

1

History of comparative cognition



Background

Observing animals in their natural habitat often calls attention to interesting and unusual behaviors. As an example, early in the twentieth century, inhabitants of the British Isles noticed that some birds were using their beaks to poke through the lids of milk bottles that were delivered to houses. By puncturing the lid, the birds were able to get the cream that floated to the top of the bottle, no doubt annoying the humans who had purchased the milk. The bottles were often attacked by swarms of birds as soon as they were left at the door, and there were even reports of flocks following milk carts on their delivery route (Fisher & Hinde, 1949). Because this habit started in a small village and spread across a large geographical region, many people believed that the birds were learning the behavior by watching other

birds open bottles. In other words, social learning *could* explain how the behavior was transmitted so quickly in a population.

The only way to verify that social learning explains the transmission of bottle opening by birds is to examine the behavior under controlled experimental conditions. This may occur either in the lab or in the natural environment, although many researchers favor the former because it is easier to control factors that may influence or bias the results in a lab setting (although that in itself is debatable). Either way, researchers examining the role of social learning in bottle-opening behavior of birds would need to consider alternative explanations. For example, did one bird have to see another bird open a bottle to be able to do this? Did the birds have to interact in order for the behavior to be transmitted? Is it possible that individual birds were following other birds to a milk bottle, tasting the cream, and then approaching new milk bottles on their own which they learned to open through trial-and-error? If the birds were learning from other birds, what conditions made this learning possible?

This list is only a subset of the possible questions that scientists could ask regarding social learning in birds and there is no guarantee that any one researcher, or even any group of researchers, will be able to answer all of them. Often new questions arise as research progresses and, in some cases, scientists return to the natural environment for more detailed observations of the behavior under study. This general approach of combining field observations and controlled laboratory experiments exemplifies the subject matter of this text: comparative cognition.

Chapter plan

This chapter provides a brief overview of the historical and intellectual influences that led to the contemporary field of comparative cognition. An interest in animal cognition has been documented for much longer than is reported here: theories of animal cognition were presented by early philosophers such as Aristotle (384–322 BC) and later by Rene Descartes (1596–1650), among others. The approach in this chapter is to first define the hallmarks of research in comparative cognition and then to focus on three modern, scientific perspectives that, together, influenced the emerging field of comparative cognition. In doing so, this chapter outlines the intellectual traditions that laid the groundwork for the discipline.

Students and researchers in any field must be aware of the intellectual and social influences that led to the development of their field. This allows them to place current scientific advances within historical context and to interpret the significance of research findings that are presented through published journals, research conferences, academic courses, or the popular media. An inherent component of any scientific investigation, therefore, is the understanding that research advances are built on prior work; understanding these influences will facilitate further progress in that knowledge of the past can direct future endeavors.

For the field of comparative cognition, this tradition emerged from the work of early experimental psychologists who devised carefully controlled experiments to examine behavioral responses to environmental events, the work of early biologists who were interested in the evolution of animal behavior and conducted studies in naturalistic settings, and the work of early cognitive psychologists who considered the underlying mental representations that might guide behavior. After detailing these historical influences, the chapter concludes by characterizing the modern interdisciplinary trends in comparative cognition and suggests some likely future directions for the field.

1.1 Hallmarks of comparative cognition

Researchers in the field of comparative cognition study a wide diversity of species, employ a variety of methodologies, and conduct their work within many different academic and research departments. Nonetheless, the field is characterized by three unifying hallmarks:

- 1. *Examination of cognitive processes.* **Cognition**, translated from the Latin *cognosco*, means *knowledge* or *thinking*. It is frequently equated with information processing in that the study of cognition examines how humans and animals acquire, store, and process information¹. A more specific definition of cognition is the “mental processes and activities used in

