Applying evolutionary theory to human behaviour: past differences and current debates

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Abstract

The aim of this paper is to provide non-specialist readers with an introduction to some current controversies surrounding the application of evolutionary theory to human behaviour at the intersection of biology, psychology and anthropology. We review the three major contemporary sub-fields; namely *Human Behavioural Ecology*, *Evolutionary Psychology* and *Cultural Evolution*, and we compare their views on maladaptive behaviour, the proximal mechanisms of cultural transmission, and the relationship between human cognition and culture. For example, we show that the sub-fields vary in the amount of maladaptive behaviour that is predicted to occur in modern environments; Human Behavioural Ecologists start with the expectation that behaviour will be optimal, while Evolutionary Psychologists emphasize cases of 'mis-match' between modern environments and domain-specific, evolved psychological mechanisms. Cultural Evolutionists argue that social learning processes are effective at providing solutions to novel problems and describe how relatively weak, general-purpose learning mechanisms, alongside accurate cultural transmission, can lead to the cumulative evolution of adaptive cultural complexity but also sometimes to maladaptative behaviour. We then describe how the sub-fields view cooperative behaviour between non-kin, as an example of where the differences between the sub-fields are relevant to the economics community, and we discuss the hypothesis that a history of inter-group competition can explain the evolution of non-kin cooperation. We conclude that a complete understanding of human behaviour requires insights from all three fields and that many scholars no longer view them as distinct.

Keywords: human behavioural ecology, evolutionary psychology, cooperation, gene-culture co-evolution, cultural group selection

1 Applying evolutionary theory to human behaviour

The application of evolutionary theory to the study of human behaviour has a long and contentious history (Boakes 1984; Laland and Brown 2011). Over this history, the fields of economics and the biological sciences have drawn inspiration from each other, but the social and biological sciences have also been in apparent conflict (Hodgson and Knudsen 2008; Witt 1999). In order for communication between different academic fields to be successful, individual researchers need to meet the challenge of incorporating the most recent advances from multiple disciplines. This challenge is certainly not straightforward, but is aided by inter-disciplinary journals, such as the *Journal of Bioeconomics*. The aim of this paper is to contribute to this inter-disciplinary discussion by presenting a brief summary of some of the current debates at the interface of biology, anthropology, and psychology, thereby provide readers with information about the issues that are being discussed at this relevant junction.

Our approach is, in itself, somewhat controversial: we present a number of sub-fields within the evolutionary human behavioural sciences (namely Human Behavioural Ecology, Evolutionary Psychology and Cultural Evolution) and draw distinctions between some of the underlying assumptions of the research conducted under each of these headings. Other researchers have argued instead that the sub-fields are highly complementary and exhibit a large degree of overlap (Alcock 2001). We agree with this latter statement to some extent, and we have previously discussed the fact that some research topics have been successfully viewed from multiple perspectives (Brown et al. 2011; Laland and Brown 2011). In addition, we acknowledge that several researchers have successfully combined more than one of the approaches within their own research and have bridged between the sub-fields (e.g., Kaplan and Gangestad 2005). However, we also believe that the distinctions between the sub-fields are real; for example, the sub-fields differ significantly in methodology, views on which evolutionary processes are relevant, and consequently on the most likely explanations for important aspects of human

behaviour. Evolutionary epistemologists, like Donald Campbell, have argued that science progresses by scientists considering the adequacy of different proposals against the best evidence we can bring to bear on the subject (Heyes and Hull 2001). If so, science will progress best when whatever differences exist are clearly delineated. Hence, in this paper we take for granted the many agreements between the three areas and focus on the differences. Indeed, many current practitioners, particularly younger scientists, do not conceive of themselves as members of separate fields and view the issues that once divided them on their way to solution.

We first provide a brief introduction to human sociobiology, as exemplified by Wilson's (1975) book, *Sociobiology: the New Synthesis*, given that many of the current debates within the field stem from discussions that surrounded the conception of this field. The next sections then provide short summaries of the three main sub-fields that characterise current research – Human Behavioural Ecology, Evolutionary Psychology and Cultural Evolution (for a more detailed discussion, see Laland and Brown 2011). The following section then examines some of the key debates between the sub-fields, including questions of whether human beings exhibit maladaptive behaviour in modern environments, and what the relationships are between human cognition and our evolving culture, focusing particularly on the debates between Evolutionary Psychology and Cultural Evolution. As an example of where the differences between the sub-fields are relevant to the economics community, we discuss alternative perspectives on cooperative behaviour between non-kin. We conclude that the disagreements between the sub-fields are indeed over substantive scientific issues that need to be settled by future research.

2 Human sociobiology

In 1975, Edward O. Wilson, a Harvard professor of entomology, published *Sociobiology: the New Synthesis*, in which he promoted recent advances that were being made within the field of

evolutionary biology. Naïve group-selectionist views were being rapidly overtaken by the 'gene's-eye' perspective, as exemplified by the work of William Hamilton, Robert Trivers and George Williams. This new perspective was revolutionising the application of evolutionary theory to non-human animals, and the ground-breaking research of Hamilton, Trivers and others has been hugely influential in the field of animal behaviour to this day (e.g., Danchin et al. 2008). More controversially, Wilson (1975; 1978) applied these theoretical advances to human behaviour (Human Sociobiology), providing evolutionary explanations for topics such as aggression, religion and homosexuality. Despite gaining many followers, Wilson's comments on human behaviour resulted in hostile attacks from some critics (e.g., Allen et al. 1975; Rose et al. 1984), including accusations of genetic determinism, storytelling and ignoring the influence of culture on human behaviour. Partly as a result of this hostility, many researchers who were applying evolutionary principals to the study of human behaviour mostly sought to distance themselves from Wilson's sociobiology during the 1970s and 1980s, and the term 'Human Sociobiology' has generally fallen out of favour. However, other researchers, such as Sarah Hrdy, have been keen to highlight that sociobiological theory contributed a considerable amount to our understanding of animal behaviour and provided fertile ground for more recent applications of evolutionary theory to human behavior (Segerstråle 2000). In addition, Wilson embraced the emerging field of cultural evolution (Lumsden and Wilson 1981), and Wilson has continued to call for greater integration between the biological and social sciences (e.g., Wilson 1998).

