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Volume 2

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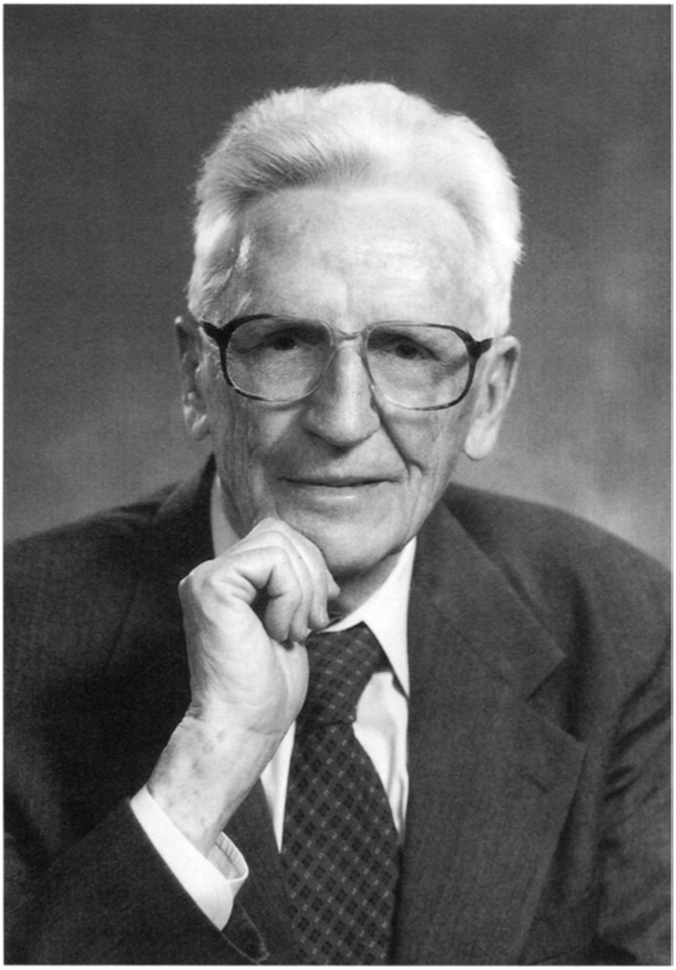

Donald R. Griffin

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August 3, 1915

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Harvard University, B.S. (1938)
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Donald Griffin discovered, with Robert Galambos, the phenomenon of echolocation in bats. He carried out extensive studies of bat behavior, demonstrating conclusively that bats use echolocation to catch flying insects. He also conducted fundamental studies of homing in birds, bird navigation, and honeybee communication. He has written extensively on the topic of awareness in nonhuman animals.

The History of Neuroscience in Autobiography, Volume 2

Donald R. Griffin

I might be called a "WASAG," for white Anglo-Saxon agnostic, and I have been most fortunate in my relatives, friends, and general circumstances. My ancestors have been in the United States for at least three generations; some were part of the original Mayflower company, and one was a refugee from the slave revolts in Haiti. Two came from Ireland, including my great grandfather Thomas Francis Griffin (1820–1907). He must have led a full and fascinating life between his arrival at the age of 15, and his financial success in building up a prosperous foundry business that by the 1890s was selling carwheels to railroads literally around the world, from St. Petersburg through Europe and North America to Vladavostok. This emigrant boy was a distant cousin of the Irish playwright Gerald Griffin (1803–1840), but unfortunately he left no recollections, and we know only that he began by working on the new Mohawk and Hudson railroad as it was being expanded westward from Schenectady. To quote my father's recollections, "In the 1830s the Mohawk and Hudson was a very small affair . . . with some 20 miles of track, two locomotives,. . . . half a dozen cars made out of stage coach bodies, and . . . a few horses to pull the cars when the locomotives broke down." Curiously enough, my mother's great grandfather, Asa Whitney, was superintendent of the Mohawk and Hudson. By the 1890s the thriving Griffin foundries produced such superior carwheels that the Whitney foundry in Philadelphia went bankrupt.

Mary Whitney Redfield Griffin (1885–1968) read to her only child so much that my father feared I would never learn to read myself. My favorites were Ernest Thompson Seton's books and the National Geographic *Mammals of North America* with colored illustrations by Louis Aggassiz Fuertes. My father, Henry Farrand Griffin (1880–1954) had strong literary interests and was a scholarly amateur historian. A few years after he graduated from Yale in 1903 his father's financial affairs collapsed in 1907 and he became a reporter for the *New York Evening Sun,* covering among other things Theodore Roosevelt's Bull Moose Campaign and the sinking of the Titanic. After turning to advertising about the time I was born (August 3, 1915) he developed high blood pressure in his 40s and retired gradually to Barnstable, Massachusetts where he read widely, wrote numerous unpublishable essays, tried to improve on standard translations of selected Greek and Roman classics, and published two historical novels (H. F. Griffin, 1941, 1942).

My uncle, Alfred C. Redfield (1890–1983), encouraged my boyish interests in biology from time to time. A great grandson of William C. Redfield (1789–1857), who discovered the cyclonic nature of storms, he was an enthusiastic bird watcher in his youth, and by the 1920s he was a comparative physiologist at Harvard. His interests gradually shifted to ecology and he was one of the scientists who founded the Woods Hole Oceanographic Institution.

After fourth grade my schooling was highly irregular and at times consisted of tutoring at home by my father and a retired school teacher, as well as 2 years at Phillips Andover that were interrupted by illness; but it sufficed for admission to Harvard in 1934. My most vivid memory was the forbidding white-haired principal of the Barnstable grammar school delivering an impassioned sermon on the hideous doctrine of evolution, culminating with "Do any of *you* believe your grandmother was a monkey?" The occasion was the death of the famous plant breeder Luther Burbank who, we were assured, had been struck down by the Lord because of his blasphemous advocacy of biological evolution.

