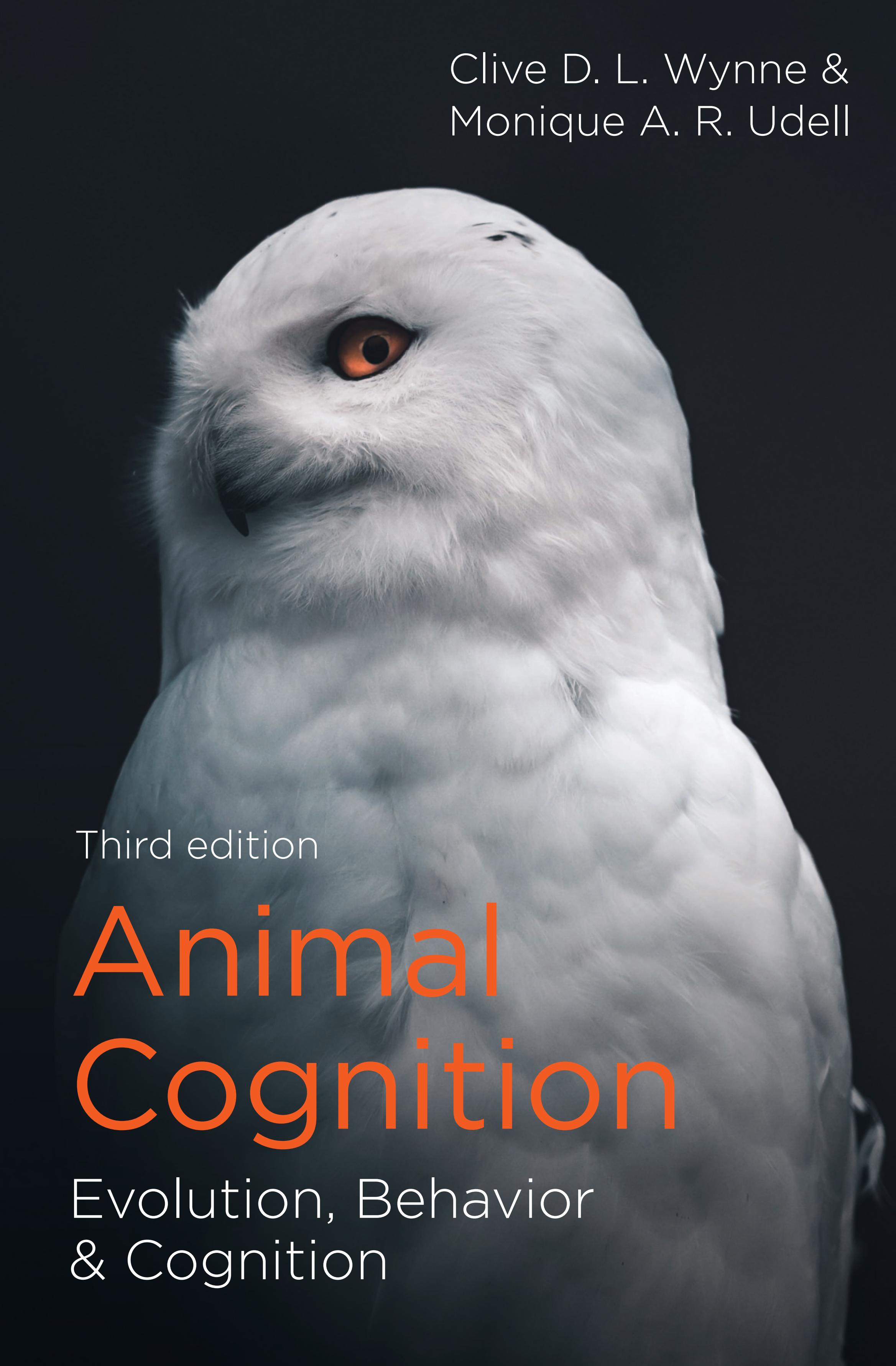

Clive D. L. Wynne &
Monique A. R. Udell

Third edition

Animal Cognition

Evolution, Behavior & Cognition

ANIMAL COGNITION

Also by Clive D. L. Wynne

Dog is Love: Why and How Your Dog Loves You (2019)

Do Animals Think? (2004)

ANIMAL COGNITION

EVOLUTION, BEHAVIOR AND COGNITION

THIRD EDITION

CLIVE D. L. WYNNE

MONIQUE A. R. UDELL

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For my mother, and in memory of my father
– Clive D. L. Wynne

To my family
– Monique A. R. Udell

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PREFACE TO THE THIRD EDITION

Twenty years have now passed since the first edition of *Animal Cognition* was published, and eight years since publication of the second edition. In an active field of research, even eight years is a long time. We have been thrilled to watch the field we love develop in so many different exciting directions. Where twenty years ago, studies on animals kept as pets, including dogs and cats, were quite rare, studies on domestic animals are now one of the fastest-growing areas of research in animal cognition. This offers the wonderful bonus that it is very easy for any reader to join in these research programs. A great deal of the science of animal cognition requires little or no special equipment, and thus it is very easy for anyone to become involved if they have a cooperative dog or cat in their household (e.g., you will learn how to conduct a preference assessment in Chapter 5). Of course, studies continue on stalwart laboratory animals like pigeons and rats as well. Research on lab animals offers the benefits of tremendously tight control over the experiences that are offered to the animals, and thus they will always play an important role in the science of animal cognition. Investigations of species in zoos and other captive environments are also considered, sometimes in comparison to counterparts living in other environments, in order to understand the relative influence of evolution and environment on cognition. One such example, comparing behavioral synchronization by dogs and wolves living in different environments, can be found in Chapter 9. In addition, the study of animal cognition on wild animals living freely in their native habitats continues apace. In some cases, more attention has been given to previously understudied species: for example, the question of how the process of metamorphosis impacts memories will be discussed in Chapter 10, with a focus on frogs and insects.

This third edition of *Animal Cognition* has been thoroughly updated to reflect advances in the field. This edition also contains more callout boxes to give you the opportunity to dig deeper into the scientific literature and to encourage you to look for examples of animal behaviors or the concepts identified in the text in your own environment, or try out experimental methods for yourself.

The preface for the first edition of this book stated the aims of that volume, aims that remain true in this new edition:

> This book wants to convert you to a different way of looking at animals. It wants you to be amazed at what animals can do –

> but amazed with a critical glint in your eye. This book wants to convince more people to find out what makes animals tick.
>
> If you have an interest in animal cognition but have not studied animal behavior before then this book is for you. You may be studying psychology and wondering how much of our human cognition is shared by other species. Or you may be studying biology and wondering how complex animal behavior can get. Or you may just be curious about the animals you see around you or hear about through TV documentaries. Though I have assumed no specific prior knowledge of psychology or biology, the tone I have adopted is a somewhat critical one. I think the truth about animal minds is interesting enough without having to embellish it with fanciful stories that are unlikely to stand closer scrutiny.

Some other points we made in the preface to the earlier editions remain valid here. This book is intended as a text for undergraduate students at universities and colleges. It can function as a stand-alone text for a class on animal cognition – possibly with the inclusion of some of the papers listed as further reading. It can also serve as a component of a broader class perhaps entitled "Animal Learning and Cognition," "Animal Behavior and Cognition," or "Comparative Psychology." More advanced students can use the chapters of this book as springing off points to pursue the topics covered here in the primary research literature.

Finally, it is our pleasure to acknowledge the help of those who have made this book possible. We thank the reviewers who provided highly constructive comments making each revision stronger and guiding our focus toward new areas of scientific interest. Our thanks also to Luke Block and Verity Rimmer at Macmillan International Higher Education, who shepherded the book to publication so skillfully. Of course, responsibility for the errors that remain rests with us.

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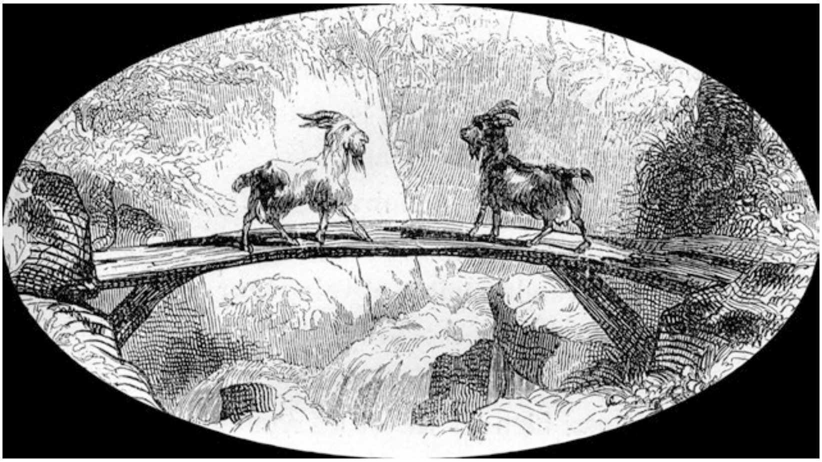
AUTHOR BIOGRAPHIES

Clive Wynne, Ph.D., is currently a Professor of Psychology at Arizona State University, USA, where he is founding director of the Canine Science Collaboratory. In addition, he is Research Director at Wolf Park in Indiana. In recent years, Clive's research interests have focussed on dogs and their wild relatives, but over the last thirty years he has studied the behavior of animals ranging from pigeons to dunnarts (a mouse-sized marsupial) and from bats to Galapagos tortoises. He received his PhD from the University of Edinburgh. Always fascinated by the things animals do, in recent years, he has developed an additional interest in how people relate to animals. When not working, he talks to his dog – even though research from his own lab suggests dogs are quite indifferent to what people say to them.