¹ Life on earth is classified according to a biological taxonomy, originally developed in the eighteenth century by Carl Linnaeus (see Chapter 9 for details). The system divides living organisms into progressively smaller groups, based on shared physical traits, according to the following scheme: Domain; Kingdom; Phylum; Class; Order; Family; Genus; and Species. Humans would be classified as follows: Eukarya (Domain); Animalia (Kingdom); Chordata (Phylum); Mammalia (Class); Primates (Order); Hominidae (Family); Homo (Genus); and sapiens (Species). An organism’s scientific name, also called the binomial name, consists of the genus and species which are usually derived from a Latin or Greek root. These are written in italics with the genus name capitalized. Thus, humans are *Homo sapiens*. According to this classification, humans are part of the Kingdom Animalia but, for succinctness, this book will use the term ‘animal’ to refer to all non-human animals and ‘human’ to refer to *Homo sapiens*. In addition, the scientific name will be provided in parentheses the first time that a species is mentioned in each chapter.

perceiving, remembering, thinking, and understanding and the act of using these processes” (Ashcraft & Klein, 2010, p. 9). Any cognitive process, therefore, is internal: it happens inside the organism’s brain. Although scientists have developed some very clever tools and tests to examine these internal processes, cognition is typically inferred from some behavioral measure. For example, in studying memory, a researcher may test whether humans can repeat a list of words or whether rats will return to a location where they found food after different delay intervals. The researcher then uses the behavioral data (i.e. verbal recitation or number of visits to a food location) to make inferences about time-dependent effects on memory retention.

2. *Experimental procedures.* Research in comparative cognition typically involves some experimental manipulation. Behavior that was initially observed in the wild is often ‘moved’ into the laboratory for controlled empirical study. In other instances, researchers conduct experiments in an animal’s natural habitat; one of the best-known examples is the study of European honeybee (*Apis mellifera*) communication by von Frisch. Von Frisch determined how honeybees indicate to other bees where to find food by moving food sources to different locations and then observing how the forager bees ‘dance’ when they return to the hive. There are many other examples of outstanding research using this naturalistic approach, despite the fact that it is more difficult to control extraneous variables outside of the lab.
3. *Evolutionary framework.* A guiding principle in comparative cognition is that cognitive abilities emerge through the same evolutionary process that shapes physiological traits (i.e. natural selection). Some researchers examine whether a given cognitive ability in humans is present in animals (e.g. counting, planning for the future, or understanding social relationships among group members), with the goal of understanding more about human cognition (e.g. if humans have unique cognitive abilities, what does this tell us about how this species processes information?). In other cases, researchers compare cognitive processes across species with the goal of understanding how and why these processes evolved. It is important to note that not all researchers in comparative cognition study a variety of species; in reality most focus on one or two. Yet, their findings are interpreted from an evolutionary perspective in that they reveal how a particular cognitive process may function in relation to certain environments.

These hallmarks of comparative cognition are exemplified in research by Galef and his colleagues that aimed to explain why some male grouse end up with a disproportionately large number of matings. In the natural environment, grouse mate on ‘leks,’ locations where males gather and display by fluttering their wings, rattling their tails, and vocalizing. Females observe the males during these displays and then select the male grouse with whom they will mate. It *appeared* that females were making their mate decisions based on the males’ behavior but, despite extensive examination, observers could find no clear difference between males that would explain why some of these animals attracted more females. This led to the idea that females simply observe the mate choice of other females and then copy them (e.g. Bradbury & Gibson, 1983).

Galef tested this social learning hypothesis by studying mate-choice copying of another ground-dwelling bird, the Japanese quail (*Corturnix japonica*). In a series of tightly controlled lab experiments, he and his collaborators recorded the reactions of female quail to male quail that they had observed interacting with other females. For example, in one experiment they determined which of two males a female preferred. Then, the female observed her ‘nonpreferred’ male interacting with another female quail. This observation session was enough to

Researcher profile: **Dr. Bennett Galef**



Figure 1.1

Dr. Bennett Galef.