Wild mammals have fascinated me as long as I can remember—certainly since the age of 10. By the time I was about 12 my enchantment with trapping furbearers in the North Woods led to a few ill-fated efforts to trap local mammals; but even skinning roadkills was beyond me until a friend of my parents demonstrated the simple procedure of lifting the edge of the skin and cutting where it was still attached to the underlying muscle. Badly misaligned teeth required frequent trips to an orthodontist, and as a reward for putting up with this monthly tooth wiring I was taken to the Boston Museum of Natural History on Berkeley Street. After I had become familiar with the public exhibits I was encouraged to frequent the museum library, where a thoughtfully supportive librarian introduced me to scientific journals. In time I met curators Francis Harper and Clinton V. McCoy who encouraged a redirection of my enthusiasm for trapping furbearers to collecting small mammals and making them into study skins. Curiously enough McCoy was my laboratory teaching assistant in elementary zoology a few years later. At age 15, the age at which my great grandfather had emigrated from Ireland, I subscribed to the *Journal of Mammalogy.*

Collecting small mammals and reading about them at the museum library led me to hope I could describe a new subspecies of *Peromyscus* from Cape Cod based on variations in ratio of tail length to body length. This aspiration was based on the numerous papers by Outram Bangs describing new subspecies of small mammals from islands off the New England Coast, almost all of which have long since been relegated to synonomy. The books and papers I read told me that the red-backed vole *Clethrionomys* (then *Evotomys*) *gapperi* was found in damp mossy woodlands. But when I caught several on Sandy Neck, a very dry barrier beach with pine and oak woods, I came to realize that scientific papers were not always correct in every detail.

Trappers and deer hunters in Massachusetts were supposed to report to the Division of Fish and Game the number of various species they had taken. Doubtless encouraged by my father, I wrote to the appropriate authorities and obtained lists of the numbers of each species reported from each county. I wondered whether the populations of each species could be estimated from the numbers trapped. This required assumptions about how many could be taken without reducing the population and presumably causing a decline in numbers taken in subsequent years. All this was of course naive guesswork, and I remember Uncle Alfred diplomatically pointing out that the proportion of those killed and reported to those actually present must have been very different for deer and weasels.

Another redirection of my enthusiasm for trapping was to dream of becoming a fur farmer. I spent hours during school study hall planning and sketching the cages I would build. I bought by mail order live traps similar to the current "Have-a-heart" types and caught a few muskrats and skunks, for which I constructed substantial and roomy cages. But I was disappointed that my captives spent most of their time in the roomy nest boxes and very seldom showed themselves voluntarily in daylight. I also kept a few chinchilla rabbits, and my indulgent parents took me to meetings of the local rabbit breeders club. One piece of advice that I recall vividly when I asked about rabbit hutch construction was "Don't try to build against rabbits."

The first time I found a live skunk in one of my wire mesh traps I naturally approached it with great trepidation. But I had read that skunks don't "shoot" unless seriously alarmed. So I decided that I could wrap the wire mesh trap and skunk in a piece of old rug, kindly donated by my mother, and carry it back to my waiting cage. The first time I tried this I nervously dropped the rug from a couple of feet above the cage. The rug protected me, but I had to ask for another piece for later captures. By the time I was driving a car at 16 I became confident enough to carry well wrapped traps in an automobile without mishap. This led to requests from family friends for humane removal of skunks living under their houses.

In 1932, when I was 17, I visited the Oliver Austin bird banding station at Eastham and was invited to spend a couple of weeks with the Austin family while collecting small mammals on the station grounds and learning about bird banding from the Oliver Austins, father and son, and Maurice Braun who is well known for his later work at Hawk Mountain, Pennsylvania. The Austin station was then one of the largest in North America in terms of numbers of birds banded per year. I learned how the Austins were catching small birds in cage traps, and helped them catch shorebirds with mist nets which were then quite new. They allowed me to band birds in Barnstable as a substation of the Austin enterprise.

My mammal collecting had only occasionally brought me into contact with bats; as I recall I had made a study skin of only one *Eptesicus fuscus,* but it was only natural to think of combining my interest in small mammals and banding birds. When I heard of a colony of bats in the attic of an abandoned frame house the Austins let me try a few of their bird bands on these bats. Recoveries the next year showed that the bats tolerated bird bands reasonably well (Griffin, 1934). From 1933 to 1938 I banded as many bats as I could catch at nursery colonies in buildings and in caves where they hibernated. I perfected what I have come to call the "Tom Sawyer fence whitewashing method" of recruiting college friends to participate in studies of animal behavior under natural conditions by letting them in on the secret that it is great fun.

Recoveries of banded little brown bats (*Myotis lucifugus*) showed that they migrated between caves in Vermont and nursery colonies as far away as Cape Cod (Griffin, 1940b, 1945; Gifford and Griffin, 1960; Davis and Hitchcock, 1965). Homing experiments yielded returns after displacement as far as 50 miles. But the real surprise from bat banding has been longevity records up to 20 years or more (Hall et al., 1957; Griffin and Hitchcock, 1965; Griffin, 1980; Roer 1971; Lehman et al., 1992; Sommers et al., 1993). I will never forget hearing Alan Grinnell, who accompanied me on a trip to Vermont caves in search of banded bats, exclaiming "He's older than I am!" Lifespans of several years must be quite common, because I once recaptured 8% of a large group after 8 years, and some 10- to 12-year-old females were pregnant or lactating. Analyses of animal longevity are often confused by assuming that all marked animals not recaptured have died. But banded bats often move between colonies, so that many more must have survived than were recaptured.

At Harvard I concentrated heavily on biology and one quarter of my courses were in chemistry. Although I never used chemistry, faint memories have often helped me judge the plausibility of scientific ideas. I was only a B student, but John Welsh encouraged me to study activity rhythms of bats (Griffin and Welsh, 1937). The tutorial plan was still taken seriously at Harvard, and I was fortunate to have Jeffries Wyman as my tutor. He had me read elementary material on physical chemistry but also tolerantly supported my interests in migration of bats and birds. Physiology was the order of the day, and animal behavior was considered too vague for serious scientists. To satisfy a distribution requirement I took E. G. Boring's half course in introductory psychology, but had to do so against the strong advice of a junior instructor who assured me it would be a waste of time.

I cannot recall just how my interests in bats turned to their orientation in the dark. Their agile flight in totally dark caves was most impressive, and I had read elementary accounts of Spallanzani's experiments showing that blinded bats flew normally. Left to my own devices I might never have even heard of the physics professor George Washington Pierce, but Talbot Waterman and James Fisk told me I should ask whether his new apparatus for studying "supersonic" sounds might respond to bats. He was already studying the high-frequency sounds of grasshoppers, with a biology student, Vincent Dethier, to help him identify them.

Once I worked up the courage to knock on his door, I found Pierce a jolly fellow whose apparatus clicked and rattled delightfully whenever my bats were at all active. They were emitting definite sounds well above the range of human hearing, but we had difficulty detecting any of these sounds when they were flying around the room. We were therefore appropriately cautious about concluding that these sounds were used for orientation (Pierce and Griffin, 1938). As described elsewhere (Griffin, 1958, 1980) when I returned to studying bats with fellow student Robert Galambos we found that the initial difficulty had been that both the bats' emission of sounds and the sensitivity of Pierce's apparatus were quite directional, and that we had to aim the apparatus straight at an approaching bat to reliably detect these sounds.