Monique Udell, Ph.D., is an Associate Professor of Animal Sciences at Oregon State University, USA, where she directs the Human-Animal Interactions Laboratory and teaches courses on Animal Behavior, Cognition, and Learning. Her research focuses on the development of cross-species bonds in both wild and domesticated animals, and the impact that these bonds can have on the behavior and success of both species. This includes bonds shared between humans and the animals they live with, work with, or care for. While much of her work has focused on domestic dogs, cats, horses, and captive wolves, she has studied a wide range of species out of a desire to better understand social behavior across the animal kingdom. In her free time, you will find her exploring the beauty of Oregon with her family.



1 EVOLUTION, ADAPTATION, COGNITION, AND BEHAVIOR: AN INTRODUCTION

> Let man visit Ourang-outang in domestication, hear expressive whine, see its intelligence when spoken; as if it understood every word said – see its affection – to those it knew – see its passion and rage, sulkiness, and very actions of despair; and then let him dare to boast of his proud pre-eminence.
>
> Charles Darwin, *Notebook C*, p. 79, 1987

We live with animals[1] – we always have, and we probably always will. As an inhabitant of a desert city at the start of the twenty-first century, Clive shares his home with a dog (loving but not terribly smart), a cat (aloof and seldom seen), spiders (mostly, but not always, harmless), occasional scorpions (terrifying!), and many other smaller hopping, scurrying, and biting things. Monique lives in damp Oregon with a dog – and numerous box elder beetles. Farmers and agriculturists over the last few thousand years have lived with many large domesticated mammals and a few birds. Before agriculture, humans hunted and were, in their turn, preyed upon by the various beasts that surrounded them. No matter our attitude toward animals, they are always among us.

But what are we to make of them? Do they think? Do they have minds? Are they conscious? What is it like to be a bat (as the philosopher Thomas Nagel famously asked in 1974)? Or a cat? Or an ant? Going back as far as records can show, people have treated animals as if they were people. Simple people, perhaps, but people nonetheless. This tendency to view animals as people is called *anthropomorphism* (from the Greek *anthropos*, human, and *morph*, form), and it seems to be an ancient and irresistible urge. Some of the earliest artworks in the world – paintings on the walls of caves in southern France that date back 30,000 years – depict human bodies with an animal head, suggesting that the people of those times viewed animals as having human-like qualities. We defy anyone, no matter how hard-nosed, not to adopt an attitude to Clive's cat, Peppermint, that involves treating her as a small child. We could probably

1 People are animals, too. However, for ease of reading, we stick to the tradition of calling humans "humans" and the rest "animals."

write a computer program (and not a very long program at that) that could convincingly simulate Peppermint's behavior, and yet Clive could never for one moment treat her with the same attitude he adopts toward a computer. The tug of anthropomorphism is just too strong.

Anthropomorphism, then, is our most natural, spontaneous, and everyday way of considering animals. And yet anyone who has ever observed and reflected on the behavior of an animal for a little while knows this cannot be right. Animals are not little people. Peppermint is not a baby; a dog with a gray beard is not a wise old man (or even a foolish old man). It may be emotionally satisfying to treat them that way, but we know it cannot be true. Cats and dogs and all other animals have their own mental lives to lead. In the case of domesticated species, these may overlap quite satisfactorily with the roles we have created for them, but reflection tells us naive anthropomorphism must be wrong. We must consider the psychology of animals in their own right. Box 1.1 considers one example of anthropomorphic projection onto animal behavior: the case of sexual pleasure.

Box 1.1 The popular view of animals

A while back, a friend came to Clive with a story he had read in the newspaper. Dolphins, chimpanzees, and humans are the only species to indulge in sexual activity solely for pleasure, not for procreation, said the newspaper report. Had Clive heard of this, the friend wanted to know, and was it true? As so often, we were astonished at the absurdity of the popular presentation of animal minds. What does it mean to say that some species indulge in sex for recreation not procreation? It would seem to imply that all the other species of animals on this planet engage in sexual activity only when they want to have offspring – that they know the connection between sex and pregnancy – surely a wildly improbable conjecture.

What is known of sexual activity among dolphins? In bottlenose dolphins, male groups of typically two or three individuals harass groups of females and young until they can separate a female from the group. They then keep this female captive, taking it in turns to have sex with her over a period of several days or weeks. In an in-depth study of 255 cases of dolphin mating behavior in Western Australia, Richard Connor et al. (1996) reported that 82 percent of these involved coercion on the part of the male dolphins. Of the remaining 18 percent, they could not be certain; some coercion may have taken place beneath the water's surface where they could not see it.

It would be anthropomorphic to claim that female dolphins do *not* experience pleasure in sex under these circumstances just because human females would not, but Connor and colleagues' results do not encourage the belief that female dolphins are uniquely privileged in terms of their opportunities for sexual pleasure.

When we look at animals, having recognized that they are not people, we still can't help seeing them from our human perspective – this is called anthropocentrism. Just as tourists visiting a new country make the foreign more manageable by making comparisons with home, so, in considering animal psychology, we inevitably start with our human minds and compare what animals do with what we do. Are they intelligent or conscious? Do they think or feel? All these are anthropocentric questions. We know we are intelligent and conscious, and we think and feel; therefore, we ask whether other species share these states. Anthropocentrism is a more subtle problem than anthropomorphism. Since we are human, we can probably never be entirely free from anthropocentrism. But just as astronomers gradually came to recognize that Earth is not at the center of the solar system and developed a cosmology that places our planet appropriately, at a particular point in the solar system in a certain galaxy, so we may hope that we can develop an animal psychology that moves humans from the central position and that sees each species as being at the center of its own world.

On minds, thought, and intelligence in animals

So what of "minds," "mental life," "thought," and "intelligence"? Are these anthropocentric terms, to be avoided by a mature animal psychology? That depends on what these words mean. If by "mind" you mean something different from your body, something like a nonphysical soul in which your intimate essence resides even beyond the death of your body, then the question of whether animals can have minds becomes one for your spiritual adviser, not an animal psychologist. In this book, however, we use the terms "mind" and "mental life" in a more down-to-earth manner. Here they refer simply to the totality of the behavior of an animal and the operations it performs to create those behaviors. These include perception: seeing, hearing, and senses we do not share (like the magnetic sense of pigeons); simple behaviors (like having a sense of when dinner is coming); through to the most complex cognitions, such as what psychologists call "theory of mind" – an individual's understanding that other beings have minds, too.

We are less convinced that the term "thought" can be made to do useful work for a modern animal psychology. Though others who have considered this question disagree (e.g., Marc Hauser, 2000), to us "thought" implies language. Though there are certainly mental operations that do not involve language, we would not consider these as thought. Furthermore, our assessment of the attempts to teach language to apes is that this enterprise has been unsuccessful (see Chapter 12). Consequently, we do not believe that animals think in the way we mean that word when we apply it to members of our own species. It is, in our view, unhelpful anthropocentrism, verging on anthropomorphism, to talk of thought in nonhumans. Talking about "thinking" animals tricks us into believing we understand animal mental life better than we really do. (For more of Clive's views on animal thinking, see Wynne, 2004.)

"Intelligence" is another problematic term for animal psychology. Even in our own species, arguments rage over what constitutes intelligence, where it comes from, and how to measure it. But even if we accept that, for humans, there exists a package of problem-solving skills that can be effectively measured and labeled "intelligence," it is not clear what this means for nonhumans. Talk of intelligence is often linked to attempts to form a single scale of intelligence, with some species at the top (humans, inevitably) and others at the bottom (marsupials, perhaps, or insects). Modern comparative psychologists take the more Darwinian view that each species has its own problems to solve and has therefore evolved its own skills to solve them. All the species that we see around us today have evolved for exactly the same length of time, and each has adapted to a unique niche. As we shall see in the chapters that follow, different niches make different demands on their occupants, and these include different cognitive demands.

