[1st draft of a review eventually published in a much revised version in *Trends in Cognitive Sciences, 3,* (1999) 489-50.]

Cognition, Evolution, and Behavior
by Sara J. Shettleworth, Oxford University Press, 1998. $45.00 (paper, xii +688 pages) ISBN 019511048X

Anthropomorphic accounts of animal behaviour may rarely stand up to rigorous scrutiny, but a theoretical concept which originated in discussions of human cognition translates surprisingly well into Sarah Shettleworth's long review of information processing capacities in animals. This is Fodor's modularity thesis — animal information processing is accomplished by a wide variety of modules which are domain specific, encapsulated and so on.

A stated aim of the book is to argue for an adaptationist approach to cognition. The way in which modularity suits the adaptationist approach is especially obvious when it is applied to sensory mechanisms which are unfamiliar to us, but readily understandable as ecologically appropriate, such as echo- location in bats, detection of objects via electrostatic fields in fish living in turbid waters or the use of sky-polarization compasses for homing in diurnal insects and vertebrates. These examples, among others, are the starting point of Shettleworth's treatment of Perception and Attention, which sets the stage for subsequent chapters covering topics such as memory and discrimination learning.

However, an equally important theme of the book is the inherent interdisciplinarity of questions which arise about how animals are able to deploy their specialised sensory adaptations, and whether such information processing in animals has any relation to the study of human cognition. Shettleworth has a joint appointment in Departments of Psychology and Zoology her book integrates material which would otherwise be covered separately in psychology texts (experimental studies of laboratory animals often performing very artificial tasks) and those used in zoology departments (attempts to study the evolution, development and function of the natural behaviour patterns of a wide range of species, under the general heading of "Behavioral Ecology"). This book attempts to synthesise the two approaches to animal behaviour by explicitly endorsing the concept of evolved adaptations while organizing the material according to psychological categories such as "Simple Recognition Learning" (which encompasses habituation, perceptual learning and social imprinting) as well as ecological categories such as "Foraging and Measuring Rate".

Zoologists such as Tinbergen analysed animal behaviour in term of hierarchically organized input-output relationships termed instincts. Why it is appropriate to use the information processing meaning of "cognition" in these contexts, and why Shettleworth reviews also the corpus of data arising from the very different tradition of behaviourist or associative theories of animal learning can be illustrated the standard uses to which some of the unfamiliar sensory capacities are put.

Most animals are mobile and many need a high degree of sensitivity to their own geographic location. This applies particularly to central place foragers, which include

many bees and ants as well as the species (rats and pigeons) most used by experimental psychologists. This means that no matter how fixed and innate the geographic sensing modules are, they are used to monitor local and transient information — animals need to *learn* about the location of their own nest or hive, their own current position, and the location of changing food sources.

It is therefore not just a co-incidence that information processing was introduced into animal psychology by E.C. Tolman's use of the term "Cognitive Map". The current consensus seems to be that this is a misnomer, because, at least for social insects and rats, the representation of space is predominantly in terms of self-motion, and observed behaviours can be explained by the flexible combination of path-integration vectors, "snap-shot" views of visual landmarks and memorized routes. But in view of the computational load imposed by path-integration (dead-reckoning) and the flexibility with which different sources of geographic information are typically utilized this does not make spatial orientation any less interesting. Shettleworth's conclusion is that asking the question "does this animal have a cognitive map?" is less useful that asking "how does this animal represent space?"

A relatively recent subdivision of the "cognitive map" idea comes from careful studies of the accuracy of cache recovery in food hoarding birds. A number of species including marsh tits in Europe and scrub jays in the Western US regularly cache and recover food items in the wild. Laboratory studies suggest that the cognitive processes involved are "episodic-like" in that birds remember "where", "what" and in some cases "when" in relation to caching activities.[1,2] This is at the same time "anthropocentric" research to use Shettleworth's term, since it derives some impetus from human cognitive phenomena, but also a contribution behavioural ecology. Other anthropocentric examples are Triesman-like visual search (which can be related to the use of "search-images" in foraging), Posner-like studies of attention via eye-movements in primates and Gibson-like use of optic flow by flying insects (especially when landing).

Shettleworth reserves the term "anthropomorphic" for unjustified imputing of humanlike cognitive attributes to other species. This applies to a large fraction of research on imitative learning in animals as well as attempts to hold conversations with chimpanzees. Chimpanzees not only do not engage in small talk, but they appear to fail to notice any difference in the probability of attracting the attention of a human experimenter wearing a dark scarf over her eyes as opposed to her mouth. This bolsters the case for saying the human species has many cognitive modules not shared with the species that happens to be our closest living relative, and perhaps for saying that the set of cognitive modules available to any particular species may be unique.

But many of the behavioural phenomena described here are extremely widespread. Shettleworth says that data on time interval judgements are "suggestive of pretty wide phylogenetic generality among vertebrates" (p 355), and Weber's Law, habituation, and anticipatory response shifts along the lines of Pavlovian conditioning can be found in just about every species studied from *C. elegans* which has only 302 neurons to the chimpanzee which although lacking human cognitive modules appears to anatomists to have a brain which is remarkably like ours, though a third the size.[3] Shettleworth generously concludes that behavioral ecologists interested in Optimal Foraging Theory would have had to invent the Skinner box if he hadn't done so first. There thus remains scope for general theories about the biological origin and neural mechanisms of what

Davey[5] has called "global adaptations" as well as continuing behavioural explorations of the natural history of cognitive diversity.

Previous attempts to resolve the tension between evidence for some forms of species-general learning mechanisms, and the undoubted primacy in animal behavior of what Shettleworth calls "evolved predispositions" include the book by Gallistel[4], which is frequently referenced, as well as that by Davey.[5]

Shettleworth's text is encyclopaedic in scope, measured in its opinions, and written in a more accessible style than either of these predecessors. Its range, recency and reasoned advocacy should be widely welcomed. Zoologists and psychologist will learn more about each other's literatures by reading it. In summing up Shettleworth returns to the theme of modularity. The book undoubtedly succeeds in demonstrating the variety of adaptively specialized cognitive modules that are available for study in the natural world and it is arguable that animal cognition is if anything even more modular than human information processing[6], but that does not preclude, especially in the vertebrate brain, rich interactions between modules, and a wealth of possible permutations of module taxonomy. It is likely that in the near future an interdisciplinary account of animal cognition will need to incorporate results from neuroscience and molecular genetics. Although these disciplines are only occasionally alluded to here practitioners of them will find this a useful compendium of behaviors they may wish to get their teeth into. The primary audience for the book is however the students on courses in comparative cognition to whom it is dedicated.

References

1. Shettleworth, S.J. and Krebs, J.R. (1982) How marsh tits find their hoards: the roles of site preference and spatial memory *J. Exp. Psychol.: Anim. Behav. Process, 8*, 354-75

2. Griffiths, D., Dickinson, A. and Clayton, N. (1999) Episodic memory: what can animals remember about their past? *Trends Cognit. Sci. 3*, 74-80

3. Semendeferi, K, Damasio, H and Frank, R (1997) The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains *J. Human Evol. 32,* No.4, Pp.375- 388

4. Gallistel, C.R. (1990) *The Organization of Learning,* MIT Press

5. Davey. G. (1989) *Ecological Learning Theory,* Routledge

6. Coltheart M. (1999) Modularity and cognition *Trends Cognit. Sci. 3*, 115-120

Stephen F. Walker
Department of Psychology
Birkbeck College, University of London
Malet Street, London WC1E 7HX, UK
phone (+44) 020 7631-6590
fax (+44) 020 7631-6206
email s.walker@bbk.ac.uk