3 Human Behavioural Ecology

During the 1970s, anthropologists had already begun to apply contemporary concepts from evolutionary biology, such as optimality modelling and evolutionary game theory, to

observational data gathered from a diverse range of human populations (Chagnon and Irons 1979). One of the key concepts within this sub-field, now referred to as Human Behavioural Ecology, is the idea that human behaviour is extremely flexible, and adaptive behaviour can be produced in response to a broad range of environmental variables (Borgerhoff-Mulder and Schacht 2012). Typically, Human Behavioural Ecologists appeal to the 'phenotypic gambit' (Grafen 1984), which allows researchers to test the prediction that behavior is fitness-optimizing in the particular environment under study without recourse to understanding the mechanisms involved. Such mechanisms could include a combination of genetic adaptation, physiological plasticity or culturally transmitted information. These researchers thus do not generally concern themselves with the mechanistic processes that are the central focus of the other major sub-fields. Early proponents of Human Behavioural Ecology, such as Richard Alexander, Napoleon Chagnon and William Irons, attempted to explain human behaviour based on the assumption that individuals behave in a manner that maximises their reproductive success, with particular emphasis on foraging and reproductive behaviour. A strength of this approach is that it typically tries to explain concrete human behavior in real-world environments. Most Human Behavioural Ecology research has focused on non-Westernised societies with small-scale subsistence patterns and a relative absence of modern contraceptive technology (Borgerhoff Mulder and Schacht 2012). However, other researchers have pointed out that there are good evolutionary reasons to expect that Human Behavioural Ecology approaches can be effective when applied to data from Westernised societies (Laland and Brown 2006), and the field of Human Behavioural Ecology has broadened since its inception to incorporate research on a wider range of populations and research topics (Nettle et al. 2013; Brown 2013), including consideration of the processes of cultural evolution (Borgerhoff Mulder and Schacht 2012).

4 Evolutionary Psychology

The term 'evolutionary psychology' has a long history, including appearing in William James' (1890, p. 146) *Principles of Psychology*, and could be used to refer to any evolutionary perspective on the human mind. Given the remarkable size of the human brain and its unique products like language and cumulative culture, every student of human evolution is an evolutionary psychologist. However, the term Evolutionary Psychology is now commonly used to describe a highly influential school of the human evolutionary sciences that was founded by Donald Symons, Leda Cosmides and John Tooby (e.g., Symons 1989; Tooby and DeVore 1987; Cosmides and Tooby 1987; Tooby and Cosmides 1992). Since the 1980s, Cosmides, Tooby, David Buss and Steven Pinker, in particular, have promoted the idea that the human brain consists of specialised psychological mechanisms that have evolved in response to recurrent selection pressures acting on our human ancestors. Evolutionary Psychologists argue that the most important stage of history for understanding the evolution of the human mind is the Pleistocene epoch when our ancestors were living as hunter-gatherers on the African savannah (Cosmides and Tooby 1987). Evolutionary Psychologists aim to describe the evolved psychological mechanisms that underlie human cognition, with an emphasis on domain-specific information processing devices that provide human beings with a universal toolkit of mental adaptations. These researchers argue that selection will have favoured psychological mechanisms that are suited to efficiently solving problems within specific domains, and this perspective has been applied to a broad range of topics, including mate choice, aggression, social exchange and morality (Buss 2005). While critics argue that Evolutionary Psychology will benefit from incorporating advances from adjacent research fields (Bolhuis et al. 2011), Evolutionary Psychology is perhaps the most impactful of the contemporary approaches, in terms of numbers of practitioners and wider dissemination. For example, Steven Pinker's (1994) book *The Language Instinct* is one of the most highly cited books in the entire field.

5 Cultural Evolution

The idea that Darwin's theory of natural selection can be applied to entities other than genes was endorsed by Darwin (1871) himself, when he applied the idea of natural selection to language evolution and proposed an important role for traditions in human evolution. The gene itself was not part of Darwin's pre-Mendelian vocabulary, of course. The idea of universal Darwinism has since spread to many scientific disciplines (Plotkin 1994). Researchers within the field of Cultural Evolution have applied evolutionary theory to human cultural traits and have shown how mathematical models can be used to understand how the frequencies or distributions of different cultural variants change over time (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). More broadly, the field of *gene-culture co-evolution* investigates how genes and culture co-evolve (Laland et al. 2010; Richerson and Boyd 2010a). Culture is pragmatically defined as 'information capable of affecting individuals' behaviour that they acquire from members of their species through teaching, imitation, and other forms of social transmission' (Richerson and Boyd 2005). Numerous factors can influence the process of information transmission, such as biases in how individuals learn, biases in which model is chosen, and preferences for learning or remembering some cultural variants over others (Richerson and Boyd 2005). Cultural Evolutionists thus assume that rather domain-general psychological mechanisms can bias the acquisition of particular behaviour patterns (Sterelny 2012); for example, 'copy the majority' (or plurality) is a learning rule that can potentially be applied across numerous cultural domains. These relatively domain-general forces are generally weak at the individual level, agreeing with Tooby and Cosmides (1992) in this regard, but they can act as very powerful evolutionary forces when acting on populations over the evolutionary time scale to cumulatively "design" complex technologies and social institutions that are far beyond the capabilities of any one innovator (Boyd et al. 2011a). While the field of Cultural Evolution could once be criticised for failing to stimulate new empirical research, a sustained and rapidly expanding empirical

program began in the late 1990s (e.g., McElreath et al. 2005; Mesoudi and O'Brien 2008; Henrich and Broesch 2011; Morgan et al. 2012), including large cross-cultural collaborative projects (e.g. Henrich et. al. 2005, 2010; Henrich and McElreath 2002).

