

The evolutionary approach to human behaviour

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Why do some women of a certain age opt for plastic surgery in an attempt to preserve their youth? Why do the husbands of Dogon women in Mali insist that their wives spend five days a month living alone in a small dark hut? Why are step-children at greater risk of fatal abuse than a parent's natural offspring? And just what is it that makes a man with a fast car and a strong chin that much more attractive than your basic Mr Average?

At first glance, these would seem to be four entirely unrelated questions, each requiring a completely different explanation. But, as in most things, first impressions can be misleading. In fact, there is a theory that explains all of these phenomena, that reveals the natural connections that exist between them. This is the theory of evolution by natural selection. Our aim in this book is to demonstrate that by adopting an evolutionary perspective on human behaviour and psychology, we can provide a coherent unified explanation of human social evolution and adaptation.

In order to do this, we first have to recognise that humans are animals like any other, and that we can thus explain our behaviour using the same models used to explain the behaviour of lions or blackbirds or baboons. Inevitably, some people find this suggestion disturbing. They don't really like being lumped in with the rest of the animal kingdom. Even Alfred Russel Wallace, co-founder with Darwin of the theory of evolution by natural selection, couldn't accept that humans were actually animals. He preferred to think that, at the crucial point, God intervened to place humans on the side of the angels, so placing us a cut above the rest of creation. The

same argument still persists today, although ‘culture’ now replaces God as the means by which we are able to rise above the beasts. Of course, in a very real sense, this is true: the impact of culture on human behaviour is enormous and not to be underestimated. The very fact that you are sitting here reading this book is testament to that fact. As clever as our closest relatives, the chimpanzees, are, they do not write books, play musical instruments, undergo psychoanalysis, build skyscrapers or launch spaceshuttles. Only we do.

As humans, we have been able to transform the natural world to suit us and, by virtue of our capacity for language, we have also been able to create and live in ‘virtual worlds’ – worlds where intangible ideas and imaginary flights of fancy are as important and meaningful as solid objects. Ever since modern humans first evolved, we have been transforming both nature and, as a consequence, ourselves to the extent that we have become less dominated by nature, with culture playing a more prominent role. Consequently, understanding human nature is not a problem for biology alone. As Malik (2000) puts it: ‘Culture is not a mere encrustation upon human nature, like dirt on a soiled shirt. It is an integral part of it because human nature can only be expressed through human culture’ (see also Plotkin 1998).

On the other hand, human nature and culture both have biological roots. Unless you are a Creationist, you have to accept that humans have been subject to the same processes of evolutionary change as all other living things on earth. A full understanding of human nature therefore requires an understanding of biological as well as sociological processes. Indeed, it is actually impossible to separate the two. We are products of an interaction between biology and culture, or to put it in its more familiar guise, nature and nurture, genes and environment. To separate the two is a false dichotomy. Many would argue that human nature cannot be reduced to mere biological processes – and they would be right. But to infer from this, as many do, that biology is now completely irrelevant (see many of the papers in Rose and Rose 2000) is to commit an egregious logical error. In what follows, we shall try to show that those who espouse this view could not be more wrong.

The resistance to biological explanations of our behaviour is in part a reaction to an over-enthusiastic application of evolutionary theory to humans in a way that seems to leave no room for cultural influences (see, for example, Pinker 1997, Baker 2000, Dennett 1995). It smacks too heavily of genetic determinism for some people and therefore questions human morality and free will. Their view seems to be that we must resist acknowledging our biological roots because, if we accept them, this must mean that our biological inheritance is solely responsible for determining our behaviour: biology as destiny. This is to commit what has been dubbed the ‘naturalistic fallacy’ (that the way things are is the way they ought to be) so that criminals are ‘born, not made’, and men can’t help philandering because ‘it’s in their genes’.

But to understand our evolutionary history and recognise its antecedents in the animal kingdom is not to deny what it is to be human. In fact, it can only add to our understanding of the human condition, and possibly even help us overcome human frailty. It can explain why we have to teach our children to share (since they won’t do it naturally); it can shed light on why people prefer to gossip about their neighbours than solve problems in differential calculus; it can even help explain why our seas are over-fished despite our best efforts to regulate such practices.

In fact, an evolutionary perspective on human behaviour and psychology, far from promoting the view that we are automatons driven relentlessly by our genes, actually highlights our inherent flexibility or ‘**phenotypic plasticity**’ – the ability to vary responses according to circumstances, to learn from experience, to recognise and exploit opportunities as they arise. Above all else, we shall show that phenotypic plasticity

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is the most important of the human evolutionary adaptations, and that any accusations of genetic determinism are simply misplaced. Before we can begin to look at human behaviour from an evolutionary perspective, however, we need to be clear about what we mean by the term ‘evolutionary’.

NATURAL SELECTION

The first thing to establish is that evolution is not a theory, but a fact. The fossil record shows that species have changed through time; they have diverged and transmuted and become entirely new species. This is all (literally) hard evidence, and as such very difficult to question. The ‘theory’ bit of evolution comes in with respect to the process by which these changes occurred. This was Charles Darwin’s (Darwin 1859) and Alfred Russel Wallace’s great insight: the theory of natural selection. As theories go, this one is particularly straightforward and easy to grasp, being based on just three premises and their logical consequence (Dunbar 1982):

Premise 1: All individuals of a particular species show variation in their behavioural, morphological and/or physiological traits – their **‘phenotype’**. (This is usually known as the Principle of Variation).

PHENOTYPE

Premise 2: A part of this variation between individuals is **‘heritable’**: some of that variation will be passed on from one generation to the next or, to put it even more simply, offspring will tend to resemble their parents more than they do other individuals in the population. (The Principle of Inheritance).

HERITABLE

Premise 3: There is competition among individuals for scarce resources such as food, mates and somewhere to live, and some of these variants allow their bearers to compete more effectively. This competition occurs because organisms have a great capacity to increase in numbers, and can produce far more offspring than ever give rise to breeding individuals – just think of frogspawn, for example. (The Principle of Adaptation).

Consequence: As a result of being more effective competitors, some individuals will leave more offspring than others because the particular traits they possess give them some sort of edge: they are more successful at finding food or mating, or avoiding predators. The offspring of such individuals will have inherited these successful traits from their parents, and ‘natural selection’ can be said to have taken place. Through this process, organisms become ‘adapted’ to their environment. The success with which a trait is propagated in future generations relative to other variants of that trait is called its **fitness**. Fitness is a measure of relative reproductive success – that is, relative to alternative variants of the same trait; strictly speaking, it is a property of traits. (This is sometimes known as the Principle of Evolution).

FITNESS

It is important to notice here that we have deliberately avoided mentioning the terms **DNA** (the genetic code) and **gene** or anything suggesting that the mechanism of inheritance in Premise (2) entails a particular biochemical process. This is because the theory of natural selection as originally conceived by Darwin and Mendel (who identified the mechanism of inheritance missing in Darwin’s original formulation) makes no mention of genes as we know them today. As Dawkins (1983) has pointed out, Mendel’s theory of inheritance is constructed entirely in terms of phenotypic characters and makes no assumptions about the process of heredity other than that

DNA, GENE

there is fidelity of copying between parents and offspring. Any mechanism that allows fidelity of copying ensures that natural selection will take place. In so far as the theory of natural selection is concerned, learning is as much a bona fide mechanism of evolutionary inheritance as the genetic code.

