

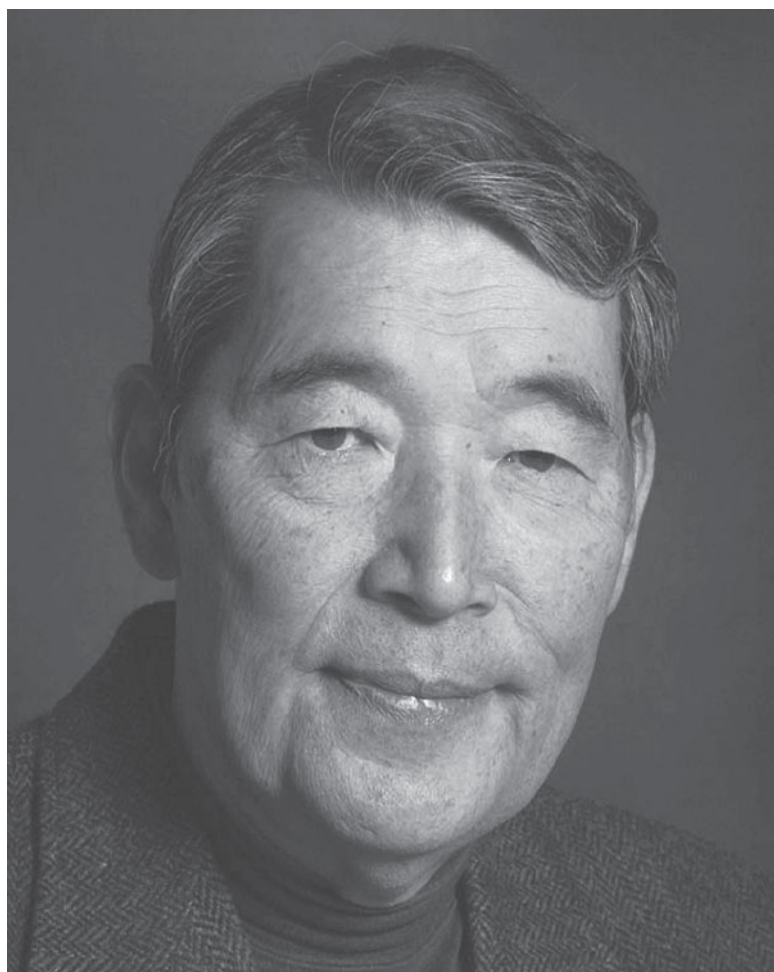


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Masakazu Konishi
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Masakazu Konishi

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Masakazu (Mark) Konishi has been one of the leaders in avian neuroethology since the early 1960's. He is known for his idea that young birds initially remember a tutor song and use the memory as a template to guide the development of their own song. He was the first to show that estrogen prevents programmed cell death in female zebra finches. He also pioneered work on the brain mechanisms of sound localization by barn owls. He has trained many students and postdoctoral fellows who became leading neuroethologists.

Masakazu Konishi

I was taken by surprise when Larry Squire asked me to write an autobiography, because I did not expect to die soon. My mother used to say that I should not do anything for her after her death, because she could not see it. True, I shall not be able to see what will be written about me. So, here is my version that I can see. I thank Larry and his committee for including me in this group of distinguished scientists.

My Origin

I was born on February 17, 1933, in Kyoto as the only child of “Nishijin” weavers. The section of the city known by this name is famous for silk sashes and kimono. My parents lived in a rented row house and worked at home using looms and silk provided by their contractor. My parents received little education, because they too grew up in poor weavers’ homes. My father went to school only for the first 2 years to learn how to read and write simple sentences, whereas my mother was told that all she had to learn was to read price tags, because teenage girls in her social “class” tended to become maids for rich families. Apparently, her father neglected the registration of her birth (1901) for 3 years. This meant that she would be 3 years older than other kids in her school class. Her father avoided this potential embarrassment for her by not sending her to school. My mother was forever bitter about her father’s misjudgment.

The pacific war (1941–1945) started when I was 8 years of age. The first bad thing that emerged with the war was the militarization of schools. Teachers treated little children like soldiers. The whole school started daily with the broadcasting of the national anthem and a speech by the principal. Otherwise, the war did not seem to affect the life of ordinary people until the United States started to bomb cities and food shortage became acute. To cope with this situation, we planted edible plants wherever we could find space, including schoolyards. One half of the playground in our school was converted to underground bomb shelters and arable lands by the little hands of pupils. I raised edible plants in our backyard and on the roof of our house where I used boxes filled with soil to grow plants such as pumpkins. My pet rabbits, which I raised on weeds, became important sources of proteins. As the country was entering the last phase of the war, the differences between rich and poor became small, because there was little that money could buy. This equalization was perhaps the only unintended benefit of the war. My mother appeared to thrive

under these conditions, because she was so used to deprivation. While my father had to work in a military factory in another city, she managed to find a source of black market beef for distribution with profit.

