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Book Reviews

Spatial Representation in Animals. Edited by S. HEALY. Oxford: Oxford University Press (1998). Pp. x+188. Price £45.00 hardback, £22.50 paperback.

Because of several recent developments in the field of animal orientation, the *Journal of Experimental Biology* dedicated its entire January 1996 issue to the topic. With 33 papers, that compilation has two major advantages: it offers a fairly complete survey of the field, and it is downloadable for free from the World Wide Web. Any publication that appears now in the field will obviously be measured against that issue. Healy mentions in the introduction of her new book that her goal is not a comprehensive survey of the field. Rather, the book's envisioned niche is in making the topic accessible, interesting and attractive for students. This is an honourable goal, given that choosing a thesis topic in the field implies resisting the temptations of mainstream science, rapid fame and huge grants (unless you happen to study the hippocampus). It means studying a topic that is almost purely intellectual fun, but in a grand way! Convincing students that the fun is worth the hardships, and that there is sufficient unknown territory to explore, is a tall task. Before I return to the question of whether this goal is reached, I give brief accounts of the eight chapters of the book.

Cheng & Spetch review the many ways in which mammals and birds use arrays of landmarks for the precise location of familiar locations in space, and explain experimental procedures to determine how animals remember space. Their comparison of humans, rodents, birds and bees reveals that different species store the same landscapes in very different ways. Cheng & Spetch advocate expanding modern learning theory into animal orientation, and to ask questions such as: is there blocking and overshadowing in landmark learning? Unfortunately, this is the only chapter with suggestions for key avenues of future research.

With only a single chapter, the venerable field of arthropod orientation is underrepresented in this book. But that is probably fine, given that another book on arthropod orientation appeared recently (Lehrer 1997). Collett & Zeil produce veritable fireworks of ingenious experiments and 'landmark findings' on the use of landmarks by spiders, crustaceans and insects. It is hard not to notice the elegance and sophistication of these behavioural experiments when compared with many vertebrate studies. All the examples in Collett & Zeil's chapter are closely linked to the real-life biology of the species in question, which will make this chapter stimulating for students outside the field of animal orientation as well.

Path integration helps animals to return home even when they have ventured too far out to encounter any familiar cues in their immediate surroundings. Etienne et al. review how animals, from spiders through hamsters to humans, evaluate distances and directions travelled in the past to compute the direction of home. I found here and in other chapters that comparisons between species are made somewhat in vacuo, without an attempt to unravel the evolutionary causes of differences. A few years ago, this would have gone unnoticed. For a century, comparative physiologists have compared species merely for the sake of getting a more complete picture of mechanisms realized in the animal kingdom. Even if attempts were made to link mechanisms with adaptation, such attempts were often compromised by naïve pan-adaptionism. But today, as more and more workers realize the necessity of linking mechanistic with ultimate perspectives of behaviour, mere reports of differences between species leave us somewhat unsatisfied.

How pigeons find their way home when displaced hundreds of kilometres away from any familiar terrain has long fascinated researchers. Bingman presents convincing evidence that pigeons use both landmarks and odour gradients when close to the loft. However, no one would argue that using landmarks in familiar environments means that they are also used when they cannot be seen. But this is exactly the argument Bingman and other proponents of the olfactory navigation hypothesis adhere to. In essence, they suggest that pigeons use cues that have been shown not to exist (Wiltschko 1996): reliable odour gradients that extend over hundreds of kilometres and whose properties can be deduced from the pigeon's experience close to the loft. There are alternative explanations for why anosmic pigeons fail to navigate over long distances (Wiltschko 1996), and so the olfactory navigation hypothesis rests on shaky foundations.

Fish have been somewhat neglected in the study of landmark learning. But Braithwaite's chapter on spatial memory in fish contains a few jewels that may (hopefully!) lay the ground for a new direction in animal orientation. At present, we know very little about how orientation capacities evolve in the face of selective pressures posed by specific environmental conditions. This is because many workers in animal orientation treated interindividual variance, the raw material for evolution, as noise, which needed to be eliminated by averaging large numbers of measurements from different animals. But Braithwaite shows that not only is there different usage of orientation cues during ontogeny, but there are also fascinating differences between individuals of a population and between populations. This could be the beginning of a new evolutionary behavioural ecology of landmark navigation.

The evolutionary approach, although not in the context of landmark learning, is taken to perfection in Berthold's chapter on avian long-distance migration. Berthold describes mechanisms used by birds to locate far-away places, and combines biogeography, phylogenetic reasoning and elegant breeding experiments to explore how, and why, the genetic programs that determine a bird's choice of migration destination have evolved.

The chapter by Save et al. on landmark use and the cognitive map in rats is really only about landmark use. The cognitive map remains something of a holy grail for some workers studying animal orientation, while many seem to assume that it exists a priori. There are probably twice as many different uses of the term cognitive map in this book as there are chapters, but the term, as originally coined 50 years ago, has a single definition which yields straightforward, and testable, predictions (Bennett 1996). To date, there is no evidence for cognitive maps in rats (Benhamou 1996) or any other nonhuman animal (Bennett 1996). Even if the required experiments are performed, which is subtle and difficult, and even if animals pass some critical tests, the results are often hard to interpret (Menzel et al. 1998).

In the final chapter, Sherry & Healy review neural mechanisms of spatial representation. In fact, their review is heavily centred around the hippocampus and its possible function as a long-term storage site of spatial information; the recent exciting development in cortical spatial working memory is not covered. The involvement of the hippocampus in spatial memory is supported by several lines of evidence. For example, comparative studies reveal that food-storing birds have larger hippocampi. Sherry & Healy also review research on place cells: neurons whose activity is correlated with particular positions of the animal in space. I was surprised to see that the groundbreaking work of McNaughton and coworkers is not described. Through simultaneous recordings from several dozens of hippocampal cells (e.g. Wilson & McNaughton 1994, and references therein) it has been possible to gain insight into the very ways brains store, distribute, organize and retrieve information (Wallenstein et al. 1998).

The chapters are well written and intelligible. The choice of subjects does cover the field more or less appropriately and with a minimum number of chapters, so the book offers a compact overview over most of the recent directions in animal representations of space. In my view, the attempt to create a book that stands out against the aforementioned volume of the *Journal of Experimental Biology* would have been even more successful had the editor proceeded as follows. First, one might have included different topics, for example a section that elaborates on the ecology of spatial memory more thoroughly (cf. the work of Kamil, Balda or Stamps, and others) and another chapter on cognitive maps in humans. After all, humans are excellent experimental animals because they can describe their perception of space, and draw maps of how they think a landscape looks (e.g. Mallot). There are fine studies on how spatial representation changes through child development (e.g. Cornell), or how different cultures describe space in different terms (e.g. Levinson). Second, a book addressed to a new audience of energetic young scientists should map out future directions of research within each field. With very few exceptions, such directions are not given. Third, through careful editing and cross-referencing of articles, a book on such a diverse field as this could emphatically point out how merging the ideas from different traditions might generate wholly new perspectives. Such new perspectives are not described explicitly in this book. But they can be sensed, simply from the observation that even some of the best chapters, such as those by Collett & Zeil, and Berthold, are worlds apart in terms of language and philosophy. There is still a lot of unexplored territory between these approaches, and it is great that this book contains that message, albeit between the lines!

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