This perhaps surprising conclusion is important for much of what follows for two reasons. First, it allows us to avoid unnecessarily fruitless arguments about whether or not a particular behaviour is genetically determined. This frees us up to consider behavioural strategies as genuine Darwinian entities subject to the influence of natural selection – a device that evolutionary biologists like Maynard Smith (1982) have long exploited without any sense of discomfort (see Dunbar 1995a). Second, as a consequence, it allows us to consider culture (which is transmitted only by learning: see Chapter 13) as part and parcel of the Darwinian world, and hence a legitimate object for evolutionary analysis.

BOX 1.1

Speciation and the evolutionary processes

Not surprisingly perhaps, the theory of evolution has been dominated by what we might properly refer to as genetically determined characters. This is because biologists have been mainly concerned to explain the evolution of species, and these are defined by their phenotypic traits (that is, appearance). In this respect, genes are the proper mode of inheritance.

The phenotype is produced by an interaction between the individual's genetic makeup (or '**genotype**') and the environment. The source of variation is genetic mutation, whereby physical changes occur in DNA (the genetic code). These mutations result in changes in protein synthesis and ultimately to changes in the way that phenotypic traits are expressed in the organism. Selection acting on the phenotypic characters results in those genes that produce these characters being passed on to the next generation in greater numbers.

One of the consequences of natural selection is that, over time, individuals tend to track their environments and the ecological niches that become available to them. For example, among birds, a seed-eating niche requires a different beak shape (thick and robust for cracking seeds and nuts) to a nectar-feeding niche (a long thin pointed beak that can get into the nectaries of flowers). Exactly these kinds of changes in beak morphology are found among the finches of the Galapagos islands.

The finches were discovered by Darwin himself and helped him to formulate his theory of

the origin of species. On the Galapagos islands today, there are 14 different species of finch that are all descended from a single ancestral species. Radiation into all the available niches and subsequent reproductive isolation between individuals of the original ancestral species gave rise to this diverse array and provide us with one of our best examples of evolution in action. Grant and Grant (1993) have shown that small changes in beak shape and size among these bird populations from one year to the next can be attributed directly to the effects that these have on birds' abilities to survive and reproduce as climatic and vegetation conditions change.

Although genetic mutation is the engine of natural selection, the processes of adaptive radiation and reproductive isolation are essential elements in the origin of new species. Reproductive isolation occurs when individuals within populations are prevented from breeding and, consequently, genes are not freely exchanged throughout the population. This can occur because of the formation of geographical barriers: for example, a new mountain range may arise and divide a species' population in two with the result that mating can only occur within each sub-population instead of throughout the entire population as before. As a consequence, the two populations diverge from each other genetically due to the action of mutation, natural selection (that is, adaptation to local conditions) and 'drift' (random changes in gene frequencies not driven by natural selection).

ASKING THE RIGHT QUESTIONS

While a good understanding of evolutionary theory is obviously essential if we are to understand why humans behave in the way that they do, it is also important to realise that just as there is more than one way to skin a cat so there are a number of different reasons for asking ‘why?’ in the first place. Understanding the reason why a particular question is being asked is all important since this determines the kind of the answer that one can expect. In a seminal paper, the ethologist Niko Tinbergen (1963) identified four ways in which to ask the seemingly simple question: why?

First, one might wish to know what motivates an animal or a person to behave in a particular way at a particular moment in time; that is, what is the immediate or *proximate* cause of the behaviour. An answer to this question might be couched in terms of the impact that stimuli have on the nervous system and the manner in which this triggers the appropriate response in the organism. It answers questions about mechanisms that produce behaviour, and hence is sometimes referred to as the *mechanistic* cause.

Alternatively, one might wish to know why an individual performed the behaviour in a particular way; what was it about their upbringing or development that led to them adopting a particular way of performing actions (the developmental or *ontogenetic* cause of the behaviour)? An answer to this type of question would require an investigation into the factors that shape development throughout the lifespan, including both their genetic inheritance and the impact of learning on the individual.

Another reason for asking why is to understand the evolutionary history of the behaviour; when did it arise in the first place and why did it follow the particular evolutionary path that it did? This is known as the *phylogenetic* or historical cause. To answer this kind of question, one needs to look back at the fossil record and identify the changes that occurred through evolutionary time.

Finally, one can ask why the behaviour increases an animal’s ability to survive and reproduce. This is known as the functional or *ultimate* cause. This is the causal explanation most closely linked to natural selection. Since natural selection works by a process of differential reproduction across individuals, we need to understand why a particular behaviour promotes (or hinders) the production and survival of offspring in order to identify and assess the impact of particular selection pressures.

For example, take the question: why does a woman suckle her baby? This can be answered in terms of:

- (i) *Proximate or mechanistic cause*: the baby was crying and/or the mother’s breasts were full of milk.
- (ii) *Developmental or ontogenetic cause*: the mother learned to care for babies while she was growing up by observing other females suckling their babies. In addition, she may have an innate (built-in) tendency to show positive caring behaviours toward infants that is triggered by the presence of a young baby.
- (iii) *Phylogenetic or historical cause*: humans are mammals and like all members of this group, they produce milk with which to feed their offspring. This explanation would also include an account of how mammals evolved from their non-mammalian ancestors: what sequence of changes was involved in moving from a species that laid eggs (and perhaps reared its young in a nest) to one that could nurture and grow its offspring inside its body and then feed the young with milk once they were born?
- (iv) *Functional or ultimate cause*: By suckling her offspring, a mother provides them with all the nutrients and energy they need to survive and grow, thus increasing

their chances of surviving to maturity, thereby passing the mother's genes on to future generations.

As should be apparent, each of these explanations tackles a different 'level' of explanation that is logically quite independent of the others. An understanding at one level does not presuppose or necessitate an understanding at any of the other levels; nor, more importantly, does it commit us to any *particular* explanation at any of these other levels (the same function may be subserved by several different proximate mechanisms, and may arise either genetically or by learning). On the other hand, being able to provide answers at two or more levels at the same time can be helpful. If we can provide mutually consistent answers at all four levels, for example, then we can be fairly confident that we have achieved a full account of the phenomenon under study. For example, demonstrating the existence of a proximate mechanism that would produce the functional consequences we have inferred strengthens the case for both levels of explanation.

The thing to avoid at all costs, however, is confusing one level of explanation with another. To argue about whether mothers suckle their babies in order to stop them crying or in order to ensure that they survive (and so propagate their mother's genes) is pointless: both explanations are right, and there is no reason, other than personal bias, to think that any one level is 'more correct' or should take precedence over any of the others.

When studying non-human animals, it is usually quite easy to keep levels of explanation separate. However, with humans it is often much more difficult – especially with regard to proximate and ultimate levels of explanation. This may be partly a consequence of human consciousness and self-awareness. We are often aware that there is a functional explanation underlying our behaviour, even though we recognise that any particular instance is motivated by more proximal factors. To go back to our previous example, mothers may feed their infants because they are crying, but they may also be aware that feeding is essential to promote the growth and continued survival of the baby and this could therefore be regarded as a proximate cue prompting them to suckle their offspring. This ability to recognise and understand the long-term consequences of our actions may explain why we occasionally confuse different kinds of explanation.

