CHAPTER 5

Evolutionary psychology

Researchers committed to an evolutionary perspective on humanity were initially united in the face of widespread hostility to human sociobiology. However, in the 1980s, as the number of investigators using evolution to study human behaviour increased, subgroups began to emerge with different opinions on how best to proceed. One such subgroup was dominated by academic psychologists searching for the *evolved psychological mechanisms* that they envisaged underpinned any universal mental and behavioural characteristics of humanity. While the intellectual roots of some of these practitioners could be traced to human sociobiology, or to the study of animal behaviour, the majority were fresh recruits who sought to differentiate themselves from human sociobiology, and restyled themselves as *Darwinian* or *evolutionary psychologists.* For Leda Cosmides and John Tooby, two of the pioneers of this new discipline, evolutionary psychology owed little intellectual debt to Edward Wilson but did draw inspiration from the writings of Bill Hamilton, Robert Trivers, and George Williams. Tooby, a Harvard-trained anthropologist who had worked closely with Irven DeVore, and Cosmides, a psychologist also from Harvard, were brought by Donald Symons to Santa Barbara where they founded the first Center for Research in Evolutionary Psychology.

The 'Santa Barbara school'[1] were concerned that human sociobiologists and behavioural ecologists had neglected psychological adaptations:

> In the rush to apply evolutionary insights to a science of human behavior, many researchers have made a conceptual 'wrong turn', leaving a gap in the evolutionary approach that has limited its effectiveness. This wrong turn has consisted of attempting to apply evolutionary theory directly to the level of manifest behavior, rather than using it as a heuristic guide for the discovery of innate psychological mechanisms (Cosmides and Tooby, 1987, pp. 278–9).

The evolutionary psychologists stressed how the environments that contemporary human populations experience differ massively from those experienced by our ancestors. Modern houses, cities, and social institutions are relatively recent innovations in evolutionary terms, and hence they suggested that there is a mismatch between our ancient psychological adaptations and our modern, artificially constructed world. As a result of this mismatch, they argued, researchers should not expect human behaviour to be adaptive. For evolutionary psychologists, any failure on the part of human sociobiologists and human behavioural ecologists to find optimal human behaviour would only demonstrate that these researchers were working at the wrong level (Symons, 1987).

Nevertheless, if evolutionary psychologists are correct in their reasoning that human beings walk around with stone-age minds in their heads, then the manner in which people

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1 As Tooby, Cosmides, and Symons all work at the University of California at Santa Barbara, this strand of evolutionary psychology has become known (perhaps somewhat disparagingly) as The Santa Barbara Church.

think should betray their ancestral selective environments. They proposed that evolutionary biology was best used to generate hypotheses of the adaptive problems that the human mind had to solve in the selective environment of our ancestors. Following Bowlby (1969), this past environment was described as the *environment of evolutionary adaptedness* (EEA), which was generally conceived of as the Pleistocene[2] environment inhabited by our Stone-Age hunter–gatherer ancestors. With a good understanding of these adaptive problems, evolutionary-minded researchers would be able to determine the design features that any cognitive programme must have to be capable of solving them. This would help them to develop models of how the mind works. Thus, with evolutionary psychology, the primary focus of attention shifted from behavioural adaptations to evolved psychological mechanisms.

The evolutionary psychologists' approach was also influenced by the changing face of psychology which, by the 1980s, had long abandoned behaviourism and was in the throws of the cognitive revolution. The use of animals as research tools had been jettisoned in favour of the computer as an analogue of human cognition. Minds could be described in terms of information processing in which representations of the world were constructed on the basis of information from sensory inputs, while cognitive decision rules determined motor outputs. Research into artificial intelligence revealed that, to solve even supposedly simple cognitive tasks, minds required pre-specified procedures or information. This led evolutionary psycho-

[2] The Pleistocene is the period from 1.7 million to 10,000 years ago.

logists to propose that 'innate psychological mechanisms' guided decision-making. Psychologists were increasingly developing computational theories of informational processing problems that specified what had to happen if a particular function was to be accomplished (Marr, 1982). Evolutionary psychologists believed that, with sufficient information about our ancestors' way of life, evolutionary theory could be put to use to construct computational theories of adaptive information processing problems.

Cosmides and Tooby's visionary writings were to provide the defining features of the field, and trigger the rapid growth of this new movement. By the 1990s evolutionary psychology had blossomed into a thriving programme of research, with important contributions from Jerome Barkow, David Buss, Bruce Ellis, Martin Daly and Margo Wilson, Steven Pinker, Roger Shepard, Donald Symons, and many others. With the publication of Barkow, Cosmides, and Tooby's (1992) landmark volume *The Adapted Mind,* a stream of popular books in this new genre followed, notably David Buss's (1994) *The Evolution of Desire*, Robert Wright's (1994) *The Moral Animal*, and Steven Pinker's (1997) *How the Mind Works.*

As noted in the introduction, however, the term 'evolutionary psychology' is used in a divergent manner by different researchers. Confusingly, some anthropologists or archaeologists describe themselves as doing 'evolutionary psychology' because they identify with the Santa Barbara perspective. Conversely, prominent evolutionarily minded psychologists, such as Henry Plotkin (1994, 1997), disagree with the modular and adaptationist school of thought championed at Santa Barbara. Many researchers have endeavoured to broaden evolutionary psychology to encompass all evolutionary approaches to the study of human minds and behaviour (Daly and Wilson, 1999; Buss, 1999; Barrett *et al.*, 2001; Heyes and Huber, 2000), but others, including Cosmides and Tooby, see important distinctions between the various schools. Moreover, many evolutionary anthropologists, human behavioural ecologists, and human sociobiologists have been at pains to differentiate themselves from evolutionary psychology and recognize major theoretical and methodological distinctions between the approaches (Smith *et al.*, 2000).

In this chapter we will focus our attention primarily on research in line with the narrower conception of *evolutionary psychology* as defined by Cosmides and Tooby, because it remains the dominant school of thought within the field, and the broader usage is more diffuse and difficult to characterize. Nonetheless, it is important to bear in mind that a significant number of researchers describing themselves as evolutionary psychologists take issue with aspects of this version, some see no important divisions between the various schools of thought, and some utilize methods and lines of reasoning that we describe as sociobiology, evolutionary anthropology, human behavioural ecology, or the comparative method.

Key concepts

The distinctive theoretical concepts of evolutionary psychology are: first, a focus on evolved psychological mechanisms as the adaptations that underlie human behaviour; secondly, the use of the concept of 'environment of evolutionary adaptedness' (EEA) to reconstruct the adaptive problems faced by our ancestors; and thirdly, an emphasis on *domain-specific* mental organs or modules as evolved solutions to ancestral problems. In this section, we describe each of these concepts in greater depth, and then go on to depict the methodology of evolutionary psychology.

Evolved psychological mechanisms

According to Cosmides and Tooby (1987, p. 281): 'natural selection cannot select for behavior per se; it can only select for mechanisms that produce behavior.' A psychological mechanism is the term they gave to such mental adaptations, the information processing circuits in our brains that shape behaviour. For other researchers (for example, Buss, 1999), psychological mechanisms are defined more broadly to include context-specific emotions, preferences, and proclivities. Psychological mechanisms are assumed to exist in the form that they do because they recurrently solved a specific problem of survival or reproduction over evolutionary history.