The people of Kyoto were lucky, because the city was never bombed, when all major cities were literally reduced to ashes. I recall seeing hundreds of miserable looking and crippled refugees in the Kyoto train station immediately after the bombing of Osaka, which is a large city some 40 kilometers away. Although Kyoto was spared, we suffered from food shortages, which were more severe after the war than during the war, because an economic chaos followed the war's end. My father and I would go to countryside to buy rice or anything edible including watermelons from farmers. They did not take cash, because there was nothing the money could buy. We took used clothes including my mother's for exchange. This experience also prompted my father to buy and sell used clothes. This was the first time my father succeeded in business well enough to rent a nice store near the center of the city. As the postwar chaos subsided, so did his business.

My mother lived and worked alone since my father's death at 60 years of age. My grade-school friend Tatsuo Naito kept me informed of her after my departure for the United States, because he delivered mail in her neighborhood. When he wrote me that she could no longer take care of herself at 81 years of age because of senility and deafness, I decided to bring her to Pasadena, California. I had no other choice as her only son. Putting one's parent in an old people home was thought to be the worst thing a child could do to his parents. Nothing was harder than taking care of my mother, because we could not communicate with each other. Judging from her attitude, I was different from other people, although she would tell my guests that I was her "brother." Fortunately, she had no other illnesses until her death at 89 years of age. Despite the hardship, I experienced some enlightening moments. Watching TV about marine life, she said "I did not know the octopus swims the head first." This was her first time to see an octopus that moved. Another time, when I took her out for a drive, she was amazed to see men running on the street with their upper body uncovered. She said "They are naked." Even then grown men did not run "naked" on city streets in Japan, while some women walked bare-breasted in our neighborhood. People did not see any sexual connotation in the milk-producing organ. My mother also caught a live quail that flew into our house and kept it in a cage until I came home. I had never expected this depth of observation and reasoning by a person who seemed to have lost her rational mind.

Early Schooling

My father read storybooks for me before I learned how to read in school. My mother occasionally asked our janitor neighbor to help me with arithmetic. I am bad with numbers to this day. When I was a third-year pupil, our teacher,

Mr. Goto, asked our science class how we could turn two wheels in opposite directions with one belt. I instantly answered that twisting the belt would do it. He looked astonished and said emphatically “Yes, you are right.” I knew this trick, because I used to play with my mother’s spinning wheels. Nothing gave me more confidence than his praise, and I began to get better grades. As the only child, my best playmates were animals including insects, fish, birds, rabbits, and dogs. When Mr. Goto showed us how two spiders fought upon meeting each other on a stick he held horizontally, I was so happy to see that even our teacher (God for us) played like me.

When I finished my grade school education, I did not have any role model to follow. My parents did not have any ideas, although my mother complained that our relatives were against giving me higher education. One of my school friends told me that he was going to a private agricultural middle school in the southern suburb of the city. I decided to join him because of my aspiration for ranching. I loved American cowboy movies mainly because of the animals that appeared on the screen. However, the school quickly disappointed me, because I was bored by the subjects taught and by the bad teachers. I looked around to find that there was a new public high school with an agriculture section near the opposite end of the city. The question was how to transfer to this school. My parents knew a local politician who had some connection to the city school board. He apparently smoothed the way for me to move to the new school. Later I returned his favor by volunteering to work for his election to the city government. All I did was to broadcast loudly his name from his small election headquarters as Japanese politicians still do today. I liked the new school, but I quickly switched from agriculture to the liberal art section that was added after my arrival, because I started to mix with kids who were preparing for college entrance examinations. These kids also had middle-class hobbies such as tennis and skiing. Because I was already hiking a lot by myself or with my dog, I joined the mountaineering club. Most of its members also belonged to the biology club, which I led. The club activities helped me come out of my only-child cocoon.

There was only one biology instructor, Mr. Yoshida who was also my homeroom teacher with whom we had lunch everyday. He did not teach well, but I liked him because of his bear stories. He had gone to Hokkaido University in Sapporo. This island is known for big brown bears like the grizzly bear of North America. They kill a few people every year. The teacher had a little book that contained scary yet fascinating stories about how bears murdered people. The university was also known for the impact of an American professor named William S. Clark from Amherst College. When he was leaving Sapporo after 2 years as the head of the then Sapporo Agricultural College, he told his disciples (24 students), “Boys be ambitious.” Indeed, some of them became leaders in the Meiji era (1868–1912), which signaled the rise of modern Japan. Every Japanese child read about William S. Clark, because this story was in a school textbook. Our high school principal also worshipped

William S. Clark. I thought that I should prepare for the entrance examinations of this university. Japanese universities use only written tests for deciding admission or rejection. Neither high school grades nor letters of recommendation are used. This was a saving grace for me, because not only were my grades average but also few teachers would have written good letters for me. Our principal once confronted several members of my biology club to ask if they were seriously studying for the college examinations. He said that he asked us because our parents had asked him about us. I was sure that my parents never asked such a question, because they did not know how one gets in a college. Because applicants from Hokkaido alone did not make the entry competitive enough, the university let the applicants from far away areas to take the tests in Tokyo. I traveled to the capital for the first time. When I told my biology teacher Mr. Yoshida that I passed the exams, he was incredulous at first. No wonder, because I pretended not to study for the tests. The principal congratulated me and asked me to send him a portrait of William S. Clark if I found one in Sapporo. I gladly obliged.