The flip-side of this is that we often assume that because we are, for the most part, conscious of our motivations, then we must be conscious of all our decision-making processes. This leads people to question whether we would be able to work out the sometimes complicated calculations that seem necessary to explain behaviour: for example, calculating kinship relations (see Chapter 3) or maximising the rate of energy intake (Chapter 4). However, these are calculations for which evolution has worked out the answer, so we don't actually have to do them in our heads. People who question the abilities of humans to make these calculations often have no problem believing that desert ants find their way back to their nestholes using polarised light and trigonometry. With the ant, it is more obvious that natural selection has created animals with this ability programmed into them and that the ant's brain (such as it is) has very little to do with it. However, certain aspects of human behaviour may operate in exactly the same manner. Studies of humans therefore have to be very explicit about (a) the type of explanation they are attempting to provide and (b) whether evolution has selected for a cognitive ability or an unconscious pre-programmed 'rule of thumb'.

BOX 1.2

Reductionism vs holism

Opponents of the evolutionary approach to the study of human behaviour often argue that biology is a reductionist science (explanations for phenomena are given in terms of lower level phenomena, for example genes or, even more extreme, chemistry). In contrast, they argue, human behaviour is complex and can only be studied holistically in terms of cultural or sociological explanations. In part, this view derives from the work of the French sociologist Émile Durkheim who argued (at the end of the nineteenth century) that cultural phenomena cannot be studied biologically, but rather must be explained by reference to other cultural phenomena.

The claim that the evolutionary approach is necessarily reductionist rests on a misunderstanding of what evolutionary explanations entail, probably because of the significance attached to genes in all evolutionary explanations. However, reference to the (genetic) fitness of traits (or behaviour) does not necessarily imply that the trait (or behaviour) is genetically determined, but rather that it has genetic *consequences* in terms of the numbers of extra offspring it allows the bearer to produce. In effect, the reductionist argument confuses two different levels of explanation: ontogenetic arguments (genes as *developmental* determinants of behaviour) with functional arguments (gene replication as the measurable *consequence* of behaviour). In such cases, the genetic consequence of a well-chosen behavioural decision could simply be the propagation of the gene(s) for a brain complex enough to make smart decisions; it would thus have nothing at all to do with the particular behavioural outcomes.

In addition, it is important to note that evolutionary explanations are never couched solely in terms of lower level phenomena such as genes or other chemical processes. The genetic fitness of behaviour is the outcome of a decision (which requires some kind of cognitive machinery to support it) in the context of a whole range of ecological, demographic and social factors. The latter are crucial to a proper evolutionary understanding of behaviour because they determine the costs and benefits that the organism assesses when choosing between two or more courses of action. As a result, the behavioural strategies of most higher organisms (and, a fortiori, humans) are very flexible and are fine-tuned to the particular circumstances in which the individual finds itself.

Were this not so, such large-bodied long-lived species as birds and mammals would not be able to survive since they experience many variations in their environment over the course of their lives which require a flexible response. Indeed, behavioural flexibility of this kind may have been crucial to the evolutionary success of these species (a phenomenon known as the **Baldwin Effect**).

In effect, then, evolutionary explanations of behaviour (sometimes referred to as *behavioural ecology*) are necessarily holistic in that they inevitably refer not just to lower level disciplines (genetics, chemistry, cognitive psychology) but also to other 'higher' level disciplines (history, economics, cultural processes) as well as to variables at the same logical level (the behaviour of competitors and predators, the interests of offspring and allies). For further discussion, see Dunbar (1995a).

Once the nature of the question being asked has been established, the next thing to do is decide on an appropriate research strategy to determine the answer. This may sound straightforward, but in the field of evolutionary psychology it has led to some rather heated debates. Essentially, the arguments put forward hinge on how the term 'biological adaptation' is defined. It is to these that we now turn.

APPROACHES TO THE STUDY OF HUMAN BEHAVIOUR

The broad field of study that we characterise as human evolutionary psychology (that is, the evolutionary-oriented study of human behaviour and cognition) is currently divided into two quite distinct camps who disagree fundamentally on some key issues. In this section, we summarise their basic positions. In the following section, we will try to draw them together into a unified framework.

HUMAN BEHAVIOURAL ECOLOGY

On one side of the fence, there are those individuals who take a functional perspective and consider a trait to be biologically adapted if it increases the fitness (the number of genes passed to future generations) of those who bear the trait relative to those who do not. Individuals working in this field adopt an approach that is virtually identical to that taken by behavioural ecologists who study non-human animals (see, for example, Krebs and Davies 1997). That is, human behavioural ecology (HBE) focuses on measuring differences in reproductive success between individuals in relation to differences in the behavioural strategies that they follow (Smith et al. 2000). Because many of those who adopt this perspective were originally trained in anthropology, they are sometimes referred to as ‘Darwinian anthropologists’ (DA).

This kind of study usually involves observing and quantifying the study subject’s natural behaviour and correlating this with measures of their reproductive output or some appropriate proxy of this. Alternatively, in the time-honoured tradition of comparative analyses established by Darwin himself, it can take the form of large cross-cultural studies based on survey or census data. Due to its focus on reproductive outcomes it has been dubbed the ‘counting babies’ approach (Crawford 1993).

The HBE approach makes extensive use of formal mathematical modelling to generate testable predictions. Since mathematics has a unique capacity to turn people off, we would enter a plea here for its importance. Mathematical modelling allows us to do two important things, namely (1) to evaluate the effect of our assumptions and (2) to explore the interactions between several contributing factors that influence a given behavioural outcome. The first is important because it forces us to specify exactly how we think a process works in a way that is difficult to fudge. The second is important because humans are notoriously bad at being able to visualise the consequences of more than one explanatory variable at a time: we have trouble thinking in anything more than two dimensions and this limits us to thinking about one cause and one effect. Evolutionary analyses are particularly susceptible to this problem because they invariably involve trade-offs between two driving variables (a cost and a benefit) as well as a pay-off (the fitness consequences) even when there is only one benefit for a particular action.

Because the use of mathematical modelling in this way is a feature of all mature sciences (Dunbar 1995a), we shall not shirk from presenting mathematical treatments where these are relevant. However, in deference to most people’s tolerance of these matters, we will confine our treatments to verbal expositions wherever possible. Indeed, it is a maxim of good modelling that any mathematical model that cannot be explained in simple English is probably so poorly understood by the modeller as to be wrong.

Many of the studies conducted using the HBE approach have been conducted in environments that are thought to have remained stable for many thousands of years –

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for example, the !Kung San tribe of Southern Africa (Lee 1979, Howell 1979) or the Yanomamö of Amazonia (Chagnon 1974, 1988) – or at least largely uninfluenced by western culture – for instance, the Kipsigis (Borgerhoff Mulder 1988a, b) and the Gabbra of Kenya (Mace 1996a, b). There is thus a temptation to assume that studying these tribal peoples is close to studying our ancestors, and that the traits possessed today can therefore be considered to have increased the fitness of individuals in the past as well as in the present day. In other words, that selection pressures operating today are identical to those that operated in past environments.

This may not always be true, of course, for any one of several reasons. First, there is much archaeological evidence to show that even hunter-gatherer lifestyles have changed considerably over the course of the last 10 000 years or so (Caro and Borgerhoff Mulder 1987, Shennan 2000). Second, there are examples where individual behaviour is found to be sub-optimal, suggesting that we might be witnessing time-lag effects as individuals adjust to new selection pressures (for example, Borgerhoff Mulder 1988a, 1995). Finally, behaviours that confer selective advantages today need not have been selected for that purpose in the past: they may have evolved for another reason entirely, and later become secondarily co-opted into their present role by a change in environmental circumstances – a process known as exaptation (Gould and Vrba 1983).

