Introduction: Mechanisms of Animal Behaviour

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Introduction: The Study of Animal Behaviour

This book comprises four volumes, roughly dealing with the four main problems in animal behaviour, namely the causation, development, function and evolution of behaviour. The way in which these four topics were assigned to the different volumes is pragmatic, and there is bound to be some overlap. Nevertheless, we feel that the division of the study of animal behaviour into these four questions, is helpful and will lead to a better understanding of the subject. In this we follow Niko Tinbergen, one of the founding fathers of behavioural biology, who first identified these four problems in a publication from 1963 (Chapter 2 of the present volume). Animal behaviour was studied before Tinbergen, and it is instructive to dwell briefly upon the prehistory of the field. The scientific study of animal behaviour is also called ethology, a term used first by the 19th century French zoologist Isidore Geoffroy Saint Hilaire but then used with its modern meaning by the American zoologist Wheeler (1902). Ethology is derived from the Greek *ethos*, meaning 'character'. There is some resemblance with the word 'ethics', which is derived from the same Greek word. This is perhaps not so surprising, seeing that ethics is basically about how humans ought to behave. Unfortunately the word 'ethology' is often confused with the word 'ethnology' (the study of human peoples), with which it has nothing in common. The term 'ethology' is not used as much as it used to be, although there is still an active animal behaviour journal bearing this name. Instead of 'ethology', nowadays many authors use the words 'animal behaviour' or 'behavioural biology' when they refer to the scientific study of animal behaviour.

Early days

Scientists and amateurs have studied animal behaviour long before the word 'ethology' was introduced. For instance, Aristotle had many interesting observations concerning animal behaviour. The study of animal behaviour was taken up more systematically mainly by German and British zoologists around the turn of the 19th century. The great British naturalist Charles Darwin (1809-1882), in his classic book on the theory of evolution by natural selection (Darwin, 1859), devoted a whole chapter to what he called 'instinct'. As early as 1873, the British amateur investigator Douglas Spalding recorded some very interesting observations on the attachment behaviour of young domestic chicks to abnormal objects, a phenomenon that was later called 'imprinting', after the German 'Prägung' (see the paper by Konrad Lorenz reproduced here as Chapter 24). At the beginning of the twentieth century, the behaviour of animals was also studied in the context of learning by the Russian physiologist Ivan P. Pavlov (1927) and the American psychologist Edward L. Thorndike (1911). Learning is discussed in Chapter 34.

Lorenz and Tinbergen

In the middle of the twentieth century, the study of animal behaviour became an independent scientific discipline, called ethology, mainly through the efforts of two biologists, the Austrian Konrad Lorenz (1903-1989) and the Dutchman Niko Tinbergen (1907-1988). It can be said that Lorenz was the more philosophical, theoretical of the two, whilst Tinbergen was very much an experimentalist, who together with his students and collaborators conducted an extensive series of field and laboratory experiments on the behaviour of animals of many different species. Lorenz put forward a number of theoretical models on different aspects of animal behaviour such as evolution and motivation. He was also the more outspoken of the two men, and some of his publications met with considerable controversy. In 1973 Lorenz and Tinbergen were awarded the Nobel Prize for Physiology and Medicine. They shared their prize with Karl von Frisch (1886-1982), an Austrian comparative physiologist and ethologist who had pioneered research into the dance 'language' of bees.

Behaviorism

The emphasis of the North American psychologists on learning was epitomized in the rise of behaviorism in the 1930's. Behaviorism was a very influential school of thought initiated by the American psychologist John B. Watson (1878-1958), with his book 'Behaviorism' (1924). Essentially, Watson considered psychological phenomena to be physical activity rather than some kind of mental event. Watson proposed that we cannot make any scientific statements

about what might be going on in our minds, and that introspection was unreliable. Rather, psychologists can only investigate the physical manifestations that we can observe in the form of behaviour. For behaviorists, psychology is the study of behaviour and of the external physical factors that influence it. They believe that it is not possible to make scientific statements about mental processes. This may sound odd to us, but at the time, behaviorism was extremely influential in science and beyond. Within North-American psychology it was the dominant school of thought for several decades. Behaviorist theory also affected education practice, particularly with Watson's book 'Psychological care of infant and child' (1928). Watson once made the famous statement: "Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select – doctor, lawyer, artist, merchant-chief, and, yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors". This epitomizes behaviorist ideas about child rearing. Watson considered the upbringing of children to be an objective, almost scientific exercise, without the need for affection or sentimentality.