College Years

My parents gave me money to travel to Sapporo and live there for a while. Although my expenses were low, I knew that my parents could not afford even that level of expenditure on a continual basis. I earned some money as a day laborer and a private tutor for high school kids. My first rented room was like a prison cell of 3 m long by 2 m wide without any furniture, although all I needed was a low wooden table. I brought from home a set of bedding materials and a bicycle. I ate potatoes and herrings day after day because they were the cheapest items. To compensate for this “hardship,” the beautiful campus gave me a peace of mind and hopes. It had large elm trees and deep green lawn (the only Kentucky blue grass in Japan), meadows, streams, forests, apple orchards, and barns with horses and cows. This campus differed radically from all other former imperial universities, which had small gardens of white sand and pine trees. I was fortunate enough to receive a government loan for my undergraduate years. I even saved enough money to help my parents during the fatal illness of my father.

After the war, Japan adopted the U.S. system of college education in which students took general subjects for the first 2 years before specializing. This was a saving grace for me, because I was again thinking of majoring in agriculture for which this university was famous. As I compared zoology courses taught by the science faculty and those taught by the agricultural faculty, I became convinced that I should choose the former. Nevertheless, I found that most lectures in zoology were quite boring with a couple of exceptions. The neurophysiology course given by Professor Mitsuo Tamashige was sophisticated and interesting. He took a liking to me and invited me to use his equipment in his office, a rare privilege for a Japanese student. My project

was to show that the rhythmic movement of the foot in land snails was centrally controlled. He and his assistant Dr. Mitsuhiro Hisada also took us to the university's beautiful marine station to study the behavior and physiology of marine invertebrates. Dr. Shoichi Sakagami also gave an interesting course in which I was made aware of *The Study of Instinct* by N. Tinbergen. I thought that this was the field for me. One gets paid and praised for fooling animals with dummies. I was already doing it as a child. Sakagami and I also did field work together on great reed warblers in a large reed bed near our building. I was particularly interested in studying the response of a single territorial male to tape-playback of his own song. Portable tape-recorders were not available, and tapes were made of paper. I had to borrow a long electrical cable for my project. The vigorous response of the bird to tape-playback of his song was very exciting to me. However, I ended up writing my master's thesis on brood parasitism by cuckoos, which lay eggs in the nests of reed warblers.

I was thinking of studying abroad since my early college years. I diligently went to English conversation classes at the American Cultural Center and an Episcopal church in Sapporo. I also made a few English-speaking friends including Christian ministers, diplomats, and U.S. army officers. Among them Mr. Daniel Meloy, the U.S. consul of Sapporo, was most supportive of me. A couple of times we went on long Jeep trips across Hokkaido. He would ask whether I wanted to speak English or Japanese, which he spoke fluently. Of course, I always chose English. He gave me one of his Brooks Brothers jackets after having seen me in a black university uniform at one of his official cocktail parties for local political and business leaders who seemed to look down on me. I kept and wore the jacket for many years in the United States. Judging from what my American friends told me, the United States offered a lot of academic opportunities, although I had briefly thought about going to Oxford, because two people I knew went there to get training in avian ecology. I carefully studied the catalogues of U.S. universities at the American Cultural Center and wrote for application forms. I applied for admission to several universities including the University of California, at Berkeley (UC Berkeley), the University of Michigan, and Yale University. I chose these schools, because they were known for vertebrate zoology. UC Berkeley was the first to send me a letter of acceptance. This fast response influenced my decision. Also, my roommate told me that his father liked Berkeley as a graduate student. Yale and Michigan also accepted me. Now, my problem was how to say no to these schools without offending anyone. In Japan, this "double dealing" would have caused problems for me. So, I wrote very polite letters profusely apologizing for declining their offers. Professor Francis Evans of Michigan wrote me back congratulating me for my success at Berkeley. This gesture profoundly impressed me. I learned later that this is how most U.S. professors would respond. In contrast, Dr. Sakagami told me that I should have not directly asked for a letter of recommendation from

his boss Professor Tohru Uchida who was on a sabbatical leave at the University of Iowa. I flatly told Sakagami that it was my own business. A few days later, he told me that I could not stay for further graduate study, although I had no intention to continue there any way. It was exactly this kind of hierarchical system that I wanted to leave. I never looked back. It was ironic that I should later receive an honorary doctor's degree from Hokkaido. Sakagami came to see me in Berkeley before I finished my degree there. We did not discuss the past. I respected him as a fine scientist.

Graduate Study

I was fortunate to receive a Fulbright travel fellowship to cross the Pacific. I had only 50 borrowed dollars upon my landing in Seattle, Washington. I arrived in Berkeley on September 9, 1958. I was impressed by the streamlined administrative procedures to get me started. I got a teaching assistantship, which meant a salary of about \$1500 for two semesters in addition to a tuition exemption. I also earned additional \$300 by assisting a summer course. I originally wanted to study under Professor Alden H. Miller who was well known for his study of avian speciation. I thought I would investigate the role of behavior in speciation. However, while I was still in Sapporo I heard that Miller was abroad on sabbatical and that there was a new assistant professor named Peter Marler. Because I had read and liked his paper "Some Characteristics of Animal Calls," I immediately asked him for admission to his group. I was incredibly lucky. In addition to the teaching assistant duty I spent much time taking a few required and other courses. It took me about 2 years before I could do research full time.

