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Book Reviews

Behavior and its Neural Control in Gastropod Molluscs. By RONALD CHASE. Oxford: Oxford University Press (2002). Pp. xx+314. Price £55 hardback.

Snails, slugs, whelks and limpets are notoriously slow, but as Ronald Chase shows in this book, they are far from boring. The book starts with a short, animated introduction about the history of research on the behaviour and neurobiology of gastropod molluscs. The research in this field got off to a good start when Theodore Bullock and G. Adrian Horridge (1965) published their influential work on invertebrate nervous systems. Around the same time, many researchers were gearing up to tackle molluscan neurobiology and behaviour. Among them were Kandel, Kerkut, Kupfermann, Lever, Sakharov, Salánki, Rózsa and Tauc. They all realized the great advantages that invertebrates provided over vertebrates.

Although the behavioural repertoires of gastropods are relatively simple, their neurons are fundamentally similar to those of vertebrates. What makes them even more attractive is the fact that the central nervous system is much less complex and has fewer, larger neurons than the vertebrate brain. In addition, their neurons are often individually identifiable and easily accessible. Thus, using invertebrates as model systems opened up possibilities for research that were (and still are) not available in vertebrates.

As a result, the use of molluscs as model systems has contributed significantly to our understanding of how general behavioural processes (such as feeding and reproduction) are regulated by the central nervous system. Ronald Chase, who has worked in this field for many years (after having made the switch from research on vertebrates to invertebrates himself), rightfully notes that no comprehensive review of gastropod neuroethology has been attempted since the 1970s when Kandel published his reviews (1976, 1979), which were heavily based on research carried out on the sea hare *Aplysia*. Much has been done since then on many different gastropods; therefore, the present book is an appropriate and welcome review, especially because the author concentrates on the advances made since the 1970s. Obviously, it is not an easy task to review such a vast amount of work. Nevertheless, Ronald Chase succeeds in writing a comprehensive, and at times very entertaining, overview that conveys the advantages of working with invertebrates.

The book is divided into two parts. In the first four chapters the main aspects of the animals are introduced. Among other things, Ronald Chase explains torsion and how this resulted in primitive gastropods probably defecating on their own heads. He then explains the general features of the central and peripheral nervous system, the sensory system and the muscle system. In general, these chapters implicitly highlight the similarities to and differences from vertebrates. For those who are not so familiar with gastropods, these chapters provide an excellent introduction for what follows. In the next five chapters the main behavioural activities are dealt with one by one: regulation of the internal environment, locomotion, feeding, reproduction and defence. In each of these chapters, the author gradually works his way from the behaviour towards the underlying neural mechanisms. Finally, and fittingly, in the last chapter the author tackles how all the activities are distributed over time.

In chapter eight, some of the spectacular mating strategies that are found in gastropod molluscs are described in some detail. Naturally, the dart-shooting behaviour of land snails is included. Chase and his co-workers, including myself, have investigated this behaviour extensively in the garden snail, *Helix aspersa* (a species that Ronald Chase has been working with for many years). Another odd behaviour that he mentions is penis biting in slugs, which can result in complete removal of the partner's penis. He states that such apophallations occur simply because the long penes get knotted up. However, part of the female reproductive tract seems specialized for tightening the grip on the penis of the partner, indicating a more adaptive explanation (Reise & Hutchinson 2002). Earlier in the same chapter he also uses the term aphally in the wrong context by referring to males without a penis as aphallic. He seems to have overlooked the fact that this term is used only when a polymorphism is present, that is both aphallic and euphallic individuals are present in the population (e.g. Jordaens et al. 1998).

Despite these details, Ronald Chase has compiled a comprehensive review of the field and on the whole strikes a good balance between neurobiology and behaviour. In most cases he specifically focuses on the well-studied cases and draws parallels with similar studies done in other species. However, he is appropriately cautious about suggestive results and rather makes valuable suggestions for avenues for further research throughout the book. Finally, the book is conveniently equipped with taxonomic, neuron and subject indexes and special care has been taken to cite the most important literature. This latter feature makes it not only an enjoyable and valuable review for people working in this field but also a great starting point for anyone with basic biological knowledge who wants to learn more about gastropods' neurobiology and behaviour.

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Comparative Vertebrate Lateralization. Edited by LESLEY J. ROGERS & RICHARD J. ANDREW. Cambridge: Cambridge University Press (2002). Pp. ix+660. Price $120.00.