Watson's most famous student was Burrhus Frederic Skinner (1904-1990), who applied behaviorist ideas to the study of learning. For Skinner and his behaviorist colleagues, learning had to do with changing relationships between visible entities, not with what might be going on inside the animal's head. In particular, behaviorist learning theorists suggest that learning involves the formation of associations between a stimulus and a response. Most of their experiments involve instrumental conditioning (see Chapter 34), where a certain response by the animal (e.g. pressing a lever) is rewarded ('reinforced') with, for instance, food.

Cognitive Psychology

Within experimental psychology there came a reaction to behaviorism in what we now call cognitive psychology. In contrast to behaviorism, cognitive psychologists start with the assumption that individuals (humans and other animals) have a mental life that can be investigated. For instance, Skinner (1957) maintained that language development in children was a learning process, where responses (i.e. uttering certain sounds) were reinforced. The great American linguist Noam Chomsky (1959) wrote a lengthy and highly critical review of Skinner's book on language development, in which he suggested that language acquisition is not a case of instrumental conditioning, but the development of certain cognitive mechanisms, the so-called universal grammar. Another important publication that signalled the beginning of the cognitive revolution is a book by the British psychologist Donald Broadbent (1958) who, in contrast to Skinner, analyzed learning and memory in terms

of cognitive mechanisms rather than stimulus-response relations. Hogan (1988) has suggested that what cognitive psychologists call 'cognitive structures' are in fact the same as the causal mechanisms that were proposed by ethologists such as Lorenz and Tinbergen.

Tinbergen's Four Questions

Niko Tinbergen published a very important paper in 1963 – reproduced as the opening paper of this volume–, in which he outlined the four major questions in the study of animal behaviour, namely causation, development, function (Tinbergen called this 'survival value') and evolution. As he readily admitted, Tinbergen was not very original, as three of these questions (causation, function and evolution) had already been put forward by the British biologist Julian Huxley as the major questions in biology, and Tinbergen merely added a fourth question, development. Tinbergen's four questions are sometimes collapsed into two categories; proximate or causal questions (causation and development) and ultimate or functional questions (function and evolution). These distinctions have often led to confusion and controversy (see Hogan & Bolhuis, 2009). Bolhuis (2005, 2009) distinguished between functional questions (function and evolution) on the one hand, and questions about mechanism (causation and development) on the other. But no matter how these questions are broken up it is crucially important that students of animal behaviour be quite clear as to the type of question they are addressing when they study or speak of animal behaviour. Tinbergen's analysis is so important that we would say that you cannot really understand animal behaviour if you do not also understand the meaning of Tinbergen's four questions. Some of the more heated contemporary debates in the field of animal behaviour can often be traced to misunderstandings about the meaning of the four questions (e.g. Hogan, 1994; Bolhuis & Macphail, 2002). It is essential, therefore, that any productive discussion about animal behaviour involves participants that are capable of clearly stating which of the four questions they are addressing.

