Behavioural Neuroscience

Brain and behaviour are intrinsically linked. Animals demonstrate a huge and complex repertoire of behaviours, so how can specific behaviours be mapped onto the complicated neural circuits of the brain? Highlighting the extraordinary advances that have been made in the field of behavioural neuroscience over recent decades, this book examines how behaviours can be understood in terms of their neural mechanisms. Each chapter outlines the components of a particular behaviour, discussing laboratory techniques, the key brain structures involved, and the underpinning cellular and molecular mechanisms. Commins covers a range of topics including learning in a simple invertebrate, fear conditioning, taste aversion, sound localization, and echolocation in bats, as well as more complex behaviours, such as language development, spatial navigation and circadian rhythms. Demonstrating key processes through clear, step-by-step explanations and numerous illustrations, this will be valuable reading for students of zoology, animal behaviour, psychology, and neuroscience.

Seán Commins is a Senior Lecturer in the Department of Psychology at Maynooth University, Ireland. His research focuses on the biological basis of learning and memory, spatial navigation and the impact of stroke on cognition. Dr Commins has published extensively and has received numerous awards in recognition of his research.

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For Sinéad, Sorcha and Dara

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PREFACE

Over the last 70 years, especially since the discovery of the genetic code, scientists have become very reductionist in their approach. Many look deep into the cell, examining specific genes, molecules and their underlying machinery. Using amazing techniques, genes can be turned on or turned off; molecular pathways can be silenced or enhanced. Such approaches have brought about amazing discoveries. However, at times it feels that the whole animal has been forgotten. An animal's behaviour is not controlled by a single cell, a single gene or a particular molecule. We must take a step back, and make sure we understand the animal, its behaviour in a particular environment, its underlying physiological machinery, and, importantly, how these are all interlinked. It is only then that we will gain a more complete understanding.

Brain and behaviour are intrinsically linked. Disruptions to various brain regions and their neural circuits (e.g. by head injury) can lead to changes in behaviour. Likewise, modifications of behaviour (e.g. exercise, learning) can change neural structure. While many neuroscientists try to understand the chemical and molecular make-up of neurons and their electrophysiological properties, as well as how they communicate with each other, one job of the behavioural neuroscientist is to link specific brain regions, and even specific neurons within a brain structure, to overall function and behaviour. This is not new. Patient studies from the late nineteenth century pointed to the idea of localisation of function, that is, the concept that specific brain regions are involved in a particular behaviour. All brain regions do not contribute equally to a given function. Through decades of research we now know that some brain areas are heavily involved in language processing (e.g. Broca's area), while other areas deal mainly with memory (e.g. hippocampus), emotion (e.g. amygdala) or other functions. Patient and lesion studies provide great insight into brain and behaviour, and the emergence of functional imaging technology over recent decades probes even further, allowing multiple structures and circuits to be visualised, mapped and aligned to behaviour.

Although one of the major goals of behavioural neuroscience is to try to understand how various behaviours are mapped onto the brain, this is not as straightforward as it may seem. Animals have a huge repertoire of behaviours. They show emotions, they show different forms of memory, they hear and respond to different sound frequencies and they see different wavelengths of light. Even if we consider only mammals, some can talk, some swim, some walk and some even fly. In short, behaviours are complicated. More than this, as the mammalian brain contains millions of neurons (more than the number of stars in the Milky Way galaxy) and trillions of connections between these neurons, and each neuron has different biochemical and molecular make-up, brains are complicated.

How do scientists marry the two and map a specific behaviour onto a neural circuit? One method is to study and use a model organism that has a very simple biological make-up. So, rather than trying to study a brain containing millions of neurons, many scientists

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have successfully looked at organisms that contain a simple nervous structure, with at most tens of thousands of neurons. For example, the action potential and its properties were originally elucidated by the Nobel Prize–winning physiologists Alan Hodgkin and Andrew Huxley in the giant squid. This invertebrate has very large axons, which can be observed with the naked eye. Similarly, in 2000 a Nobel Prize was awarded to Eric Kandel for his work elucidating learning and memory processes in another invertebrate with a simple neural circuitry, the *Aplysia* (sea slug). Some of this work is described in Chapters 5 and 6.

An alternative method of investigation is to look at the behaviours and break these down into simpler components. Psychologists over the last 100 years have very successfully worked out many of the rules and conditions that govern behaviour. For example, Ivan Pavlov in 1920s showed how a neutral stimulus (a stimulus that doesn't normally trigger a response) can evoke a strong response in an animal simply by associating this neutral stimulus with another that does trigger the response. Ringing a bell, for example, would not normally evoke a salivation response in dogs unless it was associated with another stimulus (e.g. food) that does trigger this response. So, despite the seemingly daunting task of mapping behaviour onto neural circuits, it can be achieved.