Jealousy is provided as an example (Buss, 1994). In ancestral environments, males that experienced jealous emotions when they observed their partner behaving in an overly friendly manner to a rival male, and as a consequence were spurred into action, may have had a selective advantage over males who were indifferent about the possibilities of being jettisoned or cuckolded. How each male went about addressing this problem would depend on factors such as his size, the size of the rival, his personality, and so on. Some males might respond with threats or aggression towards the other male, others with signs of displeasure towards their partner, others with increased vigilance, and others by seeking out a more faithful female. At the behavioural level, it is difficult to predict how an individual will respond to such situations and there is no straightforward answer as to which behavioural strategy maximizes fitness.

However, evolutionary psychologists predict with some confidence that individuals placed in such situations will experience jealous emotions, albeit with varying degrees of intensity, so at the psychological level there is a reliable pattern to be found. Other phenomena proposed as psychological mechanisms include a fear of snakes and spiders, a preference for savannah landscapes, a capacity to learn a spoken language, preferences for particular characteristics in a partner, and a sensitivity to cheating.

Psychological mechanisms are assumed to be complex adaptations that evolved slowly and hence that are unlikely to have undergone any significant change since the Pleistocene. In many respects, they are similar to Lumsden and Wilson's (1981) *epigenetic rules* and Hinde's (1987) *predispositions*, although in some cases the cognitive procedures are specified in more detail. While there is no logical or biologically necessary connection between 'innateness' and modularity, psychological mechanisms are often described as 'innate' or as 'instincts'. For instance, Pinker (1994) describes a 'language instinct', a psychological mechanism that predisposes us to speak complex, fluent grammatical language:

> some cognitive scientists have described language as a psychological faculty, a mental organ, a neural system, and a computational module. But I prefer the admittedly quaint term 'instinct'. It conveys the idea that people know how to talk in more or less the sense that spiders know how to spin webs. (Pinker, 1994, p. 18)

The use of such terms is unfortunate because they are slippery and vague. Bateson points out that:

> the word 'innate' has at least six separate meanings: namely, present at birth; a behavioural difference caused by

> a genetic difference; adapted over the course of evolution; unchanging throughout development; shared by all members of a species; and not learned. (1996, p. 2)

Researchers rarely state which meaning is being adopted. What is worse, they may take evidence for one of these meanings as justifying the use of another (Bateson and Martin, 1999).

According to Buss (1999), evolved psychological mechanisms provide non-arbitrary criteria for 'carving the mind at its joints' (p. 52), although the critics of evolutionary psychology question whether such criteria really are non-arbitrary (Lewontin, personal communication). Buss envisages that the mind possesses hundreds, perhaps even thousands, of such specific evolved psychological mechanisms, which are assumed to be universal (or at least, relatively stable) characteristics of human nature. Anthropologist Donald Brown (1991) has documented some of these human universals. For instance, he reports how all people experience certain emotions and express corresponding facial expressions; all have a spoken language, which all have phonemes, morphemes, and syntax; all societies are structured by statuses and roles, and possess a division of labour; and all possess incest avoidance regulations. Humans also possess universals of behavioural development (Bateson and Martin, 1999). With few exceptions, all humans pass the same developmental milestones as they grow up, with most children starting to walk at 18 months, to talk at 2 years, and most reach sexual maturity by their late teens. For evolutionary psychologists, the promise of the evolutionary perspective lies in its power to assist in the discovery, inventory, and analysis of the psychological mechanisms that underpin human nature.

The environment of evolutionary adaptedness (EEA)

The concept of the environment of evolutionary adaptedness was initially developed by the British psychiatrist John Bowlby (1969), influenced by Robert Hinde, to explain why young children the world over develop a strong attachment to their mothers, and why separation can result in extreme distress, including psychiatric disorder. Bowlby argued that the overt attachment of young to their parents should not be regarded as an illness or as dysfunctional behaviour, but rather as an adaptation that in our evolutionary past greatly enhanced the survival prospects of infants. Bowlby asserted that people have lived in modern societies with agriculture, high population density, and complex social institutions for only a few thousand years, while their predecessors lived in small foraging societies for a much longer period of time. The modern world is very different from that experienced by our genus for most of its two million-year history. While attachment and separation anxiety are not necessarily of survival value in contemporary environments, Bowlby envisaged that they were of value at the time and in the environment in which they evolved. The environment of evolutionary adaptedness (EEA) is the term Bowlby gave to this past selective environment. Prior to the late 1960s, there was much confusion over the use of the term 'adaptation' (Gould and Vrba, 1982), and Bowlby's point that evolved characters may be adaptations to past environments was of considerable value.

In their writings on evolutionary psychology, Cosmides and Tooby rapidly adopted Bowlby's notion of the EEA. They also stressed how history and modern culture can change extremely quickly compared to biological evolution, leaving our evolved psychological mechanisms lagging behind:

> The recognition that adaptive specializations have been shaped by the statistical features of ancestral environments is especially important in the study of human behavior… Human psychological mechanisms should be adapted to those environments, not necessarily to the twentieth-century industrialized world. (1987, pp. 280–1)

Cosmides and Tooby reasoned that if they could establish what kind of problems our Stone-Age ancestors faced, they might be able to predict the kind of psychological mechanisms necessary to solve these problems, and hence which may be expected to have evolved.

Domain specificity

Most evolutionary psychologists believe that minds are composed of a large number of psychological mechanisms dedicated to finding quick and efficient solutions to particular problems that were of significance to our ancestors. One feature of these psychological mechanisms is that each is believed to have evolved to operate in a specific domain. Such domains include language, mate choice, sexual behaviour, parenting, friendship, resource accrual, disease avoidance, predator avoidance, and social exchange. In contrast, some (although by no means all) non-evolutionary psychologists may assume that the human mind is a general-purpose computer with processes that operate across several domains. Evolutionary psychologists have argued that from an evolutionary point of view this is highly implausible. According to Buss (1999), evolved psychological mechanisms tend to be problem-specific because:

> (1) general solutions fail to guide the organism to the correct adaptive solutions; (2) even if they do work, general

> solutions lead to too many errors and thus are costly to the organism; and (3) what constitutes a 'successful solution' differs from problem to problem. (p. 52)

Instead, humans should have evolved specialized learning mechanisms that sort experience into adaptively meaningful channels that focus attention, organize perception and memory, and call up specialized procedural knowledge that will generate appropriate inferences, judgements, and choices given the context (Cosmides and Tooby, 1987). In this respect, the mind is described as being like a 'Swiss army knife', with each psychological mechanism analogous to a single blade.

In making the argument that psychological mechanisms are domain-specific, evolutionary psychologists frequently refer to evidence that animals are predisposed to learn some things and not others. A series of elegant experiments by the Berkeley psychologist John Garcia demonstrated that what animals learn varies adaptively across species (Garcia and Koelling, 1966). Garcia gave rats food and then, sometimes after several hours, he gave them a dose of radiation that made them sick. He found that the rats tended subsequently to avoid the food, and they did so because they had learned, often after just a single trial, that food with that particular taste leads to illness. However, the rats struggled to learn an association between the other characteristics of the food and feeling sick, and were extremely slow to learn that a buzzer sound or light predicts illness. From an evolutionary perspective, this makes a lot of sense, as sickness generally results from eating rather than from noises or lights, and taste is a reliable indicator of a food's nature. Garcia's experiments suggested that animals, humans included, were *prepared* by evolution to learn some things more easily and quickly than others.

The methods of evolutionary psychology

Tooby and Cosmides (1989) outline the steps that researchers must go through to do evolutionary psychology.