During my senior year I decided it was time to branch out and take up something new as I started graduate work, looking forward hopefully to some sort of academic career. The navigation of birds struck me as a suitable thesis problem, but some of my elders and betters advised that if I really hoped to become a serious scientist I should put aside such childish interests in favor of some important subject such as physiology. I was saved from this dilemma when Karl Lashley came to Harvard as a member of both biology and psychology departments. I had read the classic paper by Watson and Lashley (1915) on the homing of terns, and persuaded him to accept me as a biology graduate student to study the homing of locally available species. Lashley stipulated that I take a couple of courses in psychology with Clifford Morgan and S. S. Stevens, and I even talked E. G. Boring into letting me audit his proseminar for first year graduate students.

The key question I hoped to answer was whether birds displaced into unfamiliar territory could determine the homeward direction and proceed directly back to their nests. In the summer of 1938 I selected Leach's petrels as a suitable species, partly because a fellow graduate student, William Gross, had been studying them at the Bowdoin College field station on Kent Island at the mouth of the Bay of Fundy. These pelagic seabirds spend about 4 days with their eggs and young in burrows on islands free of ground predators while the mate spends the same time feeding at sea. Each homing experiment entailed catching 20 or 30 petrels and transporting them in covered cages to distant release points. For releases well out in the ocean the cages were taken by launch and auto to Halifax and left with the deck officer of a freighter who released them en route to the West Indies. Many homed from distances as great as 470 miles, but their speed of return was not especially impressive. Either they might have been well oriented but spent considerable time in feeding, or perhaps they flew in some sort of search pattern that brought them to a familiar coastline (Griffin, 1940a).

In 1939–1941 I therefore turned to herring gulls and common terns nesting on Penikese Island not far from Woods Hole, and both species returned reasonably well from release points several hundred miles along the coast or inland. The speed and percentage returns were slightly better from the southwest where the bird might have encountered landmarks that were familiar from their seasonal migrations. But as with the petrels, the results were consistent with a "nothing but" interpretation that in unfamiliar territory birds either flew off more or less randomly or searched in some systematic pattern until they found familiar landmarks. To distinguish between these two possibilities I obviously had to learn where they actually flew. As we cast about for possible methods to accomplish this, Lashley suggested feeding the birds poison capsules so that after a predetermined time they would drop from the sky and, he thought, be observed and their location reported. I diplomatically refrained from following that advice, but I did seriously consider radio tracking, only to find that the smallest available transmitter was much too heavy for a herring gull to carry (Griffin, 1963).

It was Alexander Forbes, the physiologist, yachtsman, pioneer aviator, and explorer of Laborador, who encouraged the alternative of following herring gulls from a light airplane. Although nothing could have been farther from any of my previous experience or aspirations, Forbes' enthusiasm was irresistible. We first tried releasing a gull from the plane: "Wait 'til I pull the plane up into a stall, then you open the door, Griffin, and throw the gull down as hard as you can, so it'll miss the horizontal stabilizer." A nice idea at the time, except that the open door acted as right rudder and put the plane into a spin. After that we asked someone at the airport to watch our plane and release a gull when it was rocked back and forth conspicuously. It proved feasible to keep a white gull in view while circling one or two thousand feet above it, and in 1941 I bought a 6-year-old plane and followed several gulls as they started home. Once more it seemed that when released inland in presumably unfamiliar territory herring gulls did not head directly toward home, even though most of them did eventually find their way back to their nests on Penikese Island (Griffin, 1943).

During the summer of 1939 I was lucky to be awarded a fellowship (probably on the recommendation of W. J. Hamilton) to work at the newly established E. N. Huyck Preserve in Rensselaerville, southwest of Albany. After homing experiments with gulls and terns in May and June I returned to banding bats and repeated and extended the obstacle avoidance experiments that Hahn had carried out at Indiana University more than 30 years earlier (Hahn, 1908). The agility with which bats dodged 1-mm wires even when blindfolded was most impressive; I experimented with various types of ear plugs and confirmed the disorientation of bats with impaired hearing. On returning to Harvard in the fall I found that Galambos had succeeded in recording cochlear microphonics from bats at frequencies up to 90 kHz. I have described elsewhere the development of our joint experiments (Griffin and Galambos, 1941; Griffin, 1958, 1980), and Galambos has also published his recollections of our experiments (Galambos, 1995, 1996; see also

Grinnell, 1980). He was far more of a physiologist, and without his critical ideas I would very likely never have worked out such conclusive experiments showing that bats avoid obstacles by echolocation. On the other hand I was the one who knew bats, and our collaboration was intense and fruitful. We kept to our original plan that his Ph.D. thesis would be on the hearing of bats and mine on the homing of birds.

After Pearl Harbor I was fortunate to be employed in applied wartime research at Harvard in S. S. Stevens' Psychoacoustic Laboratory where I found it exhilarating to plunge directly into practical efforts to improve voice communication systems used in noisy military tanks and aircraft. Orders conveyed by radio were often so garbled that a pilot could not tell where he should fly to return to his carrier. The equipment then in use had been developed 20 years earlier for dot–dash telegraphy with a sharp peak at about 1 kHz which became painfully loud or even damaging to the ears when the gain was turned up. After laborious tests in a variety of noise fields we proved to everyone's satisfaction that one really could hear better in noise with a broad-band system. This now seems obvious, but in 1942 it appeared to be long-haired theorizing.

After several months at the Harvard Fatigue Laboratory testing equipment and developing improved gear for soldiers and airmen forced to live and fight under adverse climatic conditions, I was glad to join George Wald and Ruth Hubbard in a project sponsored by the U. S. Army Engineers. Still secret night vision devices converted infrared light into an image that allowed soldiers to see and shoot the enemy in total darkness. The only catch was that despite everything in the textbooks, the intended victims could see a dark red glow from the infrared searchlight. Working with filters that had to be locked away in a safe after each experiment, we measured the human threshold in the near infrared. At 1000 nm one could feel a slight warming of the skin at the visual threshold (Griffin *et al.,* 1947).

When I participated in competitive efforts to sell one of the Armed Forces on our conclusions, or on the virtues of a device we were recommending, it was instructive to see how the formal structure of scientific tests could be manipulated to achieve any of a wide range of outcomes, according to the preference of the advocate. Yet in my firsthand experience the Armed Services eventually reached reasonable decisions, although they often needed a great deal of persuasion. Much of this applied wartime "research" consisted of gathering evidence that would convince officials of relative simple matters of scientific fact that were obvious very quickly once one studied the matter sensibly.