In some cases, of course, the inference that a behavioural trait that is adaptive today was also adaptive in the past may, in fact, be perfectly accurate. However, there is no way to prove this if the only evidence available is based on current reproductive differentials. To be able to state with any confidence that behavioural traits accorded the same reproductive benefits to individuals in the past as they do in the present, we must be able to demonstrate that past conditions were the same as those which promote the behaviour in contemporary populations, and that the trait has been transmitted faithfully across the generations. This is true not only for studies of humans, but also for non-human animals. Such evidence is obviously very hard to come by, especially for humans, due to our sketchy knowledge of palaeoenvironments and the ethical restrictions preventing human breeding experiments (something which is much less of a problem for studies of non-human animals).

It is thus very difficult to validate claims concerning traits as the product of selection, and any such claims should be treated rather cautiously. Essentially, all behavioural ecologists, whether they study human or non-human animals, play what Grafen (1984) has called ‘the **phenotypic gambit**’. As Smith (2000) puts it: ‘this means taking a calculated risk to ignore the (generally unknown) details of inheritance (genetic or cultural), cognitive mechanisms, and phylogenetic history that may pertain to a given decision rule and behavioural domain in the hope that they don’t matter in the end result’. Evidence of current fit between behaviour and its functional consequences is then taken as sufficient evidence to justify the claim that this provides an explanation for the evolution of the behaviour or trait in question. Taking shortcuts of this kind is considered quite normal in science (Dunbar 1995a).

These limitations aside, ‘counting babies’ and estimating current reproductive benefits of a particular trait provide valuable information about how natural selection is acting in the present and can provide insights into the evolutionary process overall. It is an approach that has proved enormously successful in the study of animal behaviour and shows no sign of being any less productive when applied to human behaviour. Furthermore, as Caro and Borgerhoff Mulder (1987) point out, concentrating on current fitness differentials is a cautious approach to adopt when asking evolutionary questions, since it relies only on features that can actually be measured. This is not to deny the impact of past selection pressures, for, as Betzig (1989) has warned, we

shouldn't ignore the history in natural history. But equally, we shouldn't extrapolate beyond the bounds of our data. Our ability to demonstrate that a trait is a product of past selection is much more limited than our ability to identify the pressures that maintain a trait in the present. Conversely, of course, being able to demonstrate a selective advantage that is likely to maintain a trait in the present is no small achievement, since the evolutionary processes that operate in the present are those that guide a trait's evolution in the future.

In short, studies that look only at current adaptiveness do not ignore our evolutionary history; rather, they are simply not designed to confront the issue at that particular level of analysis. Their real interests lie in determining whether or not evolutionary considerations (such as maximising fitness) underpin individual organisms' behavioural decisions and in studying the dynamics of the evolutionary process.

EVOLUTIONARY PSYCHOLOGY

On the other side of the fence from the human behavioural ecologists – and facing in an entirely different direction – are those who consider themselves to be practising evolutionary (or Darwinian) psychology (EP). As might be expected, workers in this area study human adaptation from a largely psychological perspective and their parent discipline is not behavioural ecology but cognitive psychology. The aim of EP is to identify the selection pressures that have shaped the human psyche over the course of evolutionary time, and then test whether our psychological mechanisms actually show the features one would expect if they were designed to solve these particular adaptive problems (for example, choosing mates or detecting cheats). Accordingly, the human psyche is envisaged as being composed of a number of specialised 'domain-specific modules' or 'mental algorithms' rather than a small number of generalised mechanisms that can cope with the whole range of adaptive problems.

In contrast to the HBE approach, EP does not consider the demonstration of reproductive benefits necessary to determine whether or not a particular feature is an adaptation. Instead, they look for evidence of 'good design' that points to the operation of selection in the past. Evolutionary psychologists thus focus on identifying the design features of human psychological adaptations, and make no attempt to determine whether particular traits contribute to fitness differentials in the present. Consequently, most of their studies are conducted in the lab, using batteries of psychological tests or questionnaires. To date, relatively few studies in this field have looked at subjects' behaviour in a natural environment.

Clearly, this is quite a different approach to that adopted by the behavioural ecologists, and to some extent reflects the large differences between the parent disciplines from which the two arise (zoology and behavioural ecology in the case of HBE, cognitive psychology in the case of EP). While the 'phenotypic gambit' means that HBE can be agnostic about the actual psychological mechanisms that humans use to make their decisions and thus focus solely on outcomes, EP is committed to identifying these mechanisms in precise detail (while having much less interest in the outcomes). This difference in focus led to misunderstandings between the two camps when EP first emerged as a discipline and spawned a large amount of rather acrimonious debate (for example, Symons 1989, 1990; Tooby and Cosmides 1990; Turke 1990), some of which continues (albeit in more polite vein) to this day (Daly and Wilson 1999, 2000; Smith 2000; Smith et al. 2000; Sherman and Reeve 1997).

BOX 1.3

The problem of external validity

Most EP (and some HBE) studies rely on what are sometimes referred to as 'pencil-and-paper' methods rather than the direct observation of behaviour (as is perhaps more typical of most HBE studies). These typically involve giving subjects questionnaires or short vignettes of particular situations and asking them to say how they would respond if they found themselves in that particular situation. Two important criticisms can be made of this approach.

One is that what people say they will do in the benign conditions of an interview or questionnaire may be an entirely different thing to what they actually do when faced with the real circumstances. Similar problems arise when we use written sources (such as historical records or advertisements in personal columns) as sources of data on people's behaviour or intentions. As socio-cultural anthropologists have frequently learned to their cost, humans the world over are notorious for the fact that they will often tell you what they think you want to hear rather than what they actually believe to be the case. In some cases, this may be out of a sense of politeness to the interviewer, but in other cases it may be because the way they would actually behave when push came to shove would be considered morally reprehensible.

Although this will always be a problem with studies that rely on self-report by subjects, it is not an insurmountable problem providing we are aware of it. Questionnaires, for example, can be designed with questions that allow lying to be detected, while written sources can always be treated with a healthy dose of scepticism (if only because the victors in a contest invariably seek to rewrite the history of an event in their favour). However, lying is in itself an evolutionarily interesting phenomenon for two reasons: (a) it forms part and parcel of the cognitively complex social processes underpinned by Machiavellian intelligence (see Box 6.1) and (b) it reflects the role of culture in modulating the conflict between indi-

vidual selfishness and the benefits of group co-operation (see Chapters 2, 4 and 9).

The second criticism of the pencil-and-paper approach is that such tests are invariably carried out on a very small sample of modern humans. In terms of sheer number of studies, the workhorse of these studies is the North American undergraduate, most of whom are white, middle class and (culturally) Euro-American. Evolutionary psychologists would be inclined to argue that, since what they study are the universal aspects of the way the human mind is designed, one group of subjects ought to be much the same as any other, just as livers from one group of humans are much the same as the livers from all other humans.

While this is a defensible position (and conveniently avoids accusations of racism), two notes of caution should be sounded. First, there are genetic differences between human races that have real behavioural and fitness consequences (Cavalli-Sforza et al. 1994). (Two examples that we discuss further in Chapter 13 are sickle cell anaemia – a defence against malaria – and lactose tolerance – the ability to drink milk as an adult.) It may be heuristically unwise not to check that all human minds really do have the same construction. Second, everything depends on whether we are measuring a fundamental *cognitive mechanism* (such as the way memories are coded and stored in the brain) or the *behavioural outcomes* of a cognitive mechanism. While the former may well be universal traits, the latter are strongly affected by current circumstances (in particular, the costs and benefits that drive behavioural decisions). Moreover, socio-cultural anthropologists would insist that the construction of the human mind itself is influenced by local cultural perspectives. While the latter position is certainly debatable (see Dunbar 1995a), it may be unwise to ignore this possibility altogether since, at least at a superficial level, it may turn out to have some validity.