1. Use evolutionary theory as a starting-point to develop models of adaptive problems the human psyche had to solve.
2. Attempt to determine how these adaptive problems manifested themselves in Pleistocene conditions, and endeavour to establish the selection pressures.
3. Catalogue the specific information processing problems that must be solved if the adaptive function is to be accomplished. Develop a computational theory.
4. Use the computational theory to determine the design features that any cognitive program capable of solving the problem must have, and develop models of the cognitive programme structure.
5. Eliminate alternate candidate models with experiments and field observation.
6. Compare the model against the patterns of manifest behaviour that are produced by modern conditions.

To discourage 'just-so' story-telling, Tooby and Cosmides (1989, p. 41) state

> The desire to leapfrog directly from step one to step six must be resisted if evolutionary biology is to have any enduring impact on the social sciences.

For illustration, consider the example of altruistic behaviour presented by Tooby and Cosmides (1989). The first step is to look to evolutionary theory, where Hamilton's (1964) inclusive fitness theory predicts that individuals ought to be more likely to behave altruistically to close kin.

The second step requires knowledge of our ancestors' selective environment: cooperative exchanges between closely related members of a foraging band might have been critical for survival amongst our Pleistocene ancestors. The third step leads to the reasoning that, for humans to confer benefits on kin, they required cognitive programmes that allow them to determine what are reliable cues indicating relatives and how closely related is a particular individual. As a consequence, the fourth step leads to the conclusion that humans must have psychological mechanisms that allow them to extract this information, and decision rules that use this information to recognize kin. The fifth and sixth steps might, for instance, involve devising experiments that test whether individuals can recognize kin and how they do so, or investigating how people act towards kin and non-kin across different societies.

Buss (1999) outlines two strategies for generating and testing evolutionary hypotheses: a theory-driven strategy similar to the approach of Tooby and Cosmides and an observation-driven strategy. This second approach requires individuals to develop a hypothesis about adaptive function based on a known observation, and to test further predictions based on the hypothesis. Pinker (1997) describes this latter method as 'reverse-engineering', as it starts with the end-product and attempts to reconstruct the steps that led to this point. Other evolutionary psychologists embrace a broader range of methods (Daly and Wilson, 1999). Indeed, in the following section we will describe prominent case studies that test evo-lutionary hypotheses using psychological experiments, questionnaires, and through analysis of published data records.

Case studies

Here we present three case studies that illustrate the evolutionary psychology approach. We first describe experimental evidence of a psychological mechanism for detecting cheaters. We then examine a study on human mating preferences, and finally look at an evolutionary analysis of homicide.

Psychological mechanisms for detecting cheats

If reciprocal altruism has been important in our evolutionary past, then evolutionary psychologists reason that humans should possess psychological mechanisms that render them sensitive to detecting cheats; that is, individuals that take the benefits from a social exchange without paying the costs.

Statements such as 'If you take the benefit, then you must pay the cost' are known as conditional rules. They can be represented in abstract terms as 'If P, then Q'. One widely used experimental paradigm for exploring people's ability to detect violations of conditional rules has been the Wason selection task. Psychologist Peter Wason (1966) wanted to know whether people think by testing hypotheses and devised an experiment to determine whether they were good at detecting violations of conditional rules. He found that people reason logically only in restricted contexts and that the subject matter people are asked to think about seems to affect how well they do on these tests. Consider the task to detect violations of the abstract rule 'If a person has a 'd' rating, then the documents must be marked code 3' depicted in Figure 5.1a. Wason found that typically less than 25% of people answer this task correctly. You can try this test for yourself before reading what the correct answer should be.

a. Abstract problem
Part of your new clerical job at the local high school is to make sure that student documents have been processed correctly. Your job is to make sure the documents conform to the following rule:

If a person has a D rating, then the documents must be marked code 3

You suspect the secretary you replaced did not categorize the student's documents correctly. The cards below have information about the documents of four people who are enrolled at this high school. Each card represents one person. One side of a card tells a person's letter rating and the other side of the card tells that person's number code. Indicate only those card(s) you definitely need to turn over to see if the documents of any of these people violate this rule.

D	**F**	**3**	**7**

b. Drinking age problem
In a crackdown against drunk drivers, Massachusetts law enforcement officials are revoking liquor licenses left and right. You are a bouncer in a Boston bar, and you'll lose your job unless you enforce the following law:

If a person is drinking beer, then he or she must be over 21 years old

The cards below have information about four people sitting at a table in your bar. Each card represents one person. One side of a card tells what a person is drinking and the other side of the card tells that person's age. Indicate only those card(s) you definitely need to turn over to see if any of these people are breaking this law.

Drinking beer	**Drinking coke**	**25 years old**	**16 years old**

Adapted from Figure 3.3 and examples given in Cosmides & Tooby (1992).

Figure 5.1

Most people presented with this abstract problem selected only the D card, or the D and 3 cards, as necessary to check for violations. In fact, the right answer is to turn over the D and 7 cards. This is because, to establish that every D card has a 3 on the flip side it is clearly necessary to turn over the D card, but also important to establish that the 7 is not a D. Whether the 3 is a D or not is irrelevant, as the rule does not insist that D is the only rating with the code 3. Now compare your performance with the task shown in Figure 5.1b. Surprisingly, despite the fact that the drinking age task depicted there is logically exactly the same, people consistently perform better on this task, with approximately 75% of subjects giving the logically correct response of 'drinking beer' and '16 years of age'. In both tasks, individuals are given a conditional rule of the form If P then Q *(*i.e. if D then 3, or if beer then over 21), and asked what they need to do to determine whether this rule has been violated. The rule is violated only when P is true but Q is false, and thus in both cases the answer is to check P (the D or beer card) and not Q (the 7- or 16-years-old card).

Such experiments suggest that human reasoning changes depending on the subject matter about which one is reasoning, but prior to an investigation by Leda Cosmides there was no satisfactory theory that could account for these content effects. As part of her doctoral dissertation at Harvard University, Cosmides set out to establish whether the contexts in which people reason logically made sense in evolutionary terms. In particular, she was interested in the hypothesis that a history of reciprocal altruism among our ancestors would have fashioned us with a cheater detection mechanism that biased our reasoning.

In an elegant series of experiments that expanded Wason's findings, and for which she was awarded the AAAS Behavioral Science Research Prize, Cosmides found that when subjects are asked to look for violations of conditional rules that express social contracts their performance improves dramatically (Cosmides, 1989; Cosmides and Tooby, 1992). According to Cosmides, the reason most people get the abstract problem wrong but the drinking age task correct is that only in the latter case does logic coincide with cheater detection (Cosmides and Tooby, 1992). The drinking age task has a content equivalent to 'If you take the benefit, then you pay the cost'. Here drinking beer is the benefit, being over 21 is the cost, and drinking alcohol under age is cheating by violating a social norm. Cosmides's experiments ruled out alternative explanations, such as that performance was better on some tasks than others because the content was more familiar. Even when subjects were given an entirely unfamiliar rule, such as 'If a man eats cassava root, then he must have a tattoo on his face', they responded with a high level of success provided the preamble gave them sufficient information to establish that the rule was a social contract. Most compelling of all, Cosmides was able to switch the order of the rules so that the logically correct answer conflicted with the social contract theory, and subjects responded in a manner consistent with the cheater detection hypothesis (for a description of these experiments see Cosmides and Tooby, 1992).

Cosmides and Tooby argue that people are tuned to attend to situations in which people take the benefit without paying the cost. Although not all psychologists accept Cosmides and Tooby's interpretation of these findings, few would dispute that Cosmides's experiments have reinvigorated this area of research and made a valuable contribution to the field. It remains an intriguing and highly plausible possibility that our minds are equipped with cognitive adaptations for social exchange, of which one procedure is a psychological mechanism dedicated to looking for cheats.

