Cephalopod Cognition

Cephalopods are generally regarded as the most intelligent group among the invertebrates. Despite their popularity, relatively little is known about the range and function of their cognitive abilities. This book fills that gap, accentuating the varied and fascinating aspects of cognition across the group.

Starting with the brain, learning and memory, Part I looks at early learning, memory acquisition and cognitive development in modern cephalopods. An analysis of the Chambered *Nautilus*, a living fossil, is included, providing insight into the evolution of behavioural complexity. Part II surveys environmental responses, especially within the active and learning-dependent coleoids. The ever-intriguing camouflage abilities of octopuses and cuttlefish are highlighted, alongside bioluminescence, navigation and other aspects of visual and cognitive competence.

Covering the range of cognitive function, this text underscores the importance of the cephalopods within the field of comparative cognition generally. It will be highly valuable for researchers, graduates and senior undergraduate students.

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To the next generation

ASD and LD: To Nitzan and Pia

JM: To Charlotte and Nicky

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Preface

In July of 2012, at the Francis Crick Memorial Conference on Consciousness in Human and Non-Human Animals, a group of researchers signed The Cambridge Declaration on Consciousness. What was important about this declaration was that it firmly stated that consciousness can emerge in animals that evolved along different evolutionary tracks, including cephalopod mollusks. This recognized what researchers in cephalopod behaviour, starting with the ground-breaking work of J. Z. Young and Martin Wells over 50 years ago, have been maintaining, that these animals are ‘learning specialists’ and capable of ‘complex cognition’. The chapters of this book will help define and discuss this cephalopod cognition, giving insight not just into how their brain and behaviour work, but also a comparative view that can be contrasted to research in ‘traditional’ vertebrates.

Cognition has been difficult to define and has been described more or less broadly over the years (Shettleworth, 2010). In general terms, Neisser (1967) defined it as ‘all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered and used’ (and see chapter 6, this volume, by Mather et al.). Deukas (1998) defined it similarly as ‘the neuronal processes concerned with the acquisition and manipulation of information by animals’. Richardson’s (2010) definition that cognitive systems ‘disambiguate confusing, incomplete and rapidly changing data, while generating equally unique, yet adaptive responses’ reminds us that this information processing is not static and works across time. Shettleworth (2010) starts with a definition that is similar to these, but points out that many believe it to be too broad. She notes that cognition might need to be declarative (knowing that) rather than procedural (knowing how). Similarly, cognition might need to act on mental representations. First-order operation (operating directly on perceptual input) would not be cognitive, whereas second-order ones (acting on first order ones) would be. She reminds her readers that without experimental analysis, it is impossible to tell what kinds of processes are reflected in a behaviour, a point nicely analyzed by Webb (2012) for insects. She also notes that different kinds of animals might accomplish functionally similar behaviour in different ways, an important point for the comparison of cephalopod cognition with that or animals from other phyla (see the chapter 7, this volume, by Jozet-Alves et al.). All of these ideas are incorporated in different ways in the chapters of this book.

Although comparative cognition was probably not even defined when Martin J. Wells was doing research in the 1950s and 1960s, his work definitely fits into that category and was also the basis for much of the work we are doing on cephalopod cognition now.

His initial orientation was physiology, but Wells moved the study of octopus learning from visual to tactile, and located a second area in the brain concerned with learning. He conducted many of the lesion studies that laid the groundwork for our understanding of the brain's control of behaviour (see chapter 4, this volume, by Hochner & Shomrat). But his investigation of the function of the optic gland was a pioneering step in the understanding of invertebrate neuroendocrinology. He was always interested in cardiovascular physiology and his work was the foundation for later study in this area, particularly by Ronald O'Dor. Later in his career he became intrigued with the lifestyle and adaptation of nautiloids, and while he may have underestimated their ability (see chapter 2, this volume, by Basil & Crook), he laid the foundation for further research in this area too. And we still find his book, written in 1978, a useful source of information (Wells, 1978).

Part I: cognition, brain and evolution

Cephalopods are often described as amazing brainy creatures; this is probably why they are the first invertebrates considered as 'sensitive' beings and, hence, the use of them is now regulated by a European directive. This is fully explored in the first part of this book. Given the absence of parental care to the eggs and juveniles, Darmaillacq et al. (chapter 1) highlight how the cuttlefish is a suitable model to address developmental questions. They review the remarkable memory and other cognitive skills from embryonic stages. From a comparative point of view, Basil and Crook (chapter 2) illustrate learning in the ancient cephalopod *Nautilus pompilius*. This chapter addresses how *Nautilus* can be used for a better understanding of evolution of cognition and neural complexity in its more derived relatives, the coleoid cephalopods (octopuses, cuttlefish and squid). In contrast, Kuba et al. (chapter 3) underline the interest in the 'sophisticated' octopus as a model to study object play, a high-order behavioural emergence in the animal kingdom. Hochner and Shomrat (chapter 4) underline the spectacular functional and structural similarities of memory systems between octopus and mammals, despite very different brain organization. Lastly, chapter 5 by Grasso gives an authoritative account of current understanding of the octopus nervous system and a clearly personal view of the functional architecture. The hierarchical system proposed in this chapter could be applied in robotics and cybernetics, and the ideas are challenging and may be controversial.