ENVIRONMENT OF EVOLUTIONARY ADAPTEDNESS

ENVIRONMENT OF EVOLUTIONARY ADAPTEDNESS

One important source of disagreement between the two approaches centres around the concept of the **Environment of Evolutionary Adaptedness** (or **EEA**). This issue arises out of the fact that EP and HBE disagree about the extent to which we can expect humans to be adapted to current environments. HBE argues that humans are likely to be well adapted to current environments due to a capacity for rapid shifts in phenotype as a consequence of increases in brain size and a capacity for flexible ‘off-line’ planning of action (Smith 2000). EP on the other hand takes the view that the massive cultural changes that have taken place in the last 10 000 years have occurred at a pace that is simply too fast to allow human brains (and hence behaviour) to adapt. The psychological adaptations we possess today were selected for in our past environment of evolutionary adaptedness (EEA) (Bowlby 1969, 1973) and are not geared for the modern world. Consequently, EP argues that, a priori, there is no reason to expect any modern behaviour to be adaptive since present environments are so different from those in which the behaviour evolved (Cosmides and Tooby 1987).

As defined by Tooby and Cosmides (1990), the EEA is no particular point in time or space, but is ‘a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations’. Put more simply, the EEA is the conglomeration of selection pressures that have operated on humans over the course of evolution and, in this sense, it is really quite uncontroversial. However, most authors (including Tooby and Cosmides themselves: see Tooby and Cosmides 2000, p. 1170) have operationalised this definition by placing the EEA at some time in the **Pleistocene** (roughly the last 2.5 million years) prior to the advent of agriculture 10 000 years ago and the cultural revolution of the last 40 000 or so years. By doing so, they imply that modern environments and modern selection pressure do not form part of the human EEA. Consequently, we are, as Eaton et al. (1988) would have it, ‘Stone agers in the fast lane’. The world to which we are adapted no longer exists, but, due to evolutionary lags, we continue to behave as though it does; consequently, our psychological mechanisms inevitably result in behaviour that no longer produces reproductively successful outcomes.

PLEISTOCENE

All this is, of course, entirely possible, and examples can no doubt be quoted from studies of animals. However, it is equally plausible that (as HBE assumes) human behaviour does, in fact, produce adaptive outcomes in the modern world, and there is at least as much evidence from studies of animal behaviour (including, for example, optimal foraging theory) to support this claim. The a priori assumption that behaviour is currently maladaptive has no firm evidence to support it (other than the studies which assume that this is the case in the first place).

In addition, there are two further problems with the EEA concept. One is that human evolutionary history has in fact been a mosaic process in which different components arose at different stages under very different ecological environments (Foley 1995a; Strassman and Dunbar 1999). Identifying the EEA with a particular period in time overlooks the fact that some components of a phenomenon may predate others. Second, as Malik (2000) points out, ‘we humans have not simply been dropped into an alien environment. *We created that environment . . .* If the brain is “wired up” to create modernity, why is it not wired up to cope with it?’ In other words, there is no a priori reason to suppose that current behaviour shouldn’t be adaptive. It is, instead, an empirical issue that can only be tested by measuring current fitness differentials.

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BOX 1.4

Human evolution

The last common ancestor between the great apes and the line leading to modern humans (the hominids) lived around 5 to 7 million years ago. The earliest certain members of our lineage, the **australopithecines** (meaning 'southern apes'), are found as fossils dating from 4.5 to around 2 million years ago (MYA).

The australopithecines walked on two legs (bipedal) like modern humans, but had brains approximately the same size as modern great apes. Although capable of fully bipedal locomotion, they had long arms and rather long, curved finger and toe bones suggesting they were also at home in the trees. The australopithecines are often viewed as the first primitive step towards modern humanity, but they were, in fact, a highly adapted species in their own right. Their unique form of locomotion, for example, was not just a 'transitory' step between life in trees to life on the ground, but was a stable and successful adaptation in itself that remained essentially unchanged during the period that australopithecines were alive.

The australopithecines were a highly successful group of animals in their time, persisting for nearly three million years and diversifying into a number of different species. They can be divided into two main groups, the gracile forms and the robust forms. The gracile forms were small and slender, with a diet that included both plant and animal matter. The robust forms, by contrast, became highly specialised for a tough, vegetarian diet, evolving massive jaws and enormous cheek-teeth (molars). The robust forms survived the longest (until around 2 MYA according to the fossil record) and were contemporaneous with the earliest fossil specimens of our own genus, *Homo*.

The genus *Homo* is thought to have arisen from one of the gracile australopithecines. The earliest *Homo*, distinguished by an increase in brain size relative to the australopithecines, belongs to the species *Homo habilis*, from around 2.5 to

2 MYA. *Homo habilis* means 'handy man', and was so named because the first evidence of tool use was associated with these fossils (however, there is now some evidence to suggest that australopithecines may have used simple tools: Asfaw et al. 1999). When first discovered, *H. habilis* was considered to be a distinct species and one of our direct ancestors. As the number of fossil finds has increased, evidence is accumulating to suggest that the fossils making up *H. habilis* should in fact be regarded as at least two (if not more) species (*H. habilis* and *H. rudolfensis*) – see Tattersall (2000) for review – and some workers dispute whether they are, in fact, members of the genus *Homo* at all (Wood and Collard 1999). This increase in the number of species makes it much harder to know which (if any) was ancestral to the line that led to modern humans. The human family tree is very bushy, with lots of side branches representing an adaptive radiation of hominid species in the newly emerging savannah environments of the Pleistocene.

A more advanced form of hominid, *Homo erectus*, with a further increase in brain size and larger stature, arose around 2 MYA. Like *H. habilis*, *H. erectus* was initially thought to be a single species, but more recent finds suggest that there are at least two different species (*H. erectus*, and an earlier species *H. ergaster* that was found only in Africa). *H. erectus* is the first hominid to be found outside Africa (there are many sites in southeast Asia with *H. erectus* fossils) and it is the first to be associated with fire. They also made use of more advanced tools than *H. habilis* but the form of the tools remains remarkably stable through time; there are no advances or innovations made to improve their form. This stasis has fascinated archaeologists and palaeoanthropologists alike, and there has been some speculation about the psychological capacities and attributes of these individuals based on tool form (Mithen 1996).

Irons (1998) recommends adopting a different concept in which to situate human behavioural and psychological studies: the **adaptively relevant environment**. He argues that the adaptively relevant environment of an adaptation consists of those features of the environment that organisms must interact with to confer a reproductive advantage and that, as a rule, there are only a few key features that need to be present for an adaptation to confer its advantage on its possessors. Environmental novelty may therefore disrupt some adaptations but not others; it all depends on whether or not the key features with which the adaptation needs to interact have been affected. So there are undoubtedly some modern behaviours that are non-adaptive (deliberate lifelong use of contraceptives to avoid all chance of reproduction, addictive drug use and modern eating habits, to name but a few) due to a very recent historical origin (for example, only 40 years or so in the case of the contraceptive pill), but some traits (such as mate choice or parenting strategies) continue to be adaptive since the adaptively relevant environment still persists.

