

## **EVOLUTIONARY PSYCHOLOGY *SENSU LATO***

A review of *The Oxford Handbook of Evolutionary Psychology* edited by Robin Dunbar and Louise Barrett. Oxford University Press (2007), 720 pages, £49.95 (\$98.50), ISBN: 0198568304 (hardback).

WILLIAM M. BROWN<sup>1,2</sup> AND MICHAEL E. PRICE<sup>1,2</sup>

<sup>1</sup>Centre for Culture and Evolutionary Psychology, <sup>2</sup>Centre for Cognition and Neuroimaging, Brunel University, West London, Uxbridge, Middlesex, UB8 3PH, UK  
E-mail: william.brown@brunel.ac.uk

The rise of human evolutionary psychology (EP) has been impressive. For students in the early 1980's, *Evolutionary Biology and Human Social Behavior* (CHAGNON and IRONS 1979) was the only advanced edited volume on human sociobiology. The first advanced edited volume to overtly synthesize human sociobiology with cognitive science, *The Adapted Mind* (BARKOW, COSMIDES and TOOBY 1992), did not appear until more than a decade later. In testimony to EP's growth as an empirical science, several more such synthetic books have appeared since *The Adapted Mind* and the *Oxford Handbook of Evolutionary Psychology* (OHEP) is a new and welcome addition to this list.

OHEP consists of 46 chapters, divided into seven sections: (1) philosophical issues, (2) the comparative approach, (3) neurobiology and cognition, (4) development, (5) mating, reproduction and life history, (6) the self and social world, and (7) cultural evolution. Coverage is thus broad and diverse, but some common themes do emerge. The most fundamental commonality is, of course, that all contributors are committed to a theoretical perspective that is, to one degree or another, rooted in evolutionary theory. Many contributors also share something of distaste for what they consider to be the narrow adaptationist modularity of "*sensu stricto*" EP (more on this below).

OHEP's organisation and contributors provide readers with a particularly strong interwoven demonstration of Tinbergen's levels of causation. For example, the neurobiology and cognition section does a splendid job of describing brain evolution and its associated controversies between the developmental constraints and mosaic accounts. Another important feature of this section is that we are presented with the latest on mirror neurons and other aspects of social cognition. One complaint, however, is that there is little in this section on neurogenetics, a

criticism to which we will return later in this review. In other sections of the book, two aspects for which the editors and contributors must be commended are the chapters on life history strategies in human evolution and on human psychological development. Furthermore, the book's final chapters provide multiple insights on cognition and our cultural capacities.

One criticism is that there is more emphasis on human development and social cognition than on the phylogeny of both. However, Section Two picks up part of the slack here by presenting powerful arguments from the comparative approach with a heavy emphasis on primates. Fortunately we are treated with a chapter on social cognition in non-primates in this section. The volume could have benefited greatly by the inclusion of more non-primate comparative work. Because some of our evolved psychological mechanisms are probably products of convergent evolution, an in-depth treatment of the comparative work in avian and cetacean species would have been particularly useful. Further, some of the controversies presented in OHEP (discussed below) become less problematic when more taxonomic groups and levels of analysis are considered.

An aspect that sets OHEP apart from similar volumes is a general focus on topics that the editors feel are not addressed adequately by what they refer to as EP *sensu stricto*. By *sensu stricto* they mean those evolutionary psychologists, epitomized by JOHN TOOBY and LEDA COSMIDES, who believe that the brain is composed of a large number of functionally specialized cognitive adaptations, that behaviour is properly regarded as adaptation-execution as opposed to fitness-maximization, and that human culture is, first and foremost, the product of specialized information-processing mechanisms that were selected for ancestrally.