Six months resumption of my junior fellowship in the first half of 1946 provided a fine opportunity to apply to bats what I had learned about acoustics with S. S. Stevens and especially from Francis Wiener of L. L. Beranek's Physical Acoustics Laboratory. He loaned me a 640AA condenser microphone, which at the time was by far the best available to record sounds above the frequency range of human hearing. The cathode ray oscilloscope showed at a glance that the sounds emitted by bats were even briefer in duration than Pierce's apparatus had revealed; rather than being broadband noise bursts, they were frequency modulated chirps sweeping downward by an octave during 1 or 2 msec (Griffin, 1946, 1950, 1958).

Having been at Harvard for 12 years it was obvious that I should move out into the real (non-Harvard) world. I knew some of the biologists at Cornell, including William Wimsatt who was then teaching anatomy at the Harvard Medical School. I let Bill know that I would be delighted to become Cornell's comparative physiologist. Howard Adelmann was building up a department of Zoology, and his screening included asking me to prepare outlines of three courses in vertebrate, invertebrate, and general physiology. Brought up to believe that physiology was one subject that was best not divided along phylogenetic lines, I managed to persuade him that I should give one full course in comparative physiology, and a seminar on cellular physiology.

I am deeply appreciative of Adelman's vigorous support even when it was not at all what he had probably anticipated. He was a true scholar, and although I strongly disagreed with his political opinions, he was a tower of intellectual strength. His own work in experimental embryology had included two years with Spemann in Germany, but had shifted to intensive analyses of the history of embryology and anatomy that led to his monumental books on Vesalius and Malphigi. It seemed at times that I was the only colleague who was willing to listen patiently to endless monologues about the problems of truly accurate translation.

In the present period when talented scientists are so much more numerous than suitable positions, I am somewhat embarrassed to recall my extreme good fortune when, during the summer of 1947, the University of Rochester offered to make me a full professor and chairman of its biology department. I was, and still am, flabbergasted that a good university would offer me such a responsible position after only one year as an assistant professor. Nothing appealed to me less than academic administration, but with two small children I could not afford to turn down such an offer. Fortunately for me, and I think also for the University of Rochester, Adelmann was able to twist whatever dean's arms were necessary and I was promoted to tenured associate professor. Although I did not realize it at the time, this episode reflected the beginning of an exponential growth phase in academic science.

I was delighted to find a Cornell graduate student, W. C. Curtis, son of a plant physiologist, ready to work with me. He began by measuring the ability of bats to avoid wires of various sizes, showing better than chance avoidance even with wires 0.26 mm in diameter. Although Galambos and I had at first thought that bats could scarcely use their vision at all since plugging the ears made them so helpless, Curtis confirmed and extended the published work of Eisentraut showing that they did indeed have at least rudimentary pattern vision. We also wondered whether owls might use echolocation, but Curtis found that although barn owls could avoid obstacles in very dim light, they were disoriented in total darkness.

During the war years I had worked out detailed plans for improved homing experiments that I hoped would clarify the sensory basis of bird navigation. The gannets nesting on Bonaventure Island in the Gulf of St. Lawrence seemed ideal because they are large and white and thus easily followed from the air. Furthermore they are strictly pelagic and normally do not fly far from the ocean, so that inland release points would certainly be unfamiliar territory. But research support adequate for rental of a suitable airplane was unheard of. Then suddenly I learned from Laurence Irving and Pete Scholander at Swarthmore College that, *mirabile dictu,* the federal government was still supporting research projects, even though the war had ended. There was now an agency called the Office of Naval Research ready to award research contracts at a biological research station at Point Barrow, Alaska. Even more astonishing was that they did not really care what one studied, provided it was in arctic Alaska. What I really wanted to do was follow homing gannets over New Brunswick and Maine, but of course there were interesting birds nesting on the north coast of Alaska, including large white species such as snow geese and swans. So my proposal to the ONR explained that in order to study the homing of snow geese and swans in Alaska I had first to develop and perfect the method of airplane following, which could be accomplished more effectively with gannets from Bonaventure Island in 1947, to be followed by similar studies in Alaska in 1948.

A Cornell graduate student, Ray Hock, and his wife, Ann, helped me catch gannets nesting at the top of cliffs on Bonaventure Island, and we transported them by local boat and Navy jeep to Caribou, Maine. With a three-place Piper Super Cruiser fitted with an extra fuel tank in place of the third passenger I managed to follow gannets for as long as 10 hours. Most of them did return to their nests, but their flight paths deviated greatly from a straight line between Caribou and Bonaventure Island (Griffin and Hock, 1949; Griffin, 1964).

These airplane observations, together with a thorough analysis of all the data then available, persuaded me that almost all bird homing could be accounted for without assuming that the birds could choose the correct homeward direction when released in unfamiliar territory (Griffin, 1944, 1952). This conclusion, which in retrospect seems so narrowly overconservative, was very much in keeping with the basic ideas on which I had been brought up at Harvard in the 1930s. Everything that animals did was to be explained in the simplest possible terms; Jacques Loeb or Frankel and Gunn (1961) were models to be emulated. For example, when I used to discuss the problems of bird navigation with my student friends one far-fetched idea we played with was that the birds might conceivably use the sun or stars for directional guidance. But this was outrageous speculation, and a typical response was to ridicule the notion that a bird might carry around in its head a nautical almanac to determine the appropriate direction for migration or homing from the constantly changing azimuth of the sun or a star. The possibility that birds might distinguish Polaris from other stars was so outlandish that I don't think anyone even dared to mention it.

The English physicist Wilkinson (1952) likened homing birds to gas molecules, and his equations could be made to fit reasonably well with the data then available on homing performance—including my airplane observations. Yet small nagging doubts remained, for some reports of homing pigeons, and especially Lack and Lockley's experiments with Manx Shearwaters, were difficult to reconcile with this "nothing but" explanation that seemed most reasonable and appropriate.

Only a few years later Matthews (1968) in England and Kramer (1961) in Germany demonstrated that well-trained homing pigeons really do show much better than random homeward orientation within a few minutes after release in unfamiliar territory. In 1948 an even more startling development shook up my whole scientific viewpoint when I first heard of Karl von Frisch's experiments on the waggle dances of honeybees. At first I was incredulous, even though his earlier work on color vision in bees and hearing of fishes was well known and highly regarded. Good God, if mere insects communicate abstract information about distance and direction, where does that leave Loebean tropisms? If bees do something like that, how can I be so sure that homing birds simply search for familiar landmarks?