Another point to remember, and one very nicely pointed out by Sherman and Reeve (1997), is that a reliance on the concept of the EEA means that the EP approach is just as limited as that of HBE when it comes to identifying traits as the products of selection. As we have pointed out, HBE studies of current reproductive success and adaptive function may not enlighten us about past adaptation, since we cannot know for certain that the environment has remained constant, or that the behaviour actually evolved for the purpose it now serves. However, these are arguments that can also be levelled at the study of psychological mechanisms, since these are just as much an aspect of the phenotype as particular behavioural traits (that is, they are both products of a gene-environment interaction), and as such are just as likely to be confounded by significant changes in the environment (Sherman and Reeve 1997).

Identifying psychological mechanisms as adaptations thus requires a good knowledge of the EEA in which the traits evolved, and evidence that the traits have been transmitted faithfully through time for the same purpose that they serve today. If the EEA cannot be characterised satisfactorily, then it is, at best, a heuristic convenience and, at worst, an unsupported assumption. Consequently, EP will then be as limited as HBE in its ability to illuminate the process of evolutionary adaptation. By the same token, if we can be confident about the nature of past environments and the EEA, then both the EP and HBE approaches may be equally useful, if used cautiously.

Finally, a note of caution. It is important to remember that identifying selection pressures that create or maintain adaptations can often be extremely difficult. We should beware of concluding that a trait is maladaptive simply because we cannot see an obvious advantage to it. Sometimes, the selection processes involved can only be identified after a very careful detailed analysis. The so-called 'demographic transition' that has resulted in a dramatic reduction in birth rates among those who live in western industrialised countries may be a case in point (see Chapter 6). The claim that a trait has no function or is maladaptive may simply be a statement of ignorance. As a general rule of thumb, therefore, the conclusion that a trait is maladaptive should be an explanation of last resort after all other possible adaptive explanations have been excluded (Dunbar 1982).

TOWARDS A UNIFIED APPROACH

In what follows, it may appear as though we are defending the position of HBE against that of EP. This is only because workers in EP have tended to be more vocal

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and upfront in their criticism of the HBE approach. However, this should not be taken to imply that we find the HBE approach preferable to that of EP. As we have pointed out, different questions require different answers and both EP and HBE are needed to answer those concerned with human adaptation. Rather, our aim is to try to bridge the gap between the two approaches and develop a single coherent theoretical framework for the study of human behaviour and cognition. Indeed, on a broader front, what follows in the rest of the book might be seen as an attempt to provide a single overarching theoretical framework for the behavioural sciences, in particular psychology (a discipline that is notoriously fragmented into a number of sub-disciplines that spend most of their time trying to ignore each other).

One of the main sources of antagonism between the HBE and EP camps focuses on the issue of whether current behaviour and reproductive differentials are relevant to the study of adaptation. The view of the EP camp is that studies of current reproductive differentials tell us little about the process of adaptation, because (by definition) adaptations are the result of past selection pressures. The pressures that operate today on a particular trait to produce reproductive differentials tell us nothing about the pressures that led to the evolution of the trait in the first place. The human eyeball, for example, displays abundant evidence that it is adapted for visual perception, and an investigation of visual processes reveals more about the nature of that adaptation than a comparison of the reproductive success of sighted versus blind individuals. Thus, in order to discover the nature of human psychological adaptation, EP looks for similar evidence of ‘good design’ (Williams 1966). This approach is perfectly valid and quite uncontroversial: if one wants to look for evidence of good design, reproductive differentials are not particularly illuminating.

However, in the early days of EP, this assertion was often made in a way that implied that not only were reproductive differentials not useful to the EP approach, but they were not useful *at all* in the study of human behaviour and adaptation. Symons (1990), for example, asserted that ‘studies of adaptiveness (that is, current fitness differentials) have no significance *in and of themselves*’. Some even went so far as to suggest that studies of current fitness were not sufficiently Darwinian. John Tooby was quoted by Symons (1990), for example, as stating that ‘the study of adaptiveness merely draws metaphysical inspiration from Darwinism, whereas the study of adaptation is Darwinian’.

This was very unfortunate since in most cases, the EP contingent was not, in fact, arguing that measuring reproductive differentials was pointless per se, only that it was not a useful way to help *them* to achieve their particular goals (see also the recent debate between Daly and Wilson [2000] and Smith et al. [2000]). Indeed, in a paper that has been held up as a defining example of the EP view, Tooby and Cosmides (1990) insist that ‘there is nothing wrong per se with documenting correspondences [between behaviour and reproductive success] and in fact such investigations can be very worthwhile’ – a more conciliatory (if condescending) view than that with which they are usually credited. However, for the most part, this recognition of the value of HBE was not apparent in many early EP writings (Symons 1989, 1990; Barkow 1990) and, in some cases, still isn’t today (see Buss 1995).

Not surprisingly, human behavioural ecologists were a little irritated by the implication that they didn’t understand evolution properly. With their background in animal behavioural ecology and theoretical evolutionary biology, human behavioural ecologists can legitimately claim to understand evolution extremely well. If a particular study does suggest that their data on current function can necessarily explain past selection without offering supporting evidence for this assumption, then this is, properly

BOX 1.5

Modern human origins

The traditional view assumes that modern humans arose from the populations of *H. erectus* that emerged out of Africa around 1.0 to 1.5 MYA. After colonising Eurasia, these pre-human populations subsequently underwent independent evolution in different parts of the world to produce the various human races seen today. This is known as the **multi-regional hypothesis**. Although evolution occurred independently, proponents of the multi-regional hypothesis assume that there was sufficient gene flow between the populations to prevent reproductive isolation and speciation from occurring (although this would have required gene exchange across a geographical range that biologists would consider unusual, even for highly mobile species like birds).

During the late 1980s, an alternative hypothesis was proposed, based on evidence from molecular genetics. Known as the '**Out-of-Africa**' or 'African Eve' hypothesis (see Stringer and McKie 1996), this suggested a much more recent origin for modern humans. This hypothesis argued that all living humans share a recent common ancestor (or very small number of ancestors) that lived in Africa some time between 100 000 and 200 000 years ago. After occupying virtually the whole of sub-Saharan Africa, one population crossed the Levant landbridge around 70 000 years ago and, over the next 30 000 years, spread rapidly across Eurasia and into Australia, finally breaching the Bering Strait to cross into the New World by around 15 000 years ago.

The principal evidence on which the Out-of-Africa hypothesis was based came from molecular genetics, and particularly from an analysis of variations in the molecular composition of mitochondrial DNA (Cann et al. 1987, Stoneking and Cann 1989). Mitochondria are the tiny elements within living cells that are primarily responsible for providing the cell's energy; thought to have originated as bacteria that successfully invaded living cells at an early stage in the evolution of life on earth, they are not part of the DNA that makes up the chromosomes in the cell's nucleus, but instead are passed on only through the maternal line in

the cellular matter (cytoplasm) that surrounds the nucleus in the egg.

Comparison of the number of differences in the base pair sequences of mitochondrial DNA from individuals of different living races suggested that all modern humans share a recent common ancestor (or very small group of ancestors). In addition, all non-African peoples (plus a small number of Africans) share a smaller number of mitochondrial DNA variants, suggesting an even more recent common ancestor (dated to around 70 000 years ago).