To take an example from the Australian bush, are rabbits more intelligent than wallabies because they are smarter at evading foxes? A fox is a very unfair challenge to a wallaby. Australian marsupials have had only 200 years to try and figure out how to evade foxes, after millions of years adapting to the challenges of a climate that, though often harsh and very dry, was without foxlike creatures. Should we call the wallaby smarter than the rabbit because it can go longer without water and feed on drier foods?

However, so long as we stay away from attempts to rank-order the intelligence of different species, the term might still be a useful one. Used carefully, as a shorthand term meaning "wide-ranging problem-solving abilities," intelligence seems like a very natural way of describing an important aspect of behavior.

Finally, what about "cognition" – what does that term mean? In this text, "animal cognition" simply means the full richness and complexity of animal behavior. To many psychologists, "cognition" implies behavior driven by internal representations of the world. We prefer to remain agnostic on the question of internal representations because we believe that seeking simple, parsimonious explanations is central to the scientific approach. That means that we look for ways of explaining complex behavior in terms of the simplest possible behavioral rules. This is particularly apparent in Chapter 6 of the present text, where we consider animal reasoning. But even if it can be demonstrated that a particular, apparently complex, behavior can be explained with simple behavioral rules, we still believe it is reasonable to call that behavior cognitive. Therefore, "cognition" will not be defined here in a way that demands the involvement of internal representations.

Historical background: Darwin, Wallace, and the minds of beasts

Though, as we have seen above, an interest in the behavior of animals is evident in the earliest human artworks, the modern study of animal behavior began with Charles Darwin and his theory of evolution (1859). Darwin's originality lay not so much in arguing that all living things had evolved from earlier forms – others, including his own grandfather Erasmus Darwin, had suggested as much before. Darwin's breakthrough was to propose a plausible mechanism for how such evolution could have taken place. In each generation, Darwin observed, more young are born than can survive to have offspring of their own. These young are very variable – they are not simple clones of their parents. Inevitably, some of the offspring vary in ways that make them more or less likely to survive and have young of their own. In modern terms, they vary in fitness. Darwin reasoned that if some of the qualities that make some individuals better able to have offspring are inherited, then we have a mechanism for evolution. Those individuals with higher fitness will tend to leave the most offspring, and consequently, the species will change to contain more fit individuals. Of course, just as in any game of chance, the environmental conditions can change abruptly so that those who were previously less fit suddenly find themselves better suited to the environment. But, on average, over long periods of time, natural selection ensures that the most fit organisms survive and have young.

In general, we can say that the Darwinian mechanism for evolution is a process of variation (many different offspring are born), selection (some of these offspring survive to have young of their own), and variation again (the survivors from one generation are the parents of the next). The outcome of this process is a species continually improving its suitability to the environment around it. This suitability is technically known as "adaptation," and it is a central tenant of modern biology that organisms are adapted to their environments. Box 1.2 explores the power of the adaptionist approach to animal behavior.

Box 1.2 Can it be right to eat your own young?

The power of a scientific approach lies not just in explaining the obvious cases but in dealing with situations that at first blush seem impossible for a theory to account for.

The cornerstone of the adaptive approach to animal behavior is that animals act to perpetuate their genes into future generations. Broadly speaking, they do this by ensuring their own survival so that they can find mates and then by rearing their offspring. The amount of energy different species put into different aspects of this project vary greatly, but the theme is clear – animals strive to get their genes into future generations.

The real test of this theory lies in trying to explain situations where an animal seems to act to *prevent* its genes from passing forward into future generations.

One especially challenging case is that of animals that, far from caring for their young, actually eat their own offspring. The technical name for this phenomenon is filial cannibalism, and it is quite widespread in the animal kingdom. Filial cannibalism has been observed in a number of species, including hamsters, cats, dolphins – and several species of fish. Eating one's own young happens often enough that it cannot simply be dismissed as some kind of rare and anomalous behavior, and it does not just involve the eating of already dead or perhaps diseased offspring.

How might an adaptive approach account for such a strange course of action by such diverse animals?

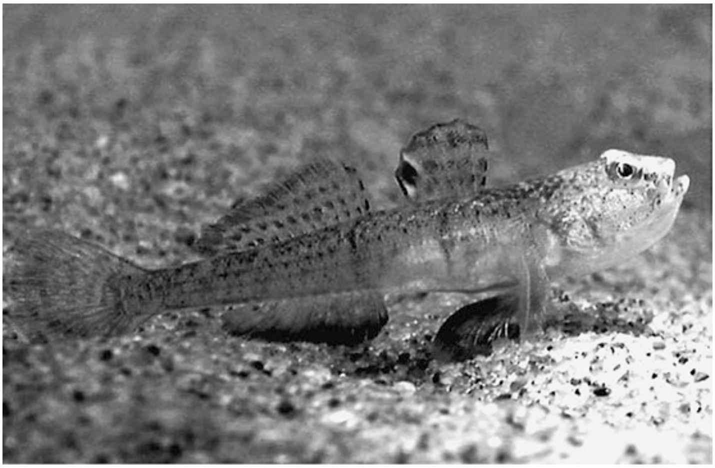


Figure 1.1 Sand goby

Source: Courtesy of Kai Laindstrom.

Hope Klug et al. (2006) made a detailed study of the reasons why the sand goby, a small sandy-colored fish that lives in European waters from the Baltic to the Mediterranean, eats its own eggs (Figure 1.1). In sand gobies, it is the males that care for the eggs.

How might eating one's eggs leave a father fish with a net adaptive benefit? There are several possibilities: Perhaps the energy gained by eating the eggs could aid future survival or reproduction; perhaps the fish eat inferior eggs and will invest the energy they gain in the upkeep of superior eggs; or perhaps the parents weed out slower-developing young and thereby give themselves time to have another clutch of eggs before the breeding season is over.

Klug et al. (2006) tested one hypothesis: an excessive density of eggs leads to such a high rate of egg death that eating some – and thereby reducing the density – actually enables more eggs to survive. Klug and colleagues found that the father fish did indeed eat more of their young if the eggs were packed in a high density rather than a low density. This effect was strongest when there was a lack of oxygen in the water. In another experiment, they simulated the impact of cannibalism by removing some of the eggs themselves so that they could see whether it was really the case that if some of the eggs were removed, the total number surviving would increase or at least not decrease. This was indeed what they found – again especially under conditions of low oxygen in the water. Overall, then, Klug and colleagues were able to demonstrate that by removing some of their eggs, father fish were able to obtain an energetic benefit for themselves with no decrease in the number of their offspring that survived.

From the beginning, Darwin believed that behavior and psychology were part of the evolutionary process too. He expanded on these thoughts in his private notebooks and letters (see Box 1.3), in *The Expression of the Emotions in Man and Animals* (1872), and in *The Descent of Man, and Selection in Relation to Sex* (1877). What struck Darwin were the commonalities between human and nonhuman psychology. In his private notebooks, he allowed his feelings to show more than in the works he prepared for publication. The quote at the start of this chapter shows how impressed Darwin was by the human-like behaviors of the first orangutan displayed at the London zoo.

Darwin's proposal of a plausible mechanism for evolution, his detailed analysis of how evolution could account for the then-known facts of biology, and his belief that human psychology was also an evolved trait in which some commonalities with other species could be expected combined to launch a new science of comparative psychology, "comparative" here meaning the comparison of different species.

One of the first to pick up the challenge of studying the psychology of nonhuman animals from a Darwinian evolutionary perspective was one of Darwin's closest followers, George Romanes. Unfortunately, rather than develop controlled ways to study animal behavior, Romanes relied on anecdotes collected from others' observations. Where Darwin was a masterful compiler of observations from correspondents all around the world, Romanes was far more gullible. At the start of his 1884 book, *Animal Intelligence*, Romanes described how he had considered restricting himself only to anecdotes about animal intelligence that had been recorded by "observers well known as competent." This essential constraint, however, he dismissed as too limiting; "I usually found," Romanes continued, "that the most remarkable instances of the display of intelligence were recorded by persons bearing names more or less unknown to fame."

Not surprisingly, Romanes's claims of fellow feeling among ants, fetishism in dogs, and intelligence throughout the animal kingdom raised hackles among his more careful contemporaries. In 1894, another early British animal psychologist, Conwy Lloyd Morgan, published his *Introduction to Comparative Psychology*. In it, Lloyd Morgan dismissed Romanes's over-vivid interpretations and argued for more careful interpretations of animal behavior. However, it fell to an American, Edward Thorndike, in his 1898 volume, *Animal Intelligence: An Experimental Study of the Associative Process in Animals*, to introduce the experimental method into the study of animal psychology. Just two years before the start of the twentieth century, with the introduction of experimental rigor, animal psychology became a science.