I lost no time in setting up my own observation hive, with help from Cornell apiculturists, and saw for myself the striking correlation between the pattern of the waggle dances and the distance and direction to the food source. I even managed to work it into the laboratory of my comparative physiology course as an "unknown." The students first estimated from the dances where the bees were informing their sisters that food was located, and then they checked to see where marked bees were gathering concentrated sucrose solution from artificial feeders. I was so fascinated by this revolutionary discovery that I helped arrange for von Frisch and his wife to visit the United States for a series of lectures. They flew from Graz in the Austrian province of Styria, passing through Vienna, which was still occupied by the Russians, and on to Frankfurt where they watched in amazement the almost continuous shuttle flights of American planes to blockaded West Berlin. In Ithaca they charmed everyone, and the only problem was that when they wanted to walk through the countryside almost every motorist stopped to help these elderly people with their walking sticks. It was a nuisance to explain to driver after driver that they really liked to walk.

One of the requirements of the lecture series at Cornell was that the Cornell University Press should have the option of publishing von Frisch's lectures. He readily agreed, and within a few weeks I received a manuscript describing the same marvelous material he had presented in his lectures. But it was typed single-spaced on thin paper with strike-overs and a very few places where German word order prevailed over English usage. In my youthful innocence I did not realize that a university press would have its evaluation affected by such mechanical details. I became increasingly puzzled when several weeks went by without any response from the press, especially since I was fending off fervent pleas from other university presses to let them see the manuscript. Finally I was told that there was great doubt that the manuscript was publishable at all, but that one of their readers was revising it into acceptable form. Adelmann and I were outraged when we learned that an elderly professor of apiculture had indeed rewritten the first chapter to read like a Department of Agriculture bulletin, even inserting long paragraphs on his own experiments dealing with the amount of hay that should be piled around beehives to enable bees to survive the winter.

Seeking independent opinions I circulated samples of von Frisch's original and the proposed revisions to colleagues in other departments. The philosopher Max Black supported me fully, and Mike Abrams, Professor of English, asked if he might please use my samples in his freshman English class—von Frisch's passages as models, and the revisions as horrible examples of what to avoid. In the end Adelmann and I won our battle and Cornell University Press did publish *Bees, Their Vision, Chemical Senses and Language* (von Frisch, 1950) which was of course a great success, and is still in print. But I was so ashamed that I never told von Frisch about the whole affair.

By 1951 I had returned to further experiments on bat echolocation. It seemed appropriate to investigate whether they could discriminate between different objects. Thinking that a bat would do its best to avoid obstacles that blocked its escape path, an interested student and I built various types of boxes with an entrance hole in the middle of one wall, so that a bat released there would have a choice of escaping by flying right or left toward two identical openings leading out into a large flight chamber. We reasoned that if one of these two flight paths was obstructed the bat would of course choose the unencumbered passageway, and that having established this we could then go on to set up different obstacles at the two ends of the box and learn whether the bat could distinguish those offering the best escape route. But the bats (*Myotis lucifugus*) frustrated us at every turn. Either they developed position habits, always flying to the right or left regardless of the obstacles, or they flew toward the cluttered opening instead of the open one.

In late August, in what I thought of as a last ditch effort to salvage something from a summer's work, I took my apparatus for the first time out of doors where bats were pursuing flying insects. I had no reason to think that this would lead to anything interesting, but having watched bats (*Eptesicus fuscus*) hunting over a small pond near the Cornell campus, I wondered whether their orientation sounds might be different from those I had been recording in the laboratory. At that time the best way I could record bat sounds was to photograph their waveforms displayed on a cathode ray oscilloscope, using an ancient 35-mm motion picture camera modified so that the film moved continuously. Because most of my apparatus required AC power I had to use a gasoline engine-driven generator to power the station wagon full of gear. The long, deep parabolic horn around the 640AA condenser microphone was the only piece of apparatus left over from Pierce's supersonic detector of the 1930s. Because it was impossible to aim the parabola at a bat flying 50 feet above the pond and at the same time watch the oscilloscope, I threw together a crude audible detector by feeding the ultrasonic signal into the second detector stage of a portable radio.

The results were unexpectedly spectacular (Griffin, 1953a, 1958). Although Galambos and I had learned a decade earlier that bats increase the repetition rate of their orientation sounds when approaching obstacles, the increases in pulse rate during insect pursuit were very much greater. The "put-put-put" from the portable radio as a bat approached speeded up as it closed in on a moth or beetle to a buzz of up to 200 pulses per second. Neither I nor anyone else had previously suspected that bats might catch small flying insects by echolocation. We had always thought of echolocation as a collision warning system, and it seemed out of the question that small insects could return strong enough echoes to be audible to a rapidly moving bat. It is difficult now to realize how great a shift in viewpoint was necessitated by this evidence that bats use echolocation to locate and intercept small moving targets. Echolocation of stationary obstacles had seemed remarkable enough, but our scientific imaginations had simply failed to consider, even speculatively, this other possibility.

Yet my evidence from field observations was not entirely conclusive. For instance, one critic suggested that the increase in repetition rate was analogous to the faster yelps of his dog in hot pursuit of a rabbit. Final resolution of this question had to wait another decade when collaborative experiments with Frederic Webster in Cambridge showed that echolocation really was used at least by some insectivorous bats in their efficient capture of small flying insects in the dark (Griffin et al., 1960).

Having come to realize that bat echolocation was a highly versatile mode of perception, it was natural for a zoologist to wonder whether it might differ among the many groups of bats. It was difficult to convince some of my colleagues that this was a significant question. One expert in hearing, Nobel laureate Georg von Bekesy, told me it would be a waste of time to examine those queer-looking bats from the tropics: a bat is a bat, those sounds are simply noise bursts, and nothing more is likely to be learned from comparative studies of echolocation. But F. P. Moehres had already discovered that the horseshoe bats use a very different type of echolocation than the bats we had studied, and Harold Trapido at the Gorgas

Laboratory in Panama persuaded me after rather extensive correspondence to dispatch 20 packing cases of apparatus by air freight to Panama; he showed me where to catch several species of bats with habits very different than those previously studied in North America and Europe.

The first of my two months in Panama was spent tracking the air freight shipment which had gone astray, but when it finally arrived I was able to learn very quickly that orientation sounds and echolocation differed greatly in bats that fed on insects, fruit, fish, or blood of large animals. The most striking result was that I could not detect any orientation sounds at all from most of the small neotropical fruit-eating bats such as the very common *Carollia perspicillata,* though they collided with obstacles when their ears were plugged; I was for a time back with Spallanzani and Jurine: hearing was necessary for obstacle avoidance but the bats seemed to fly silently. It turned out that the problem was microphone sensitivity and much lower emitted intensities. When Alvin Novick returned to Panama a year later with the newly developed plastic diaphram electrostatic microphones he could detect at least faint orientation sounds from all the neotropical bats. These initial studies in Panama in 1953 and 1954 opened up a whole new truly comparative vista of echolocation adapted to a variety of feeding habits (Griffin and Novick, 1955).