6 Some current debates between the sub-fields

Having given a brief overview of the main sub-fields within the human evolutionary behavioural sciences, we now highlight some potential points of contention where, in our opinion, the sub-fields exhibit either quantitative or qualitative differences in their underlying assumptions about human behaviour (for more extensive discussions, see Brown et al. 2011; Laland and Brown 2011; Boyd et al. 2011a).

6.1 Do human beings exhibit maladaptive behaviour in modern environments?

While all three sub-fields agree that the evolutionary mechanisms they postulate tend to commonly produce adaptive behaviour, the sub-fields are rather more distinctive in the extent of maladaptive behaviour that they predict. Many Evolutionary Psychologists argue that, because the human brain is a highly complex, slowly evolving organ, human beings are likely to exhibit an 'adaptive lag', meaning that much of human behaviour is sub-optimal in modern environments (Tooby and Cosmides 1992). Any culturally evoked changes in human behaviour since the end of the Pleistocene are therefore assumed to be largely irrelevant to our understanding of the evolved human mind. For Tooby and Cosmides (1992), culture is part of the environment that, along with many other environmental influences, may trigger alternative developmental pathways, much as identical jukeboxes might play different tunes in different environments if that is how they were programmed. Barrett (2012) uses a norm of reaction

model of how the development of the organism responds to environmental inputs. In this formulation, evolved mental modules include a function that maps environmental variation onto behaviour. If human mental adaptations can be characterised as norms of reaction that were calibrated for hunting and gathering lifeways in Pleistocene environments, then many maladaptive mismatches between cognitive adaptations and the environment should exist in the vastly different lifeways of complex societies in the Holocene.

In contrast, human Behavioural Ecologists argue that their research has shown that real-world data often provide a good fit to models that assume optimal behavioural responses to current environmental parameters (Borgerhoff Mulder 1991). Human Behavioural Ecologists start with the assumption that behaviour will be adaptive, but are willing to accept that maladaptive responses may occur, either as a result of critical environmental triggers or stimuli being absent, or as a result of culturally transmitted information. Whether behaviour is adaptive or maladaptive, in terms of genetic fitness, is tested empirically, generally by using long-term datasets. For example, these researchers have considered conspicuous puzzling cases like the transition to low fertility in the course of modernization, where fertility appears to be sub-optimal (Kaplan 1994; Borgerhoff Mulder 1998). The answer Kaplan (1994) gives to the puzzle of the demographic transition is that, in the unprecedentedly wealthy societies of many contemporary populations, we inadvertently over-invest in the quality of our offspring and have too few of them; this is the same sort of mismatch explanation as Evolutionary Psychologists might give. In contrast, other Human Behavioural Ecologists have pursued the possibility that sufficiently complex optimality models, involving trade-offs between quality and quantity of offspring, can shed light on patterns of family size in post-demographic transition societies (e.g., Lawson and Mace 2011; Lawson et al. 2012). Human Behavioural Ecologists generally do not envisage high levels of mal-adaptations in modern environments, because they hold a less

domain-specific view of the underlying mechanisms than do Evolutionary Psychologists (Borgerhoff Mulder et al. 1997).

Evolutionary Psychologists, Human Behavioural Ecologists and Cultural Evolutionists do appear to agree that maladaptive behavioural responses can result from cultural processes. The social learning strategies that are studied by Cultural Evolutionists could lead to the acquisition of maladaptive information (i.e., information that fails to enhance genetic reproductive success) in some instances, as long as the learning strategies themselves are favoured by selection (Richerson and Boyd 2005). Take the issue of whether or not to learn from people other than your parents. On the one hand, doing so will expose a learner to much more cultural variation than is likely to be present in just two parents, and, to the extent that learning biases let learners chose adaptive traits, the more variation the better. On the other hand, some harmful cultural variants may arise that exploit general purpose decision-making systems to the detriment of the learner's genetic fitness. For example, Newson and colleagues (2007) used a combination of models, experiments and survey data to argue that the main cause of the modern decline in fertility was a sharp increase in the ratio of non-kin to kin in social networks, leading to the spread of fertility-limiting cultural information between unrelated peers. Weak general-purpose biases, such as 'copy the majority', can sometimes be inadequate defence against specific maladaptive ideas, perhaps explaining the demographic transition and other oddities of modernity (Newson and Richerson 2009). The trade-off of increased power of biases against the risk of acquiring fitness-limiting ideas might well have been optimized by selection in past societies, and the risk of acquiring maladaptive information might have increased substantially in modern environments, for example because mass media exposes us to many attractively packaged cultural variants designed by advertisers to increase their sales, not the recipients fitness.

Given that the cognitive mechanisms underlying human culture are assumed to have been selected for their overall fitness-enhancing properties, the extent of the 'adaptive lag' is likely to be less extreme than envisaged by some Evolutionary Psychologists (Laland and Brown 2006). Cultural Evolutionists differ from Evolutionary Psychologists in highlighting the potential for cultural transmission to produce fitness-maximizing solutions to novel problems, including those produced by human culture itself. While Cultural Evolutionists certainly have no quarrel with the idea that the developing organism has many circuits that respond adaptively to evolutionarily relevant environmental inputs and maladaptively to novel ones, culture is, in their view, a completely different system. Culture is a system that fairly quickly evolves novel solutions to novel problems. In this respect, cultural evolution is like a faster version of genetic evolution (Perreault 2012), and, like genetic evolution, generates design and functionality in traits. The speed of cultural evolution allows it to explore a very large design space. For example, Arctic people developed light, swift, safe boats to hunt seals using driftwood and skins, while European mariners developed large stout wooden sailing ships to pioneer a global commerce in bulk goods. Knowledge of how to make and operate such complex devices must be transmitted with reasonable fidelity so that weak relatively general-purpose cognition can, generation by generation, invent and select improvements in the designs of artifacts and social systems (Tennie et al. 2009). Where cultural processes induce environmental changes, selection can favour culturally-transmitted solutions, or generate selection pressures acting on the human genome (Laland et al. 2010; Richerson and Boyd 2010a; Stearns et al. 2010; Courtiol et al. 2012).