Sex differences in mate choice

As natural selection operates through the differential reproduction of individuals, any psychological mechanisms that guide reproduction should be especially strong targets of selection. As a consequence, courtship and sex have been a principal focus of evolutionary psychology (Buss, 1994). Indeed, the great bulk of research in evolutionary psychology has been focused on human mating behaviour. One question that has received considerable attention is whether evolution has fashioned us with preferences for particular characteristics in the opposite sex that influence our choice of mating partners.

Trivers (1972) proposed that females should seek to mate with males who show the ability and willingness to invest resources connected with parenting such as food, shelter, territory, and protection. There is now considerable experimental evidence from studies of animals that females frequently best maximize their reproductive success by prioritizing gaining access to resources. Perhaps humans are no different in this regard. Evolutionary psychologists have reasoned that, from the perspective of our ancestors in the EEA, women faced the burdens of internal fertilization, a nine-month gestation, and lactation, and consequently would have benefited by selecting mates who possessed and were willing to provide such resources (Buss, 1994). They also suggested that females might be selected to favour males that display cues indicating their wealth, such as status, or their potential to accrue substantive resources in the future, such as intelligence, hard work, and ambition.

In contrast, in most mammals male parental investment is small compared with that of females, and hence males can most effectively maximize their reproductive success by prioritizing mating with many females and by choosing females that are fertile. Evolutionary psychologists argue that thousands of generations of selection have favoured the evolution of psychological mechanisms in males that render the prospect of many sexual partners desirable and females of high fertility attractive (Buss, 1994). As human female fertility is highest in the early twenties, men are predicted to prefer younger to older women. Some researchers have suggested that standards of beauty reflect an evolved preference for physical traits that are generally associated with youth, such as smooth skin, good muscle tone, and an optimal waist-to-hip ratio.

To test these hypotheses, psychologist David Buss, currently at the University of Texas, Austin, carried out an extensive series of cross-cultural studies to determine whether human mate choice shows consistent patterns the world over (summarized in Buss, 1994). One investigation involved Buss and his collaborators interviewing over ten thousand people in thirty-seven different cultures (Buss *et al.*, 1990). On the basis of these analyses, Buss concluded that there is a broad cross-cultural consensus about what attributes are important in a mate, and that the sexes show the distinct patterns predicted by evolutionary psychology reasoning. For instance, Buss found that:

> Women across all continents, all political systems (including socialism and communism), all racial groups, all religious groups, and all systems of mating (from intense polygyny to presumptive monogamy) place more value than men on good financial prospects. (1994, p. 25)

In contrast, men typically placed more value than women on the physical attractiveness of their partner:

> Men worldwide want physically attractive, young, and sexually loyal wives who will remain faithful to them until death. These preferences cannot be attributed to Western culture, to capitalism, to white Anglo-Saxon bigotry, to the media, or to incessant brainwashing by advertisers. (1994, p. 70)

Buss also uncovered clues suggesting an evolutionary past that favoured men that had short-term mating in their sexual repertoire:

> sexual fantasy … lust, the inclination to seek intercourse rapidly, the relaxation of standards, shifts in judgements of attractiveness, homosexual proclivities, prostitution, and incestuous tendencies are all psychological cues that betray men's strategies for casual sex. (1994, p. 85)

However, we suggest that these findings need to be kept in perspective. Buss's study found that mutual attraction, dependable character, emotional stability, and a pleasing disposition were the four traits deemed most important to mate choice by both sexes. Good financial prospects was on average rated only the twelfth most important factor influencing mate choice in females, and good looks were rated only tenth by males. Moreover, Buss found that, for most traits, knowing where a person lives tells you more about what he or she values in a mate than knowing the person's gender, indicating that sex differences are comparatively unimportant compared with cross-cultural differences. For instance,

> The trend for men to value chastity more than women holds up worldwide, but cultures vary tremendously in the value placed on chastity. At one extreme, people in China, India, Indonesia, Iran, Taiwan, and the Palestinian Arab

> areas of Israel attach a high value to chastity in a potential mate. At the opposite extreme, people in Sweden, Norway, Finland, the Netherlands, West Germany, and France believe that virginity is largely irrelevant or unimportant in a potential mate. (Buss, 1994, p. 68)

In addition, the criteria on which standards of attractiveness are judged vary greatly from one culture to the next, with some cultures, for instance, preferring plump to slim builds, and others preferring dark to light skin colour. Moreover, much of the research in this area is carried out by giving questionnaires to university and college students, and one might question to what extent students in different countries really represent distinct cultures. It would be interesting to find out whether the reported sex differences remain if the studies were carried out on groups such as the Hadza (Tanzania), Ache (Paraguay) or Mapuche (Chile). The reliability of questionnaires and self-reports has also been queried (Nisbett and Wilson, 1977; Aunger, 1994), which may be a particularly acute problem in studies of sexual behaviour. Nonetheless, Buss's analyses provide some of the broadest evidence to date that evolved psychological mechanisms may be universal features.

Homicide

All around the world the folk literatures of distinct cultures abound with Cinderella stories involving a cruel or evil step-parent. For Martin Daly and Margo Wilson, two psychologists at McMaster University in Canada, the ubiquity of these stories reflects a genuine, dark, and disturbing aspect of human societies. Daly and Wilson have used an evolutionary psychology perspective to inform a study of homicide, leading to a number of novel questions, hypotheses, and conclusions. In fact, it was in the flyers to Daly and Wilson's (1988) pioneering book *Homicide* that the phrase 'evolutionary psychology' was first coined. A clear prediction made from Daly and Wilson's evolutionary perspective was that, as they are unrelated, substitute parents will generally tend to care less for children than natural parents, with the result that children reared by people other than their natural parents will more often be at risk. Raising a child involves considerable costs and substitute parents may be less likely than natural parents to experience the emotional rewards that make the costs of parenthood tolerable.

In an extensive analysis of data on infanticide in Canada and the United States, Daly and Wilson documented the fact that there was a very real and substantially elevated risk to children residing with one natural parent and one step-parent. For instance, the American Humane Association detected 279 fatal incidences of child abuse in 1976, of which 43% dwelt with a substitute parent, considerably more than would be expected by chance. Another survey of child abuse in Canada in 1983 gave a similar pattern of results. Daly and Wilson argued that poverty, which is also associated with child abuse, does not explain the association between abuse and step-parenthood. According to Daly and Wilson, the more common social science explanation for the difficulties encountered in step-relationships is that these difficulties are in fact caused by the 'myth of the cruel step-parent' and by the fears of the child. The evolutionary psychology view appears to present a more compelling description of the observed patterns of behaviour.

Daly and Wilson also used their evolutionary perspective to investigate adult murders outside of the family. In a 10-year survey of Canadian homicide, they found that the predominant form of murder involved men killing unrelated men. In fact, in accounting for single sex murders among adults, Daly and Wilson recorded 2861 male–male cases to 84 female–female cases, showing the former to be 34 times as frequent as the latter. A survey of 35 studies of homicide from around the world revealed that this difference between the sexes is found in every single population in which it has been investigated. According to Daly and Wilson, there is no known human society in which the level of lethal violence among women even begins to approach that among men.