Box 1.3 Charles Darwin, Alfred Russel Wallace, and mental continuity

Darwin would never have thrived in the "publish or perish" atmosphere of contemporary academia. Between his first sketch of the theory of evolution by natural selection in 1842 and the publication of *On the Origin of Species* in 1859 lies a gap of 17 years (Brown, 2003). In that time, Darwin disclosed his theory to only a handful of his closest confidants. Historians wonder when Darwin would finally have found the courage to publish his theory had it not been for a letter he received from another biologist and explorer, Alfred Russel Wallace, in 1858. Wallace was recovering from malaria in the Spice Islands in Indonesia when the idea of evolution by natural selection came to him. He immediately wrote Darwin, who was stunned by the similarities between his own theory and Wallace's and overcome with anxiety as to how to deal with the difficulty he now faced. How could Darwin be fair to Wallace and yet maintain his own position as the originator of the theory of natural selection? Two of Darwin's friends, to whom he had shown earlier drafts of his theory, proposed that Darwin and Wallace jointly present their theory to a scientific society in London. This was done, though neither Darwin nor Wallace was present in person at the meeting: Wallace was still overseas, and Darwin was mourning the loss of a son to scarlet fever.

In most accounts of the origin of the theory of evolution by natural selection, this is where Alfred Russel Wallace disappears from the story. It is less widely known that in at least one crucial respect Darwin and Wallace differed in their thoughts on evolution. Darwin, as the quote from his notebooks at the beginning of this chapter makes clear, believed that the theory of evolution by natural selection applied to humans. And not just to our physical characters, but to our thoughts and feelings as well: to our minds. Wallace on the other hand drew a line at humanity. He wrote:

> Neither natural selection nor the more general theory of evolution can give any account whatever of the origin of sensational or conscious life. The moral and higher intellectual nature of man is as unique a phenomenon as was conscious life on its first appearance in the world, and the one is almost as difficult to conceive as originating by any law of evolution as the other.
>
> Wallace, 1869, p. 391

We know that Darwin disagreed with this statement because the letter he wrote to Wallace to say so has survived:

> If you had not told me I should have thought that they [Wallace's remarks on the evolution of the human mind] had been added by someone else. As you expected, I differ grievously from you, and am very sorry for it. I can see no necessity for calling in an additional and proximate cause in regard to Man.
>
> Darwin, in Marchant, J. (1975), Vol. 1, p. 243

Wallace's position that the theory of evolution can tell us nothing about the interesting psychological qualities that human beings have is the dominant position among academic psychologists and lay people today. Take, for example, this introductory statement from a textbook on cognitive psychology:

> Whenever higher mental processes are involved, we heartily disagree that human and animal behaviour are necessarily governed by the same principles. We regard the human as a specialized product of evolution, as an animal whose cognition is also specialized.
>
> Lachman, Lachman & Butterfield, 1979, p. 42, cited in Wasserman, 1993

This was not Darwin's view, and it is not the view we will be pursuing here. The evidence gathered in this book indicates that the mind has evolved and is evolving. Sure enough, there are differences between the minds of humans and those of other animals – just as there are differences between the mind of the mother digger wasp that supplies her eggs with a stunned, but not dead, cricket for them to feed on once they hatch and the mind of the pigeon that finds its way home after a displacement of hundreds of miles from its home loft. There are differences between the minds of different species, just as there are differences between the heads, arms, and feet of different species. But the minds of animals, just like their bodies, are adapted to the environments in which they live. Minds, just like bodies, are the product of evolution by natural selection.

The story of animal psychology in the twentieth century can be told in two parts. For the first half of the century, psychologists in the English-speaking countries developed the laboratory experimental method for studying animal behavior that had originated with Thorndike. They took a particular interest in the kinds of animal cognition covered in Chapter 5 – learning about cause and effect. They found that many species' abilities in this domain were remarkably similar, and so they concentrated on a limited number of species that were easy to work with, particularly rats and pigeons. It was during this period that behaviorism came to the fore. Behaviorists believe that a science of psychology must confine itself to the study of the only thing that can be observed – behavior. Some behaviorists go farther and prohibit all forms of speculation about anything other than observable behavior, thereby excluding from consideration even concepts such as "memory" or "attention." Meanwhile, especially in continental Europe, other scientists were taking an interest in more complex behaviors such as counting (Chapter 4) and reasoning (Chapter 6). In addition, it was particularly the Europeans who developed an interest in studying animal behavior in the wild. Strong fieldwork-based traditions developed in Germany, Austria, and the Netherlands. It was through this tradition that great discoveries were made, such as the dance language by which honeybees communicate the locations of good sources of nectar to each other (Chapter 11). The Europeans' interest in complex behaviors and field studies led to an emphasis on the variety of behavior in different species and a diversity of theoretical approaches. The school of animal psychology that grew out of the fieldwork tradition is known as ethology.

One of the most important insights to come out of ethology concerns four questions proposed by founder ethologist Niko Tinbergen in 1963. Tinbergen (1907–1988) was a Dutch behavioral biologist who moved to the University of Oxford in England after the Second World War. From there, he played a pivotal role in defining the discipline of ethology and disseminating it to the English-speaking world. Tinbergen's insight was recognizing that there are several directions from which behavior must be studied if it is to be fully understood. Specifically, Tinbergen identified four different questions that must be asked and answered about behavior for a complete explanation.

The first question is the function of a behavior. Function is meant here in an evolutionary sense as a consideration of the adaptive purpose of behavior. Often the adaptive advantage of a behavior is straightforward, as when a mother wolf suckles her young. But in other cases, the function of a behavior in preserving an animal and its offspring may be difficult to uncover. The example of fish that eat their own eggs, described in Box 1.2, is one that was particularly difficult to understand from a functional perspective.

Tinbergen's second question concerned the phylogeny of behavior. That is to say, how does the behavior vary among more or less related species? This view can help us to understand how the behavior evolved.

The third of Tinbergen's questions concerns the development of behavior in an individual's lifetime – technically "ontogeny." This includes consideration of the conditions in early life that are necessary for a behavior to develop and how the behavior changes as the animal ages. It also includes a consideration of learning, such as the learning about cause and effect (considered in Chapter 5) and reasoning (Chapter 6).

Finally, Tinbergen insisted that behavioral scientists must consider mechanism – how a behavior is caused in an animal's brain and how it is caused by its ability to learn from experience.

Few behavioral scientists can claim to address all four of Tinbergen's questions at any one time, but an awareness that behavior is a function of multiple levels of causation and that we should not lose sight of any of them is a powerful legacy of this original thinker.

The development of animal psychology in the second half of the twentieth century is a story of an opening of communication between the two originally distinct traditions. Behaviorism lost its preeminent position in animal psychology in the 1960s. Scientists studying animal behavior in laboratories in the English-speaking countries began to absorb the more biologically informed views of their continental cousins. Around this time, cognitive psychology began to take center stage from behaviorism. The rise of a cognitive approach freed animal psychologists from a concern mainly with learning (in the sense of learning about cause and effect, as in Chapter 5) and enabled them to study a much wider range of phenomena.

Many who work in animal cognition feel the need to line up with one school of animal psychology or another. They may be behaviorists, who disparage the wild speculations of those who call themselves cognitive psychologists or object to the relative lack of control in most field studies carried out by ethologists. Or they may be cognitive psychologists, who criticize behaviorists for not permitting themselves to look at the more interesting and complex aspects of animal behavior. For their part, ethologists sometimes argue as though only their work, because it observes animals in their natural habitats, can be considered to be the “true” science of animal psychology. But science is not sports. We do not have to cheer for one team or another. On the contrary, this tribal attitude is quite antithetical to a scientific frame of mind. Since the purpose of this book is to come to a well-rounded appreciation of the minds of animals, we borrow what we find useful from all three schools of animal psychology. From the behaviorists, we take a concern with finding watertight experimental designs and an impatience with unnecessarily complex explanations. From the cognitive psychologists, we take a willingness to consider very complex behaviors as part of our field of interest. Finally, the ethologists make us aware that behavior is part of a toolkit of adaptations that animals use in the wild in the daily struggle for survival.

A cautionary tale and a canon

Clever Hans: the horse with the intelligence of a 14-year-old child

Clever Hans was a horse who lived in Germany at the end of the nineteenth century. Hans’s trainer was a schoolteacher, Mr. von Osten. Under von Osten’s tutelage, Hans was able to answer a great variety of questions put to him by von Osten and other interested people. Hans was most famous for his ability to answer arithmetical questions. By stomping his foot the appropriate number of times, Hans was able to answer questions involving addition, subtraction, multiplication, and division, with both integers and fractions. Asked, for example, “what is 2/5 plus ½?”, Hans stomped his foot 9 times, followed after a pause by 10, to indicate 9/10. Hans’s mathematical abilities went beyond simple arithmetic to include calendar reckoning (“If the eighth day of a month comes on Tuesday, what is the date for the following Friday?”) and clock reckoning (“How many minutes has the large hand to travel between seven minutes after a quarter past the hour and three quarters past?”), and he could also answer questions requiring words as answers, such as “What is this lady holding in her hand?” and “What does this picture represent?” Hans provided word answers by reference to a table of letters. In this table, each letter of the alphabet could be identified by Hans stomping his foot the requisite number of times to indicate the column and row of the letter required. Clever Hans, Mr. von Osten, and the table of letters are shown in Figure 1.2.