As an undergraduate at Princeton, Bennett Galef had planned to major in chemistry with a minor in art history and then begin a career as a forensic art historian. After attending courses in chemistry, physics, and calculus, he ended up majoring in psychology – not because he particularly liked it, but because he held the all-too-common misconception that it would be an easy major. His senior thesis examined concept formation in humans, and he graduated with honors standing and the requisite coursework under his belt, but only two courses in animal learning (Galef, 2009). It was only in preparation for his comprehensive exams and PhD dissertation that Galef began reading ethology texts, including Tinbergen’s classic studies of animal behavior in the natural environment (Tinbergen, 1951, 1958). Through these texts, he found his passion for the burgeoning field of comparative cognition.

Upon graduating, Galef was hired as an assistant professor at McMaster University in Ontario, Canada, where he stayed until his retirement in 2008. At McMaster, Galef began the research that would make him a prominent member of his field. In 1971, he reported the finding that rat pups learned to choose particular foods based on the food choice patterns of adults. The adults had been trained previously to avoid a tasty, yet toxic food and instead to eat a far less palatable food. The pups, even without personal exposure to the toxin, also favored the less palatable, safe food, but only when they observed adults making this food choice (Galef & Clark, 1971). This was the first systematic demonstration of social learning across generations in a controlled laboratory setting. (Social learning will be detailed in Chapter 13.)

Since then, social transmission of behavior, particularly food choice and mating, has been the focus of Galef’s research. From his perspective, social learning lies at the intersection of biology and psychology: Galef has approached the topic as such, spending time conducting both field and laboratory research. He has served in important roles that span the fields of psychology and biology, including editor of the journal *Animal Behaviour* and president of the Animal Behavior Society. His interdisciplinary framework has enabled Galef to develop new hypotheses and theories regarding the ‘hows’ and ‘whys’ of social transmission, evidenced by his numerous empirical papers, book chapters, and edited volumes.

According to Galef (2009), “As I have told my students, probably far too often, I see a life in science as a marathon, not a sprint. Ask simple questions arising from clearly stated hypotheses. Use simple experimental designs and transparent statistical analyses. One step at a time, experiment after experiment, frequently replicating your main effect, until you understand what you set out to understand and can be quite sure that, when others attempt to repeat your procedures, they will get the same results that you did. And if not, you will know why not.” (p. 304).

increase her preference for this male bird (White & Galef, 1999). In other words, watching a male bird interacting with another female makes him more attractive. Moreover, when females mate with these males, they lay more fertilized eggs than when they mate with males that they have not observed interacting with other females (Galef, 2008; Galef & White, 1998; White & Galef, 1999). This work helped to determine that social learning has a profound impact on reproductive behavior (at least in this avian species).

1.2 Influence: theory of evolution by natural selection

Prior to the end of the nineteenth century, most people believed that all animals (including humans) were distinct and that each species had arrived on earth in its current form. This ‘arrival’ was explained, most commonly, by divine creation. These ideas were challenged by Darwin’s theory of evolution, detailed in *On the Origin of Species* (Darwin, 1859) and *The Descent of Man and Selection in Relation to Sex* (Darwin, 1871). Other scientists and philosophers had discussed evolution, the idea that one type of animal could descend from another type of animal, but Darwin’s hypothesis of how this occurred was novel. Alfred Russel Wallace independently came to similar conclusions (Wallace, 1870) although it was Darwin’s published works that engendered excitement, inquiry, and controversy.

1.2.1 Tenets of the theory of evolution by natural selection

The basic tenets of Darwin’s theory can be simplified to the following three points:

1. *Variation*: Individuals within a species display variability in both physiological and behavioral traits. Many of these variations reflect random mutations of genetic material, although Darwin elaborated his theories without benefit of this knowledge.
2. *Heritability*: Offspring inherit traits from their parents. Again, Darwin had no understanding of the mechanisms explaining trait heritability, which occurs through transmission of genetic material.
3. *Survival and reproduction*: If a certain trait promotes survival or reproduction, individuals possessing this trait will have a greater chance of transmitting traits to their offspring.

