General Introduction

'... In the primeval struggle of the jungle, as in the refinements of civilised warfare, we see in progress a great evolutionary armament race— whose results, for defence, are manifested in such devices as speed, alertness, armour, spinescence, burrowing habits, nocturnal habits, poisonous secretions, nauseous taste; and for offense, in such counter-attributes as speed, ... ambush, allurement, visual acuity, claws, teeth, stings, ... [and] poison fangs.' – Cott (1940), cited in Dawkins and Krebs (1979) as the first ever use of the arms-race analogy applied to predator-prey interactions.

For any animal, there is a strong selection pressure to eat and not get eaten. All living organisms need energy to survive, and animals get their energy from food. Broadly speaking, food comes in one of two forms; plants, in which case the eater is a **herbivore**, or other animals, in which case the eater is a **carnivore**. The great advantage to being a carnivore is that the food comes pre-processed into a high-energy form almost guaranteed to be suitable for the eater's requirements; carnivores are made of meat and their food is made of meat - what could be a better match? From the carnivore's perspective someone else had to do the hard work of finding an edible plant, overcoming whatever defences the plant may have had, harvesting the plant, evolving and maintaining the long and complex gut necessary for converting the plant cellulose into useful animal material, and so on. All the carnivore has to do is eat the animal that ate the plant. However, this is not a trivial matter.

Some carnivores are scavengers; they eat animals that are already dead, either from natural causes, or as a result of another animal's actions. The advantage for the scavenger is that its food puts up no resistance! This is true in both the short and long term. Dead food cannot fight back in the short term, and there is usually no long-term selective pressure on an animal to develop mechanisms to prevent it from being scavenged after death[1]. Some of the structures that an animal has evolved which help to protect it while alive (such as a thick hide) persist after death and might make things difficult for a scavenger but, in principle, there is no evolutionary arms race between scavengers and their food. However, there is a lot of competition for dead meat. Other scavengers will want a piece of the action, so there is both an evolutionary and, often, a real-time race between scavengers. The first scavenger on the scene is likely to get the best pickings. This being the case, there is strong selection pressure on a scavenger to help things along a bit by arriving *before* the food is actually dead. This crosses the bridge between scavenging and predation[2].

---

[1]It is conceivable that, in cases of voluntary cannibalism, where an animal allows itself to be killed and eaten by close relatives (as occurs in matriphagous spiders – for instance, see Kim and Horel, 1998), post-mortem defences against non-related scavengers might increase fitness. However, we are not aware of any documented evidence for such adaptations.

[2]We are not for a moment suggesting that all predators evolved from scavengers in this way. However, there is no doubt that most predators will scavenge if the opportunity arises, and that scavengers are not too picky about their food actually being completely dead before they start to eat.

One of the main characteristics of predation is that predators have a detrimental effect on the fitness of their individual prey. As Joe Fetcho (1991) eloquently and succinctly put it, 'Being eaten alive abruptly ends all chances of future reproduction and is not favourable from an evolutionary viewpoint'.

However, starving to death is not good news from an evolutionary (or personal) perspective either. We are thus confronted with the absolute inevitability of an evolutionary arms race between predators and their prey. The pressure of the race is not equally balanced between competitors, since predators will usually live to fight another day if they fail in any particular attack, while failure of a prey's defence system is likely to be fatal to that individual[3]. Nor does predation always seriously damage individual prey fitness; predators will often target old or diseased prey that may have little chance of further reproduction anyway. And, of course, in the long term, predation is a major drive for prey evolution by weeding out less fit individuals.

Ecological factors tend to stabilise the situation so, if a prey species starts to lose the arms race, then its population decline puts resource pressure on its predators, whose population may then decline in response, thus relieving pressure on the prey, and so on. There is a huge ecological literature on such matters (see, for example, Barbosa and Castellanos, 2005). Nonetheless, if the arms race becomes too weighted to one side or the other, then the losing side is likely to drop out of both the race, and existence, by becoming extinct (possibly taking its competitor with it, if there is strong ecological coupling between them). It is, therefore, true to say that a snapshot of extant life on Earth today shows us the suite of animals who are still active competitors in the race between predators and prey.

A vast range of adaptations has evolved in both predators and prey in their endless struggle with each other. If we take an apex predator (i.e. one sitting on top of the food chain, that is not itself subject to predation), such as a lion or a polar bear, then size and strength and teeth and claws come to mind. On the prey side, too, size and strength are primary defences – nothing (except, occasionally, humans) predates on large, healthy adult elephants or whales. At the other end of the size scale, we have the gossamer delicacy of a spider's web, beautiful to the human observer and lethal to the flies it entraps. And there is cryptic and warning colouration; on the one hand, camouflage that makes a prey virtually undetectable to its predators, and on the other, garish colours that broadcast the presence of the wearer with such brazen confidence that the would-be predator suspects that the prey has an alternative defence such as poison.

