like to gossip because knowing who has been up to what is important when fitness depends on co-operation in small communities.' 'We don't all talk the same language because that would make us more likely to interbreed with foreigners (which would be bad because it would weaken the ties of hunter-gatherer communities)'. 'We don't copulate with our siblings because that would decrease the likelihood of interbreeding with foreigners (which would be bad because, all else being equal, heterogeneity is good for the gene pool)'. I'm not making this up, by the way. Versions of each of these theories can actually be found in the adaptationist literature. But, in point of logic, this sort of explanation has to stop somewhere. Not all of our traits can be explained instrumentally; there must be some that we have simply because that's the sort of creature we are. And perhaps it's unnecessary to remark that such explanations are inherently post hoc (Gould called them 'just so stories'); or that, except for the prestige they borrow from the theory of natural selection, there isn't much reason to believe that any of them is true.

The high tide of adaptationism floated a motley navy, but it may now be on the ebb. If it does turn out that natural selection isn't what drives evolution, a lot of loose speculations

will be stranded high, dry and looking a little foolish.

Induction over the history of science suggests that the best theories we have today will prove more or less untrue at the latest by tomorrow afternoon. In science, as elsewhere, 'hedge your bets' is generally good advice.

As for Sachs, I wouldn't think of arguing that we are either mostly happy or mostly good. But I doubt that's because of what our minds were selected for. Maybe the real trouble is that our neurones aren't hooked together quite right, or that some of our hormones aren't entirely reliable; with the effect, in either case, that getting some of the things we want isn't compatible with getting the others. Or that some of them we can't have at all. Anyhow, for what it's worth, I really would be surprised to find out that I was meant to be a hunter-gatherer since I don't feel the slightest nostalgia for that sort of life. I loathe the very idea of hunting, and I'm not all that keen on gathering either. Nor can I believe that living like a hunter-gatherer would make me happier or better. In fact, it sounds to me like absolute hell. No opera. And no plumbing.

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**Jerry Fodor** is collaborating with Massimo Piattelli-Palamarini on a book about evolution without adaptation.

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