Because mitochondria are inherited only through the maternal line, this means their evolution is not affected by the complexities of inter-sexual selection. Hence, their evolution represents a relatively unblemished record of the descent history of particular lineages. In addition, because their function as the cell's powerhouses buffers them against the impact of natural selection due to environmental change, any changes that do occur in their genetic code are likely to be a consequence of random mutations rather than active selection. Since mutations normally occur at random, the number of differences between the mitochondrial DNA of two individuals can be used (with appropriate corrections for back mutations and other statistical effects) to estimate the length of time since they last shared a common ancestor (the so-called **molecular clock**).

The Out-of-Africa hypothesis has a number of important implications for how we interpret human ancestry. First, it suggests that the Neanderthals of Europe and western Asia could not have been direct ancestors of modern humans (Europeans or otherwise) – a fact confirmed by molecular evidence that their DNA is sufficiently different from that of all modern humans to indicate a much deeper common ancestor around 600 000 years ago (Krings et al. 1997). Second, it rules out the possibility that any modern human races evolved out of different populations of *Homo erectus*. Third, the speed with which early modern humans colonised Eurasia and Australia suggests that they were characterised by an

BOX 1.5 cont'd

Modern human origins

extraordinary level of behavioural flexibility in the face of environmental and geographical challenges for which their long evolutionary history in Africa could not have prepared them.

While these two views of modern human origins have remained locked in sometimes vitriolic dispute for the past decade (for example, Templeton 1993), the weight of genetic (including Y-chromosome sequence data) and fossil evidence has, over the intervening years, come down increasingly strongly in favour of the Out-of-Africa hypothesis (or something very close to it) with a consensus date for the origin of all

modern humans somewhere around 150 000 years (Stoneking 1993, Aiello 1993; Cavalli-Sforza et al. 1994, Lahr and Foley 1994, Relethford 1995, Hammer and Zegura 1996, Ingman et al. 2000). More importantly, both mitochondrial and nuclear DNA (for example, the Y-chromosome, which is passed down only through the male line) suggest that the ancestral breeding population at the common origin was very small (about 5000 individuals of each sex). The latter represents the individuals whose DNA has contributed to all living humans, not necessarily the total number of individuals alive at the time.

speaking, a failing on the part of an individual researcher rather than an indictment of the HBE programme as a whole. However, we caution once again about drawing an absolute rift between past and current function (or between the selection forces responsible for a trait's original evolution and those currently responsible for its maintenance): in some cases (and this may be especially true of behaviour), current function does reflect past function.

However, we could take the more ambitious view that, so far from being irrelevant, studies of current fitness can help to provide a more complete explanation than the EP approach can achieve alone. If studies of current fitness and psychological mechanism coincide, then we can be much more confident in the evolutionary explanations we advance since, in essence, what we are doing is providing an explanation at both the proximate and ultimate levels of explanation. Because the two approaches are (and should be) complementary, cooperation between them should yield an outcome in terms of understanding that is more than just the sum of its parts. Indeed, when all is said and done, biologists actually use both fitness (the HBE approach) *and* evidence of design (the EP approach) as equally appropriate alternatives for identifying adaptation (Dunbar 1993a).

Another source of antagonism between EP and HBE was (and still is) related to the adoption of the phenotypic gambit (Grafen 1984) in behavioural ecological studies. Behavioural ecologists assume that individuals behave 'as if' they are attempting to maximize their fitness. As pointed out above, when they do this, behavioural ecologists make no assumptions about the underlying cognitive mechanisms that produce behaviour. Instead, they choose to ignore these processes altogether and focus on the outcomes of behaviour. However, EP researchers (for example, Symons 1990) have sometimes over-interpreted the nature of the 'as if' assumption. They take it to imply that the human mind operates using one general-purpose rule that states 'maximize the number of offspring raised to maturity'. Such an all-purpose rule would be unlikely to result in adaptive behaviour, since, as the EPs point out, efficient functioning in everyday life requires achieving a large number of proximate goals that are only distantly related to reproductive goals (Symons 1990). Again, this is a misunderstanding of what each approach is trying to achieve. The question as to whether or not the

mind is made up of a number of 'domain-specific' modules is irrelevant to HBE studies in just the same way that studies of fitness differentials are irrelevant to the study of good phenotypic design. Behavioural ecologists have always made it clear that their use of the language of conscious decision-making is a convenient metaphor for evolutionary processes and does not imply anything about the underlying cognitive processes that might be involved.

The emphasis on behavioural outcomes in HBE studies has also been criticised on the grounds that 'Natural selection cannot select for behaviour *per se*; it can only select for the mechanisms that produce behaviour' (Tooby and Cosmides 1990). This has been interpreted as meaning that behaviour is not an appropriate focus for the study of human adaptation. As before, the message of the EPs was actually less condemnatory than is often reported. Tooby and Cosmides (1990), for example, state that 'Turke [1990] argues that behaviour can be an adaptation just as much as any other phenotypic property can be and, depending on exactly what is meant by the word behaviour, we agree with him'. If behaviour is taken to be the manifest phenotypic expression of an underlying cognitive trait, then, for Tooby and Cosmides (1990), it is appropriate to consider it an adaptation. However, it seems likely that they want to argue for a stronger interpretation than this, namely that behaviours cannot themselves be viewed as something whose design is honed by natural selection (in the sense that eyeballs represent a good design for vision); only psychological mechanisms can be viewed in this way. This is certainly a defensible position, and in fact, most studies of HBE implicitly make the same assumption when they play the phenotypic gambit.

However, one could equally take the position that expressed behaviour is 'visible' to natural selection in a way that brain processes are not. It is behaviour that operates 'out in the world' and, since natural selection acts in the world, it is behaviour that maximises fitness. Furthermore, the nature of neurobiological growth and learning mechanisms means that different patterns of neural activity can lead to the same behaviour and, by the same token, different behaviours can occur as the result of the same neurological processes. If this is the case, then what exactly is being selected – neurological structures or the behaviours they produce? While it makes sense to argue that the physical structure of the brain can be subject to evolutionary change, it is also clear that behaviour can be subject to the process of natural selection. That, after all, is exactly what learning is all about.

This particular aspect of the dispute between EP and HBE is especially puzzling since just those kinds of human behaviour that the behavioural ecologists concentrate on have long been a legitimate focus of interest within psychology where it traditionally falls under the rubric of social psychology. Within traditional psychology, social psychologists and cognitive psychologists generally get along fine (or, more accurately perhaps, simply ignore each other) and view their particular specialisations as complementary. They study different aspects of psychology using different methodologies but, as far as we know, neither has ever accused the other of being completely misguided or irrelevant to the issue of understanding human psychology. The different types of psychologist can adopt this neutral view of each other because they constitute quite separate fields within modern psychology, and do not have any overarching framework (such as evolutionary theory) in common.

However, if EP – which is in effect cognitive (plus developmental?) psychology with evolution added – has greater explanatory power as a consequence of taking a strong evolutionary stance, then HBE could be seen as social psychology with evolution added. Indeed, evolutionarily informed studies of human psychology provide the

role model for how the various branches of psychology could be reunited under a single intellectual umbrella. HBE studies provide a perfect example of how social psychology could be improved enormously by conducting studies that lie within an immensely solid theoretical framework. In short, evolutionary psychology is not just the study of universal cognitive mechanisms, but rather the wrapping together in a single unified framework of all of psychology's rather disparate sub-disciplines.