Hans was no fairground spectacle trained for profit to hoodwink the unwary. A group of experts called on the schoolteacher von Osten and his horse, put them through their paces, and declared there was no trickery involved – Hans the horse had the intelligence of a 13- or 14-year-old child. This committee of experts included an African explorer, the director of the

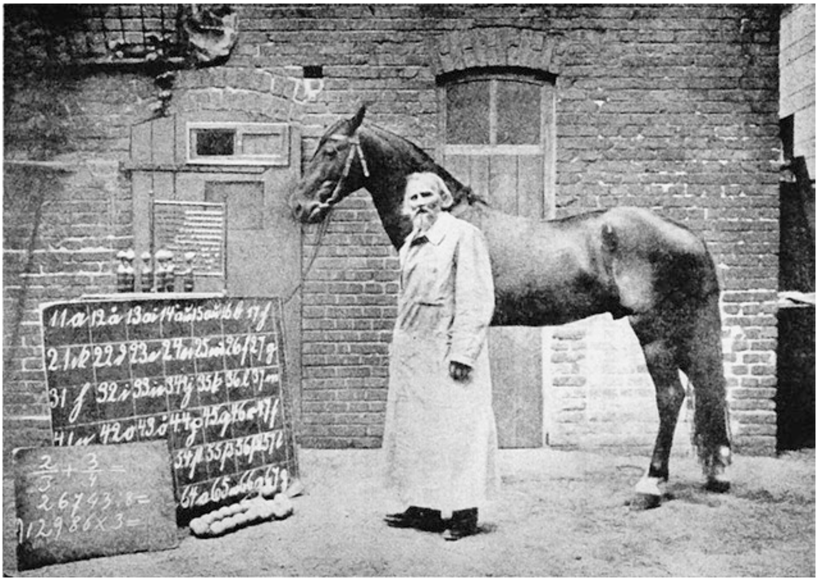


Figure 1.2 Clever Hans with his trainer Mr. von Osten

Note: Examples of the kinds of arithmetic problems Hans could solve are shown on the small board in the bottom left corner. The larger board behind it is the table of letters of the alphabet Hans used to answer questions requiring a word answer.

Source: Pfungst (1911/1965).

Hannover zoo, the leading psychologist of the day (Professor Stumpf of the University of Berlin), and two experts on horses from the Prussian cavalry. All were convinced of the horse's ability to count and solve arithmetical problems. Professor Stumpf was interviewed in the newspaper:

> Concerning the question whether the horse was given some sort of aid, Prof. Stumpf expressed himself freely. He said: 'We were careful to state in our report that the intentional use of the means of training, on the part of the horse's teacher, is out of the question, … nor are there involved any of the known kinds of unconscious, involuntary aids.'
>
> Frankfurter Zeitung, Sept. 22, 1904

Despite the unanimous acclamation of this committee of experts, some were still suspicious. Oskar Pfungst, a research student with Stumpf, decided to make a detailed study of Hans and his trainer. Pretty soon, Pfungst began to notice some strange aspects of Hans's performances. For one thing, although Hans could answer questions put to him by many different people (which was one of the aspects of Hans's performance that had convinced the commission that Hans's feats were genuine), he could do so only if that person already knew the answer and if the person putting the question was visible to him. Pfungst put von Osten in a tent to question Hans, and Hans's performance collapsed. These observations led Pfungst to the idea that the horse was relying on visual cues from his interrogator. Careful investigation of the behavior of the person testing Hans led Pfungst to this conclusion:

> As soon as the experimenter had given a problem to the horse, he, involuntarily, bent his head and trunk slightly forward and the horse would then put the right foot forward and begin to tap, without, however, returning it each time to its original position. As soon as the desired number of taps was given, the questioner would make a slight upward jerk of the head. Thereupon the horse would immediately swing his foot in a wide circle, bringing it back to its original position.
>
> Pfungst, 1911/1965, p. 47

The crucial detail here is the "involuntarily" in the first sentence. It is not surprising or remarkable that a horse could be trained to tap his foot in response to very slight movements on the part of the questioner – circus animals are routinely trained in this way. What is remarkable and important about Hans is that there was no suggestion that von Osten knew he was making these signals, nor did the many other people who questioned Hans successfully. The horse was picking up on very slight movements of the head that his questioners did not even realize they were making.

The involuntary, unconscious nature of the signals that Hans's questioners gave the horse is very important for two reasons. First, it shows that Hans really was very clever – just not clever in the way von Osten believed. Hans's ingenuity lay not in understanding arithmetic, spelling, the calendar, and so forth but in an astonishingly acute eye for the body language of the people around him. Who would have guessed that the way one nods one's head gently while watching a horse tap its foot could be used by that animal to guess how many taps are required? This was indeed a clever horse. The second reason that what has become known as the "Clever Hans Phenomenon" is important to anyone interested in animal cognition is what it implies about studying animals. Whenever a human experimenter gets together with an animal subject to test some aspect of that animal's cognition, steps must be taken to ensure that the animal does not have the opportunity to pick up on signals that the experimenter gives off unintentionally. It is not enough for the experimenter to go into the experiment with the honest intention of not giving any signals – the story of clever Hans tells us that for a signal to be recognized by an animal, it is not necessary that the experimenter intend to give this signal or even know he is giving it. The only conditions where we can be certain that unintentional cueing is ruled out are where the experimenter cannot be seen (or heard, or picked up in any other way) by the subject and where the experimenter does not know the correct answer. Nowadays, these conditions are usually built into the critical tests in any experiment, but this cannot simply be assumed, and it is always important to check.

Lloyd Morgan's canon: the most awesome weapon in animal psychology

Conwy Lloyd Morgan published his *Introduction to Comparative Psychology* in 1894 in response to Romanes's *Animal Intelligence* of ten years earlier. Morgan was concerned that Romanes's rich interpretation of fanciful anecdotes was getting the fledgling science of comparative psychology off to a bad start. For one thing, no science can be based on facts that are unreliable. Furthermore, it is a principle of science that simpler explanations are always preferred to more complex ones. The reason for this is that an unlimited number of more complex explanations always exist for any observation. The trick is to find the most parsimonious explanation for what we see – the one based on the fewest principles. It may seem easier at first to use richer, more complex explanations for what animals do. However, if these turn out to be red herrings, so much time will have been lost. It is far better in the long run to be safe, secure, plodding, and confident that the knowledge we have amassed so far is reliable.

> In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale.
>
> Morgan, 1894, p. 53

This statement has become known as Lloyd Morgan's canon or principle. It is certainly not without problems of its own. How, for example, can we tell what is a "higher psychical faculty" and one "lower in the psychological scale"? The whole notion of a psychological scale is now considered outdated. Nonetheless, if we take Lloyd Morgan to be saying that we should not get carried away with what look superficially like astonishing animal performances but instead experiment carefully to find the simpler explanation underlying the behavior, then his canon can continue to do useful work in comparative psychology.

Now and the future

As Thorndike complained over a century ago, if one poor dog finds its way home from twenty or thirty miles away, you can be sure that the story will be all over the papers and the evening news. Every weekend pigeon fanciers release thousands of pigeons over much greater distances, the majority find their way home, and nobody sees any need to comment on it. Stories about animals in the media emphasize the improbable, the rare, and the downright untrue. And yet, as we hope this book will show, the truth is often far stranger than fiction. The amazing skills pigeons use to find their way home is just one example.

Animal cognition – the study of the mental lives of animals – is a very new science. Unlike the older sciences, there is no great mass of accepted fact through which a student must wade before she can hope to make an original contribution. There is no reason why any reader of this book could not expect to make a contribution to our understanding of the minds of animals. We hope that reading this book will inspire some to do so.

Further Reading

Desmond, A., & Moore, M. (1994). *Darwin*. London: Michael Joseph.

Darwin's life, including the dispute between Darwin and Wallace mentioned here, is recounted in this book.

For a more extended account of Darwin's life, see Browne, J. (1996). *Charles Darwin: A Biography, Vol. 1 – Voyaging*, and (2003) *Charles Darwin: A Biography, Vol. 2 – The Power of Place*. Princeton, NJ: Princeton University Press.

Plotkin, H. (2004). *Evolutionary Thought in Psychology: A Brief History*. Oxford: Wiley-Blackwell.

This book offers an excellent brief introduction to the history of evolution and psychology.