One of the aims of this book is to highlight the extraordinary work that has been achieved to date in the field of behavioural neuroscience. The book demonstrates how scientists have attempted, through the use of multiple techniques and the examination of various species, to understand our behaviour in terms of their neural mechanisms. More than this, the book aims to be student-centred; it acts as a resource to bring together experimental findings from many neuroscientists working in a particular area. Through the use of multiple illustrations and step-by-step explanations, the current understanding of the biological processes underlying a particular behaviour is clearly laid out.

Each chapter follows the same general format. Initially, there is a description of a specific behaviour; this is then followed by a detailed analysis of the brain regions and neural circuitry involved in the behaviour. Finally, cellular and molecular changes that occur within the circuitry are described, to offer explanations of how such a behaviour occurs. As well as mechanistically explaining a particular behaviour, the book aims to be thought-provoking. Students will, at the end of each chapter, realise that the explanation is not complete. They will hopefully get a sense that scientists are still working to understand more and more, and that this work is ongoing and always changing. This will provide students with an insight into the work of the scientist and allow them to think about how future experiments should be designed and what still needs to be addressed in the field. To promote this further, each chapter ends with a series of questions and discusses some of the unresolved issues in the field. A final aim of the book is to promote a sense of enthusiasm in a new generation of behavioural neuroscientists, who will hopefully be inspired to understand more.

The book contains 16 chapters. As the student moves through the book, the behaviours become more complex. Some behaviours are currently well mapped at the neural and cellular level, and these are described in detail. As the book introduces more complex behaviours, the current knowledge of the exact neural circuitry and molecular machinery underlying such behaviours is less complete. However, the key brain structures and the underlying properties of the neurons contained in these regions are described, as well as an analysis of how they contribute to a particular behaviour. In addition,

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the book does not limit itself to one particular species but includes work on many. The various species are selected on the basis that they represent the best model of a particular type of behaviour. Further, by using different species, students will get to know the anatomy and brain structure of a range of animals, including zebra finches, bats, owls, *Aplysia* (sea slugs) and rats. Each chapter is also associated with a major subdiscipline within behavioural neuroscience, including learning, plasticity, fear conditioning, motor response, taste aversion, navigation and circadian rhythms.

Specifically, Chapters 1 through 4 provide an introduction to neurons and the brain and how neurons communicate with each other, and discuss in general the various brain regions and their functions. In addition, a brief introduction to the various techniques used in behavioural neuroscience is provided, followed by a description of the principles of behaviour and how different behaviours can be measured in the laboratory. These chapters may provide a useful starting point and an introduction to the area of behavioural neuroscience for undergraduate students.

In Chapters 5 and 6 students are introduced to the *Aplysia*, a small marine invertebrate, and consider why this animal makes for a perfect model in understanding the mechanism of learning and memory, despite not having a brain! Chapter 5 describes how habituation and sensitisation, considered to be among the simplest forms of learning, play an important role in the survival of this marine animal. The chapter describes the work of neuroscientists, particularly the Nobel Prize–winning laureate Eric Kandel, who have shown how habituation and sensitisation can be produced in the lab, and how the neural circuitry and molecular mechanisms underlying these behaviours have been elucidated. Chapter 6 follows directly from the previous one and describes a more advanced form of learning: classical conditioning. While we accept that the *Aplysia* may have a very simple learning repertoire, is it possible that the *Aplysia* can also be classically conditioned, as Pavlov's dogs were? The chapter describes how the *Aplysia* can be conditioned, and the site of change within the neural network and the molecular events associated with learning are also examined.

Before examining various mechanisms of learning in the vertebrate brain, students are introduced to the concept of synaptic plasticity (Chapters 7 and 8). If learning and memories are to be stored in the brain, there must be a mechanism to allow this to happen. Long-term potentiation (LTP) is one very plausible mechanism (Chapter 7). The student is introduced to the basic concepts of LTP, how LTP is elicited and the molecular underpinnings of such a phenomenon. The latter part of the chapter looks at the evidence that LTP is a realistic model of how mammals learn. Chapter 8 describes the idea that not only can the strength of synapses be enhanced (potentiated), but synaptic strength can also be reduced. This synaptic depression or LTD is described in two areas of the mammalian brain (the cerebellum and hippocampus), along with a description and discussion of the cellular and molecular mechanisms.