I was lucky again to receive an excellent fellowship in my third year. My first project in the Marler laboratory was to determine the acoustic properties of song that birds use for species recognition. I chose birds with simple songs like the Oregon junco (*Junco oreganus*) to be able to modify the song with ease. The laboratory had a portable tape recorder (Magnemite 610) in which turning of the reels was done by a coiled spring as in old phonographs. I had to spin a heavy flywheel by hand to start the machine turning and crank up the spring every so often. The machine basically worked flawlessly and I recorded many songs in the Berkeley hills. I used my first Kay sonagraph in the Marler laboratory to look at the acoustic properties of songs. How do I change recorded songs though? Computers were not available then. I recall asking people at the Haskins Laboratory whether they could synthesize birdsongs with their Visible Speech machine, which scanned and converted cutout patterns (holes in paper) into sounds. Years later I got to know Alvin Liberman, who was one of the designers of the machine. He did not remember any letter from me. He said that he would have helped me, if he had read my letter. If I could see sounds on magnetic tapes, I might be able to cut and paste together different parts of a song. I either figured it out by

myself or learned from someone that the magnetized parts of the tape might pick up fine iron particles. I got hold of iron powder and passed tape through a mound of it. I was delighted to see patches of iron powder corresponding to the song syllables in the trill type song of Oregon juncos. Assuming that the constant silent interval between syllables was important for species recognition, I cut and pasted tape to make the interval highly variable. When I played back this type of song in the field, wild juncos responded to it. This result was a great disappointment for me, because I had expected no response. Also, this project turned out to be very time-consuming; I could do field experiments only during the spring breeding season. I had to become realistic, because I was in my third year of graduate study.

Also, graduate students had to take an oral examination before submitting their theses. Although I was far from writing a dissertation, I decided to take the examination in my 4th year. I had a star-studded exam committee consisting of Ledyard Stebbins (plant evolution), Michael Lerner (population genetics), and Sherwood Washburn (human evolution). Because Stebbins and Washburn liked my term papers, they basically passed me without asking any hard questions. I was afraid of Lerner, because he was more quantitatively oriented than the others, but he asked what I had expected from him. He also asked if I knew anything about Lysenko. I knew a lot about this crazy Russian agronomist, because he was a hero among communist students in Sapporo. Later when I happened to see Professor Lerner in the cafeteria, he invited me to his table. He told me about new things he was thinking about. I did not understand anything he said!

So far as my dissertation research was concerned, I decided to go in a new direction. The idea of central coordination was hotly debated between ethologists and psychologists. It goes back to the turn of the last century when people like Friedländer and Biedermann carried out simple but clever experiments to prove or disprove the theory. Later people like Erich von Holst and James Gray performed sophisticated behavioral experiments to obtain evidence for or against central coordination. Peter Marler covered central coordination and endogenous rhythms quite extensively in his animal behavior course, because central coordination was at the core of the Lorenz-Tinbergen model of instinctive behavior. It was Donald M. Wilson who used neurophysiological methods to provide the most convincing evidence for central control of wing beating in the locust. While I was in Berkeley, Wilson joined our department and served on my thesis committee, which also included the famous Frank Beach of sexual behavior from the Department of Psychology. Wilson later moved to Stanford and invited me from Princeton to give a couple of lectures in the course he and Donald Kennedy were teaching. Shortly after this visit Wilson died in a rafting accident. I always wonder what Wilson would be doing if he were alive today. His work triggered a bandwagon effect in which other people tried to replicate his finding in every possible preparation. In retrospect, it is interesting to realize

that the idea of central coordination did not affect the students of birdsong at that time, because few of them were interested in neurophysiology. Also, mechanistic views of birdsong simply did not exist.

I thought that the relationship between vocalization and hearing resembled that between motor coordination and sensory feedback. It was already known that humans could not speak normally when auditory feedback was removed or delayed. I thought that similar experiments in birds had to be done. I was also aware that I could not fail in this project, because either positive (deafening affects song) or negative results were worth publishing. I checked the literature on the subject and found Johann Schwartzkopf who developed a method for removing the avian cochlea in 1949. He also reported that the flute-like quality of a learned social call in adult bullfinches (*Pyrrhula pyrrhula*) gradually became shrill after deafening, although this operation did not affect other vocalizations. Similarly, Messmer and Messmer, for whom Schwartzkopf deafened blackbirds (*Turdus merula*), heard some abnormal sounds from these birds. However, I could not check the accuracy of their impressions, because they had no pictorial way to visualize birdsongs before the age of the sonagraph, which apparently did not reach German zoology laboratories until after 1956.