According to Darwin, this cycle continues across generations such that individuals with the trait promoting survival and reproduction will begin to outnumber those without the trait. This principle is often paraphrased as ‘survival of the fittest’ in which **fitness** refers to the ability to survive and reproduce. The process by which inherited traits become more (or less) prominent in a population, due to differences in fitness, is called **natural selection**.

Darwin’s description of evolution by natural selection provided a theoretical framework for many fields of science, including modern-day comparative cognition. Put another way, if physiological traits are shaped by evolutionary pressures, so are cognitive traits. Moreover, if there are physical similarities between species due to common ancestry, there are likely to be similarities in behavior, emotion, and thought processes (i.e. cognition) as well. Finally, the idea that humans evolved, through variation and selection, from other animals, does not mean that humans are ‘descended from chimpanzees’ or any other species of animal that is alive today. Rather, humans and chimpanzees both evolved from a common ancestor that lived approximately 4–6 million years ago. This common ancestor was neither a chimpanzee nor a human, and there is no reason to believe that it was more chimp-like than human-like.

1.2.2 Adaptations

To examine cognitive processes within an evolutionary framework is to consider how a cognitive trait might improve fitness in a particular environment. Evolution produces **adaptations**, byproducts, and random effects (Buss, 2004), but only adaptations are the result of natural selection.

History of comparative cognition

That is, only adaptations provide some evolutionary advantage to the individual. Adaptations, therefore, can be defined as traits that improve fitness; these have been selected for because they increase survival and reproduction. Some of an organism's adaptive traits can already be seen at birth (e.g. reflexes such as sucking); in other cases, input from the environment may be necessary for the adaptive trait to develop (e.g. language). Finally, some adaptive behavioral traits may not appear until later in life because they depend on developmental processes (e.g. human bipedal walking).

It is sometimes difficult to ascertain whether a particular trait is an adaptation because the fitness advantage it provided in the past may not be the same across evolution. In other words, a particular characteristic may be providing a valuable service now, without having been selected for that function in the past (i.e. without being an adaptation). These adaptations to one environmental problem that can be co-opted to solve another are called **exaptations**. Lewens (2007) provides an illustrative example: many people find that a screwdriver is very good at lifting lids from paint cans, but that is not what a screwdriver was originally designed to do. Some physiological traits fit the same pattern. Bird feathers probably evolved for thermoregulation but then served the important function of early flight. As another example, primate hands probably have evolved for manual dexterity, but humans also use them to hold a wedding ring which symbolizes a monogamous relationship. This symbol arguably helps with social bonding and co-parenting, leading to increased fitness of offspring. Yet, one would not propose that the structure of fingers is an evolved trait for pair-bonding and offspring survival.

The difficulty of defining and identifying adaptive traits led Williams (1966) to conclude that "evolutionary adaptation is a special and onerous concept" (1966, p. vii). The 'onerous' problem is compounded with cognitive traits because, even with contemporary species, cognition must be inferred through other measures. Fossil records and artifacts provide minimal information on the behavior of extinct animals, although they can be used to infer what animals were capable of doing (e.g. pterodactyls could fly and the early human ancestor *Homo habilis* created basic tools). In some cases, scientists compare cognitive abilities of contemporary species that share a common ancestor as a means to understand whether a particular cognitive trait is an adaptation. It is important to remember, however, that different animals will often employ different solutions to the same problem. Mate and offspring recognition is a perfect example: this is a survival problem that must be solved by birds and mammals, particularly for species in which both parents contribute to rearing the young. Most animals rely on sensory abilities, such as vision or olfaction, to recognize their mate and offspring, but the particular mechanisms that accomplish this task vary across species. The female emperor penguin (*Aptenodytes forsteri*), for instance, has the amazing ability to use vocal calls to identify her mate, who has been incubating their egg for over 2 months, within a colony containing a cacophony of hundreds of vocalizing males (Figure 1.2).