Although much progress has been made in understanding learning and memory mechanisms in simple invertebrate systems, the task in localising learning and memory circuits in the mammalian brain is much more difficult, especially given the sheer numbers of neurons involved and the complexity of the neural system. The trick is to use a simple learning paradigm, like classical conditioning, but one in which the stimuli involved are well defined and provoke an automatic response. Our eyes are very sensitive; if someone

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blows into them we immediately close the lids to protect them (which parallels the defence reaction of *Aplysia*). This reaction is automatic but, importantly, it can paired with other stimuli to evoke a response. Chapter 9 introduces the student to eye-blink conditioning. It outlines the neural circuit in the cerebellum involved with this simple learned motor response and the cellular and molecular changes that occur with conditioning.

An eye-blink response is an automatic motor reaction and therefore does not require too much cognitive processing. What about higher-order brain processing such as emotions? Can we, for example, learn fear? Fear is fundamental to an animal's survival. Some animals have an innate fear of other animals, but fear can also be learnt. If we place a sharp object in an electrical socket, the chances are that we would never, ever do this again. We have learned to be afraid. In Chapter 10, the student is introduced to the amygdala, a brain region heavily involved in emotions, especially fear. The chapter describes how fear conditioning can arise through a network of circuits involving the amygdala. Then some of the known biochemical and molecular mechanisms underlying fear conditioning are described.

Animals have another very important defence mechanism. If we eat something in a restaurant and a couple of hours later we take ill, the likelihood of eating that food again or indeed even visiting that restaurant again is very low. Chapter 11 describes taste-aversion conditioning, a behaviour that also involves the amygdala, among other brain structures. While many of the previously described learning responses require multiple training trials, this form of learning is special; it typically involves only a single trial. We do not have to eat food and fall ill multiple times before we avoid it; once is sufficient. Like in previous chapters, in Chapter 11 the student is introduced to the neural circuitry involved in this behaviour and the molecular and cellular underpinnings.

The ability to locate the source of a sound is essential for most animals. In humans, the skill is clearly important in a range of scenarios from identifying the source of a speaker during a conversation to identifying the location of a car when crossing a busy road. In some animals this ability takes on an even greater importance. For example, in the case of the barn owl, identification of the origin of a sound as a potential food source is needed for its very survival. Chapter 12 shows how the physical features of an owl's head and how its brain deal with sound information coming at slightly different frequencies and timing combine to provide an aural map of space. This, in turn, allows the animal to identify exactly from which direction the sound has originated.

Having the ability to locate a sound source and react to it is certainly an impressive skill, but how do you use sound to navigate your environment? The impressive skill of echolocation is performed by many animals, but bats are most adept at this ability. Chapter 13 introduces the student to different bats and how they can identify various elements of complex environments using sound echoes. Specifically, the chapter describes the various neural pathways of the bat brain, with a particular emphasis on the auditory cortex. In addition, how neurons respond to different sound frequencies, allowing the animal to judge distances and velocity, is described. This knowledge is critical for a bat to identify moving prey as well as to avoid obstacles when flying.

Many animals navigate their environment without using echoes. The complex behaviour of knowing where you are, where you want to go and how to get there is explored in Chapter 14. Although complete knowledge of a circuit involving all aspects

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of spatial navigation is currently unknown, the role of a particular brain structure, the hippocampus, in navigation is described in this chapter. In addition, the student is introduced to specialised cells found in hippocampus and surrounding areas that aid this behaviour. The work described in this chapter was recognised in 2014 by the awarding of the Nobel Prize to John O'Keefe, Edvard Moser and May-Britt Moser.

Language is considered to be a distinctively human form of communication. It is so complex that it might be considered nearly impossible to understand its basic components and neural underpinnings. However, scientists do have a model that resembles language acquisition in humans: birdsong learning. When a baby hears sounds emanating from its parent's mouth, these sounds are repeated and remembered. With time, the sounds the baby makes, in the form of words, match exactly with those of the parents. In addition to hearing sounds from others, children also depend on hearing the sounds that they themselves emit. Can each of these components be matched in the songbird? Chapter 15 examines how some birds acquire their distinctive song by learning from their parents and by using their own aural feedback. The neural circuits of such behaviours are also examined.

Finally, many of our behaviours, implicit and explicit, are governed by biological rhythms. We are active during the day and fall asleep at night. Our sleep cycles between REM (rapid eye movement) and non-REM states. Body temperature, secretion of hormones and other physiological changes follow a set rhythm. Over a longer period, many animals hibernate during the winter months before waking up in spring. How are these rhythms governed? Chapter 16 introduces the student to the suprachiasmatic nucleus, the brain's master circadian clock, and describes some of the mechanisms that control our biological rhythms.

Because of the nature of science and the volume of work currently being done, there are many behaviours that I have not included in this book; furthermore, while I have done my best to capture the state of current knowledge in each chapter, there may be some relevant information that I have missed or have not fully captured. I apologise in advance for this.

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