I read Schwartzkopf's paper in German to learn his methods. This was not a big problem, because I had learned enough German in my undergraduate years in Sapporo. His illustrations of relevant anatomical structures and head-holding devices were very helpful. The main problems were the tools that I needed for his methods. The Marler laboratory was not equipped to do surgeries. The most advanced surgical technique the laboratory used was laparotomy, that is, making a hole in the bird's body wall to see the gonads. I learned this method from Alden H. Miller and introduced it to the Marler laboratory. Deafening and laparotomy methods required a dissecting microscope and a light source that could illuminate the bottom of a small hole. The question was how to direct a light beam into a small hole without obstructing the view with the light source itself. Today, we can buy a dissecting microscope like the Zeiss Operating Microscope that comes with a vertical illuminator. Another graduate student who knew the method of vertical illumination told me how to solve the problem. According to his idea, I should use a mirror, which is coated only on one side, and place it 45 degrees relative to the optical axis of the dissecting scope. So, what this arrangement did was to allow me to see the bottom of the hole through the mirror, while this was directing some light into the hole. Where do I get such a mirror? He told me how to make one by exposing one side of a large cover glass to smoke from a candle.

My next problem was to find materials for making fine fishhooks. Schwartzkopf put a small wire hook at the end of a probe like a thin chopstick. He inserted the hook through a hole made in the bony cavity containing the cochlea. I looked for fine but relatively stiff wires without success.

Then, it occurred to me that light bulbs contained wires holding the filaments. I collected a few burned out light bulbs. They did contain fine tungsten wires that were just perfect for making those hooks. Actually, I have never found a better material. As soon as I discovered this fact, I asked everyone around to save burned-out light bulbs. The remaining problem was how to adjust the angle of the bird's head relative to the optical axis of the dissecting microscope, because the scope was on a fixed stand. I needed a small table that could be tilted around a pivotal point. I went to a junkyard and found a material suitable for the above purpose and that was an automobile rear-view mirror. I replaced the mirror by a plastic plate and constructed a simple device for holding the bird's head. The plastic table could be moved up and down around the ball joint that came with the mirror. When I was almost finished with my research, the Marler laboratory got a National Science Foundation (NSF) grant that included a dissecting microscope with a vertical illuminator! I gave my operating table to Fred (Fernando Nottebohm) who used it for his thesis on chaffinches in Cambridge, England. I recall seeing the table in one of Fred's laboratories at the Rockefeller University years later.

I operated on several species of songbirds using the Schwartzkopf methods. Most of the data in my thesis came from these species. As I worked on larger birds and also more abundant species like the domestic chicken, I found that I could remove the cochlea through the ear canal instead of a hole made in the skull. In recent years, I have taught several people to deafen zebra finches (*Taeniopygia guttata*) with this method using Zeiss Operating Microscopes. The Marler laboratory had a menagerie of animals ranging from fish to unusual mammals like kinkajous and a badger. No one seemed to be bothered by the crowing of my roosters, which I kept in an old greenhouse for plants in the central courtyard of the building. When the Animal Behavior Field Station was built up on the Berkeley hills, I moved some of the chickens there to make clean recordings. When Fred and I met there, we would return to his apartment for lunch with steaks and red wine as in his country, Argentina. Because we did not have enough soundproof boxes to house a large number of birds individually, I put all my deaf passerines in separate cages within a penthouse on the roof of the Life Science Building. I lined the penthouse walls with cheap sound absorbing materials. I spent most of my daytime sitting there listening and recording, because nothing was automated as it is today. I made about 3000 sonagrams for my thesis. I still have them in my office. To make one sonagram took a few minutes. I sometimes read a book while I was making sonagrams. The first set of data came from the chickens, because they matured much faster than wild birds. I knew enough about the vocalizations of chickens from my childhood experience. It was particularly interesting to see how deaf chickens failed to respond to vocal signals such as cackling and aerial alarm calls of their flock

mates. Sonagrams of several vocalizations showed no systematic differences between normal and deaf roosters.

Around this time a German named Erich Bäumer published a paper on chicken vocalizations. I could guess what vocalizations he was referring to from his German descriptions. He was kind enough to send me his tape recordings upon my request. I made sonagrams of his recordings and compared them with my own recordings. He and I agreed on all identifiable adult vocalizations. Pictorial catalogues of animal voices with their functional significance were rare at that time except for the one by Marler for chaffinches. I also noted that there were graded and discrete signals (I used the terms *analogue* and *digital*; D. Wilson did not like the term *digital*, because the signal was not digital in the true sense of the word). Marler had already pointed out this distinction in his theoretical essay of 1961. Later he also found examples in the voices of several primate species. The chicken results were neither discouraging nor encouraging. Had I just worked on chickens, what would I have concluded? Auditory feedback is not necessary for avian vocalizations?

I had reasons to expect that deaf songbirds would develop abnormal songs. It was already known from the work of Thorpe in the chaffinch and also from the work in progress in the Marler laboratory with the white-crowned sparrow (*Zonotrichia leucophrys*) that young birds memorize tutor songs before they can sing. This fact suggested to me that auditory feedback should be indispensable for vocal reproduction of tutor song. I thought that the only way this expectation could be shown wrong would be to have a situation in which vocal memory somehow directly controls vocal motor centers of the brain. This possibility was inconceivable, because birds have to know how their song sounds to know the degree of match between the memorized and vocalized songs. I was, therefore, delighted to see the dramatic effects of deafening on the development of song in the white-crowned sparrow. All other songbirds I used also developed abnormal songs. In my thesis, I summarized my thoughts above in a model in which birds use auditory feedback to match their vocal output with a stored song template. I also reported that deafness did not affect the song of adult white-crowned sparrows. Although recent studies appear to contradict this conclusion, a systematic study of the relationship between age and the effects of deafening in zebra finches by Lombardino and Nottebohm showed that the song of birds 5 to 6 years of age remained unchanged after the operation for a much longer time than that of younger birds.