Finally, to fully understand adaptations, it is helpful to also consider the other products of evolution that are not the result of natural selection. **Byproducts** are side effects of adaptations (e.g. a belly button is the byproduct of the adaptive umbilical cord; Buss, 2004) and **random effects** (sometimes called noise) are chance mutations (e.g. the particular curvature of one's belly button) that do not provide any survival or reproductive advantage. Both byproducts and random effects may disappear across evolution, particularly if there is an evolutionary cost to maintaining these traits (e.g. a chance mutation that produces brightly colored feathers on a bird may make them more conspicuous to predators). On the other hand, environmental conditions may change such that a trait which provided no fitness advantage when it emerged may be adaptive in the future, in which case it would be more likely to be passed on to the next generation.



Figure 1.2 Emperor penguin colony with cubs in Antarctica.

1.2.3 Speciation

The concept of adaptation helps to explain the emergence of different species across evolution. To Darwin and his contemporaries, a species was a group of animals that resembled each other; a primary task of biologists during this period was to classify different animals into groups, based on shared physical characteristics. By the mid-twentieth century, with advanced knowledge of molecular biology, species were defined based on genetic similarities which map very closely to physiological attributes. On a general level, a species is a group of animals capable of interbreeding and producing fertile offspring. That is, different species cannot breed together, although there are a few notable exceptions (e.g. dogs and wolves). It is unlikely that humans and chimpanzees could produce new baby organisms (even with current reproductive technologies) because the eggs and sperm would not join properly. But the common ancestor of humans and chimpanzees was a species that bred together, very effectively, until approximately four to five million years ago.

Wallace (1870) explained how more than one species can evolve from a common ancestor based on the idea that subpopulations of a single species may display a trait that becomes adaptive when environments change. An animal's environment may change due to extraneous factors, such as the meteorite impact that led to the extinction of dinosaurs. A more common scenario is that small groups of animals move to a new habitat that provides better foraging, shelter, or reproductive opportunities. Some of these animals may possess a physiological or behavioral trait that had no fitness benefit in the previous habitat, but now provides a reproductive or survival advantage in the new conditions. These traits are more likely to be passed on to the next generation, but *only* in the group of animals that moved to the new environment. The separated groups, originally members of the same species, may diverge to the point that they can no longer breed together, a process called **speciation**. This tight link between physiological traits and local environmental conditions is illustrated by one of Darwin's best-known examples, shown in Figure 1.3.

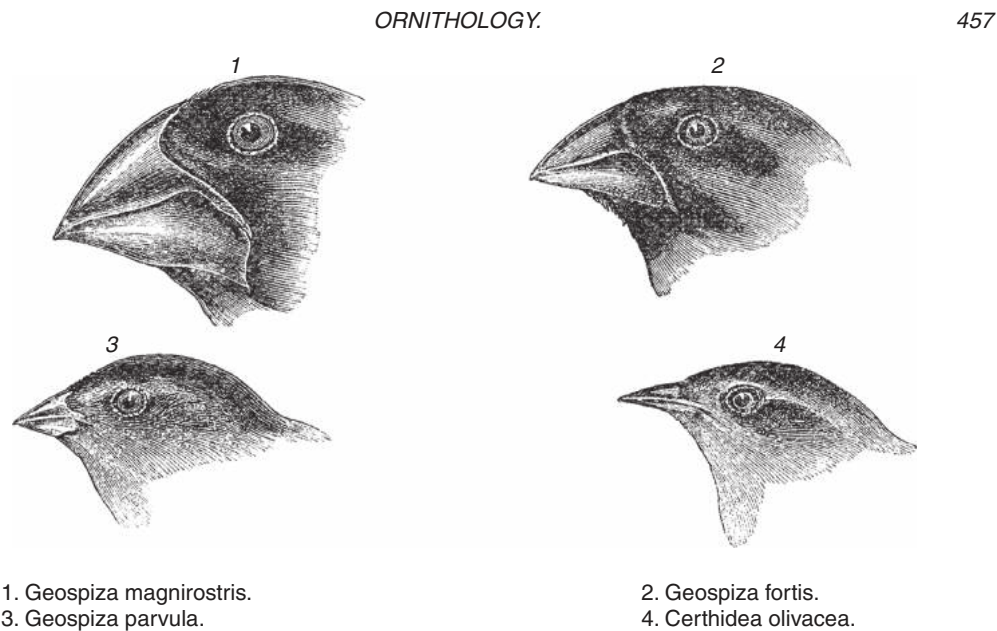


Figure 1.3 Finches with beaks adapted to different diets observed by the Charles Darwin in the Galapagos Islands during his voyage on the Beagle.