Tinbergen's four questions are sometimes also called the four whys, because they represent four ways of asking 'why does this animal behave in this way?' Let's consider a bird singing at dawn, say a male song sparrow (*Melospiza melodia*). The question is: why is this bird singing? This seems a perfectly straightforward question, but in fact it is much more complicated, because it can take any of four different forms. These different forms reflect Tinbergen's four whys. The first of the four questions concerns causation: what causes the bird to sing? Another way of asking this is: what are the mechanisms underlying the male's singing behaviour? These mechanisms involve the 'machinery' that operates within the animal and which is responsible

for the production of behavioural output. The topics include the stimuli or triggers of behaviour whether they be internal or external, the way in which behavioural output is guided, factors that stop behaviour and the like. These are questions concerning the *causation* of behaviour. Sometimes this is called motivation (e.g. Hogan, 2009). The question of the causation of behaviour is the subject of the papers reproduced in Volume 1 of this book. The second question is about development: how did the singing behaviour of the bird come about in the lifetime of an animal? It turns out that a male song sparrow does not sing immediately after it has hatched from the egg, but that it takes quite some time before it has developed a song, a process that involves learning. Such questions that concern *development* of behaviour, sometimes also called ontogeny, are the subject of the papers reproduced in Volume 2 of this book. The third question has to do with function: what is the function of the bird singing; what is it singing for? This question has to do with the consequences of singing for the singer's fitness. Does singing help the bird keep intruding males away from his nest? Or does it simply serve to attract females? The topic of function, its methods of enquiry and main findings is discussed in the papers reproduced in Volume 3 of this book. The fourth question concerns evolution: how did this behaviour come about in the course of evolution? Behaviour does not leave many fossils behind and so the study of its evolutionary history requires the development of special methods. These methods, based on taxonomy and comparisons among species, are the subject of the papers in Volume 4 of the present book.

We hope to have made it clear that the question 'why does this bird sing?' is not very useful, as it can have four different meanings. It can be very confusing if a biologist studying birdsong does not make it clear which of the four 'why questions' he/she is asking, and it could lead to futile arguments concerning whether the bird is singing to attract mates or because it learned its song. The same problem arises in all other areas of animal behaviour and so it is very important to make it clear which of the four questions is to be addressed in any study. Of course, it is possible that a particular investigator wants to address more than one question at the time. This is perfectly legitimate, as long as it is made explicit which of the questions is addressed at what time. A famous example of this is an experimental paper by Tinbergen and his associates (Tinbergen et al., 1962) on the behaviour of blackheaded gulls (*Larus ridibundus*). After the chicks have hatched, the adult birds remove the empty eggshells from the nest. Tinbergen et al. investigated both the causation and the function of this behaviour using elegantly simple field experiments and reported results for both questions in the same paper. There is also considerable overlap between some of the four questions. For instance, the development of behaviour is essentially a causal problem, but may also involve functional aspects. The evolution of behaviour (Volume 4 of the present book) often depends on mechanism. For instance, emergent properties of an

animal's sensory and perceptual capabilities (mechanisms) may create opportunities for sexual selection to evolve extravagant traits (see Volume 3). Finally, questions in one domain (e.g. function) can provide clues for questions in another domain (e.g. causation). For instance, a number of bird species cache food, some for a few hours, others for months (Vander Wall 1990). It is plausible that the ecological circumstances that have given rise to these different forms of food caching may have also influenced the animals' ability to memorize spatial locations. In fact, a large number of studies at a mechanistic level (e.g. learning, memory, cognition, neuroethology) are concerned with the spatial memory of food caching versus non-food caching birds (Bolhuis & Macphail, 2001). A recent volume that addresses Tinbergen's four whys, and their relevance for modern behavioural biology is Bolhuis & Verhulst (2009).