Of many memorable events in the Marler Laboratory, trips to Inverness (a coastal area north of San Francisco) were my favorites. White-crowns nest in coastal chaparrals. We would arrive there the night before and camp out on the meadows. Peter always brought the whole family including his wife Judith, their young son Christopher, and a Basenji dog. In the evening,

we would talk around the campfire. Chris would babble before going to sleep. His babbles appeared to contain some elements of English to my ears, which were accustomed to the babbling of Japanese babies. Peter was very interested to hear my impression. Another story that must be told is about Fred. When Peter took us to the Chiricahua Mountains in New Mexico to collect nestlings of slate colored juncos (*Junco hyemalis*), Fred got lost and spent all night wandering the mountains. He was carrying a nest with young birds until they died. Fortunately, a passing ranger truck picked him up as he finally hit a road in the morning. As he came back to our campsite, he gobbled a breakfast and threw it up right away before he went to his tent to sleep half a day. Had he disappeared, would we know of the existence of the song control system today?

Postdoctoral Period

After I finished my thesis work in Berkeley, I had to go out of the country, because I had an exchange visitor visa. Instead of going back to Japan where I had no place to return to anyway, I chose to go to Germany for 2 years. This duration may sound very short by today's standard, but many of my graduate classmates opted for teaching jobs right after getting their doctorate. At 30 years of age I was also younger than many of them who had families to feed. On my way to Germany I attended my first International Congress of Ethology in Leiden, the Netherlands (1963). Peter Marler managed to send two of his students, Keith Nelson and me, as speakers, which were more like plenary speakers of today. I could see big stars like Konrad Lorenz, Niko Tinbergen, William Thorpe, and Otto Koehler in the audience. After my talk Don Wilson congratulated me and Koehler came to me to ask if I would publish my results in "his" journal, which was then called *Zeitschrift für Tierpsychologie*. I was so flattered that I simply said yes and kept my promise. John Emlen of the University of Wisconsin approached me to ask if I would be interested in a position in his department. My ego was boosted again later when the German Ornithological Society invited me to speak at their annual meeting in Berlin. The eminent president of the society, Erwin Stresemann, introduced me as "*Ein Wandervogel aus Japan, der Deutsch spricht*." (A German-speaking migratory bird from Japan). My talk received very favorable comments in the society journal (*Journal für Ornithologie*).

Although my primary purpose in Germany was to learn more about the auditory system of birds under Professor Johann Schwarzkopf, it did not work because his new laboratories in Tübingen were not ready. I was also appalled to see primitive university laboratories in postwar Germany. In sharp contrast, facilities in Max-Planck Institutes were close to the U.S. standard then. Because my time was limited, I decided to move to the Max-Planck group led by Otto Creutzfeld in Munich to map the receptive fields of

neurons in the cat's visual cortex using intracellular recording methods. I learned a lot about the techniques from my coworker Satoru Watanabe from Japan. This work did not go far, because we could not hold neurons long enough to map their receptive fields. However, this failure was well compensated by my frequent visits to the Max-Planck Institut für Verhaltensphysiologie in Seewiesen where Konrad Lorenz was the director. I thought that the Institute was a heaven for ethologists. Lorenz told me that I should feel like a member of the institute. Their seminar series brought interesting speakers including the young Jane Goodall fresh from Africa. Her slide showing a chimpanzee inspecting a dead mouse deeply impressed Lorenz. He said, "That is human!"

There were several Seewiesen people whose work caught my attention, including Dietrich Schneider (silkworm moth pheromone), Friedlich Schutz (sexual imprinting in ducks and geese), and Jürgen Nicolai (African parasitic birds). Walter Heiligenberg who later became one of my best friends was a graduate student under Lorenz. Jürgen Aschoff, who was famous for his study of circadian rhythm, invited me to come to see his department in a nearby village, Erling-Andechs. He had a lot of Japanese art objects that his famous father (medical professor) received from some 40 Japanese medical students he trained. There was not a dull moment, because Aschoff knew how to spend time for useful purposes. He asked me to give a talk for him alone. When I used the term "*template*" in this talk, he proposed an equivalent German term "*Sollmuster*" I really liked this term, because it is so expressive. *Soll* means "should or must" and *Muster* "pattern." I used it in the German summary of my white-crown paper in Koehler's journal. Koehler liked the word and asked me how I got this nice term.