And then there are the fakers – the prey that pretend to be poisonous but are not, and which mimic the warning colours of their more honest neighbours. Life is a struggle, and almost any adaptation of any animal has some role in the conflict between predator and prey. Even an extreme adaptation that apparently handicaps its owner may, in fact, act as an **honest signal** to advertise superior fitness. This can put off predators that then look for easier targets, while simultaneously attracting mates who fancy enhancing their offspring's life chances with a share of such an obviously superior set of genes.

What this book is about

What is **neuroethology**? The term refers to the study of the neural control of natural animal behaviour from a comparative biological perspective. Behaviour arises from the activity of the nervous system and neuroethology, therefore, includes the analysis of

[3]The so-called 'life-dinner principle': the fox is running for its dinner, but the rabbit is running for its life (Dawkins and Krebs, 1979).

neural circuits and their modulation from the lowest molecular level through to the highest systems level. What distinguishes neuroethology from straight neuroscience, however, is that this analysis is always considered in terms of the natural function of the output, and that function is necessarily constrained by both the biology of the individual and the biological and physical characteristics of the environment in which it operates. These, in turn, are constrained by the developmental and evolutionary history of the animals (and plants) involved. A neuroethologist is, therefore, interested in how and why animals in their natural environment respond to natural stimuli in the way that they do. The 'how' is the main concern of the *neuro* bit of the word, which refers to the neural mechanisms of behaviour, and the 'why' is the main concern of the *ethology* bit of the word, which refers to the study of behaviour that a free animal displays in the wild. The animals can include everything from jellyfish to humans, which makes it a pretty broad topic.

This book is about the neuroethology of some of the fascinating and spectacular adaptations within the subject of predation, predator avoidance and escape. For the predator, the first and most essential stage in the hunt for food is usually **detection**, closely followed by **localisation** in 3D space. For a predator to launch a successful attack, it must not only know that a prey item is out there, but must also know precisely where 'there' is. In cases such as the auditory system of the owl, we have a detailed knowledge of how this is accomplished within the bird's brain. For prey, early detection is equally important, but localisation perhaps less so. The prey needs to know the approximate direction of danger, so that it does not flee directly into its jaws, but it does not usually need really precise information. In fact, there is plenty of evidence to show that some randomness in escape is a real advantage to the prey. If even the prey does not know in advance exactly where it is going, then the predator certainly cannot second-guess it and get there first to welcome it.

The next crucial stage is **decision**. Both attack and escape are expensive and potentially dangerous. For the predator, a failed attack both costs energy and reveals its presence, thus reducing the chance of a successful second try. For prey, keeping still might be the best tactic unless and until it is sure that it has been spotted and an attack is imminent (Broom and Ruxton, 2005). Many predators have sensory systems that are highly tuned to detect movement, and premature escape may simply draw attention to the prey. Furthermore, escape costs energy, and it also incurs an **opportunity cost**, in that it interrupts whatever else the prey might be getting on with, which could have been something really useful, like mating or eating. In relatively simple systems, such as the crayfish escape tail-flip, we are starting to gain some insight into how such 'economic' decisions are made, although we are still a long way from a full understanding.

Finally, there is **action**. At this stage, speed is often crucial. The predator needs to grab the prey before it can react and escape and, conversely, the prey needs to escape before it is grabbed. It is here that we see some of the most dramatic specialisations – giant neurons, electrical synapses, massive muscles, and catapult mechanisms to enhance power output. Here also we see trade-offs. Ultra-high speed reactions require simple neural circuits, and simple neural circuits imply a lack of flexibility. Some of the fastest escape reactions are, indeed, quite stereotyped in their form and, in some cases, not only have predators adapted to predict the prey escape trajectory, they even deliver the particular stimulus needed to trigger 'escape' straight into their own mouths, as in the amazing tentacled snake (see Chapter 8)!

Of course, many predators are prey items themselves, doubling the pressure on survival mechanisms. There is little point in being massively focussed on capturing what is in front of you if you, yourself, then fall victim to an attack from behind. It is, therefore, perhaps not surprising to find that sometimes the neural and muscular machinery that evolved for escape purposes has also been usurped (or perhaps co-evolved) within the same species for the purpose of attack. We will see a beautiful example of this when we consider archer fish, which perform what is essentially a rapid escape manoeuvre, but use it to reach their prey before competitors get there first. It is also not surprising that, in such cases, the design principles for escape do not always match those needed for attack. We have already seen that the intrinsic variability in escape trajectory that facilitates the evasion of predators would be positively detrimental if the same animal used it when in predator mode, because now the emphasis must be on precision of movement. So, although the same basic pathways and apparatus may be deployed by the same individual in two subtly different behaviours, each of which requires speed, there must be refinements that adapt the output for the purpose of attack (targeted) and escape (variable) behavioural requirements.

How this book is organised

The book mostly consists of a series of 'case study'-based chapters, whose sequence broadly follows the three major themes outlined in the previous paragraphs: **detection, decision and action**. However, chapters often contain information relevant to two, or even all three, themes. After all, a fundamental aim of science is to understand how things work and, where we have information for a single system that goes from stimulus detection at the start, through central integration and decision-making all the way to motor output, we thought it would be a pity to force it apart so as to conform to an abstract organisational plan. One benefit of this is that individual chapters can, if desired, be read in isolation, with some assurance that most, if not all, of the information contained within the book on that topic will be found within that chapter.