Causation: The Mechanisms of Behaviour

The rest of the chapters in the present volume are concerned with Tinbergen's causation question, or, in contemporary terms, with the mechanisms of behaviour. The internal factors involved in the causation of behaviour are often called motivation. The second section of the present volume has a number of papers dealing with models of motivation. Chapters 3 and 4 are the presentations of the two founding fathers of the field, Lorenz and Tinbergen, at the Symposium of the Society for Experimental Biology, held in Cambridge in 1949. Lorenz outlines his views on motivation from a comparative perspective. In this paper he describes his famous 'psychohydraulic' model of motivation, where the level of motivation is represented as the amount of water in a reservoir. Lorenz's model has received considerable criticism, perhaps partly because the hydraulic metaphor was considered to be an oversimplification. Nevertheless, even this simple model made sense of a number of behavioural phenomena that ethologist had been unable to explain previously. Lorenz's model also incorporated the effects of external stimuli as possible 'releasers' of behaviour. A classic empirical study that clearly shows the interplay between internal factors and external stimuli in the causation of behaviour is that by Baerends et al. (1955) on the courtship behaviour of the male guppy (*Lebistes reticulatus)*. In a brief paper (Chapter 4), Tinbergen presents his hierachical view of the motivational mechanisms of behaviour. It is interesting to see how much Tinbergen's schema is reminiscent of neurons making synaptic connections. The following chapter has a paper by Dutch ethologist Gerard Baerends (who was a student of Tinbergen at Leiden), which is a kind of implementation of Tinbergen's hierarchical view in actual behaviour. The early models by Lorenz and Tinbergen were followed by more complex ones, involving the possibility of feedback (see Toates (1986), for a detailed treatment of the concept of feedback). A concept used by many was that of

homeostasis, where behavioural output was thought to be regulated relative to certain standard values, somewhat like the way a thermostat regulates the temperature in a room. In Chapter 6, ethologist and psychologist Jerry Hogan discusses this concept in the context of motivation in some detail. The early models made use of the idea of energy. For instance, in his 'psychohydraulic' model, Lorenz introduced the concept of 'action-specific energy' , an entity that could build up inside the animal, and could be released by the appropriate stimuli. Energy models of motivation were criticised by British ethologist Robert Hinde in a paper that is reproduced here as Chapter 7. Hinde was one of the leading figures in the generation following Lorenz and Tinbergen (he was a student of Tinbergen at Oxford). Hinde argued that particularly Lorenz's model of energy building up in the animal's nervous system was naïve and not consistent with actual data. In the subsequent chapter, Hogan evaluates the different views on motivation, and argues for a re-appraisal of energy models. Hogan argues that a build up of motivational energy is often a rather good way of analysing behaviour. He discusses several examples where the causal factors for a particular behaviour are twofold. On the one hand, there is often some kind of motivational mechanism that somehow increases the probability that a behaviour will occur with time, along the lines of a Lorenzian energy model. On the other hand, in many cases behaviour is influenced by a circadian pacemaker. Hogan discusses dustbathing in chickens as an example of a behaviour that is under the influence of these two systems. Another example is found in human sleep, discussed in detail in Chapter 11 in the next Section, on biological rhythms.

The German Jürgen Aschoff and the American Colin Pittendrigh were the two towering figures in the study of the biological rhythms underlying behaviour. Chapter 9 is a review by Ashoff of the influence of circadian clocks on the behaviour of humans and other animals. In Chapter 10 we reproduce one of a series of classic papers by Pittendrigh and Daan on circadian rhythms in nocturnal rodents. In the last chapter in this Section, Dijk and Lockley provide a review of the research done on the human sleep-wake cycle. As indicated in Hogan's paper on energy models of motivation (Chapter 8), the prevailing view – first put forward by Borbély (1982) and in a quantitative version by Daan et al. (1984) – is that sleep is influenced by two factors: a homeostatic process (known somewhat mysteriously as 'process S') and a circadian rhythm (see also Fig. 6 in Chapter 8). Process S can be measured as increasing power of the EEG spectrum measured in awake subjects, and is very much reminiscent of the 'energy' factor in Lorenz's model. The combination of the homeostatic factor and the circadian rhythm has proved to be a powerful explanation for the characteristics of the human sleep/wake cycle.

Where Tinbergen's hierarchical model only hinted at the underlying neural and endocrinological factors involved, the next section of Volume 1 is concerned

with these factors themselves. Chapter 12 is Lehrman's classic analysis of the hormonal influences on reproductive behaviour in the ring dove. The paper – a chapter in an important early book on sexual behaviour edited by Frank Beach – shows clearly the interaction of internal motivational factors (in this case hormone levels) and external stimuli. Another classic study showing the effect of the sex hormone testosterone on sexual behaviour in male rats is by Beach and Holz-Tucker (1949). Behavioural endocrinology is now a burgeoning field that has its own journal, Hormones & Behavior. A recent textbook on behavioural endocrinology is Adkins-Regan (2005). Chapter 13, by Harris and Michael, is a pioneering study concerning the interplay between hormonal and neural factors influencing behaviour. The study suggests that the hypothalamus is important for, in this case, sexual behaviour. It has become apparent that this brain structure plays a crucial role in behavioural motivation.