Why should there be a universal sex difference in homicidal aggression amongst humans? Daly and Wilson explain how evolutionary biology provides an answer. Trivers (1972) argued that across all sexual species, the sex that makes the greater parental investment tends to become the crucial resource limiting the fitness of individuals of the less investing sex, so that selection favours competition among the latter for access to mates. In humans, females are the sex making the greater investment in raising offspring and males could father many children if they had access to multiple mates, potentially many more than an equivalent female. There is strong evidence that the selective history of our ancestors was one that involved mild but sustained polygyny; in fact, such is the norm in many human societies today. While females are likely to have been competing among each other for quality males too, the variance in male fitness was probably greater than the variance in female fitness. In other words, the successful males are big winners with many wives and offspring, and the losers may do extremely poorly, while virtually all females have some intermediary level of reproductive success. From this evolutionary perspective, where there are big rewards for competition between males for access to females, the entire life history of males may favour higher risk strategies. The more intense the competition, the more likely it becomes that selection will favour psychological mechanisms in males rendering them prone to risky competitive tactics, including escalated fighting even to the point of death. Daly and Wilson (1983) showed that this hypothesis is supported by related studies of risky behaviour in humans. For instance, they pointed out that males are more prone to dangerous driving and suffer elevated rates of mortality on the roads. Another example is that 93% of robberies and 94% of burglaries in the United States in 1980 were perpetrated by males. Males are not poorer than females but they would seem to be more prone to taking risks. Daly and Wilson hypothesize that the risks that males take may reflect a past history of selection that has fashioned their minds for competition.

Critical evaluation

Much of the criticism levelled at evolutionary psychology is identical to that directed at sociobiology; indeed, many critics see no meaningful distinction between these two schools (e.g. Rose and Rose, 2000). Rather than repeat ourselves, we refer the reader back to the penultimate section of Chapter 3, where we discuss these charges. To reiterate briefly, allegations of genetic determinism or prejudice on the part of leading sociobiologists or evolutionary psychologists are usually unfounded; charges of reductionism are misguided; however, criticism on the grounds of 'Just so' evolutionary story-telling and a superficial reading of the relevant literature are frequently justified. Here we concentrate on evaluating the distinctive characteristics of evolutionary psychology, focusing on issues related to the environment of evolutionary adaptedness, domain specificity, and their general evolutionary perspective.

Evaluating the concept of the EEA

Early work by evolutionary psychologists asserted that the human mind was fashioned over the last two million years for a past world of hunting and gathering on the African plains of the Pleistocene. For instance, Cosmides and Tooby wrote:

> Our species spent over 99% of its evolutionary history as hunter–gatherers in Pleistocene environments. (1987, pp. 280–1)

Daly and Wilson (1999) point out that much of the dissatisfaction with the EEA concept has derived from an equation of the EEA with a stereotype of a Pleistocene African savannah. Cosmides and Tooby have informed us that they never adhered to this stereotype, and that their early writings on the EEA were simplified to reach an 'evolutionarily-naive' audience that tended to regard all human behaviour to be of utility in current environments. Unfortunately, a damaging EEA-as-Pleistocene-African-savannah stereotype pervades the evolutionary psychology literature.

What is wrong with the notion of the human EEA as a particular time and place? The problem is that comparatively little is known about the lifestyle of our ancestors throughout the Pleistocene. Consequently, the EEA concept has engendered a wealth of undisciplined speculation and story-telling in which virtually any attribute can be regarded as an adaptation to a bygone Stone-Age world. A stereotypical notion of the EEA implies that the Pleistocene hunter–gatherers exhibit little variability in time or space, which a number of researchers have pointed out is false when one considers that Stone-Age peoples lived not only on the African savannah, but in deserts, next to rivers, by oceans, in forests, and in the Arctic (Foley, 1996; Boyd and Silk, 1997). The evolutionary psychology literature makes common reference to the observation that 'humans spent 99 per cent of their evolutionary history as hunter–gatherers'. Yet every human descends from ancestors collectively subject to natural selection for three and a half billion years, which leaves the '99 per cent' figure arbitrary.

Neither is a description of our ancestors as 'hunter–gatherers' a sufficient account of their life history to be able to reconstruct the relevant selection pressures. Wasps, rats, and blue tits are all hunter–gatherers in the sense that they both hunt live prey and gather other foods. Of course, they do not exhibit the cooperative, coordinated, socially organized, linguistically guided hunting and gathering that modern human hunter–gatherers exhibit, but the point is that it is not known whether our ancestors during the Pleistocene did so either (Foley, 1996). Many authoritative archaeologists and anthropologists believe that *Homo erectus* and even Neanderthals lived completely different lives to modern hunter–gatherers. To what extent they had sophisticated linguistic abilities, hunted large game, shared food, and had home bases, for example, is open to dispute. If, as many believe, these characteristics emerged as late as the upper Paleolithic, around forty thousand years ago, any focus on the earlier Pleistocene would be misplaced.

More recently, Tooby and Cosmides have clarified their position:

> [The EEA concept does not refer to a single] place or habitat, or even a time period. Rather, it is a statistical composite of the adaptation relevant properties of the ancestral environments encountered by members of

> ancestral populations, weighted by their frequency and their fitness consequences. (Tooby and Cosmides, 1990a, pp. 386–7)

However, this conceptualization may be problematic in a different sense. Can the 'new' EEA concept be put to use, in the manner that Tooby and Cosmides (1989) originally claimed, to develop models of adaptive problems the human psyche had to solve? How could one compute a 'statistical composite' of all the relevant environments encountered by our ancestors, and weight them accordingly? Comparative analyses of animal abilities suggest that many human behavioural and psychological traits have a long history. Some human behavioural adaptations, such as maternal care or a capacity to learn, may even have evolved in our invertebrate ancestors. Many perceptual preferences will be phylogenetically ancient. For example, an understanding of causal relationships may be common to mammals and birds. Much social behaviour, such as forming stable social bonds, developing dominance hierarchies, an understanding of third-party social relationships, and coordinated hunting, probably evolved in our pre-hominid primate ancestors. A capacity for true imitation may also have evolved in pre-hominid apes. Yet if researchers are going to use the EEA as Cosmides and Tooby originally outlined, they need to identify a particular time period and class of ancestor when the relevant psychological mechanisms evolved, and then weight that and all subsequent environments accordingly. In principle, EEA supporters could carry out a phylogenetic analysis to determine the earliest known ancestor exhibiting a trait. In practice, this is never done and, as little is likely to be known about that particular ancestor and most of its descendants, it would be an extremely time consuming exercise that would generate only vague speculation.

Perhaps the real virtue of the EEA concept is more modest. The EEA encourages researchers to recognize that humans, like all species, exhibit *some* adaptations to past environments that are not necessarily of current utility. The originator of the EEA concept, John Bowlby, was concerned with the mother–child relationship, which we might envisage has a degree of constancy across environments and over time. There is a strong argument that the EEA concept was important in developing an understanding of childhood separation anxiety and attachment (Hinde, 1987). Similarly, researchers do not need to know the precise conditions in which humans evolved to make the reasonable guess that salts and sugars may not have been in abundant supply so that their reinforcing properties may not have been counterbalanced by regulatory processes operating against consuming excess (Bateson and Martin, 1999). The question is what proportion of human behavioural traits can be assumed to have evolved in all relevant past environments?

In conversation with us, John Tooby suggested that one doesn't need to know when traits *first* evolved to use the EEA concept, as the behavioural regulatory machinery would have been modified by selection up until the Pleistocene. This line of reasoning brings researchers back to the position where knowledge of stone-age conditions is all that is needed to reconstruct the selective environment of our ancestors. However, this argument is based upon a number of assumptions, including that there was genetic variation in psychological traits up until the Pleistocene, that no significant mental structure carries any historical legacy of selection prior to the Pleistocene, that there has been no meaningful selection on psychological mechanisms since the Pleistocene, and that evolutionary change occurs at a particular rate. These assumptions are not in themselves unreasonable, but they remain highly disputed.