Thus, Cultural Evolutionists expect that many types of temporal and spatial mismatches between ancestral human adaptations and their current environments will be solved by cultural evolution fairly quickly; for example, the development of protective clothing and shelter technology systems has allowed human beings to survive in environments with extreme low temperatures. Cultural evolution seems to explain why humans have been, if anything, more

successful in the Holocene than in the Pleistocene. We have undergone a veritable adaptive radiation of locally adapted economies using domesticated plants and animals. At the same time, the disease and nutritional environments created by the cultural evolution of agricultural subsistence systems have put intense selective pressure on those aspects of human biology for which cultural fixes have proven elusive (Laland et al. 2010; Richerson and Boyd 2010a; Stearns et al. 2010); for example, an increasing proportion of starchy food in the diet following the adoption of agriculture has selected for increasing the number of copies of the enzyme amylase, which is secreted in saliva to begin the digestion of starch (Perry et al. 2007). More broadly, many organisms change conditions and factors in their local environments, a process known as *niche construction*, and thereby produce an organism-induced change in the selective environment (Odling-Smee et al. 2003). Niche construction activities lead to feedback loops between organisms and their environments that alter the selection pressures on the organisms and their descendants, for example, leading to the fixation of alleles that would otherwise be deleterious and allowing the persistence of organisms in otherwise hostile environments (Odling-Smee et al. 2003). The potency of human cumulative culture allows *cultural niche construction* to modify selection on human genes (Laland et al. 2001), and socially transmitted information thus has the ability to shape natural selection pressures, allowing genetic and cultural variation to co-evolve and novel evolutionary episodes to occur (Laland et al. 2000; Kendal et al. 2011).

In summary, the three sub-fields have strong commonalities. All three take it for granted that humans possess evolved psychological mechanisms that produce adaptive responses to environmental cues, as long as the environment is not too dissimilar to ancestral environments. All three agree that mismatches can occur when modern environments are very dissimilar to those of our ancestors. All three agree that cultural transmission (or contagion) processes can sometimes lead to the adoption of behaviour patterns that are maladaptive at the level of gene transmission. However, Cultural Evolutionists and Human Behavioural Ecologists agree that

culture itself can quickly evolve solutions to novel problems, resulting in culturally constructed environments that fit with our previous adaptations, or that instead lead to new bouts of genetic evolution (Laland and Brown 2006), while, in contrast, some Evolutionary Psychologists maintain that cultural evolution has limited explanatory power (Pinker 2010). Thus, the type of adaptive lag envisaged by Cultural Evolutionists differs from that of the Evolutionary Psychologists. For Cultural Evolutionists, mis-matches are generally self-induced and can result in both cultural and genetic responses, with gene-culture co-evolutionary processes potentially minimising the mis-match between current environments and previous adaptations.

Tooby and Cosmides (1992) provided a sweeping critique of the "Standard Social Science Model" and its heavy dependence on the concept of transmitted culture, and they proposed a radically cognitivist alternative. Cultural Evolutionists agree that a blank slate model of human cognition is untenable, but argue that cognitive constraints on transmitted culture are considerably weaker than Evolutionary Psychologists allow. If so, the SSSM is quite right to stress the importance of culture if wrong in *its* radical attempt to deny any importance to genetic evolution and the products of genetic evolution, such as important elements of cognition. Cultural Evolutionists take the massive adaptive radiation of humans in the Holocene based upon culturally transmitted technology and social institutions, and the lack of a massive mismatch of Pleistocene-adapted people to Holocene environments, to be some of the best evidence available for the gene-culture coevolution and cultural niche construction picture of human evolution.

6.2 What is the evolved function of cognition and culture?

Evolutionary Psychologists originally viewed the human mind as consisting of evolved psychological mechanisms that are content-specific computational processing devices adapted for Pleistocene hunting and gathering existence (Tooby and Cosmides 1992). (See the discussion

below on improvisational intelligence for a discussion of a different, more recent evolutionary psychological hypothesis about human cognition.) In contrast, Cultural Evolutionists focus on relatively general-purpose learning mechanisms that produce biases in behavioural outcomes depending upon the context of learning in addition to the content of the transmitted information (Richerson and Boyd 2005; Boyd et al. 2011a); for example, a prestige-bias ('copy prestigious individuals') can lead individuals to acquire information about diet, hunting techniques or mates (Henrich and Gil-White 2001). The human mind is likely to contain both domain-specific and domain-general psychological mechanisms, allowing for some apparent integration between these perspectives. Our sensitivity to pain in the human head and face is clearly a domain-specific adaptation to protect the relatively fragile and important organs of the head from damage. Many such domain-specific adaptations likely exist. Therefore, the relative importance of more domain-specific versus more domain-general mechanisms in directing human cognition and behavior appears to be an empirical question that is amenable to resolution.

However, the sub-fields have different hypotheses about the main adaptive function of human cognition. According to Cultural Evolutionists, the strongly cognitive picture of the Evolutionary Psychologists got the main adaptive problem of the Pleistocene wrong. Tooby and Cosmides (1992) have argued that humans evolved cognitive adaptations to the statistical regularities of Pleistocene environments. If so, Barrett's (2012) reaction norm model of phenotypic flexibility would be adequate. However, according to Cultural Evolutionists, the ancestral world was insufficiently regular to favour numerous highly specific cognitive adaptations, and selection instead favoured a smaller number of more general rules. As it turns out the Pleistocene was a stunningly variable environment that was statistically quite unpredictable (National Research Council 2002). While early records of climatic variation only resolved low-frequency glacial cycles with time scales of tens of thousands of years, paleoclimatologists have recently discovered that glacial environments became increasingly

packed with high amplitude noisy variation on times scales of decades to millennia over the last eight glacial cycles (Loulergue et al. 2008). The Pleistocene is also the culmination of a 50-million-year-long trend toward drier climates and polar cooling that increased spatial variation in the Earth's habitats (Zachos et al. 2001). According to Boyd and Richerson (1985), social learning would be most useful in environments with lots of unpredictable variation that is concentrated in events with durations too long for adaptation by individual learning but too short for genetic adaptations to evolve, just the sorts of variation that typify the Pleistocene. Human cultural complexity and brain size increases appear to have roughly paralleled this increase in climatic variability (Richerson et al. 2005).