A more general and systematic approach to the study of the neural mechanisms underlying behaviour became known as neuroethology (Ewert 1980; see Chapter 16). Chapter 14, by von Holst is his own English summary of his famous paper (with Mittelstädt) on reafference (von Holst & Mittelstädt, 1950). This paper introduced the concept of an endogenously active central nervous system providing a command to action, which continued until the "expected" sensory stimulation was received. In many ways it laid the foundations for modern cognitive neuroscience. The following chapter is a classic neuroethological study by Lettvin et al., analysing the neural mechanisms of visual perception. Chapter 16 is a review by one of the pioneers of neuroethology, Jörg-Peter Ewert. His work amounts to an analysis of the neural implementation of classical ethological concepts such as key stimuli and releasing mechanisms. These chapters illustrate that in the early days of this new discipline, researchers concentrated on the study of the neural mechanisms of perception and movement, often in insects or lower vertebrates. More recently the study of the brain mechanisms of behaviour is also directed toward higher cognitive processes such as learning and memory or spatial orientation. Often, the terms behavioural neuroscience or cognitive neuroscience are used to describe these disciplines. Now the combination of an extraordinary array of powerful techniques from electrophysiological recording to molecular analyses of RNA sequences allows researchers to delve deeper into the connection between behaviour and its neural substrate. Sherry (2005) provides a concise overview of some of the key concepts in behavioural neuroscience.

A recent development in the study of causation is that of animal cognition. It is becoming increasingly clear that animals have many cognitive capacities that previously had been thought to be the preserve of humans. Initially, following Darwin's ideas, as expressed in *The Descent of Man* (1871), apes and monkeys were considered the closest equivalent to humans when it came to cognition. For instance, in the search for animal equivalents of human speech

and language, attempts were made to teach apes simple forms of language, either by imitating human speech or by using symbols or sign language. These attempts were not successful (for a classic critical analysis see Terrace et al., 1979) and there is general agreement among linguists (e.g. Pinker, 1994; Hauser et al., 2002) that apes do not have language in the way that humans have (see Radick, 2007, for a recent review). More recently, it has become apparent that non-primates often have cognitive capacities that were thought to be the preserve of primates (Bolhuis & Wynne, 2009). Thus, researchers increasingly look to songbirds for an animal model of human speech and language (Bolhuis & Gahr, 2006; Gentner et al., 2006). In addition, for other higher cognitive abilities it has become apparent that birds often outperform monkeys and apes. The last chapter in this volume is an example of this research, involving meta-tool use in crows. These birds are capable of cognitive feats that are absent in monkeys and not as well developed in chimpanzees. A recent introductory chapter on animal cognition is provided by Emery & Clayton (2005). Shettleworth (1998) has written a monograph on animal cognition from an evolutionary perspective. For a textbook and a more general monograph on animal cognition see Wynne (2001, 2004).

Development and Learning

Volume 2 of this book is mainly concerned with Tinbergen's question of the development of behaviour, or what he called 'ontogeny'. During the early days of ethology there was a certain amount of scientific rivalry between mainly European ethologists and North American experimental psychologists, who also studied animal behaviour in what was usually called comparative psychology. The European ethologists emphasized that animal behaviour is a biological phenomenon, and as such has an evolutionary history. This is exemplified by the use of the word 'instinct', for instance in the title of Tinbergen's classic book 'The study of instinct' (1951). The term 'instinct', which is rarely used in contemporary behavioural biology, referred to the heritable components of behaviour that are subject to natural selection.