Another caveat for the EEA argument is that, at best, it can only be partly true. Human beings cannot be exclusively adapted to a past world and not at all adapted to modern life, otherwise we would not be able to exist. It would be puzzling if our ancestors really started to thrive as soon as they left their EEA, yet it is in the Holocene, the period since the Pleistocene, that we see the explosion in human numbers and human colonization of the globe. This population growth suggests that a significant fraction of human characteristics remain adaptive even in modern environments which share features with those of our ancestors. Any assumption that natural selection on humans has stopped, that no genetic variation underlies human psychological characters, and that measuring human fitness is a waste of time, is questionable. This is well illustrated by a study by Pawlowski, Dunbar, and Lipowicz (2000) which demonstrated that taller men are reproductively more successful than shorter men, suggesting that, in contemporary populations, there is active selection for stature in male partners, perhaps brought about through female preference or competition amongst males. This study shows that, even in the modern world, with widespread use of contraception and extensive medical care, natural selection is still in operation.

Moreover, the view that modern human populations are adapted to an ancestral Pleistocene habitat is misleading because it portrays humans as passive victims of selection rather than as potent constructors of their niche. It is a distortion to regard evolution as a process by which organisms solve problems set by the environment (Lewontin, 1983a). Niche-construction theory represents one increasingly accepted strand of evolutionary genetics that lays emphasis on the fact that organisms themselves *modify* important components of their selective environments (Odling-Smee *et al.*, 1996; Laland *et al.*, 1996; 2000). For humans, our capacity to create solutions continuously to self-imposed problems reflects the fact that we are very adaptable creatures. Moreover, to a degree that surpasses other species, human mental processes must contend with a constantly changing information environment of their own creation (Flinn, 1997). The flexible nature of our learning and culture allows us to survive and flourish in a broad range of settings. This adaptability means that, rather than being adapted to a particular environment, humans adapted to a broad range of environments that they and their ancestors were involved in constructing.

Psychological traits may be domain-general

One contentious aspect of evolutionary psychology is the stress laid on domain-specific psychological modules. Many researchers believe that evolutionary psychologists have overplayed the modularity of the human brain, and maintain that minds have many domain-general features. Cosmides and Tooby (1987) characterize the difference between the standard social science view and their perspective as representing a choice between two models of the mind, one that lays emphasis on a small number of domain-general processes versus another stressing a large number of domain-specific modules. However, domain-general and domain-specific represent poles of a continuum. Evolutionary psychologists are surely correct to point out that there are efficiency benefits to be gained by mental division of labour and that at times evolution would favour specialization of psychological processing. Yet one can also have too much specificity. It would simply not be feasible to construct a brain that allocates a specific psychological module to every conceivable event an individual might encounter, as the costs in terms of neural circuitry and information processing would be huge. There is no intrinsic virtue to mental specificity; general solutions will be favoured when they can do a good enough job at low cost. For example, human beings may have a psychological module that leaves them predisposed to fear snakes, but they do not have modules that discriminate between dangerous and harmless snakes, or constricting and poisonous species, despite the fact that one can envisage some utility to such discriminations. Domain-general processes are no more incompatible with evolutionary theory than domain-specific processes.

Garcia's experiments are frequently hailed by evolutionary psychologists as demonstrating the gene-biased nature of classical conditioning in particular, and more generally the inadequacy of associative learning theory (the idea that we learn by forming associations between events). Yet associative learning is widespread and has general properties that allow animals to learn about the causal relationships among a wide variety of events (Mackintosh, 1974; Dickinson, 1980). Learning can occur via quite simple rules; for example, one theory known as the Rescorla–Wagner rule (1972) has proved useful in explaining the results of experiments on foraging in honey bees, avoidance conditioning in goldfish, and inferential reasoning in humans. Even some of the most enthusiastic supporters of a modular view of the brain (e.g. Shettleworth, 2000) accept that, while what is learned may vary adaptively across species, how it is learned does not. Natural selection may have fashioned us to be prepared to form some associations more readily than others, and built in some motivational priorities, but many psychologists regard this as more tinkering with the general system than constructing an independent set of species-specific learning processes (Bolhuis and MacPhail, 2001).

Cosmides and Tooby (1987) have argued that learning should not be regarded as an alternative to evolutionary explanations. However, our capacity to learn is an unusual adaptation. It has a property that makes it different from other adaptive responses of phenotypes to the environment, such as calluses on the hands (Buss, 1995); namely, that it is an information gaining subsystem. Its function is to acquire and store information about the world, information that will generally guide behaviour towards adaptive goals but information that nonetheless could not be specified in our genes. Rather than fashioning us with brains hardwired to recognize apples as food and sand as not food, natural selection has given us a flexible information gaining problem solver, with instructions to seek food when blood sugar levels are low and to recognize apples as food because they taste good while sand doesn't. A rule like 'Actions that are followed by a positive outcome are likely to be repeated, while those followed by a negative outcome will be eliminated' is domain-general in the sense that it can be equally applied to behaviour concerned with finding food, avoiding predators, or seeking a mate. This particular rule was first described by American psychologist Edward Thorndike in 1911, and is known as 'The Law of Effect'. While comparative psychologists still argue over the details and rarely specify the problem in informational terms, few would dispute that something approximating this rule governs much human learning. If researchers want to know why individuals prefer eating apples to sand, the best explanation is an evolutionary one, as our learning about foods is constrained to substances of nutritional value. However, if researchers want to know why some humans eat apples and others snails or curry, arguments based on biological evolution have comparatively little to offer. This is not to say that specialized processes play no part in learning. We may well be predisposed to adopt the behaviour of the majority, imitate the successful or experience norm violations as aversive, for instance. However, our genes specify a tolerance space for our acquired information but rarely the details within it.

Much of the debate over the merits of evolutionary psychology explanations revolves around the extent to which human developmental processes are under tight genetic regulation in which developmental outcomes are pre-specified and channelled, as opposed to a more flexible system in which pre-specification of regulatory development is minimal. Evolutionary psychologists are content to assume past selection for different properties of mind, such as altruism or jealousy. However, in the absence of any established neurobiological theory of how (or indeed whether) genes that bias the growth and connections of neurons during development influence the relevant psychological states, a fundamental part of the causal pathway is missing. Researchers cannot carry out experiments on humans to establish whether 'altruism' can be subject to selection. To our knowledge, no-one has ever shown that 'jealousy' has a genetic basis, or is heritable. We agree that it is quite plausible that natural selection may have favoured particular psychological states in specific past environmental contexts. However, given the immense developmental plasticity and flexibility of the human brain, it is also conceivable that 'jealousy', 'altruism', and many other psychological states are better regarded not as adaptations but as a by-product of our extraordinary adaptability.

Learning processes are not the only psychological processes to exhibit domain-general properties. The senses are classic examples of modular division of labour, yet share a number of functional properties, such as a sensitivity to contrast, a tendency to habituate, and a tendency to give a bigger response to a bigger stimulus (Shettleworth, 2000). Fodor (1983), a philosopher who pioneered the notion, regarded modularity as operating primarily at the level of these sensory input systems to the brain, with central cognitive processing more general across domains. Sensory inputs feed into some quite general cognitive processes, such as planning, reasoning, mental state attribution, and problem solving. It is even conceivable that cognitive modularity has been reduced during recent human evolution, allowing more integration of information and communication amongst modules (Mithen, 1996). The more extreme evolutionary psychologists appear to regard cognition as modular right through from perception to action, the implication being that modules operate in parallel and rarely interact (Bolhuis and MacPhail, 2001).