My first sortie to the tropics in 1953 was also enlivened by William and Katherine Phelps of Caracas who invited me to accompany them to the Cave of the Guacharos near Caripe where Humboldt had eloquently described how the oilbirds nest in totally dark caves. We were able to show by simple field experiments that they employ a crude form of echolocation using audible clicks (Griffin, 1953b).

In 1953 I was invited to return to the Harvard biology department, with the primary obligation of teaching introductory zoology. I approached this with considerable trepidation, and I am afraid did only moderately well at elementary teaching. But the stimulating environment and superior facilities available at Harvard did permit better research work than I would have been able to accomplish at Cornell. I also managed to avoid the bitter political problems that wracked the Cornell zoology group during the late 1950s.

I and several Harvard students continued to investigate bats' use of echolocation for insect catching, taking better and better, and bulkier and bulkier, electronic equipment to field sites where bats were actually doing their insect hunting. No such equipment was then available with battery power, so that we either relied on portable generators or persuaded neighbors to let us plug in a long extension cord. Sixteen-millimeter sound movies showed the position of a flying bat and the sound track measured the timing of their ultrasonic orientation sounds "translated" into audible clicks by crude ancestors of modern bat detectors. The big brown bat, *E. fuscus,* was the species I usually studied, but once a rare opportunity arose when migratory red bats, *Lasiurus borealis,* were actively chasing beetles over a miniature golf course in Falmouth, Massachusetts. The owner was most reluctant to allow us to wander through his premises trailing a long cable leading from microphone and parabolic reflector back to a truck full of equipment powered via an extension cord connected to one of his power outlets. But it was a unique opportunity, and we finally persuaded him to allow us to record bats over his golf course, provided that we did not tell his clients what we were doing. This required considerable diplomacy, especially when a serviceman from Otis Air Force base loudly explained to all within earshot that we must be studying radio waves from the ionosphere, even though some skeptical listeners kept asking "But why do they always point that thing at those bats?"

Neurophysiology of brain mechanisms of bat echolocation began when Alan Grinnell first exposed the dorsal surface of the brain of an *M. lucifugus* under nembutal anaesthesia and placed a simple wire electrode of the surface of the inferior colliculus. The beautiful evoked potentials so easily recorded formed the basic of his extensive studies of the neurophysiology of bat echolocation (Grinnell, 1963). These studies were extended later by Nobuo Suga and several others, so that in many ways the neural bases of auditory discriminations in bat brains are better understood than those of any other nonhuman animal, as recently reviewed by Suga (1994) and in several chapters of the book edited by Popper and Fay (1995).

The idea that bats use echolocation to locate and capture small flying insects still seemed rather radical, but my efforts to test it experimentally were stymied for many years because I could not persuade captive bats to catch flying insects. This bottleneck was broken by an entomologist, Eric Tetens-Nielsen, who invited me to bring bats to his laboratory in Vero Beach, Florida where he had a flight chamber filled with hundreds of mosquitoes. So I flew to Florida with some freshly caught *M. lucifugus* in a modified briefcase and as soon as they were released in Tetens-Nielsen's flight chamber some began to catch numerous mosquitoes with the same rapid increase in pulse repetition rate that had first indicated use of echolocation for prey capture.

The next step was to set up a similar flight chamber at Harvard where I could record the bats' sounds much more accurately and take sound movies to show the spatial relations between bat and insect along with the temporal pattern of ultrasonic sounds. We quickly switched from mosquitoes to fruit flies reared in oversized versions of the standard bottles used by geneticists.

Frederic Webster began a fruitful collaboration which included conversion of a Quonset hut he had erected in his backyard to house a trampoline into a larger bat flight chamber than the low ceilings of the Biological Laboratories could provide. Here we could, at last, elicit active insect hunting by *M. lucifugus* under controlled conditions. Although vision seemed most unlikely to guide insect hunting bats, a first step was to study insect catching in total darkness. The orientation sounds were similar, but how could we tell whether the bats were really catching fruit flies in total darkness? Because there was no way bats could gain weight in our flight chamber except by catching fruit flies, weighing them before and after a short period of insect catching in darkness finally demonstrated, conservatively, that some bats caught a fruit fly every few seconds (Griffin et al., 1960).

Another alternative to echolocation was that bats located flying insects by passive listening to sounds of their wingbeats. These were very faint, audible only if the fruit fly was almost inside one's ear canal, and the great increase in the bat's own sounds seemed inconsistent with listening for faint wingbeat sounds from *Drosophila*. But it was a distinct possibility that required serious consideration. We therefore subjected our insect-catching bats to loud sounds of both audible and ultrasonic frequencies. In broad-band audio frequency noise that was enormously louder than the flight sounds of fruit flies the bats continued to gain weight as fast as under quiet conditions. But when we played ultrasonic noises they landed on the wall and refused to continue insect hunting.

Under some conditions large numbers of bats fly close to one another in caves, especially when emerging in the evening. Listening with a bat detector to the bedlam of ultrasonic sounds leads one to wonder why the innumerable pulses from dozens of bats within a few meters of each other do not interfere with their echolocation. Yet they do not collide with obstacles, or with each other (although they do not need to intercept flying insects). This led to experiments in which we tried to measure how resistant bats were to jamming. They dodged wires successfully in noises loud enough that we had difficulty detecting their emitted sounds, which were of course much more intense than echoes from 1-mm wires. Our first experiments were limited because we could not be sure that the available loudspeakers generated all frequencies, including harmonics, of the bats' orientation sounds.

The possibility that bats had some way to overcome jamming intrigued colleagues at the MIT Lincoln Laboratory enough to justify their generous collaboration, which included developing transistorized bat detectors to replace my clumsy modified radio receiver. They also loaned us greatly superior electronic apparatus to improve our studies of bat "radar." The principal collaborator was J. J. G. McCue who worked with us extensively on bat echolocation for several years.

Having constructed a much improved noise field with multiple loudspeakers radiating broad-band ultrasonic noise from both ends of our flight chamber, we turned to a long-eared bat. *Corynorhinus townsendii* from caves in West Virginia, because they emit lower-intensity orientation sounds that we could match more adequately with our battery of loudspeakers. We persuaded them to fly back and forth through four rows of vertical wires, facing one of the arrays of loudspeakers at each end of the flight space, while we recorded their orientation sounds and their flight paths. The loudest noise we could deliver barely prevented them from successfully avoiding the wires.