The Nature/Nurture Debate

In his early papers, Lorenz (1937) postulated that behaviour could be considered a mixture of innate and acquired elements (*Instinkt-Dressur-Verschrankung*: intercalation of fixed action patterns and learning), and that analysis of the development of the innate elements (fixed action patterns) was a matter for embryologists. Lorenz's views were criticised by some of his North American colleagues, and this led to what is known as the Nature/Nurture debate. This is a crucial debate for the study of behavioural

development, and we have devoted the first section of Volume 2 of this book to some of the classic papers. The first critiques were formulated by Lehrman (1953) and Hebb (1953), and their papers are reproduced here as Chapters 18 and 19. Particularly in response to Lehrman's (1953) critique of ethological theory, Lorenz (1965) published a monograph, in which he changed his formulation of the problem, and argued that adaptation of a behavioural element to its species' environment can be influenced by information stored in the genes or from an interaction between the individual and its environment. An excerpt from Lorenz's book is reproduced here as Chapter 20. This formulation also met with considerable criticism from particularly Lehrman, who insisted that development consisted of a more complex dynamic. Lehrman (1970; reproduced here as Chapter 21) pointed out that he and Lorenz were really interested in two different problems: Lehrman was interested in studying the effects of all types of experience on all types of behaviour at all stages of development, very much from a causal perspective, whereas Lorenz was interested only in studying the effects of functional experience on behaviour mechanisms at the stage of development at which they begin to function as modes of adaptation to the environment. Thus, as Hogan (1988) suggested, Lehrman used a causal criterion to determine what was interesting to study, while Lorenz used a functional criterion. Hogan (1988) notes that both these viewpoints are equally legitimate, but that Lorenz's functional criterion corresponds to the way most people think about development. The second issue is that even behaviour patterns that owe their adaptedness to genetic information require interaction with the environment in order to develop in the individual. As Lehrman states: "The interaction out of which the organism develops is *not* one, as is so often said, between heredity and environment. It is between *organism* and environment! And the organism is different at each state of its development." (Lehrman, 1953, p. 345). This interactionist view has been developed more recently by Oyama (1985), and has gradually been adopted by most students of behaviour. Other reviews of the nature/nurture issue can be found in Gottlieb (1997) and Bolhuis (2005).

Imprinting and Birdsong Learning

The next section of Volume 2 is mainly concerned with two paradigmatic developmental processes, imprinting and birdsong learning. Both of these paradigms involve early learning, and in addition they have several characteristics that render them prime examples of how behaviour can develop. One of these characteristics is that of sensitive periods, the subject matter of Chapter 22. Briefly, sensitive periods are phases in development during which the individual is particularly sensitive to external experience. The term 'critical period' is now rarely used, because research has shown that there are no strict boundaries to the period of increase sensitivity. Bateson (1979) has discussed

the functional implications of sensitive periods in the development of behaviour. Chapter 23 is an example of Gilbert Gottlieb's classic series of experiments on the development of perceptual preferences in birds. In this paper, Gottlieb describes the different ways in which (often non-specific) experience can influence the development of such perceptual mechanisms. The next two chapters are on the phenomon that is known as imprinting. First, Chapter 24 has an excerpt of Konrad Lorenz's English version of his earlier paper (Lorenz, 1935) in which he provided the first comprehensive description of imprinting in birds. This is followed (Chapter 25) by Bolhuis & Honey's review of imprinting, involving much of the enormous amount of research that had been inspired by Lorenz's original observations. An in depth review of both filial and sexual imprinting can been found in Bolhuis (1991), while the neural mechanisms of filial imprinting have been reviewed by Horn (1985, 2004). The last chapter in this section is Konishi's classic treatment of song learning in songbirds. In this paper, the author introduced the concept of the template, which is still a much-used metaphor for essentially the central representation of the memory of the tutor song that is being copied. Catchpole and Slater (2009) have written an authoritative monograph on all aspects of birdsong, while a recent edited volume on the neural mechanisms of birdsong is Zeigler & Marler (2008). The neural mechanisms of birdsong memory have been reviewed by Bolhuis and Gahr (2006).