Having said this, however, some human behavioural ecologists (for example, Smith et al. 2000) wish to remain distinct from the evolutionary psychologists, arguing that theirs is an older more established discipline that can and should stand alone. While this is a fair point, we feel that a truly evolutionary psychology should encompass HBE studies, both for the reason outlined above and also because human behaviour is more heavily influenced by culture than that of other animals. HBE studies will not be able to provide a comprehensive explanation of human behaviour if aspects of cognition are not accounted for. Interestingly enough, the need to abandon part of the phenotypic gambit and pay more attention to psychological mechanisms is something that is becoming increasingly common in studies of animal behavioural ecology (Krebs and Kacelnik 1991, Kacelnik and Krebs 1997, Guilford and Dawkins 1992).

One further plea should be entered at this point. Not a few of those who consider themselves to be evolutionary psychologists (in the broad sense rather than the narrower EP sense) have argued quite insistently that a true evolutionary psychology should include observational and experimental studies of other animals besides humans (for example, Byrne 1995). After all, if the past explains the present, this must surely mean our distant evolutionary past as well as our more recent purely human history. In a similar vein, Heyes (2000) argues that 'human nativist evolutionary psychology' is just one of four possible routes to study the evolution of cognitive mechanisms, emphasising that comparative, developmental and phylogenetic approaches should also be considered a part of evolutionary psychology. Indeed, it would be a shame if evolutionary psychology became associated solely with the study of universal psychological traits in humans. If we seem to play down this point in what follows, it is simply because constraints of space oblige us to do so.

Another important thing to remember when considering the value of studying psychological mechanisms as opposed to behaviour is that the former often requires the verbal reporting of things that occur inside people's heads (since there is no other way to get in there). Since verbal behaviour is a phenotypic feature like any other kind of behaviour, it will also have been subject to selection, and may not provide an entirely transparent 'window to the mind' (Sherman and Reeve 1997). Trivers (1985) has pointed out that self-deception may have evolved in order to improve our ability to deceive others; after all, what could make a lie more convincing than your belief that you are actually telling the truth? Consequently (and rather ironically), evolutionary psychologists should not be dismissing behaviour as a focus of study; instead, they should be attempting to incorporate behavioural data into their research programme as a check on whether self-reports match up with actual behaviour.

One final point is that neither EP nor HBE, even when rigorously applied, can provide a complete explanation of human behaviour, since not all human behaviour is either necessarily adaptive (fitness-promoting) or an adaptation. As we pointed out at the beginning of the chapter, cultural processes must be taken into account if we are to get a complete picture of human nature. In fact, there are those (for example, Boyd and Richerson 1985) who argue that the study of cultural processes (including their mechanisms of transmission) constitutes a 'Third Way' (which they refer to as **Dual Inheritance Theory**, or **DIT**). Unlike HBE and EP, DIT explicitly takes culture

into account and then explores the effect that this has on genetic inheritance and transmission. According to DIT, culture and genes are independent but interacting systems of evolutionary change with cultural influences affecting traditional genetic selection in sometimes unexpected ways. This is partly because of differences in the way that cultural information is transmitted, how it varies between individuals and the kinds of fitness effects it produces. For example, cultural information can be passed from parent to offspring (vertical transmission), between peers (horizontal) or from teacher to pupil (oblique), whereas genetic information is only ever transmitted vertically. One of the consequences of this is that it speeds up the pace of cultural evolution compared to genetic evolution (see Chapter 13).

Although some theoretical advances have been made in this area (see Chapter 13), few studies in either HBE or EP have, as yet, acknowledged the importance of culture as an explanation for many facets of human behaviour. Indeed, even in this book, we are concerned mainly with exploring how far a biological explanation can take us, rather than trying to present a fully rounded explanation of human behaviour. Such a book will not appear for quite a few years yet, we imagine – for reasons that will perhaps become clear in Chapter 13. In the main, this is because something similar to the phenotypic gambit is being played in respect of culture by both EP and HBE: neither deny the importance of cultural processes, but they nonetheless choose to ignore them for the purposes of their studies and take the risk that the outcome won't be too badly affected by so doing. As long as this is recognised by all – biologists and non-biologists alike – there should be no problem. It is only when the 'biological' or 'scientific' gambit is misconstrued as a rejection of factors that operate at the societal or cultural level that trouble arises.

What should be apparent from this debate is that although both camps have made mistakes as to what particular research strategies can and cannot achieve, the two approaches are however entirely compatible, and could be combined to great effect. Studies that aim to look at current reproductive differentials provide extremely valuable information on the process of selection, and can highlight the plasticity of human behavioural strategies under variable environmental conditions. In addition, they provide an important empirical test of the evolutionary psychologists' assumption that current behaviour is unlikely to be adaptive and, in those instances where this assumption is upheld, they can be used to identify the component of fitness which acts as the 'sticking point' that leads behaviour off-track.

Hence, in our view, one of the most valuable contributions that evolutionary psychology can make may not be understanding the process of human adaptation as such, but the tying together of human behavioural ecology with psychological mechanisms. As we pointed out earlier, if we can answer a particular question at more than one level of explanation, our understanding will inevitably be more secure than if we can only provide an answer at just one level. Thus, if we can show that, say, our functional explanation of bridewealth payments among the Kipsigis (Borgerhoff Mulder 1988a, b, 1995) is underpinned by a proximate psychological mechanism that explains male mate selection preferences, then our functional explanation will be strengthened considerably.

*

We hope we have made clear our belief that the most powerful tests of evolutionary theory will come from applying both the HBE and the EP approaches together. There are a number of interesting questions regarding human social evolution that simply cannot be answered by using either the HBE or EP approach alone. All we can do is

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echo Blurton-Jones (1990) in saying 'there is plenty to do on evolution and human behaviour without bickering among ourselves' and fully endorse Turke's (1990) plea that we should get on and 'just do it'.

- Though originally conceived in terms of the genetic inheritance of morphological traits, Darwin's theory of evolution by natural selection does not strictly speaking make any assumptions about the mechanism of inheritance; recognising that learning is a Darwinian process allows us to explore behavioural decisions and culture using an evolutionary perspective without having to assume genetic determinism.
- Human behaviour and psychology are the products of evolution and can be investigated profitably using an evolutionary framework, although any approach that ignores the fact that culture is an integral part of the biological process will, of necessity, be incomplete.
- When investigating human behaviour, it is imperative to be clear about the level of explanation at which research is focused.
- Human behavioural ecology investigates the manner in which variation in human phenotypic expression influences reproductive outcomes.
- Evolutionary psychology investigates the design of cognitive mechanisms.
- Debate about the appropriateness of the different approaches has been intense, but often reflects a misunderstanding between what the two approaches are trying to achieve rather than a serious divide between them. Combining the two in order to provide explanations at more than one level of analysis will be the key to providing more satisfactory accounts of human behaviour.

Further reading

- Barkow, J., Cosmides, L., Tooby, J. (1992) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press.
- Cavalli-Sforza, L. L., Menozzi, P. and Piazza, A. (1994) *History and Geography of Human Genes*. Princeton (NJ): Princeton University Press.
- Cronk, L. (1999) *The Whole Complex: Culture and the Evolution of Human Behaviour*. Boulder, CO: Westview Press.
- Dawkins, R. (1986) *The Blind Watchmaker*. Harlow: Longman.
- Klein, R. (1999) *The Human Career*, 2nd edition. Chicago: University of Chicago Press.
- Malik, K. (2000) *Man, Beast and Zombie*. London: Weidenfeld and Nicholson.
- Ridley, M. (1999) *Genome: The Autobiography of a Species in 23 Chapters*. London: Fourth Estate.