This husky volume is a tribute to behavioural biologist Richard Andrew and includes an overview of his seminal work on neurobehavioural asymmetries in the domestic chick. The book bulges with contributions from his many associates, especially Lesley Rogers, who has added many innovations to this line of research. Some discoveries with chicks were both generalized and further advanced by new methods in pigeons (Gunturkun), while new evidence for brain asymmetries in fish and amphibians has been recently added (Bisazza, Vallortigara). Moreover, Hopkins summarizes many recent demonstrations of perceptual, emotional and cognitive lateralities in primates, which provide insight into the evolution of the striking cerebral asymmetries long known in humans. Included are chapters on early origins of structural asymmetry, as well as reviews of postural and motor asymmetries, lateralization of vocal and facial communication and the nonvisual senses. From this potpourri of species and diverse behavioural tests emerge some consistent generalizations, such as the specialization of the right hemisphere for fear-motivated behaviours and for use of spatial information. Given this wealth of convincing data, I was astonished to read recently from a prominent scholar of human split-brain studies, Michael Gazzaniga, that 'Non-human brains, by contrast, reveal scant evidence for lateral specialization, except for . . . a right hemisphere superiority for the detection of monkey faces' (page 1294).

The strongest asymmetries are so far evident in humans and various bird species. Although more evidence on reptilian brains is needed, it seems likely that birds and mammals have evolved, in parallel, strongly lateralized brains as a way of packing new cognitive complexity into a limited brain volume, gaining novel circuitry at the expense of bilateral redundancy.

As a visual neurobehaviourist, I focus here on visually guided behaviours. Andrew's early work showed that emotional and mnemonic abilities were strongly lateralized in chicks. For example, young male chicks attack conspecifics eight times more often while using the left eye than when using the right eye, and imprinting on the mother (or a laboratory substitute) is also largely lateralized. Then Gunturkun demonstrated that pigeons' visual learning reflects anatomical asymmetries in visual projections to higher forebrain centres (now considered homologous to mammalian visual cortex). Such asymmetries, which do not appear in mammals, are different in pigeons and chicks, which should provoke new attempts to match behavioural capacities to particular visual components by using the comparative method.

The bird behaviourists, with an evolutionary perspective, already have attempted to demonstrate that individuals with higher 'indices of asymmetry' perform some tasks more effectively, i.e. that neural lopsidedness pays off. This rule is also demonstrated by some mammalian studies; for example, chimpanzees, who use opposite hands in more distinctive ways, prove to be better foragers for insects. Rogers points out that left-eye superiority in food foraging plus a right-eye advantage in scanning the sky for predators should allow each brain half to performs its best operation as one eye is directed downward and the second eye towards the heavens. Surprisingly, human studies (without this evolutionary context) have provided as yet no direct evidence for the advantages of lateralization.

Having studied visual behaviours in fish, I was interested to find modest lateralization in two natural behaviours: eye use in viewing conspecifics and side choice in avoiding a frontal barrier. One suggested advantage of such sensorimotor asymmetry is to enhance the probability that schooling fish will all turn the same way when approached by predators. Predictions that schools of fish will more often turn in one direction or will show better group coherency for one turn direction have not yet been tested. Given the strong lateralization of aggression in chicks, it was encouraging to read of a rather strong asymmetry in one type of aggression by toads: the right eye mediates tongue striking at feeding rivals four times more often than does the left eye. Fear, aggression and sexually motivated decisions all remain to be evaluated in fish via single eye use or following unilateral forebrain lesions.

Evidence for functional asymmetries in birds is also strong when testing learning skills (visual imprinting by chicks, reversal learning in pigeons and long-term memories of food cache locations by marsh tits). Thus, it seems important to also test fish for eye dominance while learning, in tests ranging from conspecific recognition to spatial memory abilities, since these tests are more likely to reveal the evolutionary antecedents of cognitive skills in birds and mammals. Vallortigara's quotation from a neuroanatomist that fish seem to have weak commissural transfer of visual information may not be well taken, since several studies (including my own) show excellent interocular transfer of pattern discriminations by various species of fish. I suggest that severing visual commissures in fish (or in birds) may further enhance of lateral specializations of behaviour, as one clearly sees from the study of split-brain humans.

One weakness of this volume is its failure to summarize the best examples of human brain lateralization, derived from either split-brain testing or after unilateral damage to temporal, parietal or frontal association cortex. Such information from the clinic is needed to pose experiments that might answer the question: just how close does functional lateralization in a monkey or in a bird approach that in humans?

Finally, given the important demonstrations of Andrew that brain asymmetries are sometimes stronger in male than female chicks, the best of such demonstrations in human experiments are conspicuously missing from these chapters. Andrew (page 185) quotes Kimura (1999) on several human sex differences in cognition, but ignores her review of clinical experiments that show