The same principle applies to cognitive processes, even if these are more difficult to observe and track across evolution. In other words, certain environmental conditions in the past must have favored specific types of information processing. Language is a prime example: many people believe that this form of communication evolved in humans when the complexity of our social environment increased. The question of whether other animals have language and whether social complexity explains the evolution of human language is not resolved (see Chapter 12 for details). In contrast, there is clear evidence that heritable differences in another cognitive function (visual processing) have resulted in species divergence (Boughman, 2002). A subpopulation of cichlid fish living in Lake Victoria in East Africa carry genes that make them more sensitive to red light. (Cichlid fish belong to the family *Cichlidae*, which contains a number of species.) Because light colors are absorbed differently as they pass through the water, blue light is present near the surface whereas just a few meters below the surface, red light dominates. Fish sensitive to red light will be better able to find food in deeper water and red-colored mates. Fish lacking these genes are better adapted to the blue light conditions of shallow water. Although there is no physical barrier between the shallow and deep areas of the lake, fish with different light sensitivity slowly separated into two groups. With continued environmental pressures favoring one type of light sensitivity over the other, these neighboring populations became two separate species of fish within the last few hundred thousand years (a relatively short time in evolutionary history). This example makes the point that differences in cognitive processing, like physiological or behavioral traits, may contribute to evolutionary change and speciation.

1.2.4 Continuity hypothesis

The basic tenets of the theory of evolution by natural selection led to Darwin’s **continuity hypothesis**, which is the idea that trait differences between animals and humans will be quantitative, not qualitative. In *The Descent of Man and Selection in Relation to Sex* (Darwin, 1871), he wrote the following:

1.2 Influence: theory of evolution by natural selection

There can be no doubt that the difference between the mind of the lowest man and that of the highest animal is immense. An anthropomorphous ape, if he could take a dispassionate view of his own case, would admit that though he could form an artful plan to plunder a garden – though he could use stones for fighting or for breaking open nuts, yet the thought of fashioning a stone into a tool was quite beyond his scope. Still less, as he would admit, could he follow out a train of metaphysical reasoning, or solve a mathematical problem, or reflect on God, or admire a grand natural scene. . . Nevertheless, differences in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind. (pp. 104–105)

In this passage, Darwin acknowledges that humans and animals will differ – sometimes greatly – on many traits and abilities, but he believed that the difference is not in the trait, only in how it is expressed. According to Darwin, therefore, animals possess to some degree many, if not all, of the cognitive and emotional traits that humans display, even if only at an incipient level. Modern researchers, however, do not simply automatically attribute human characteristics and traits to animals (referred to as **anthropomorphism**); rather, they test these ideas experimentally. Yet, this experimental framework was not available to Darwin, who instead relied on anecdotes from people who had frequent interactions with animals, including pet owners, zookeepers, and hunters. Each provided compelling accounts of what appeared to be highly intelligent behavior in animals. Darwin was not alone in using this technique; in the early 1880s his friend and colleague, George Romanes, compiled a book of similar anecdotes, entitled *Animal Intelligence*. Here is an example of a typical story:

As a beautiful instance of the display of sympathy, I may narrate an occurrence which was witnessed by my friend Sir James Malcolm – a gentleman on the accuracy of whose observation I can rely. He was on board a steamer where there were two common East India monkeys, one of which was older and larger than the other, though they were not mother and child. The smaller monkey one day fell overboard amidships. The larger one became frantically excited, and running over the bulwarks down to a part of the ship which is called ‘the bend’, it held on to the side of the vessel with one hand, while with the other it extended to her drowning companion a cord with which she had been tied up, and one end of which was fashioned around her waist. The incident astonished everyone on board, but unfortunately for the romance of the story the little monkey was not near enough to grasp the floating end of the cord. The animal, however, was eventually saved by a sailor throwing out a longer rope to the little swimmer, who had sense enough to grasp it, and so to be hauled on board. (Romanes, 1883; pp. 474–475)

1.2.5 Anecdotal method

As many critics noted at the time, the fact that Darwin and Romanes relied so heavily on anecdotes to develop their theories of continuity was problematic. In the case of Romanes’ reports, the observations were usually made by one person, and in many cases relayed to him second, or even third, hand. In all likelihood, the stories were embellished with each retelling and few of these anecdotes were later re-examined more carefully. Even if it were presumed that the animals *did* engage in the behaviors depicted in the stories, it is difficult to judge whether the actions reflected the complex cognitive processes the writer often assumed. In Romanes’ story, it is not clear that the larger monkey threw out the rope because she understood the smaller monkey’s desire to be pulled out of the water. Nor is it obvious, as Romanes assumed, that the monkey’s frantic excitement reflects a ‘display of sympathy.’ The problem with attributing cognitive abilities to animals, based on a single subject, is often illustrated using the Clever Hans story (see Box 1.1).

Box 1.1 Clever Hans



Figure 1.4 Clever Hans, circa 1904.

Clever Hans was a horse owned by a German schoolteacher, Wilhelm von Osten, who noticed that Hans seemed to have quite an intellect. When given math problems, for example, Hans would answer by tapping on the ground with his hoof until reaching the right answer. He could even reply to questions with German words by tapping out the numbers of the appropriate rows and columns on an alphabet table. It is easy to see why he was the toast of Berlin in the early 1900s (Figure 1.4).

In 1904, a group of academics and animal trainers known as the September Commission was created to examine Hans' abilities. There was suspicion that von Osten was giving Hans signals for the correct answer. Much to their surprise, even when other individuals posed questions to Hans in the absence of von Osten, the horse answered correctly. In the end, the commission found no indication of trickery underlying Hans' performance (Candland, 1993).

Despite this, one member of the committee, psychology professor Carl Stumpf, felt that surely something must be going on. He asked his student, Oskar Pfungst, to do an investigation, focusing on the possibility that somehow Hans was being cued. After several experiments, Pfungst found that when the tester was aware of the question or answer himself, Hans did well. But when the tester did not know, Hans got the answer wrong, for example by overestimating the correct number in an arithmetic problem. Pfungst concluded that a knowledgeable tester would enact subtle body movements just as Hans reached the correct answer, effectively cuing Hans to stop tapping.

Pfungst never claimed that von Osten was a charlatan; the owner and the experimenters were unaware of their cuing and von Osten was completely convinced that his horse could solve arithmetic problems. In this way, Hans offers an important lesson on the potential biasing of results for those studying animals and humans. Indeed, most experimental protocols now ensure that 'Clever Hans Effects' are eliminated through a 'double blind' procedure in which neither the subject nor the tester knows the expected outcome.

The Clever Hans affair occurred during a period in which many such stories of great cognitive feats by animals were spreading. Many of these cases were likely the result of intentional trickery on the part of the owners, although others might have been as innocent as the actions of von Osten. Pfungst's findings served to appropriately temper the general excitement and speculation about the animal mind (Roberts, 1998), and in turn became a factor in the development of a controlled, experimental field of study.

Even without Clever Hans, many scientists were skeptical of evidence derived from anecdotes. In addition to the problem of reliability, they noted that personal recollections of a specific incident may not reflect typical or general trends in a population. In psychology, this is sometimes referred to as the 'person who' fallacy in reference to the fact that individuals often reach conclusions based on