Wynne, C. D. L. (2004). *Do Animals Think?* Princeton, NJ: Princeton University Press.

One of the present author's further thoughts on animal minds.

Web sources

https://www.pbs.org/wnet/nature/inside-the-animal-mind-introduction/2081/

This attractive multimedia site considers different forms of animal intelligence.

http://wallacefund.info/

This fascinating site attempts to restore a higher profile to the life of Alfred Russel Wallace.

http://www.pigeon.psy.tufts.edu/psych26/history.htm

Robert Cook's site contains carefully selected readings from important historical figures.

2 OTHER WAYS OF SEEING THE WORLD

> A fox invited a Crane to supper and provided nothing for his entertainment but some soup made of pulse, which was poured out into a broad flat stone dish. The soup fell out of the long bill of the Crane at every mouthful, and his vexation at not being able to eat afforded the Fox much amusement. The Crane, in his turn, asked the Fox to sup with him, and set before her a flagon with a long narrow mouth, so that he could easily insert his neck and enjoy its contents at his leisure. The Fox, unable even to taste it, met with a fitting requital, after the fashion of her own hospitality.
>
> *Aesop's Fables*, translated by G. F. Townsend

The world that we experience around us feels complete – and yet physicists tell us that there are many aspects of our environment of which we have no awareness. As I look out my office window, I see sunlight, but I have no sense of the polarization of the sun's light in the sky. I do not experience the magnetic fields generated by the computer I'm typing on and the electrical wiring of the house. My ears fail to register the many sounds of pitch higher than about 18 kHz[1] around me. Any number of chemicals in the air do not prompt my nose to register any sensation of smell. And the same is true of any other species we care to think about. My cat may hear higher-pitched sounds than I can, but her daytime vision is considerably less acute than mine.

The pioneer behavioral biologist Jakob von Uexküll was the first to suggest that the world around an animal (what he, being German, called its *Umwelt* – the surrounding world or environment) is not the same as its *Innenwelt* – its world as perceived and internalized (von Uexküll, 1934/1957). He expressed this idea in quite poetic terms:

> Here we may glimpse the worlds of the lowly dwellers of the meadow. To do so, we must first blow, in fancy, a soap bubble

1 "Hz" stands for hertz – the standard unit of frequency. One hertz is one vibration per second. One kHz is a thousand hertz.

> around each creature to represent its own world, filled with the perceptions which it alone knows. When we ourselves then step into one of these bubbles, the familiar meadow is transformed. Many of its colourful features disappear; others no longer belong together but appear in new relationships. A new world comes into being. Through the bubble we see the world of the burrowing worm, of the butterfly, or of the field mouse; the world as it appears to the animals themselves, not as it appears to us.
>
> Jakob von Uexküll, 1934/1957

This is as true for us as it is for the tick that von Uexküll took as his example. A female tick sits waiting on a blade of grass for a mammal to go by so that she can pounce and get the meal of blood she needs to feed her eggs and complete her life cycle. But the tick does not recognize a mammal as we might from its size, four-leggedness, or furriness. Just one thing tells the mother tick that a mammal is passing by – the odor of butyric acid. This acid emanates from the skin of all mammals and is, therefore, a reliable sign that the right type of beast is close by. Having fallen onto a mammal, the tick then searches for a clear patch of skin so that she can burrow into her prey for a blood meal. At this stage, it is warmth alone that tells the tick she is heading in the right direction. For the tick, the rich world surrounding her is reduced to just a couple of signs: the butyric acid that denotes a mammal and the warmth that implies blood beneath the skin. As von Uexküll puts it, "the very poverty of this world guarantees the unfailing certainty of her actions, and security is more important than wealth."

Every species has a unique perceptual world that has evolved out of the demands of the life it leads. These perceptual worlds are astonishingly varied – as varied as the niches that their possessors inhabit. There are birds that see ultraviolet, insects that see infrared, many animals that see the polarization of sunlight, bats that hear sounds three octaves higher in pitch than the highest we can hear and use sonar to "see" the flapping of an insect's wings.

Although we shall certainly peek at some animals briefly just because they possess an exceptionally interesting sensory system, we shall also focus in on one animal whose sensory systems have been particularly well-studied: the pigeon. Pigeons are very widespread around the globe, and they have a strikingly rich perceptual world, but, most importantly, focusing to some degree on the sensory world of a single species helps us recognize that sensation and perception are not toolkits of odd pieces but an integrated package working as the handmaiden of action – action directed toward solving the problems of life that an animal faces. In subsequent chapters, we shall see how different species of animals utilize their senses to solve problems that are crucial to their survival.

First, we discuss vision and then smell, hearing, the magnetic sense, and finally, the electric sense.

Vision

We do not see the world we look at: our view of the world is limited by our eyes' and brain's ability to perceive what is around us. What we see as light, physicists understand to be electromagnetic radiation. Our eyes permit us to see only a small part of the electromagnetic spectrum – wavelengths from about 420 nm[2] (violet; see Figure 2.1) to about 700 nm (red). Light from the sun includes wavelengths both shorter and longer than those we can see. Longer ones are called infrared; these are responsible for the warming effect of sunlight (still longer wavelengths are radio waves). Shorter wavelengths are ultraviolet; overexposure to these rays can cause skin cancer. Other species can see into both the infrared and ultraviolet parts of the spectrum.

In addition, our eyes do not directly report the wavelengths of light that reach them. Rather, we have just three types of color receptors – each tuned for a different range of wavelengths. That is why two colors mixed together look like a single color rather than a mixture. A mixture of red and green may stimulate two of our color receptors in just the same way as the color yellow, which lies between red and green in the color spectrum (see Figure 2.1). Consequently, we see the mixture as the intermediate color. Red and green do not *become* yellow – they only *seem* yellow. A physicist with a sensitive instrument would be able to distinguish a mixture of red and green from "real" yellow. Some species have more of these color receptors than we do and can consequently distinguish between mixtures of colors and pure colors that to us are indistinguishable. Fish and reptiles, for example, appear to have four color receptors; birds have as many as six. Other species have fewer color receptors than our three and thus experience many more potential color confusions than most of us. Dogs, along with most other mammals except primates, have only two color channels, and therefore the world of color presents itself to them something like the way it appears to red-green color-blind people. You may have noticed how much more difficult it is for your dog to find a red ball in the green grass than a blue or yellow one.

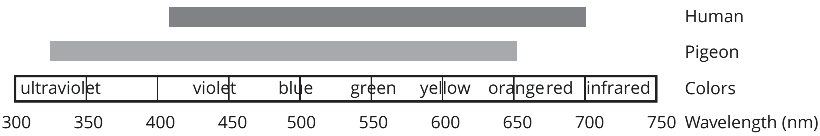


Figure 2.1 Diagram of the electromagnetic spectrum showing human and pigeon zones of sensitivity

2 The abbreviation "nm" stands for nanometer. One nanometer is one-billionth of a meter.

The sun's light has another dimension of which we are completely ignorant – polarity. Electromagnetic radiation can be thought of as waves passing through space. These waves can oscillate predominately horizontally, vertically, or at any intermediate orientation. This is their polarity. The only time most of us have any awareness of the polarity of light is when wearing polarized sunglasses. Under special conditions, though, some people can see a faint colored pattern whose orientation depends on the polarization of light. Light reflected from water or glass tends to be horizontally polarized, and so by blocking light polarized only in this direction, polarized sunglasses block the glare of reflections. Other species, however, are able to directly detect the polarization of sunlight. This can be useful in finding your way because the polarization of sunlight changes depending on the sun's position in the sky. Over 90 species of invertebrates, particularly arthropods (insects, spiders, crustaceans, and so on) have been shown to be sensitive to the polarization of sunlight, as have fish and some species of birds.

Since the polarization of sunlight changes with the position of the sun, it can be used as a compass. To do this, it is not necessary to see the sun itself – any patch of blue sky will suffice. This makes polarization a powerful aid to orientation even on largely overcast days. Orientation and navigation are the focus of Chapter 7.

Box 2.1 How to investigate the perceptual world of animals

The development in the mid-twentieth century of methods of animal training using pigeons in small boxes known as "operant chambers" – or more colloquially as Skinner boxes – provided a great boost to the study of the perceptual world of animals.

One flexible and powerful procedure used in an operant chamber is called the "Go/Nogo" discrimination. Monika Remy and Jacky Emmerton utilized this method to investigate what wavelengths of light pigeons could see (Remy & Emmerton, 1989). Thirsty birds were trained to mandibulate (open and close their beaks) in return for water only if a light was on. The light came on for 30 seconds and then went off for the same period of time. This pattern of light on followed by light off was repeated 20 times. If the pigeons mandibulated in the light, they received water, but if they mandibulated in the dark, they received no water, and furthermore, the period of time they had to wait until the light came back on again was extended by 10 seconds. The pigeons easily learned this discrimination and within a couple of days were reliably moving their beaks only when the light was on. Obviously, this discrimination of "light on" compared with "light off" can be learned only if the pigeon can see the light that is being shone at it. If the light is of a wavelength to which the pigeon's eye is not sensitive, then the birds must fail at the task. By testing the pigeons with light of different wavelengths, Remy and Emmerton were able to uncover the ultraviolet sensitivity of the pigeon's eye.