Once Konrad Lorenz invited me to his apartment to dine with a Japanese guest who spoke neither English nor German fluently enough to carry on conversation. I had no time to translate for them, because the guest nodded his head saying "yes" every time Konrad stopped talking. This response did not bother Konrad at all, and he kept talking. Later Konrad told me how he fooled a teacher who came to see him for the purpose of meeting a famous man. When Konrad saw a brightly colored male duck and a dull colored female duck dive alternately, he told the teacher "look how the duck changes its plumage colors." The teacher said "Yes." Konrad and I seldom discussed science in private conversations. One time I left a reprint of my white-crown paper on his desk in his office. Later, he thanked me and said he seldom read anything, because he did not want to change his ideas. I knew he read the paper, because he mentioned my name and work in an interview with Joseph Alsop of *The New Yorker* a year or so later. Either Lorenz or Alsop mixed the species when quoting my work. I wrote Alsop that I enjoyed his interesting article except for a small error in the story. Alsop wrote back "glad the error was small." My chairman at Princeton, John Bonner, was very excited about the article and told me that he would put a copy in my file

for future reference. I did not know that *The New Yorker* was such an influential journal.

Assistant Professorship

The U. S. consulate in Munich asked me for an explanation for returning to the United States, because my exchange visitor visa required me to return to Japan. I explained this situation to John Emlen in Madison. He might have intervened on my behalf through his connections. When I had an interview with a consular official, I explained that I really grew up as a scientist in the United States. This plea worked and I was granted a new visa to return to the United States. Also, because President Kennedy had abolished the discriminatory immigration policy against Asians, I could subsequently apply for a green card, opening my road to citizenship later. I liked the campus and surrounding areas of the University of Wisconsin. I was very sorry to miss John Emlen from the beginning of my stay there. He was not well and had to spend a large part of the year in Arizona to avoid certain maladies. I was also bit disappointed to know that I had to negotiate for set-up funds after my arrival. Apparently, offering set-up money to a new faculty member was not a norm then as it is now. While this issue remained unclear, Berkeley and Princeton approached me about a possible appointment. Because Peter Marler was moving to the Rockefeller University, his position was informally offered to me. Although Berkeley was obviously my first choice, I wondered how I would feel among my former teachers. My Japanese background came back to haunt me about the prospect of calling my former teachers by their first names. I chose Princeton in the end mostly because I was curious about good private universities in the United States.

My laboratories in Princeton were in the basement of the former psychology building where Wever and Bray discovered “cochlear microphonics” in 1930. Their hand-made wooden soundproof room was still there for my use. Wever’s group had moved to a new set of buildings outside the main campus. He and his people were very friendly and helpful to me. I learned from them about the instruments and methods for calibrating sound pressures near the eardrum of birds. Wever was conducting comparative studies of reptilian and amphibian ears. It was no accident that my first graduate student there, Geoff Manley, now an emeritus professor at the Technical University of Munich, conducted a comparative physiological study of the reptilian auditory system in my laboratories.

Although the introduction of the sonograph revolutionized research on birdsong, little was known about what songbirds could hear. I chose neurophysiological methods to answer this question. My research strategy was simple; I collected or bought birds whose songs differed clearly in the frequency domain. I recorded single neurons in one of the cochlear nuclei and determined their threshold sensitivities. The results were clear-cut: Birds

that produced high frequencies in their song had auditory neurons that responded to these frequencies. However, all birds could hear low frequencies whether their song contained these sounds or not. I found that the threshold of the most sensitive neuron in a given frequency range was close to the sensitivity measured by behavioral methods for that frequency range. Fortunately, Bob Dooling (now at University of Maryland) who was doing his thesis work under my friend Jim Mulligan from my Berkeley days had a behavioral audibility curve for canaries. I compared it with my neurophysiological results from canaries to find a very good match between the two sets of data. So, if one draws a curve connecting the most sensitive neurons in all frequency bands, one gets a curve similar to the bird's audibility curve. This relationship has been established not only in birds but also in other species including cats.

Having learned the usefulness of single-unit recording, I addressed another issue that occupied my mind. Recall how Daniel Lehrman used Kuo's interpretation of behavioral development in chicks to argue that we had to know more about behavioral development before birth instead of assuming the inborn nature of behavior. This line of argument spread fast to make ethologists apprehensive. For example, according to Gilbert Gottlieb, mallard duck embryos, which were prevented from vocalizing, discriminated poorly between the maternal call of their own species and that of chickens. He also reported that duck embryos responded to the maternal call a week before hatching. These studies got me interested in hearing in avian embryos. I checked if and when duck embryos began to hear in the egg. I showed that neurons of the cochlear nucleus in embryos became sensitive to low frequency sound about a week before hatching. As embryos developed further, neurons became more sensitive and responded to higher frequencies. The sensitivity and the range of frequency became adult-like two days before hatching.

I also did a behavioral study of song development in white-crowned sparrows. My aim was to test whether or not white-crowns reared in complete isolation from the egg could distinguish the song of their own species from that of multiple other species sharing the same habitat. I had this plan despite the fact that Peter Marler had shown not only the inability of nestlings under 10 days of age to learn even the song of their own species but also the ability of older nestlings to choose the song of their own species over the song of another species. This work showed that nestlings younger than 10 days of age could or did not reproduce the tutor song in adulthood. If such birds had been given a second chance of choosing between the original tutor song and a new song during the normal critical period, which song would they have chosen? The question is whether an early exposure to song affects a later choice of song. This was the rationale for raising white-crowned sparrows in complete isolation from the earliest stage of embryogenesis. I wanted to answer this question by collecting newly laid white-crown

eggs and incubating them and raising chicks without exposing them to any birdsong before tutoring. This project required logistical planning. For example, I took a graduate student with me to the Inverness area where we collected a few eggs. We wrapped each of these eggs in cotton and slid it into a test tube. We connected the test tubes side by side with strings into a belt, which we wore across our belly. Our own body heat kept the eggs alive. We brought back the eggs to Princeton and next morning the student drove up to Millbrook, N.Y., where Peter put the eggs in canary's nests. Incredibly, most eggs hatched. Despite this success, I began to think that the number of nestlings we could raise per year severely limited our progress. I also thought that we had to raise nestlings entirely artificially without the help of canaries. So, I decided to suspend the white-crown work.