Cultural Evolutionists thus argue that the evolved psychological mechanisms in the brain evolved in response to the challenges posed by variable environments and that culture is an important mechanism by which populations can express adaptive responses to environmental challenges. In contrast, Human Behavioural Ecology has remained relatively mechanism-neutral, relying on the ability of optimality and life history models to predict adaptive outcomes in the presence of hypothesized environmental triggers, regardless of the underlying proximate mechanisms (Smith 2000). From its inception, this field has included cultural information as one potential source of adaptive 'fit' with the environment. Cultural Evolutionists have no quarrel with the application of evolutionary models, such as life history and optimal foraging theory from evolutionary ecology to human populations (e.g. Boughton and O'Connell 1999; Borgerhoff Mulder 1991; Smith et al. 2001) but do think they have limitations. In particular the assumption that human populations are always at an adaptive equilibrium is misleading if cultures are actively evolving, a possibility that Human Behavioural Ecologists have historically ignored, or at least tried to ignore by choosing "traditional" populations, or at least traditional behavioural patterns, in *apparent* equilibrium. For example, Kennett (2005) interprets a pattern of resource use intensification in aboriginal Southern California in terms of optimal foraging

decisions interacting with climate and oceanographic change. But long term patterns of intensification occur almost everywhere in the Holocene and probably represent the relatively slow, progressive increase of technical and social sophistication made possible by the shift to warm, wet, relatively stable climates at the beginning of the Holocene.

Examples such as this strongly suggest that use of the phenotypic gambit has led to a relative neglect of culture as a transformational force in human evolution (Borgerhoff Mulder and Schacht 2012; Brown 2013). Human Behavioural Ecologists do seek the source of changes in physical and social conditions that result in changing optima over time, for example, by asking why a population changes from matriliny to patriliny in the context of increasing heritable wealth. However, some Behavioural Ecologists have argued that culture should be treated like any other proximate mechanism (Nettle et al. 2013), which leads to the neglect of how cultural transmission can radically affect the dynamics of adaptive change (Brown 2013). Much of the research within Human Behavioural Ecology involves the application of ahistorical adaptive equilibrium models that do not take into account past trajectories of cultural evolution, and culture is treated as a proximal adaptive system responding to exogenous environmental change. This approach risks ignoring the fact that the very environment to which humans are adapting is itself partly an endogenous, dynamic product of cultural evolution, an issue that closely parallels evolutionary economists' critique of neoclassical models (Nelson and Winter 1982).

In summary, while Evolutionary Psychologists (e.g., Tooby and Cosmides 1992) and Cultural Evolutionists (e.g., Boyd and Richerson 1985) have generally differed in the emphasis that is placed on more domain-specific versus more domain-general mechanisms, the difference between these sub-fields extends beyond this apparently quantitative distinction. For Cultural Evolutionists, culturally transmitted information has played a vital role in the ability of ancestral human populations to adapt to, and regulate, unpredictably varying environments, and any explanations of human behaviour that fail to take cultural evolutionary processes into account

will provide only an incomplete understanding. As discussed in the next section, Evolutionary Psychologists have instead argued that incorporating culture into the equation should have relatively little impact on how we think about the evolved human mind, as cultural content is ultimately under genetic control.

6.3 What are the proximal mechanisms of cultural acquisition?

Evolutionary Psychologists and Cultural Evolutionists have quite different views of what happens in cultural transmission. Evolutionary Psychologists hold what is called an 'epidemiological' theory of culture in which cultural variation is rather tightly limited by the cognitive psychology of representations (Sperber 1984). In the epidemiological model of culture, Evolutionary Psychologists focus on the role that evolved cognitive processes play in controlling information transmission, and they stress the importance of representations being reconstructed in the minds of the learners. For example, Tooby and Cosmides (1992) state that:

> The design of human psychological architecture structures the nature of the social interactions humans can enter into, as well as the selectively contagious transmission of representations between individuals. Only after the description of the evolved psychological architecture has been restored as the centerpiece of social theory can the secondary anti-entropic effects of population-level social dynamics be fully assessed and confidently analyzed. (p. 48)

And:

> Rather than calling this class of representations "transmitted" culture, we prefer terms such as *reconstructed culture*, *adopted culture*, or *epidemiological culture*. The use of the word "transmission" implies that the primary causal process is located in the individuals

> from whom the representations are derived. In contrast, an evolutionary psychological perspective emphasizes the primacy of the psychological mechanisms in the learner that, given observations of the social world, inferentially reconstruct some of the representations existing in the minds of the observed. (p. 118)

While these quotes suggest that information transmission is likely to have low fidelity, as a result of continual bouts of reconstruction within the minds of observers, recent work in developmental and comparative psychology shows that human culture does in fact transmit information quite accurately by cognitive systems apparently selected for that exact purpose rather than for restricting variation by strongly biasing what can be learned. For example, experiments by Tomasello, Whiten and colleagues (e.g. Tomasello 1996; Whiten et al. 2009), which compare the social learning skills of humans and great apes, have shown that young children are much more accurate imitators than are apes. Children quite faithfully replicate the arbitrary, non-functional patterns of behaviour that the experimentalists introduce into their experimental tasks. Apes largely ignore such actions and concentrate on using the demonstration for clues about how to get the reward the experimenters offer. As a result, children are prepared to learn skills that have no immediate reward, except perhaps the internal reward of "doing it right". Later, these skills often turn out to be critical to building complex artifacts and for displaying complex, arbitrary signals of group membership, such as "correct" etiquette. Experiments designed to uncover the cognitive underpinnings of cultural transmission also strongly suggest that our cognition has evolved so that infants and children could acquire the quite complex and often counter-intuitive ideas and practices of their culture (Carey 2009; Buchsbaum et al. 2011; Csibra and Gergely 2011; Harris 2012; Sterelny 2012). Psychological mechanisms in the learner and in the people acting as teachers or models are both important. Given the accurate transmission of a wide range of cultural constructions, populations of humans

can turn the same rather weak, relatively general-purpose learning schemes that underpin reinforcement-based individual learning into powerful evolutionary forces that cumulatively generate complex cultural adaptations faster than can genetic evolution acting on random genetic variation.