Another popular procedure used in the operant chamber is the concurrent operant discrimination. In this situation, the subject is given a choice of two (or more) possible responses. For example, Juan Delius et al. (1976) presented hungry pigeons with a choice of four plastic keys that they could peck to obtain food. As shown in Figure 2.2, the four pecking keys were arranged at 90-degree intervals around the box. In the roof of the box was a light fixed with a polarizing filter so that the polarization of the light crossed only one of the two pairs of pecking keys. In order to obtain a food reward, the pigeon had to peck on one of the two keys that were lined up with the polarization of the light – responses on the other keys produced no food reward. The polarization of the light changed randomly from trial to trial. The pigeons learned this problem in around 15 to 20 days of training, showing that they were sensitive to the polarization of the light.

In a later experiment with a slightly different design, Marc Coemans et al. (1990) presented pigeons in a Go/Nogo procedure with light of different polarizations that shone from a single location. The pigeons had to peck on a key if the light coming from it had certain angles of polarization but not if it was polarized in the opposite direction. Coemans and colleagues found that even after two months of daily training, their pigeons were completely unable to discriminate the light of differing polarization.

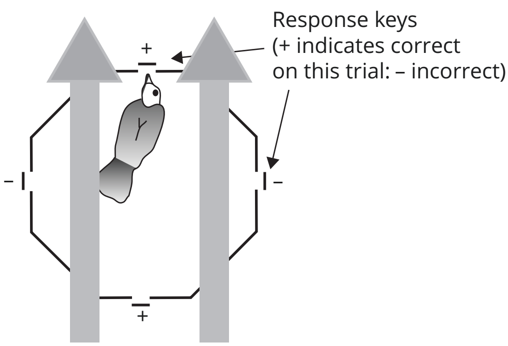


Figure 2.2 View from above of the apparatus used by Delius and colleagues to assess pigeons' sensitivity to the polarization of light

Notes: The arrows indicate the direction of polarization of light during the current trial. This changed randomly from trial to trial.

Source: From Delius et al. (1976).

These contradictory results from Delius's and Coemans's laboratories show the difficulties of working with stimuli that we as humans are unable to perceive. It is possible that stray reflections, not polarization, cued the pigeons in Delius and colleagues' experiment or that the sounds of the equipment used to shift the light of different polarizations to different keys gave the pigeons unintended cues about which key to peck. On the other hand, it is also possible that the pigeons in Delius's laboratory really do see the polarization of light and that some detail of the procedure used in Coemans's laboratory obscured the pigeons' true abilities.

The pigeon's eye view of the world: a case study in animal vision

The human eye is certainly a wonderful instrument, but there is another eye that has been well studied that has some capabilities even beyond our own – the eye of the pigeon. Box 2.1 outlines some of the methods that have been developed that are particularly useful in assessing the visual abilities of pigeons.

The first thing to notice in the pigeon is that the arrangement of its two eyes is quite different from our own. Where we see most of what we look at with *both* eyes and thus with stereo depth, pigeons have very poor stereovision. Our binocular visual field – the area we see in stereo with both eyes – is about 120 degrees out of our total 200-degree field of view. Only things that are at the periphery of our vision are not perceived with full stereo depth. Pigeons' eyes only overlap in what they see for about 35 degrees, but they have a much larger total visual field – around 340 degrees. Thus, it is very difficult to creep up behind a pigeon and surprise it because they very nearly have eyes in the back of their heads. On the other hand, very little of what they see appears to them in stereo depth. They use this small stereo part of their visual field only when considering things close up – when feeding, for example (McFadden & Reymond, 1985; Rounsley & McFadden, 2005).

Pigeons can also see into the ultraviolet domain. When looking into the distance (as they do when flying), pigeons use the large nonoverlapping, lateral fields of their eyes. It is these lateral fields that have been shown to be sensitive to ultraviolet light (Remy & Emmerton, 1989; Hart & Hart, 2007).

Pigeons have their sharpest vision when they are looking at things up close, and their acuity peaks at 10 centimeters from their eyes, which is only around 7 centimeters from the end of their beak. At this close distance, they can resolve objects around 0.06 millimeters. At greater distances, their acuity declines quickly. This is not as good as human vision (and only one-tenth what a predator bird such as a hawk or eagle can achieve), but it is excellent compared with that of many other species (Bloch & Martinoya, 1982; Rounsley & McFadden, 2005).

When looking upward and to the sides with their large lateral fields, pigeons have normal or long-sighted vision. When attending to the ground with the frontal field of the eye, however, there is good evidence that the pigeon eye is short-sighted. This combination of short-sightedness for the frontal field and normal or slightly long-sighted vision for the lateral fields means that the eye of the pigeon is perfectly graded so that the bird can see simultaneously, in focus, the ground it is standing on and the sky above it (Bloch & Martinoya, 1982; Fitzke et al., 1985). At one and the same time, the pigeon can see the grains on the ground in front of it, the distant horizon, and most of what is going on behind it clearly without having to change the focus of the eye.

As discussed in Box 2.1, some evidence suggests that the pigeon eye can perceive the polarization of light. In the real world outside the laboratory, the polarization of sunlight changes as the sun moves across the sky from dawn to dusk. Because all areas of blue sky are polarized, pigeons may be able to use polarization to figure out the position of the sun even when it is invisible, so long as there is sunlight anywhere in the sky. This would be very useful on largely (though not completely) overcast days and at dusk. The sun compass – the trick of using the position of the sun and time of day to find compass directions – is discussed in Chapter 7. An awareness of the polarization of sunlight would make it possible for pigeons to use the sun compass even when the sun itself is not visible.

We humans are trichromats – that is to say, we have three kinds of color receptors. In essence, we have one receptor sensitive to red light (a peak receptivity around 564 nm; see Figure 2.1), one sensitive to green (534 nm), and another sensitive to blue (420 nm). We perceive all the hues in between these values because colored light stimulates more than one of these receptors. A wavelength of around 600 nm, which we perceive as an orange light, for example, stimulates both the green and red receptors. This is why a mixture of yellow and red can appear indistinguishable from orange – the mixture stimulates the green and red receptors to the same extent as does “true” orange light. If we had more than just these three color receptors, we wouldn’t necessarily be fooled by mixtures of primary colors in this way.

The retina of the pigeon contains at least six different kinds of color receptors. This is how they are able to see in the ultraviolet range, but it also means that color mixtures do not so easily confuse them. Using a Go/Nogo method (see Box 2.1), Adrián Palacios and Francisco Varela (1992) were able to show that there was no mixture of 470 nm (blue) and 560 nm (yellow) that pigeons would accept as being identical to light of 520 nm (green).

Patterns and pictures

It is all very well to look at the ability of the pigeon eye to perceive different aspects of light, but that still leaves open the question of what a pigeon actually sees when it looks at something.

Several studies have investigated how pigeons recognize three-dimensional objects in the interplay of light and shade that they experience in the world. In one interesting study, Cheri Reid and Marcia Spetch investigated how pigeons could use shading and perspective in two-dimensional images to infer depth and perspective (Reid & Spetch, 1998). The pigeons were shown a large number of pairs of computer-generated images of three-dimensional objects. Some of these images are shown in Figure 2.3. For each pair of images, the one on the left represents a three-dimensional object with appropriate shading and perspective information (larger at the front than at the back). The other image in each pair was a two-dimensional outline, a shape with appropriate shading but no perspective information, or a shape with the correct perspective but no shading. Reid and Spetch were able to show, using a concurrent discrimination technique (see Box 2.1), that pigeons use

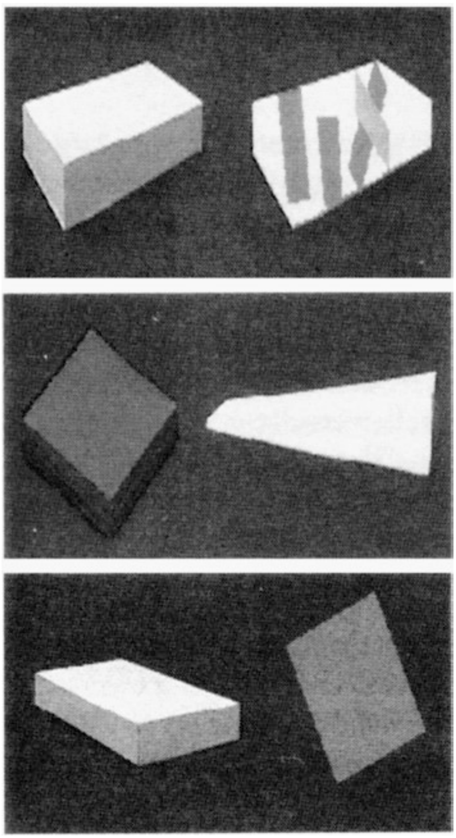


Figure 2.3 Pairs of images used in Reid and Spetch's (1998) experiment on pigeons' perception of perspective. The object on the left provides full perspective information which is lacking in the image on the right

Figure 2.4 A pigeon choosing between two objects in Spetch and Friedman's (2006) experiment

Source: Courtesy of Marcia Spetch.

both perspective and shading information to recognize the three-dimensionality of two-dimensional images.