Development of Motor Patterns

In their study of the development of dustbathing in junglefowl chicks, Larsen et al. (2000) found that individual behavior elements, as soon as they appeared, were incorporated into the normal adult sequence structure; this occurred even though the form of the elements themselves was not yet fixed. These results support the conclusion that separate mechanisms are responsible for the form of the individual behavior elements and for the organization of these elements into recognizable sequences. A similar conclusion was reached by Berridge (1994) on the basis of results on the development of grooming sequences in young rodents. In Chapter 27, Colonnese et al. call certain sequences of grooming movement "syntactic chains" to emphasize the rules controlling natural action sequences. For an earlier review of motor pattern development see Fentress & McLeod (1986).

Hall and Williams' review of their work (Chapter 28), demonstrating that in rat pups, 'suckling isn't feeding', provides a good example of what Oppenheim (1981) has called ontogenetic adaptations. Suckling behavior is qualitatively different from later feeding behavior, and it is the sole means of food intake until weaning, which according to Oppenheim (1981) qualifies it as an ontogenetic adaptation. Hall and Williams discuss two possible developmental scenarios for suckling and feeding in rats. One possibility is

that suckling merges into feeding at weaning, and the two behaviors share internal and external causal factors. Alternatively, the two behaviors are relatively separate and they share only some internal and external causal factors. Hall and co-workers found that adult ingestion is not a continuation of suckling, as the two behaviors have different internal and external causal factors. Furthermore, if pups were deprived of suckling by feeding them with a cannula, later feeding behavior emerged normally, suggesting that suckling is not a necessary antecedent for adult feeding.

The Dutch ethologist Jaap Kruijt was the first to undertake a detailed analysis of the development of social behaviour, in this case of Burmese red junglefowl. Based on his findings he proposed that in young animals, initially the motor components of behaviour often function as independent units. Only later in development, often after specific experience, do these motor components become integrated into more complex systems such as hunger, aggression, or sex. Excerpts from his classic monograph are reproduced in Chapter 29.

Development of the Brain and Social Behaviour

The next section of Volume 2 is concerned with the development of the brain and complex social behaviour. We could only include one paper on brain development, and chose a review by Mark Johnson of cortical mechanisms of cognitive development (Chapter 30). Johnson (2004) has also produced an excellent introductory text on what he terms 'developmental cognitive neuroscience', a field in which he has been a pioneer. Inspired by the work of Kruijt (Chapter 29), Hogan (1988) has introduced the concept of behaviour systems in the study of development. Chapter 31 is a more recent discussion of these ideas. A behaviour system comprises perceptual, central, and motor mechanisms that act as a unit in some situations. Hogan suggests that behavioural development is essentially the development of these mechanisms themselves and of the changes in the connections among them. Often, these mechanisms and their connections only develop after functional experience, i.e., experience with the particular stimuli involved, or with the consequences of performing specific motor patterns. The following two chapters are concerned with the effects of early social deprivation on behavioural development in monkeys. Chapter 32 has a review by Harry and Margaret Harlow of their pioneering experiments showing the profound effects of social isolation on behavioural development. In Chapter 33, Robert Hinde reviews the work from his group, showing that even brief separation from the mother can have long-lasting, profound effects on the infant's social behaviour. Hinde discusses how this research on monkeys has had an enormous influence on the psychology and psychiatry of emotional development and human bonding, for instance in the work of Bowlby on human attachment (1969, 1973).