Interestingly, an important example that Pinker and Bloom (1990), Tooby and Cosmides (1992) and Pinker (1994) use to exemplify their highly cognitively structured model of epidemiological culture is Chomsky's proposal that language learning is underpinned by a content-rich modular system. Cultural evolutionists have been major contributors to the field of evolutionary linguistics in the years since Pinker and Bloom's pioneering contribution (Richerson and Boyd 2010b). Certainly, cultural evolutionists don't deny that humans are cognitively prepared to learn and use language, but many linguists now believe that language may share most of its cognitive learning machinery with other aspects of culture (e.g. Tomasello 2008; Christiansen and Chater 2008; Smith and Kirby 2008; Evans and Levinson 2009; Hurford 2011). Chomsky's original "principles and parameters" approach to the cognitive foundations of language did not successfully deal with the vast diversity of grammatical inventions comparative linguists discovered in the late 20th Century (Newmeyer 2004). Chomsky himself has recognized the importance of evolution in explaining language but has become a minimalist regarding the cognitive structures involved (Hauser et al. 2002). Thus, what once was taken to be a convincing example of a content-rich cognitive system tightly constraining cultural variation is now plausibly an example of the dominance of cognitive adaptations for teaching and learning a more weakly constrained body of transmitted culture.

Thus, while many evolutionary psychologists emphasize the cognitive processes that allow information to be reconstructed in the receiver's mind and that structure the type of information that is likely to be received, cultural evolutionists argue for less restriction with regard to the type of information that is transmitted and point to the evidence that psychological

mechanisms favour relatively accurate information transmission, even when such information is arbitrary or maladaptive. Controversies within the field of language evolution highlight how researchers are attempting to delineate the specific evolved psychological mechanisms that underlie human social learning and that give rise to so much cultural diversity.

6.4 Is cultural evolution or improvisational intelligence the better explanation for the diversity and complexity of human behaviour?

Evolutionary Psychologists have certainly not been blind to the extremely diverse and highly creative cultural adaptations that are a human specialty. In recent papers, Evolutionary Psychologists have hypothesized that humans, uniquely among all animals, have what they call *improvisation intelligence* (Cosmides and Tooby 2001): individuals can use individual cognition to invent complex and adaptive cultural traits as needed. As Pinker (2010) puts it:

> These cognitive stratagems are devised on the fly in endless combination suitable to the local ecology. They arise by mental design and are deployed, tested, and fine-tuned by feedback in the lifetimes of individuals, rather than arising by random mutation and being tuned over generations by the slow feedback of differential survival and reproduction (p. 8449).

This proposal seems at variance with the argument in Tooby and Cosmides (1992) that general purpose intelligences are inevitably weak, the cornerstone of their hypothesis that cognitive mechanisms must be modular. On their original argument, the improvisational intelligence idea therefore must be wrong. Cosmides and Tooby (2001) admit that the evolution of improvisational intelligence is enigmatic but believe that an increase in the number of modular

structures, together with some means of dealing with the combinatorial explosion involved in keeping in mind many dimensions of a complex problem, have somehow been solved in humans.

Cultural Evolutionists argue that the improvisational intelligence hypothesis greatly overstates individual creativity relative to the power of weak, relatively general-purpose learning systems acting in concert with accurate cultural transmission in leading to the cumulative evolution of cultural complexity (Boyd et al. 2011a). Much evidence suggests that complex human "inventions" have in fact been reached by a long history of cumulative improvement by relatively small steps, a generalization well documented by the pioneering archaeologist and ethnographer Pitt Rivers in the late 19th Century (Bowden 1991) and widely supported by numerous modern studies (see Basalla 1988; Henrich 2009 and Mesoudi 2011 for overviews). Recent successful applications of phylogenetic methods drawn from biology necessarily assume a pattern of "descent with modification" on the part of some aspects of culture as well as genes (e.g. Gray et al. 2011; Mace and Jordan 2011). The role of blind variation and small incremental improvements in the evolution of even comparatively simple artifacts such as paper clips and dinner forks has been documented by Petroski (1992). Thus Cultural Evolutionists are skeptical that improvisational intelligence is a sound alternative to cumulative cultural evolution to explain the complexity and diversity of human cultural adaptations. Certainly humans improvise new solutions to problems, but such improvisation is heavily reliant on minor refinements of culturally transmitted knowledge and hence more closely fits the Cultural Evolutionists' Darwinian model than the Evolutionary Psychologists' macromutational improvisational intelligence conception.

7 A case study: non-kin cooperation in humans

The sub-fields also differ sharply over how to explain the large amount of non-kin cooperation in our species. Everyone agrees that the large-scale societies of the Holocene include a lot of

cooperation between distantly related and unrelated people. There is also widespread agreement among the sub-fields that the proximal mechanisms for ensuring cooperation include such things as reputation, sanctioning of those who misbehave, and the use of language to negotiate actions, make promises, and spread reputational information through gossip (Smith 2010). Evolutionary Psychologists (e.g. Pinker 2010) have explained human cooperation among non-relatives on the basis of selection for reciprocal exchange plus language being sufficient to create the proximal mechanisms listed above. In contrast, Cultural Evolutionists propose that a special form of group selection, *cultural group selection*, played an important role in the evolution of prosocial cognitive adaptations and that ongoing cultural group selection plays a role in the evolution of social institutions (e.g. Richerson and Henrich 2012; Turchin 2009; see also Bowles and Gintis 2011, for a case for culture-facilitated genetic group selection). The basic idea is a modernization of Darwin's tribal scale selection hypothesis in the *Descent of Man*:

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection (Darwin 1871: p. 166).