The editors feel as though EP *sensu stricto* focuses too much on the execution of specialized cognitive adaptations, and not enough on behavioural fitness-maximization (a focus of some human behavioural ecologists) or on culture as an autonomous causal influence on behaviour (as opposed to something that must be processed and produced by psychological adaptations). It is important to note that scientists within behavioural ecology proper (i.e., those who study non-human animals) probably remain largely unaware that such a debate even exists. In the spirit of synthesis among all sides of the debate, the editors invited contributions from human behavioural ecologists, gene-culture co-evolutionists, and several researchers who appear to be practitioners of EP *sensu stricto*, or at least to not have major problems with it. The theoretical perspectives presented in this book are thus diverse and eclectic, despite their common evolutionary roots, and compared to other edited handbooks on EP, this one has a far greater emphasis on human behavioural ecology and gene-culture co-evolution.

This book can to some extent be regarded as a snapshot of what the editors say "might seem like an internecine war" (p. 5) between practitioners of EP *sensu stricto* and researchers who downplay adaptation-execution and modularity while emphasizing fitness-maximization and the autonomous influence of culture. The conflict regarding adaptation-execution and fitness-maximization has been going on

for at least two decades. In brief, *sensu stricto* researchers are interested in adaptations (i.e., functional traits that were fitness-enhancing on average in ancestral environments), while human behavioural ecologists focus more on adaptiveness (i.e., on whether or not behaviour is adaptive in current environments). Too much can be made regarding this difference in focus. Clearly, an emphasis on how ancestral ecologies shaped behaviour does not preclude an investigation into that behaviour's adaptiveness in modern environments. However, most EP researchers, be they *sensu stricto* or *sensu lato*, would presumably agree that some behaviours that are fitness-enhancing in modern environments are not themselves adaptations (WILLIAMS 1992). Studying such non-adaptations and the constraints which have prevented their spread may be as empirically important as studying why some psychological adaptations fail to function adaptively in modern environments. An even older debate concerns the question of whether behavioural researchers should expect the brain to be divided up into special-purpose modules. While the editors and many contributors feel that "evolution neither entails modularity nor requires it" (p. 5), *sensu stricto* practitioners would disagree, and argue that wherever the organisation of organismal tissue (neural or otherwise) can be discerned, it takes the form of functionally specialized modular architecture.

The hoariest of all these disputes is that concerning culture's influence on behaviour. The editors and many contributors feel that culture "has remained resolutely on the sidelines of evolutionary psychology" (p. 7). By this they are probably alluding to the fact that in explaining behaviour, the *sensu stricto* focus is ultimately on psychological mechanism, rather than on cultural practice. *Sensu stricto* practitioners believe the brain to be composed of a large number of information-processing mechanisms that respond to specific kinds of environmental inputs by producing specific kinds of behavioural outputs. They regard culture as a central part of this process, both as informational input and as generated output, and claim that in order to understand culture's relationship to evolved psychology, we need to discover the design specifications of the psychological mechanisms that process and produce culture. Many contributors to the book seem dissatisfied with this *sensu stricto* view, although they disagree with it to varying degrees. McElreath and Henrich, for example, "think that psychology has a huge role to play in understanding culture" (p. 574), but argue that culture influences behaviour via mechanisms for imitating others' behaviour that seem rather general-purpose and sketchily-specified from a *sensu stricto* perspective. Crook distances himself somewhat further from the *sensu stricto* view: "Among human beings the role of culture in adaptation is presumed to be predominant although explanation in terms of genetics and the operation of evolved cognitive modules may remain important in some contexts" (p. 520). This latter opinion seems more Lockean (blank slate) than neo-Darwinian, and illustrates a danger of overlooking the fact that culture can impact behaviour only via evolved psychology: one risks becoming a perpetuator of the imaginary biology/culture dichotomy that EP is supposed to overcome.

Perhaps the greatest strengths and weaknesses of OHEP reside in its pluralism. Therein lies the rub, since science advances through conflict and the drawing of clear boundaries. Pleasing all sides of a debate will not necessarily move the field forward. When evolutionary psychologists set up the standard social science model against evolutionary *sensu stricto* hypotheses, this led to scientific advancement. Furthermore the domain-specific approach provoked researchers to think clearly about specific adaptive problems and their precise adaptive solutions. Psychological science has always been in need of theoretical grounding and specificity, and EP *sensu stricto* has delivered extraordinarily well.