If one naively treated the air between the bat and the wire obstacle as a single communication channel, the bats appeared to exceed the theoretical limits for detection of signals in noise predicted by information theory. That sounded exciting, and helped elicit the magnificent cooperation from the Lincoln Laboratory. But bats have two ears, and close analysis of our data showed how they could appear to be defying information theory. When the noise was really difficult they changed their flight paths. Instead of flying straight from end to end of the flight chamber with minor deviations to dodge wires, they began ziz-zag flight that approached the wires obliquely. This meant that echoes from the wires reached their ears at considerably different directions from the jamming noise. Figuratively speaking, the bats were using two-point interferometry. Grinnell also showed that evoked potentials could be elicited from bat brains in our jamming noise *if* the noise and signals comparable to echoes from the wires arrived from different directions (Griffin et al., 1963). I have always found these experiments quite intriguing, but when I presented a paper on bats' resistance to jamming at a meeting of the American Physiological Society, the audience turned out to number zero. Nor are these experiments mentioned in recent reviews of bat hearing and auditory discrimination.

Initially it had been a real surprise that bats used echoes from their ultrasonic sounds to avoid obstacles. Then, this sort of collision avoidance was extended by the recognition that they catch their insect prey by echolocation. But could they distinguish between different objects that returned echoes of their orinatation sounds? They chase inedible pebbles tossed into the air, suggesting that they can't tell them from flying insects. Yet no one had reported bats chasing fallen leaves or raindrops, so that this was an open question. It seemed reasonable to infer that they must have some ability to detect differences in size of sonar target, but Webster was proud to display a flash photograph of a bat grasping a tennis ball between its wings. Perhaps bat sonar is an all-or-nothing affair and they simply turn toward and attack anything that returns echoes.

To study the possibility of discrimination between different sonar targets, we tossed mealworms into the air just in front of approaching bats, and several *M. lucifugus* learned to catch these unnatural but tasty "flying" insects. When a bat had become adept at catching tossed mealworms, we began tossing up pebbles, metal spheres, and other inedible objects of roughly the same size. At first the bats attacked almost anything from BB shot to tennis balls, but after a few days some individuals began to be more selective and turn away without touching the inedible junk while still catching most of the mealworms. We presented them with spheres of different diameters, and those closest in size to mealworms were more difficult, but in time even these were rejected while real mealworms continued to be captured. This indicated something more than simple discrimination based on amplitude of echoes.

We therefore turned to disks, and in our best experiments randomly interspersed two sizes of disk between mealworms, one estimated to generate lower, the other higher amplitude of echoes. But both mealworm and disk echoes vary 100- to 1000-fold in amplitude depending on the angle at which sound waves strike them, so that this disk versus mealworm discrimination seemed appropriately challenging for our bats. After several days of practice a few individual *M. lucifugus* did learn to make this discrimination quite well, catching 80 to 90% of the mealworms, and turning away from the majority of the disks. This was impressive because measuring amplitudes of the echoes of the disks and mealworms that returned from a variety of directions showed almost complete overlap in power spectrum levels. It seemed clear that bats could not achieve this discrimination simply by learning that one sort of echo power spectrum meant a tasty mealworm and others meant a hard chunk of plastic (Griffin et al., 1965). James Simmons and his colleagues have recently proposed that bats detect the temporal patterns of echo maxima over intervals of much less than 1 μsec (reviewed by Simmons, 1989).

In 1965 discussions with Fairfield Osborn, president of the New York Zoological Society, and Detlev Bronk, president of The Rockefeller University, led to the opportunity for me to organize a research program in ethology sponsored jointly by the two institutions. I am proud to have facilitated in this way the outstanding investigations of Peter Marler, Fernando Nottebohm, and many of our younger colleagues. In 1970 I nearly dropped the telephone from my ear on hearing Frank Stubbs, a trustee of the Mary Flagler Cary Charitable Trust of Millbrook, New York inquire whether we might like to establish a field station there, which we were of course delighted to do.

Once the collaborative arrangements at Rockefeller University and the New York Zoological Society had been established, I set up a wind tunnel large enough for small birds and bats to fly for long periods where we could observe their behavior. Among other experiments Jose Torre-Bueno found that some individual starlings could be induced to fly steadily for hours while their body temperature and heart rate was measured by trailing wires. He later continued these investigations in Vance Tucker's laboratory at Duke where he built a closed-circuit wind tunnel that was sealed tightly enough to function as a respirometer. Previous measurements had indicated that flying birds, like fixed-wing aircraft, have a minimum energy expenditure at some "optimal" flight speed, with marked increases when flying faster or slower. But to every one's surprise, when starlings flew at various speeds in this apparatus their metabolic rate did not vary appreciably (Torre-Bueno and Larochelle, 1978). Starlings, and probably other birds, change their wing and body shapes to maintain efficient flight over a wide range of speeds. Once again living organisms turned out to be more efficiently complex than we had believed possible.

The sensory basis of bird navigation continues to challenge scienific explanation. One aspect of the bird navigation problem is the question of whether birds can maintain an appropriate direction of migratory flight when "flying blind" in or between layers of opaque cloud that prevent them from seeing either the stars or the ground. Previous radar observation had suggested that migrants do this, but I wished to gather more definitive data that would show just how accurately migrating birds could maintain an appropriate course when one could be sure they were in fact flying blind. With the collaboration of Larry Eisenberg of the Rockefeller University Electronics Laboratory we adapted for radar bird watching a Korean War surplus fire control tracking radar. This massive assembly of vacuum tubes and elegant machinery could track individual birds, and even insects, at ranges of a few miles. After Ronald Larkin adapted a digital computer to analyze the continuous stream of data on a target's azimuth, elevation, and range, we could plot in three dimensions the flight paths of individual birds with an accuracy of a meter or less, even when they were flying several hundred meters over our heads. When operating this apparatus I felt I *was* a bat.

On nights when ground observations and meteorological data on cloud heights were available our bird-watching radar sometimes showed a few migrants flying straight and level in seasonally appropriate directions even when they must have been flying blind (Griffin, 1973), but the density of migrants was much lower under these conditions. Apparently most birds avoid flying blind, but some at least are able to do so. How they manage to do this remains an unsolved scientific question. We also took our bird watching radar to sea, thanks to an invitation from John Teal of the Woods Hole Ocanographic Institution, and tracked numerous migrating birds and insects over the western North Atlantic. The resulting data, combined with radar tracking of free balloons to measure wind velocities where we tracked birds and insects, showed that birds must fly for at least two or three days to migrate from New England to the Caribbean, and some insects must have maintained powered flight for many days to reach the places where our radar tracked them (Larkin *et al.,* 1979; Larkin, 1991).