Modern evolutionists have learned that it is hard to make group selection on genetic variation work on large outbred populations such as human tribes. However, the same is not necessarily true if the variation on which selection operates is cultural. Neighbouring societies

are seldom very different genetically but they are often quite different culturally (Bell et al. 2009). A number of properties of cultural evolution make it easier to generate and preserve cultural variation at the level of tribes and other large groups (Richerson and Boyd 2005: 203-6). For example, social institutions usually include a system of rewards that favour those who conform to the institution and punishments for those who don't, damping down individual-level variation within groups (Bowles and Gintis 2011). Immigrants, particularly child immigrants, tend to adopt the culture of their hosts and lose the culture of their ancestors even as they interbreed and pass their genes into their host group. Prosocial emotions would have acted as biases favouring institutions that better satisfied these emotions, and many of the most powerful societies throughout history, including China, Rome, and the modern West have grown by selective immigration (Boyd and Richerson 2009). The "design space" for social institutions is very large, in part because a system of rewards and punishments can stabilize almost any pattern of behaviour (e.g. Aoki 2001). Human competition is very often between organizations: a simplified example would be that, in most modern economies, anti-competitive behaviour between firms is outlawed so that consumers can enjoy the benefits of business firms having to compete to produce better and less expensive products.

To explain the vast diversity of human social arrangements, Cultural Evolutionists thus appeal to the importance of culturally transmitted norms and institutions, whereas Evolutionary Psychologists consider that many forms of interaction between genes and the environment that occur during the lifetime of an individual may be as important, or more important, than culture in explaining differences in behaviour (e.g, Pinker 2010). Cultural Evolutionists certainly agree that gene-environment interactions during the lifespan are highly important, but their concept of the environment involves complex feedback loops between developing organisms and their socially inherited environments. Evolutionary Psychologists have been among the stoutest critics of group selection in any form, as well as doubting the cultural evolution and gene-culture

coevolution do any useful work (Footnote 1). Pinker (2010) includes these concepts in a laundry list of what he considers to be dubious evolutionary ideas:

> [I]t seems superfluous, when explaining the evolution of human mental mechanisms, to assign a primary role to macromutations, exaptation, runaway sexual selection, group selection, memetics, complexity theory, cultural evolution (other than what we call "history"), or gene–culture coevolution (other than the commonplace that the products of an organism's behavior are part of its selective environment). (p. 8996)

Evolutionary Psychologists have explained non-kin cooperation by appealing to a history of reciprocal exchange in the Pleistocene that favoured the evolution of specialized cognitive structures designed, in Cosmides and Tooby's (1992) famous example, for detecting cheaters in reciprocal exchanges. Experiments suggest that human subjects are much better at detecting violations of social contract rules compared to logical similar puzzles involving violations of other kinds of rules, such as neutral, empirically contingent rules (Cosmides 1989). To explain the fact that we cooperate in anonymous exchanges in modern societies, Evolutionary Psychologists argue that the cheater detection modules evolved in an environment where anonymous exchange was rare and are mis-calibrated for modern environments. As Cosmides and Tooby (1997) put it in general terms:

> . . . [O]ur modern skulls house a stone age mind. The key to understanding how the modern mind works is to realize that its circuits were not designed to solve the day-to-day problems of a modern American -- they were designed to solve the day-to-day problems of our hunter-gatherer ancestors. These stone age priorities produced a brain far better at solving some problems than others. For example, it is easier for us to deal with small, hunter-gatherer-band sized groups of people than with crowds of thousands; it is easier for us to learn to fear snakes than electric sockets, even though electric sockets

> pose a larger threat than snakes do in most American communities. In many cases, our brains are *better* at solving the kinds of problems our ancestors faced on the African savannahs than they are at solving the more familiar tasks we face in a college classroom or a modern city. In saying that our modern skulls house a stone age mind, we do not mean to imply that our minds are unsophisticated. Quite the contrary: they are very sophisticated computers, whose circuits are elegantly designed to solve the kinds of problems our ancestors routinely faced.

Specifically, in their functional analysis of social life, Cosmides and Tooby (1997) appear to rest their case solely on pairwise reciprocal exchange (also see Krasnow et al. 2012):

> Sometimes known as "reciprocal altruism", social exchange is an "I'll scratch your back if you scratch mine" principle. Economists and evolutionary biologists had already explored constraints on the emergence or evolution of social exchange using game theory, modeling it as a repeated Prisoners' Dilemma. One important conclusion was that social exchange cannot evolve in a species or be stably sustained in a social group unless the cognitive machinery of the participants allows a potential cooperator to detect individuals who cheat, so that they can be excluded from future interactions in which they would exploit co-operators.

Thus, even in experiments where researchers guarantee anonymity, human cognition, these authors argue, calculates as if we still live in small-scale societies where familiar others are observing and noting your behaviour and that these observers are likely to be future reciprocity partners.

In contrast, Cultural Evolutionists argue that a considerable amount of evidence supports the hypothesis that a history of cultural group selection can explain the evolution of non-kin cooperation (Boyd and Richerson 1985; Richerson and Boyd 2005; Chudek and Henrich 2011).

Most fundamentally, humans everywhere live in large groups that vary culturally and compete with one another; by definition, the winners of these competitions spread their social institutions and other aspects of their culture to daughter societies, attract immigrants from other societies and are imitated by other societies. For instance, many modern nations in Europe and Latin America follow legal codes descended from Roman law, speak languages descended from Latin, and follow religions derived from Roman Christianity. Social identity theorists have documented the mechanisms by which groups become part of our social identity (Haslam 2001), and developmental evidence suggests that young children readily learn social norms from caregivers and others (Chudek and Henrich 2011). Theoretical models have also shown that circumstances favouring social learning generally lead to conformity of behaviour, with individuals tending to copy what the majority of the population are doing (e.g., Boyd and Richerson 1985; Nakahashi et al. 2012; Perreault et al. 2012). Such conformity will tend to minimise behavioural differences within groups, providing the opportunity for cultural group selection to occur.