Below we present two major gaps in OHEP that could be corrected in future editions: neurogenetics and sociogenomics. We feel that these areas are of critical importance for human evolutionary science and may help sort out some of its philosophical controversies.

We now know that allelic variation mediates neural design and that gene expression is critical for neural functioning. Neurogenetics investigates how genetical systems influence brain development, morphology, and activation. Gene technologies have led to animal models for specific aspects of human psychology, even if the respective behavioural phenotypes do not naturally occur in these animals. In principle, these technologies can be applied to any animal, but unfortunately only mouse (*Mus musculus*), zebra fish (*Danio rerio*), fruit fly (*Drosophila melanogaster*), and nematode (*Caenorhabditis elegans*) are most often investigated. For cognitive phenotypes, there is reliance on rats as model organisms.

Importantly, conservation of gene function across distantly related species means that genes that are known to influence behaviour in one organism are likely to influence similar behaviours in other organisms. This facilitated a major advancement in our field, the application of the candidate gene approach in behavioural ecology. Expression of candidate genes reveals their contribution to behavioural variation and/or phenotypic plasticity. For example, learning evolves in laboratory populations and retaining learning capacities could have fitness costs. The cellular and genetic mechanisms responsible for learning and memory are evolutionarily conserved. The candidate gene approach to the study of behavioural ecology (FITZPATRICK et al. 2005) has implications for EP and it is conspicuously absent from OHEP.

Also insufficiently addressed in OHEP is the replicator concept from biology. Genes are catalysts whereby the reactions they catalyse influence their representation in a population. EP – the study of the evolutionary basis of information-processing mechanisms mediating behaviour – has much to gain from recent advancements in sociogenomics because the effects of strategic genes are critical for the developmental implementation of neurocognitive adaptations. Importantly, replication strategies can be in conflict with the interests of the organism itself due to different transmission rules (e.g., when some genes evade fair meiosis) or relatedness asymmetries due to sex-biased dispersal or multiple paternity. Different transmission rules between sex chromosomes and autosomes

may also cause intragenomic conflicts over behavioural choices. It is unfortunate that no contributors in this volume deal specifically with such intragenomic conflicts, as this is an area which will likely yield rich empirical advancements in EP for years to come. Advancements based on this approach are already having major consequences for cognitive and developmental psychology (CRESPI 2007; OLIVER et al. 2007).

Since the 90's there have been several edited volumes on EP, so a critical question for OHEP is whether it distinguishes itself sufficiently from its predecessors. Some evolutionary psychologists will likely feel that the volume succeeds most when it avoids largely ideological debates such as (a) whether EP underestimates the power of culture and group selection; (b) human behavioural ecology "versus" EP; and (c) domain specificity versus domain generality. Many chapters focus on theoretically-motivated empirical findings and future directions, and these are excellent contributions to the literature, more than worthy for advanced graduate courses on the subject. Thus we feel OHEP should be purchased by university libraries and EP graduate students, but with one caveat. When you read about EP *sensu stricto*, consider thinking of it as a positive development for experimental psychology, especially for those that desire further empirical synthesis with zoology. We feel that empirical issues should come first, and that this is where EP *sensu stricto* has made most of its advancements in the behavioural sciences.

Synthesis is as important for EP as it is for biology, and in both fields it requires in-depth ecological and genetic knowledge across diverse taxonomic groups. OHEP's focus on humans and closely related species falls a bit short of the mark when it comes to genuine synthesis. Not that *The Adapted Mind* (BARKOW et al. 1992) was better in this regard, but in fairness it was published 15 years ago. Many details of how gene expression adaptively influences (and is influenced by) ontogeny still need to be worked out, but there is no reason to believe that the underlying principle of adaptation by natural selection will be subsumed by the largely philosophically-oriented stance presented by many OHEP contributors against EP *sensu stricto*. Undoubtedly many of the people involved in the creating the OHEP would agree, so it begs the question as to why so much ink was spilled on ideological debates that have yielded few empirical insights. We shall let the readers and historians of science decide.

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