Although many studies have utilized two-dimensional visual scenes in pigeon research (we shall see some of these in Chapter 10), it cannot simply be assumed that pigeons perceive a two-dimensional image as a representation of a three-dimensional object in the way that a human does. In an ingenious study, Marcia Spetch and Alinda Friedman (2006) trained pigeons to discriminate between two objects of different shape that were identical in color (Figure 2.4). Each pigeon had to peck at a screen in front of one object but not at the screen in front of the other object. Some pigeons were trained on digital photographs of the objects, and the other pigeons were trained on three-dimensional models. Once all the pigeons had learned their discrimination, they were swapped over so that those that had been trained on the three-dimensional objects were now confronted by the photographs, and those that had been trained on the photographs were now shown the objects. All the birds spontaneously transferred their experience from either photographs to objects or the other way around. This result shows that pigeons do recognize a correspondence between a picture and the thing pictured.

Robert Cook and colleagues extended these findings by presenting six pigeons with a number of visual discriminations in a Go/Nogo procedure (see Box 2.1) (Cook, Qadri, Kieres & Commons-Miller, 2012). Their pigeons were presented with computer-generated images of convex and concave surfaces – in other words, images that looked rather like mountains and craters – examples are shown in Figure 2.5. Three pigeons were trained to respond onto convex surfaces (mountains) to obtain a reward: if they pecked onto concave surfaces (craters), they had to wait a few seconds in darkness before being allowed to proceed. The other three pigeons received a reward for pecking at concave surfaces and had to withhold pecks to convex surfaces. In a series of five experiments, Cook and colleagues explored whether the pigeons perceived these two-dimension images as representing three-dimensional scenes. In each experiment, they altered an aspect of how the scene appeared. Among other things, they changed the apparent height of the mountain or depth of the crater, altered the lighting conditions, moved the point of view, or changed the reflectiveness of the surface in the view that was presented to the pigeons. The outcome of all these alterations consistently indicated that pigeons can perceive two-dimensional projections as representations of three-dimensional scenes much as we humans do. Changes to the image that did not imply any change to the underlying convex or concave surface – such as a change in the direction that light shone onto the object – did not disturb the pigeons' ability to recognize what they were looking at. But changes that altered the property of the implied object itself – such as changes in the height or depth of the mountain or crater – did disturb the pigeons' ability to recognize the scene.

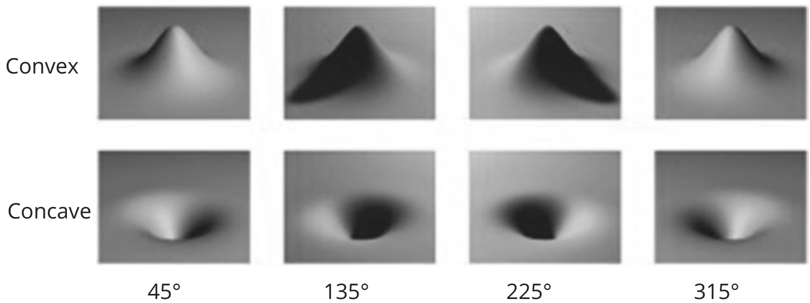


Figure 2.5 Examples of the convex (mountain-like) and concave (crater) surfaces tested by Cook et al. (2012). The columns show four different lighting directions used to produce different patterns of shadow on the surfaces

Source: Reprinted from Cook et al. (2012) with permission from Elsevier.

Apart from the shading and perspective of static objects, we also pick up information about how far away a moving object is from the way it appears to get larger as it approaches or smaller as it moves away. You can get this same impression by staring into a rotating spiral. An inward rotating spiral appears to recede away, an outward rotating spiral looms toward you. In an ingenious study, Carlos Martinoya and Juan Delius (1990) investigated whether pigeons are also prone to this illusion. Using a concurrent discrimination procedure (see Box 2.1) and precision computer-drawn spirals with windings of several different degrees of tightness that were then spun at different speeds, Martinoya and Delius established that pigeons can discriminate apparently approaching visual patterns from apparently retreating ones.

One striking aspect of human perception of the visual world is how certain features tend to stand out visually from the world around them. For instance, an object that differs in color from its background is much easier to spot than a similarly shaped object that is made up of the same texture and color as its background. Cook (1992) showed pigeons pictures with embedded square areas. Some of the target zones were made up of elements that differed in color from the background, and in others, the square target only differed from the picture elements around it in the smaller-scale elements that comprised it. Cook found that, just like people, pigeons find it more difficult to find the special square area if it was just made of different elements rather than differing in color.

How can we tell if the world looks the same to pigeons as it does to us? For one thing, do pigeons confuse similar items as humans do? Donald and Patricia Blough trained pigeons to discriminate the various letters of the alphabet and then looked at which ones the pigeons found easy to discriminate and which were more difficult. They found that the pigeons' difficulties lay mainly with the same letters (such as *A* versus *R* and *B* versus *P*) that people are also most likely to confuse (Blough & Blough, 1997).

Even though pigeons can generalize from two-dimensional images to three-dimensional objects in the way we do, it would still be a mistake to assume that pigeons perceive the visual world the same way as humans. One suggestion that pigeons' visual experience may differ from our own comes from an interesting study by Juan Delius and Valerie Hollard (1987). Objects in the world around us present themselves at many different angles. A chair with its back to you is a very different thing to look at than the same chair with the seat facing toward you, and yet both are recognized as the same object – a chair. Delius and Hollard demonstrated that pigeons could also recognize rotated objects as being the same item, no matter what the angle of rotation. The difference from the human case lies in the length of time it takes to make the recognition decision. Humans asked to identify whether two items that look similar are really the same or different take longer to make this decision the farther around one object has been rotated relative to the other. In pigeons, however, the time taken to make the recognition decision does not depend on the angle of rotation. Perhaps the pigeon's avian lifestyle has led to the development of a different system for recognizing objects. It is possible that the view of a flying animal more often contains rotated objects and that therefore birds recognize rotated forms more quickly. Whatever the fate of this hypothesis – a more recent study with a different procedure (Hamm et al., 1997) suggests that pigeons *are* influenced in their recognition decision by the angle of rotation of a stimulus – the pigeon has provided many hints of a quite different perceptual world from our own.

Smell

Smell is not usually a particularly salient dimension of perceptual experience for us, but for other species it can be very important indeed. The sense of smell enables animals to pick up low concentrations of chemicals in the air. This ability is useful for finding food (either other animals, in the case of predators, or vegetable matter for herbivores) or to avoid becoming food (by smelling the approach of a predator). But smell can also function as a simple form of communication, as when one member of a species releases a chemical that then influences the behavior of other members of that species.

We shall save for Chapter 7, where we consider animal navigation, the evidence that pigeons use olfaction when finding home from distant release sites. But there is plenty of evidence from other bird species that smell is an important sense for avians.

There is evidence to suggest that, when young, certain bird species use smell to find their nests. Eduardo Mínguez (1997) studied British storm petrel chicks at their nesting sites on Benidorm Island. Mínguez moved young chicks a little way from their nests, blocked their noses, and then observed whether they were able to find their way back or not. With blocked noses, not one of the chicks could find its nest, whereas with their noses open, they all found their way home. Caspers and Krause (2011) found that zebra finch chicks also locate their nest by smell, as do Antarctic prions (a species of petrel: Bonadonna et al., 2003).

Many animals use special chemicals, known as pheromones, as a means of communication. Male currant clearwings (a species of moth), for example, are attracted to the pheromone emitted by females of their species, as are male American cockroaches and many other insect species. Pheromones with a variety of functions have been identified in the fruit fly. These range from those that act to attract other fruit flies to others that make the fruit fly jump. Bumblebees may construct odor trails from the nest entrance to the nest core. Termites also follow odor trails. Digger wasps recognize prey using chemical cues picked up on their antennae. Several species of fish use pheromones to attract sex partners in a similar manner to that of insects (Wyatt, 2003).

Mammals of many species are able to recognize specific individuals on the basis of their smells. Turkish hamsters, for example, are able to discriminate