Part II: cognition and the environment

Of course cognitive abilities evolved through and are used in the natural environment. But it is not always easy to study them or even to theorize how they are used in the marine environment. Given that cephalopods are mostly not social animals, their cognitive ability is not, as it is in the 'higher' vertebrates, used to solve social problems and understand the actions of conspecifics. Instead, Mather et al. (chapter 6) argue that foraging in the face of predator pressure is the foundation for the development of intelligence and perhaps consciousness, particularly of octopuses. All cephalopods are mobile, and Jozet-Alves et al. (chapter 7) point out the sensory processing and cognitive competence involved in both long-distance and local movement, including laboratory investigation of the latter activities. And one of the most fascinating aspects of the cephalopods' lives is their skin display system. Josef and Shashar (chapter 8) discuss the basic aspects of benthic cephalopods' camouflage and Zylinski and Osorio (chapter 9) review the recent in-depth research on how cuttlefish use visual information about the background to produce the precise matching that they perform so well. Finally, Zylinski and Johnsen (chapter 10) challenge us to look more widely at the many species across the class. They point out that the deep-sea cephalopods, though little known, have abilities in visual cognition and body pattern production quite different from the well-known near-shore species. This range of adaptations leaves us much more to investigate about cephalopod cognition as it is adapted to a wide variety of habitats.

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Acknowledgements

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Tribute to Martin J. Wells

Martin Wells, who died aged 80 in 2009, was not only a distinguished biologist with a passion for invertebrates, but also a colourful and stimulating personality who enthused generations of students with the sheer excitement and beauty of studying animals, especially cephalopods – squids and octopuses. He began his research into cephalopod learning when he and his wife, Joyce, abandoned their PhD programs at Cambridge to move to the Stazione Zoologica in Naples, Italy, as the Director in 1953. Acting on a suggestion from J. Z. Young, who had discovered a way of training octopuses to make visual discriminations, they began studying tactile learning in octopus. They soon showed that these animals could discriminate between objects on the basis of touch, using the suckers on their arms, and that octopus suckers contain chemoreceptors so they can learn to 'taste' what they touch. This 'tasting by touching' is extremely sensitive, enabling octopuses to distinguish between snails and stones as their arms explore their surroundings at night or in murky waters.

Collaborations with J. Z. Young continued into the 1970s, building up a map of octopus brain function based on surgically 'removing bits', seeing what functions changed and then documenting exactly what was removed microscopically. This eventually resulted in octopus brains becoming the best-known non-vertebrate biological data processor ever studied. Ultimately, cephalopods' brains were so different that they were referred to as 'the only alien intelligence that humans have encountered'. A bit later Martin tried to work backward towards the origins of this intelligence by studying ancient *Nautilus* brains, but they turned out to be not very smart, so he began referring to them as 'racing snails'.

Martin also discovered that in the cephalopod brain there is an analogue of the vertebrate pituitary gland: the optic gland, closely associated with sexual maturation. Martin and Joyce's 1959 paper in the *Journal of Experimental Biology* on this topic became a classic in the literature of invertebrate endocrinology. Martin's interest in the 1970s turned to various aspects of cephalopod cardiovascular and respiratory physiology. Collaborating with colleagues from around the world, he published a series of challenging papers attempting to relate physiology to the life of the whole animal in its environment. His more recent studies on nautiluses yielded fascinating data about the physiology of an animal that regularly moves from the surface to depths of more than 700 m, and also taught us much about the reasons for the eventual failure, from an evolutionary perspective, of the shelled cephalopods (the ammonites and belemnites) that once dominated the ancient seas.

On the basis of his work in Naples, Martin was elected to a prize fellowship at Trinity College, Cambridge, in 1956, and in 1959 he was appointed a university demonstrator in the Cambridge zoology department. He soon became one of five founder fellows of Churchill College, and a tutor and director of studies in biology. In 1966 Martin was awarded a Cambridge ScD and the silver medal of the Zoological Society of London in 1968. He was made a university reader in 1976. With Joyce, he travelled extensively in search of cephalopods, and colleagues with whom to study them. Among many destinations that he visited (often as a visiting professor) were Duke University in North Carolina, Hawaii, Ghana, Dalhousie in Canada, Papua New Guinea, Australia, Texas and Uganda.

Martin approached marine biology as a 'way of life'. He used his position in Cambridge to create a global cadre of marine biologists of the cephalopod persuasion. Postdoctoral fellows and graduate students from around the world were welcomed to his laboratory, his college, his house, his marine stations and his boats. They were expected to make wine and, occasionally, garden in the Bury, his home. Perhaps only half of the world's cephalopod biologists enjoyed Martin and Joyce's hospitality over the years, but this community will never forget their influence. Several generations now hark back to it. Martin's approach was not just a scientific but also an intellectual exercise that expanded the minds of those lucky enough to be involved. He was a writer of popular science books, essays and rigorous papers, a novelist, painter and a yachtsman, talents he came by honestly as the grandson of H. G. Wells. Living with the entire Wells family shaped minds.

Martin's philosophy was always, 'Why tackle easy questions when the hard ones are so much more interesting?' I think the hardest question he ever asked was, 'Why do cephalopods need to be so smart when they die so young?' The phrase 'live fast, die young' has become a popular descriptor of the cephalopod lifestyle, but perhaps the phrase should be expanded to 'live fast and smart, to leave your offspring fewer enemies'. Martin died on the first day of Darwin's bicentenary, so a Darwinian answer seems appropriate.

Ronald O'Dor