When we asked Cosmides and Tooby whether they would accept that many psychological traits are domain-general they responded with an emphatic 'Of course!', and pointed to experimental studies of theirs that had demonstrated as much (for example, Brase *et al.*, 1998). However, a hypermodularized depiction of the mind continues to pervade much of the evolutionary psychology literature (e.g. Buss, 1999).

Adaptationism and evolutionary biology

Most evolutionary psychologists adhere to a branch of evolutionary thinking known as 'adaptationism'. Unfortunately the term 'adaptationism' is used in at least two quite distinct ways by enthusiasts and by critics of this perspective. Adaptationists take inspiration from George Williams' (1966) *Adaptation and Natural Selection*, which advocated a much more rigorous use of the term 'adaptation', and argued that natural selection was a sufficient theory to explain most of what is important about evolution. In spite of this, for their critics, adaptationists are researchers who describe virtually all characters as adaptations and who underestimate the importance of other processes in evolution. While many evolutionary psychologists are commendably disciplined in their attribution of adaptations, which are carefully distinguished from exaptations and by-products (for definitions see Chapter 4), others appear less cautious. Moreover, critics of evolutionary psychology feel that these researchers underestimate the significance of evolutionary processes other than the natural selection of genes (Lloyd and Feldman, 2001). The fact that few evolutionary psychology studies refer to the findings of modern evolutionary biology reinforces the suspicion that evolutionary psychology has become detached from recent developments in evolutionary thinking, which over the last 30 years have increasingly stressed a wide range of processes (Endler, 1986b; Futuyma, 1998). The contemporary reality is that evolution is a much more complex phenomenon than that portrayed in evolutionary psychology textbooks (Lloyd and Feldman, 2001).

Endler (1986b) identified 21 processes that are instrumental in evolutionary change, stressing that his list was incomplete. It has become clear that natural selection operates at several different levels and, unlike 25 years ago, multi-level selection models are now a common and respectable feature of evolutionary genetics. Selfish DNA such as microsatellites, and selfish genes such as transposons and segregation distorters, are examples of selective processes operating below the level of the individual, while above this level an increasing proportion of specialists accept the idea that species selection and clade selection could be important (Stearns, 1986; Lloyd, 1994; Rice, 1995; Sober and Wilson, 1998; see also the articles in Rose and Lauder, 1996). Indeed, few evolutionary psychologists appear to realize that among the converts to the idea of 'clade selection' can be found their guru George Williams (1992), previously renowned for his criticism of group selectionist arguments.

Nor is measurement of fitness straightforward (Lewontin, 1974). Endler (1986a, p. 33) writes, 'there are many different definitions and measures of fitness' and reduces the multitude of terms and methods to a core five concepts. Many evolutionary psychologists characterize Hamilton's inclusive fitness theory as the cornerstone of modern evolutionary thinking (Cosmides and Tooby, 1987; Ketelaar and Ellis, 2000), yet this represents a small subset of models used for special purposes in evolutionary understanding, and which cannot handle sexual selection, multi-locus selection, or multi-level selection (Lloyd and Feldman, 2001).

Identifying what constitutes a character that is subject to natural selection is a well recognized and stubborn problem within contemporary evolutionary biology which has countless difficulties but no universally accepted solution (Wagner, 2001). For instance, it is well known that human evolution is characterized by neoteny, that is a slowing down in development, so that in certain characteristics the anatomy of the adult human being resembles the infant ape more than it resembles the adult ape. Lewontin (2000) points out that there have been many speculations about why natural selection might have favoured a protruding chin in humans, making it an exception to the rule of neoteny. In reality, the evolution of neotenous development has produced smaller jawbones, but the dentary and mandibular bones have receded at different rates, most likely as a consequence of developmental constraints, and the chin is an incidental outcome. In other words, the chin is not a character that has been favoured by natural selection. While Cosmides and Tooby have been admirably cautious in their use of the term adaptation, few evolutionary psychologists take time to ensure that their traits truly are an integrated unit of development selected for a particular function rather than an incidental feature to which a name has been given.

Similar problems relate to identifying adaptations. It is sometimes possible to make an educated guess as to whether a character is an adaptation by drawing inferences about which traits might be expected to have been favoured by selection in the past, based on knowledge of evolutionary processes and ancestral environments (Cosmides and Tooby, 1987; Tooby and Cosmides, 1990a). The likelihood of such inferences being correct is a matter of some controversy. As investigators are rarely completely ignorant of the nature of the character that will eventually be described as an adaptation, they may be in a position to 'cheat' and devise an evolutionary story that predicts qualities of the character that are already known to exist. Under such circumstances, confirmation of the predictions through experiments or questionnaires would hardly be compelling. Researchers rarely restrict the application of this method to characters for which the relevant features of the ancestral environment are reasonably well known, or their predictions to phenomena that are not self-evident. Given the well-documented difficulties of identifying adaptations (Rose and Lauder, 1996), researchers would be well advised not to settle for a single line of evidence. Independent corroboration that the observed character has been correctly identified as an adaptation can be provided through the use of mathematical models, the comparative method, phenotypic manipulations, or by inference from the character's 'engineered' or design properties (Rose and Lauder, 1996; Sinervo and Basolo, 1996; Orzack and Sober, 2001).

There are other respects in which evolutionary psychology appears to circumvent the complexities of evolutionary biology. For instance, Cosmides and Tooby argue that:

> the complex architecture of the human psyche can be expected to have assumed approximately modern form during the Pleistocene … and to have undergone only minor modifications since then. (1987, p. 34)

This reasoning is based on the assumption that complex characters evolve slowly. However, while it is a reasonable supposition that complex traits will evolve more slowly than simple ones, evolutionary biology has not yet gained a sufficient understanding to be able to pin reliable quantitative estimates on rates of character change. It is not known if complex adaptations always take millions of years to evolve, but the evidence for those traits studied is, if anything, to the contrary. Selection experiments and observations of natural selection in the wild have, over the last 20 years, led to the conclusion that biological evolution may be extremely fast, with significant genetic and phenotypic change sometimes observed in just a handful of generations (e.g. Dwyer *et al.*, 1990; Grant and Grant, 1995; Reznick *et al.*, 1997; Thompson, 1998). Recently, Kingsolver and colleagues (2001) reviewed 63 studies that measured the strength of natural selection in 62 species, including over 2,500 estimates of selection. They concluded that the median selection gradient (a measure of the rate of change of fitness with trait value) was 0.16, which would cause a quantitative trait to change by one standard deviation in just 25 generations. While it is possible that selection gradients may be weaker when measured over larger time scales (Gingerich, 1983), it is clear that substantive biological evolution can occur in thousands of years, or less. A quotation from *Sociobiology: The New Synthesis* remains apt:

> The theory of population genetics and experiments on other organisms show that substantial changes can occur in the span of less than 100 generations [and] it would be false to assume that modern civilizations have been built entirely on capital accumulated during the long haul of the Pleistocene. (Wilson, 1975, p. 569)

Finally, given the prevalence of evolutionary psychological explanations for sex differences in human behaviour and anatomy in terms of sexual selection, it is worth reflecting on the basics that would need to be in place for such hypotheses to be viable. As an example, consider the recent interest engendered by research into human mate choice and character symmetry. Fluctuating asymmetry (FA) is a measure of the symmetry of a bilateral character (e.g. ear length or hand breadth) that fluctuates, it is supposed, in response to internal and external stress factors such as inbreeding or parasitic infection. A high level of FA (e.g. one foot longer than the other) is thought to indicate poor condition, on the assumption that it requires a sound metabolism to grow perfectly symmetrical features. Some models of sexual selection suggest that females choose a male with traits indicating that he is strong and healthy, on the grounds that their offspring will inherit these 'good genes' (Zahavi, 1975), and some researchers have suggested that symmetry (or low FA) represents such a trait (e.g. Møller, 1990).