Some chapters concentrate on a particular mechanism or modality. Thus, we have a section on vision early in the book, where the dominant theme is perception, and sections on rapid movement and power amplification later in the book, where the emphasis has switched more to action. Both of these include details from a range of animals across different phyla. Other chapters are more taxonomically based. We have a chapter on molluscan predation and escape which covers topics from jet propulsion, through inking, to colour change, and in this chapter the only real unifying feature is that the animals involved are all molluscs.

The depth with which particular topics are covered also varies. Some biological systems relevant to predation and escape have been intensively investigated over many years, often by researchers in several independent groups, and these have become recognised as 'model systems'. Examples include the crustacean escape tail-flip, and the owl auditory system. For these, we present neurophysiological information at quite a sophisticated level of detail, and they usually each occupy a complete chapter. In addition to these major case studies, other chapters consist of a collection of what might be called 'fascinating fragments'. These are shorter sections that report some particular animal or adaptation for which there is some neurobiological knowledge, but which currently lack the breadth of detail available in the major case studies. These fragments include some of the most spectacular adaptations that we have come across. Our discovery of them in the literature while researching for this book has certainly given great pleasure to the authors, and we hope that sharing the knowledge of them will give equal pleasure to the reader, and perhaps inspire the next generation of neuroethologists.

Throughout the book, we try to draw attention to common principles and adaptations when they emerge from the multiplicity of examples we present. Where animals face problems that share features, it is not surprising that evolution has come up with solutions that also share features. The role of coincidence detection in sensory systems is one such example, while the need for power amplification by small animals that make rapid movements is another. This is convergent evolution, and we will see many examples of it in the course of this book. But it is also true that evolution may find radically different solutions to problems that appear, on the surface, to be similar. An animal can only play cards from the hand that its evolutionary history has dealt it, and different hands may require different strategies to win. For example, solutions available to an animal with a hard skeleton may simply not be an option for an animal with a hydrostatic skeleton, and vice versa.

We make quite extensive use of footnotes in this book. We tend to use footnotes for snippets of information which we think are interesting, but which would distract from the flow if included in the main text. We also sometimes use them to point out exceptions to general rules that we outline, or to cross-reference to information contained elsewhere in the book.

Who this book is for

This book is primarily aimed at senior undergraduates and graduate students studying the 'biological' end of neuroscience and/or the 'neuro' end of animal behaviour. It may also provide a useful repository of information to the teachers of these students, especially in the area of neuroethology. The book is definitely *not* a general primer on neurobiology – we assume that the reader has a basic knowledge of cellular neuroscience, including the general mechanisms of action potentials and synapses, and the general layout of the nervous system. However, the theme of the book does, in places, require delving into some fairly advanced neuroscience that goes well beyond these basics, and we try to deliver this more specialist knowledge within the text itself when it is needed. These more sophisticated topics are introduced within the context of predator-prey interactions, but they are, in many cases, relevant to any advanced student of neuroscience.

We emphasised at the beginning of this introduction the huge breadth of the topic we are tackling. This necessarily means that our choice of what to include has been very personal – perhaps idiosyncratic – and we are well aware that we have omitted mention of much valuable information. If we have not included your favourite subject within the story, we can only apologise.

Acknowledgements

We are enormously grateful to the various reviewers listed below, who gave their time to reading individual chapters (and in one case, a draft of the whole thing). The valuable feedback they provided has undoubtedly improved the book – although, of course, the inevitable errors and omissions are entirely our responsibility.

John Altringham
Euan Brown
Malcolm Burrows

Catherine Carr
Verena Dietrich-Bischoff
Donald Edwards
Abdel El Manira
Melina Hale
Hans Hoffman
Paul Katz
Frank Krasne
Stefan Pulver
Stefan Schuster
Harold Zakon

We are also indebted to the various talented photographers who have kindly allowed us to use the product of their labours in our book. We acknowledge these formally within the legends of the appropriate figures, but we would like to use this space to add a more personal and heartfelt 'thank you'. We are very grateful to the BBSRC EastBio scholarship programme for their internship support of LDP during the preparation of this book.

References

Barbosa, P. and Castellanos, I. (2005). *Ecology of Predator-Prey Interactions*. Oxford: Oxford University Press.

Broom, M. and Ruxton, G.D. (2005). You can run – Or you can hide: Optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology* **16**(3), 534–540.

Cott, H.B. (1940). *Adaptive coloration in animals*. London: Methuen.

Dawkins, R. and Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society B* **205**(1161), 489–511.

Fetcho, J.R. (1991). Spinal network of the Mauthner cell. *Brain, Behavior and Evolution* **37**, 298–316.

Kim, K.W. and Horel, A. (1998). Matriphagy in the spider *Amaurobius ferox* (Araneidae, Amaurobiidae): an example of mother-offspring interactions. *Ethology* **104**, 1021–1037.