One popular theory is that migrating birds are sufficiently sensitive to the earth's magnetic field to orient their flight by some equivalent of a magnetic compass. The positive evidence consists almost entirely of weak statistical effects of earth strength fields on orientation of birds fluttering in small cages. All efforts to locate a sensory or neural mechanism that would allow such magnetic sensitivity, or to condition birds to earth strength magnetic stimuli, had then and have still led to negative results. Torre-Bueno and Larkin tested the possibility that previous negative results might be explained by assuming that birds would respond to earth strength fields only during actual flight. They tried to condition starlings to fly on one side or the other of the wind tunnel according to the direction of a magnetic field generated by appropriate coils. But once again the birds showed no sign of any magnetic sensitivity. This problem remains an exciting scientific challenge.

Another Rockefeller graduate student, James Gould, brought me back to the communicative dances of honeybees discovered by Karl von Frisch, which had so challenged my reductionist attitudes in the late 1940s. In the meantime Adrian Wenner and his colleagues had challenged von Frisch's interpretation of the dances by claiming that other bees do not use the information about direction and distance, which everyone agreed was contained in the orientation and duration of the waggle dance, but simply search for odors of flowers brought back by the dancer (reviewed by Wenner and Wells, 1990). It is impracticable to follow the actual flight paths of bees over hundreds of meters, which would be one way to resolve this uncertainty. Instead Gould devised an ingenious experiment by which he could cause dancing bees to orient the dances in a direction that was very different from the direction the dancer had actually flown to reach a scented food source. The great majority of the recruits that followed these dances searched in the direction indicated by the experimentally shifted dances rather than flying to where the dancer had actually filled her stomach with concentrated sugar solution (Gould, 1976). Von Frisch's interpretation has since been supported even more convincingly by Michelsen et al. (1992) who developed a model honeybee that caused recruits to fly in an experimentally determined direction without providing any goal-related odors.

Maturing scientists often experience what might be called the "philosopause" as they turn to more general questions than those that have occupied their attention for many years of detailed investigation. Mine has involved a growing dissatisfaction with the reductionistic viewpoints so prevalent in biology and psychology. In particular, I had begun to doubt the wisdom of totally ignoring the possibility that animals may experience conscious thoughts and subjective feelings. This led me to attempt to launch a subdiscipline of cognitive ethology (Griffin, 1976, 1984, 1992). I feel that only limited progress has yet been achieved by the small but growing group of ethologists who are trying to learn what nonhuman animals actually think and feel, but I am optimistic that in due course new blood, new approaches, and new ideas will open up this field of scientific investigation. I have often wondered why it took me so long to speak out on this subject, and I believe the chief reason has been the positivistic climate of opinion at Harvard and elsewhere in the 1930s which led me and many other scientists to believe that only reductionist explanations were worthy of critical scientific acceptance. Many surprising discoveries and much shaking up of prior assumptions were necessary before I was ready to think seriously about animal consciousness. Hindsight is always easy, and I may simply be swimming with a changing tide in the history of ideas. But it does seem that firsthand involvement in surprising discoveries is what prepared me to shift my thinking into new and I hope fruitful channels.

Reopening questions about the private, subjective experiences of animals has aroused considerable opposition from some psychologists and ethologists. One of my books (Griffin, 1984) has been called "The Satanic Verses of Animal Cognition." Most psychologists have long since abandoned the strict behaviorism of Watson and Skinner in favor of a cognitive psychology, and there has even been a small movement in behavioral ecology and ethology to consider animal cognition. Yet almost all of the scientists who study animal cognition continue adamantly to avoid any serious consideration of what life may be like to the animals themselves. Thus animal cognition has become respectable, but animal consciousness remains forbidden territory, primarily because scientists see no way to gather objective, independently verifiable data about it. As Latto (1986) put it: "Sadly for those of us who agree that (studying conscious, subjective experiences of animals) would be a desirable goal, there is no evidence that it is anything but unattainable."

Yet we are obviously conscious, and we make useful and significant, though incomplete and imperfect, inferences about the private thoughts and feelings of our human companions. We do this by observing their behavior, especially their communicative behavior, verbal and nonverbal. But we have been brought up to assume that we cannot do this with other species because they do not talk about their private experiences, if such exist. In 1974 it suddenly occurred to me that what ethologists have learned about animal communication opens up an important scientific opportunity. Many animals communicate extensively, and at least some of the messages they exchange may well be expressions of simple conscious thoughts. Insofar as this is the case, animal communication provides objective, verifiable data about what animals are thinking and feeling.

This suggestion that animal communication can provide scientists with a significant though imperfect "window" on animal thoughts and feelings has been a "lead balloon" as far as most of my colleagues are concerned. They feel that animals communicate unconsciously, or, more conservatively, that there is no way we can tell whether any of their communicative behavior conveys even the simplest conscious experiences. But it seems to me that our scientific aspirations in this area are still needlessly inhibited by vestiges of behaviorism that linger on as a sort of "mentophobia." Furthermore, many other types of evidence suggest that animals are quite capable of simple perceptual consciousness. These include versatile adjustments of behavior to cope with newly arisen challenges, together with the growing evidence from neurophysiology that all central nervous systems operate on the same basic principles. The aversion to any recognition of animal consciousness has led many behavioral scientists to discredit all such suggestions by exaggerating them into allegations that animals engage in thoughts rivaling the human level of complexity.

It has been pleasantly stimulating to become involved in a heated scientific controversy. The term cognitive ethology continues to be used even by some who are most critical of my ideas, apparently in the hope that animal cognition can be studied fruitfully even though animal consciousness remains taboo. Recognizing as clearly as my critics that studying subjective experiences in other species will be difficult, I continue to believe it is possible. One problem is that scientists who reject any possibility of progress in this area seem to require absolutely perfect proof of any statement about animal consciousness before recognizing the possibility that it may be open to scientific investigation. Yet such premature perfectionism would have seriously impeded scientific progress in attacking other difficult problems; it is difficult to understand why is it so fervently demanded in this case.

After my retirement from Rockefeller University, Harvard has generously appointed me an Associate of Zoology and allowed me to work at the Concord Field Station of the Museum of Comparative Zoology. In 1996–1997 I was even able to offer a tutorial seminar in cognitive ethology for Harvard undergraduates. Because I just love trying to solve scientific problems, and in particular trying to understand animals, along with discussions of animal consciousness I try in a limited way to study the endlessly and significantly fascinating behavior of real animals under natural conditions. Specifically, I am analyzing the role of near-field acoustic signals in the dance communication of honeybees, and seeking to understand the apparently purposeful behavior of beaver.

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