Learning

In contrast to the European ethologists' emphasis on the evolutionary history of behaviour, American psychologists emphasized the effects of learning. Pavlov (1927) had already demonstrated the importance of what we now call Pavlovian (or classical) conditioning. Earlier, Thorndike (1911) studied learning processes that are now known as instrumental or operant conditioning. Learning can be seen as being part of behavioral development; this is because learning, like other developmental processes, involves changes in the mechanisms underlying behavior over time. For example, during associative learning representations are formed of the stimuli or events that are associated, and these representations are somehow linked to each other. Representations are cognitive structures in which the external or internal environment of an individual is somehow coded or represented. Thus, after successful learning there will be behavior patterns and psychological and neural structures in the individual that were not there before the learning episode, which according to our broad definition, above, is a form of development. Many developmental processes, such as filial and sexual imprinting and bird song learning, explicitly involve learning, but they also involve other mechanisms. This raises the difficult question what the difference is between learning and other forms of development. The difference is gradual, and has to do with the specificity of the representations. In learning, representations are formed (of the stimuli or events and the relationship between them) that are specific to those external events. That is, the representation of the sound of the bell in Pavlov's dogs is only addressed when the dog hears the bell (or perhaps something that sounds very much like it, in the case of generalization). In other forms of development the influence of external experience may be non-specific, or internal causal factors may be involved. For instance, an increase in sex hormones around the time of birth may lead to the development of sexual behavior in a certain direction; one wouldn't call that learning. These differences are not substantial, however. One could say that learning is a subset of behavioral development in general. Beginning in the 1960s, ethologists and comparative psychologists noted that there were instances of animal learning that did not seem to comply with the (unwritten) 'laws of learning'. To begin with, Garcia and colleagues (e.g., Garcia & Koelling, 1966) found that under certain circumstances. the time interval between presentation of the conditioned (CS) and the unconditioned stimulus (US) in a Pavlovian conditioning paradigm could be much greater than was assumed previously, when the CS was a novel taste and the US nausea. Other work from the same researchers showed that it was much easier for rats to associate a taste with nausea than with electric shock. On the other hand, a light CS was much easier associated with shock than with nausea. These and other observations led to the suggestion that there are certain constraints on learning (discussed in Chapter 34; see Hinde &

Stevenson-Hinde, 1972 for an important collection of papers on this issue).

Unfortunately we did not have space to include some of the classic learning theory papers in this volume. The most important of these are Rescorla & Wagner (1972), Wagner (1978), Mackintosh (1975) and Pearce & Hall (1980). Chapter 34 is a paper by Roper that we think is a fine combination of a review of basic learning theory and a discussion of the biological constraints on learning. A classic textbook on animal learning theory is Mackintosh (1974), while Mackintosh (1983) is a shorter, more recent monograph. Dickinson (1980) has produced an excellent short introductory text on animal learning theory.

Concluding Remarks

Animal behaviour has grown into a highly diverse set of approaches and disciplines. Its subject area ranges from molecules and neurons to individuals and populations. One of Tinbergen's major contributions to the study of animal behaviour has been to make its goals explicit and clarify the four types of questions that can be asked of behaviour: causation, development, function and evolution. In this book we strongly advocate Tinbergen's position that behaviour can only be understood through research on all four questions. In addition, we suggest that it is made clear which of Tinbergen's questions is addressed when a behavioural problem is investigated: a problem in one domain should not be investigated with concepts from another (Bolhuis & Giraldeau, 2005; Bolhuis & Verhulst, 2009; Bolhuis & Wynne, 2009). That is why the chapters in this book are organized explicitly into four volumes that roughly follow Tinbergen's subdivision. The first volume is devoted to causation and addresses the mechanisms of behaviour, while the papers in Volume 2 are particularly concerned with behavioural development. The first major ethology textbook is Tinbergen (1951). Although obviously dated, this book is still a good read, and it is still being reprinted. Tinbergen's book was succeeded by Hinde (1970), the major textbook of the following two decades. Hinde wanted to provide a synthesis of the European and North American traditions, which is reflected in the subtitle of his book, 'A synthesis of ethology and comparative psychology'. Of later textbooks, Manning & Dawkins (1998) is particularly good, while Bolhuis & Giraldeau (2005) have produced the first edited textbook on animal behaviour. Boakes (1984) is a very good history of psychological research into animal behaviour. An inside look into the history of ethology is given by Thorpe (1979), while Dewsbury (1989) provides a North American perspective. A more recent and thorough history of the field can be found in Burkhardt (2005). Kruuk (2003) has published an excellent biography of Niko Tinbergen.

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