Several evolutionary psychology studies conclude that women find men with symmetrical features more attractive than their asymmetric counterparts and posit a 'good genes' explanation (an overview of these studies can be found in Cartwright, 2000). Yet consider some of the fundamentals that would have to be established to provide reasonable support for this hypothesis:

(1) There would have to be evidence that there is, or has been, genetic variation underlying female preferences and the symmetry of male faces.

(2) Male facial symmetry and female preferences for symmetrical faces would have to be shown to be (or have been) heritable.

(3) Male facial symmetry and female preferences would have to be shown to co-vary with fitness, or to have co-varied with fitness in the past.

(4) There would have to be evidence that male facial symmetry is, or has been, sexually selected (as opposed to naturally selected).[3]

Not only is this evidence rarely provided, but a number of biological studies have shown that the association between

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3 A good illustration of how traits seemingly fashioned by sexual selection can actually be the product of natural selection is provided by Heather Proctor's elegant studies of the mating displays of water mites (Proctor, 1992, 1993). Individuals of both sexes feed on aquatic invertebrates by sitting with their front legs spread out and pouncing on prey items that they detect through vibrations in the water. Males have taken advantage of this pre-existing female response by evolving a sexual display that involves the vibration of their front legs at the same frequency as the prey, and depositing spermatophores when the females grab them. A series of experiments and comparative analyses reveal no evidence that sexual selection has fashioned female mate choice, but considerable support for the sensory exploitation hypothesis. Yet a study that focused solely on sexual behaviour could easily draw the erroneous conclusion that the females are choosing males with 'good genes' or protein-rich spermatophores.

FA and fitness is tenuous and perhaps an artefact of selective reporting, that there are not consistent correlations among different measures of FA on the same organisms, that the human traits commonly used are rarely measured accurately enough to prevent FA from being confounded by measurement error, and that the heritability of FA for most appropriately measured traits is close to zero.[4] While it may be tempting to conclude that collecting data on human reproductive success and heritability would be ineffectual in a modern world where fitness is clouded by use of contraception, and where environments are very different from those of our ancestors, other studies have found strong evidence for ongoing selection in contemporary human populations and demonstrated the feasibility of testing these assumptions in humans (Durham, 1991; Pawlowski *et al.*, 2000; Smith *et al.*, 2000).

If evolution is a complex multi-faceted phenomenon, if many evolutionary processes, including drift and mutation, are operating at the same time, if evolutionary history is important, if selection is operating at different levels, and if evolutionary rates can sometimes be fast, it makes the business of predicting and interpreting psychological adap-

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4 Markow (1995) and Clarke (1995) both conclude that any association between FA and fitness is tenuous, speculative, and character-specific. A meta-analysis by Palmer (2000) concludes that relations between FA and individual attractiveness or fitness may be a result of selective reporting. Schlichting and Pigliucci (1998) cite studies that find no consistent correlations among different measures of stability on the same organism. Palmer and Strobeck (1997) provide a good discussion of the confounding effects of measurement error. In criticizing Møller and Thornhill's (1997) selection of studies to generate a estimate of the heritability of FA, Leamy (1997) computes its value to have a mean of 0.11 and a median of 0.03.

tations that much more difficult. However, we see no virtue in pretending that evolution is a simpler process than it actually is. Many evolutionary biologists fear that an overly simple conceptualization of the evolutionary process has, in some cases, led to erroneous conclusions being drawn (Coyne and Berry, 2000; Lloyd and Feldman, 2001). Yet modern evolutionary biology has much more to offer enthusiasts than the suggestion that the process of evolution is complicated. There are rigorous methods for detecting the action of natural selection (Endler, 1986a), for isolating characters (Wagner, 2001), for determining whether a character is an adaptation (Sinervo and Basolo, 1996; Orzack and Sober, 2001), and for drawing inferences about how characters have evolved (Harvey and Pagel, 1991) that could beneficially be used more frequently within evolutionary psychology. Rather than remaining content to rely on polemical assertions or deductive reasoning, evolutionary psychologists could directly evaluate their claim that there is little ongoing selection in modern human populations by utilizing well-established methods for estimating selection gradients and contributions to fitness (Lande and Arnold, 1983; Endler, 1986a). There is room for more evolution within evolutionary psychology.

Conclusions

It is clear that evolutionary psychology is a mixed bag. There are undoubtedly some very fine pieces of work that show genuine promise of being able to decipher the evolved structures of the human mind. The best of evolutionary psychology is as rigorous and sophisticated as any research carried out in the general area of human behaviour and evolution. However, the discipline is marred by a number of weak studies that do little more than use a Pleistocene stereotype to contrive a 'Just so' evolutionary story. Sadly, these poorer studies frequently have a sensational quality that results in their receiving considerable attention. Perhaps too much research in the field is a documentation of what is already known, accompanied by a *post hoc* evolutionary spin and a snappy press release. Other psychologists have stressed the need for more sophisticated theories than are typical of evolutionary psychology (e.g. Heyes, 2000).

It would be unfair to condemn the entire field of evolutionary psychology on the basis of the work of its weakest practitioners. The problems that are described in the previous sections are hardly irreparably damaging, and there is nothing to prevent evolutionary psychologists from using the EEA concept with greater caution, or paying greater attention to developments within evolutionary biology; indeed, some proponents clearly already do so. The evolutionary psychology perspective has brought the study of the mind well and truly into the domain of evolutionary theory, bringing with it a welcome focus on proximate mechanisms. It has proven an enormously creative approach to the study of human behaviour, and has introduced a wealth of new ideas and methods. Moreover, the evolutionary psychology literature has made important contributions to the understanding of culture (Sperber, 1996), decision making (Gigerenzer *et al.*, 1999; Todd, 2001), emotion (Fessler, 2001), language (Pinker, 1994), pregnancy (Profet, 1988; Fessler, 2002), psychological illness (Nesse and Williams, 1995), sexual behaviour and sex differences (Daly and Wilson, 1983; Miller, 1997), stigmatization (Kurzban and Leary, 2001), visual perception (Shepard, 1992), and many other topics (see Barkow *et al.*, 1992 or Barrett *et al.*, 2001 for comprehensive treatments). Yet for all the enthusiasm it has engendered, at this time evolutionary thinking makes up a very small component of psychological research. We believe that the likelihood of significant advances will be enhanced if evolutionary psychologists broaden their methodology to embrace other appropriate evolutionary perspectives, tools, and heuristics (Plotkin, 1994, 1997; Heyes and Huber, 2000).

There is one criticism of evolutionary psychology on which we have not yet dwelt, namely that it underestimates the critical role of cultural transmission processes in shaping human knowledge and behaviour. In the next two chapters we will consider evolutionary perspectives that treat culture as a much more dynamic and influential process than hitherto regarded. Maybe social scientists are right to view cultural processes as not always well specified by our genes or environment, and as having a limited autonomy from biological control. Perhaps culture is an important evolutionary player in its own right.