Further, humans are not just adept at reciprocal exchange but are also generally adept at solving problems that require high levels of cooperation, such as occur in managing commons and the provision of defense. Ethnographic analogy and palaeoanthropology suggest that ancestral societies by the late Pleistocene were quite large and that non-kin interactions would not have been uncommon (Powell et al. 2009; Hill et al. 2011). Chudek et al. (in press) review evidence that suggests that ephemeral interactions with strangers are common in the hunter-gather ethnographic record. The existence of long distant trade networks in decorative shell and valuable tool-stone in the Holocene (Baugh and Erickson 1994) and Upper Paleolithic (Klein 2009) suggests that by the latest Pleistocene at least humans were adept at establishing relationships with strangers. For example, acephalous tribes using the same institutions as mobile food foragers, but based on more productive subsistence strategies like herding and farming, can operate on quite large scales. Compared to Evolutionary Psychology, Cultural Evolution stands

out in invoking a novel evolutionary mechanism (cultural group selection) to explain the extraordinary patterns of large scale cooperation in our species.

A series of experiments conducted by Fehr and Gächter (2002) showed that cooperation in a public goods game could be sustained by *altruistic punishment* if that strategy was available. Based on this and other experiments devised by experimental economists, Fehr and Fischbacher (2003) suggest that cultural group selection and gene-culture coevolution might be required to explain human patterns of cooperation. However, laboratory experiments have failed to resolve the issue of whether humans exhibit features consistent with cultural group selection and gene-culture coevolution for prosocial dispositions. Evolutionary Psychologists Hagen and Hammerstein (2006) and Delton et al. (2011) have pointed out that, even in experiments where researchers guarantee anonymity and tell participants that the games are one-shot, human cognition might still calculate as if we still live in small-scale societies where reciprocity partners are observing and sanctioning or rewarding their behaviour. However, this criticism applies to any such experiments, including the classical experiments of Cosmides (1989), which can only tap proximal mechanisms directly and may speak rather softly about the selection pressures that led to the mechanisms. For example, a facility for detecting violators of reciprocal agreements would also be useful for detecting violations of social contracts embedded in culturally transmitted social institutions. In any case, Chudek and Henrich (2011) point out that Cosmides' classic experiment is framed in terms of norm violations, something they argue is not predicted by reciprocity theory.

Mathew et al. (in press) review evidence suggesting that human cooperation with kin and unrelated partners is both heavily institutionalized and much more extensive than in most other animals. They suggest that institutions like marriage that are plausibly subject to cultural group selection are necessary to produce high levels of kin and partner cooperation; the conventional evolutionary mechanisms of inclusive fitness and reciprocity are perhaps not sufficient to explain

the extensive small-scale cooperation humans exhibit. A hypersensitivity to the possibility of adverse effects on one's reputation or exaggerated fear of direct sanction is a plausible proximal cognitive trait that cultural group selection might have favoured by gene-culture coevolution to maintain high rates of intragroup cooperation. An increased understanding of the proximal mechanisms underlying cooperative behaviour does not directly test hypotheses regarding the evolutionary history of those traits.

A broad empirical and theoretical program is necessary to adjudicate conflicts between different evolutionary explanations of human cooperation and other important problems. Evidence for and against alternate evolutionary explanations must be sought across a series of consilient domains. Mathematical models are useful to check the logical coherence of explanations. Typically, all too many models are logically coherent and the real issue is which one best fits the data (e.g. Boyd et al. 2011b). Alternate formal models can also be fit directly to data using modern maximum likelihood based methods (Efferson and Richerson 2007; Borgerhoff Mulder and Beheim 2011). Data from microevolutionary studies demonstrating that cultural group selection and gene-culture coevolution operates in concrete cases is important (e.g. Mathew and Boyd 2011), and such studies must link microevolutionary evidence to macroevolutionary patterns. For example, some cases of culture led gene-culture coevolution due to the Holocene switch to agricultural subsistence are reasonably convincing (Laland et al. 2010, Richerson et al. 2010a). Paleoenvironmental and paleoanthropological data are necessary to understand what selective pressures acted on past human populations, and analyses of patterns of adaptive and maladaptive behaviour are often quite informative. In the case of explanations of human cooperation, as in other areas we have reviewed here, hot debates on this issue seem likely to persist for some time.

8 Conclusion

In general, researchers within the sub-fields of Human Behavioural Ecology, Evolutionary Psychology and Cultural Evolution agree that evolutionary theory can be usefully applied to the study of human behaviour. In addition, there are numerous signs that integration of the sub-fields is being achieved. For example, Human Behavioural Ecologists are incorporating cultural transmission into their models of behavioural diversity (e.g. Borgerhoff Mulder et al. 2009; Hill et al. 2009; Currie et al. 2010), and Evolutionary Psychologists increasingly make use of cultural evolution and vice versa (e.g. Atran and Ginges 2012; Norenzayan and Gervais 2012; Chudek et al. 2012). However, we believe that some of the issues that divided the three approaches in the past do remain open and that both theoretical and empirical investigations are required to resolve them. For example, there is as yet no consensus on the exact roles of genes, individual learning, and social learning in human development (e.g. Spencer et al. 2009). Within evolutionary biology itself, similarly broad issues are currently being discussed and debated, such as usefulness of the distinction between proximate and ultimate explanations (Laland et al. 2011; 2012) and the role of multi-level, group selection (Eldaker and Wilson 2011; Wilson et al. 2008), and such debates are highly relevant to researchers that are applying evolutionary principles to economics. For the novice researcher, these debates might appear daunting, but we hope that continued cross-disciplinary discussion and exchange of ideas will provide an ever richer understanding of human behaviour.

Footnotes

1) See a debate initiated by Steven Pinker's essay The False Allure of Group Selection in the online magazine *Edge* (http://www.edge.org/conversation/the-false-allure-of-group-selection).

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