Full Professorship

The sequence of events that led me to move to Caltech in 1975 seemed simple. Jack Pettigrew who was then an assistant professor at Caltech came to see me in Princeton, mainly because he wanted to see my owls, I thought. Shortly after this visit, I got an invitation to give a talk at Caltech. I was offered a full professorship, and I was quite impressed by the size and quality of space they could provide. This was in sharp contrast to Princeton where my laboratories were in the basement of one of the oldest buildings on campus. However, I had to overcome the anti-Los Angeles prejudice I acquired in Berkeley. I had to think very hard and long, before I could make up my mind. I excused myself by convincing me that even Southern California is better than New Jersey.

Caltech turned out to be a very exciting new center of neurobiology. There were already some well-known neuroscientists such as Roger Sperry, James Olds, "Kees" Wiersma, Anthonie Van Harreveld, and Felix Strumwasser. Also, Seymour Benzer was starting his famous genetic study of *Drosophila* behavior and neurobiology. I always admired Seymour for his courage to venture into this new field despite criticisms and for his devotion to science. He supported me from the day of my job interview in 1975 to the day of his death (November 30, 2007). We taught a course titled "Behavioral Biology" together until he "retired from teaching." Seymour regularly attended our lunchtime meeting called "Neurolunch" in the new Beckman Laboratory of Behavioral Biology, which housed mostly new junior faculty members including John Allman, Jack Pettigrew, Jim Hudspeth, and David Van Essen. Jim Olds and I were the only full professors in the building. This concentration of youthful neurobiologists quickly became attractive to graduate and postdoctoral applicants. I had enough space to accommodate several students and postdoctoral fellows. I could pursue songbird and owl studies simultaneously at the behavioral and neural levels.

Birdsong Neurobiology

I resumed my work on the white-crowned sparrow mentioned earlier. We had to solve a few important practical problems in bird rearing. First, we had to develop a new method of holding and transporting eggs. Our electrical engineer Mike Walsh built a battery-operated portable incubator. This allowed us to stay days at collecting sites at elevations up to 8000 ft in the Sierra Nevada where mountain white-crowns breed. Also, we did not have to drive many hours nonstop to rush the eggs to the laboratory incubator. He also built an incubator, which periodically changed the orientation of eggs as in chicken egg incubators. It was generally thought that passerines could not be raised from birth on the so called “steak food”, which consisted of beef and other ingredients as originally used for raising nestling song birds by W. E. Lanyon of Cornell University. My able assistant Gene Akutagawa found that liquid from the crop of canaries raising nestlings contained something that enabled chicks (of other passerines) to consume the steak food. We raised white-crowned sparrows from birth in complete individual isolation with this method. Gene further found that the “liquid” was not necessary if he fed predigested food for human babies to newborn white-crowns. He even figured out how to raise new born zebra finches, which normally receive partially, digested seeds from their parents. The trick was to feed babies dehusked millet, which is available in health food stores. We showed that young white crowns isolated as eggs preferred the song of their own species to alien songs sung by other inhabitants in the same area. However, some of these white-crowns initially developed a copy of the white-crown tutor song and a copy of one of the alien songs. As the season progressed, these birds dropped the alien song.

In my early days at Caltech, all postdoctoral fellows wanted to work with owls, but I began advising graduate students to work in the field of songbird research, which was to become very attractive to neurobiologists because of the discovery of the brain song control system by Nottebohm and his associates in 1976. I always liked and encouraged graduate students to start new things in my laboratory. I had some adventurous students who would do anything. Larry Katz, who tragically passed away a short while ago, was the most adventurous and skillful. I was so charmed by him that I allowed him to rent a small airplane to fly to Stanford to get a new histological tracer. Next, he suggested that we introduce brain slice techniques. So, he and I drove down to the University of California in Irvine to see slice setups. On our way home, we bought a couple of components, which Larry assembled into a functioning system within a few days. He developed a powerful new method to study the anatomical organization of neural tissues. He would inject a fluorescent tracer into the target area of neurons residing some distance away. He would then make slices of the tissues containing the

somata of the neurons. He discovered that neurons in the same area that project to different targets had different soma and dendritic morphologies. I told him that he could make big contributions, if he would apply these methods to the cat visual cortex, which was the darling of the time. So, Larry wrote his thesis on the cat's visual cortex in my laboratory. It was a big loss to the birdsong field, but it promised a big future for Larry. Rich Mooney later inherited Larry's setup to do his very original thesis work on the nature of synaptic inputs to RA, which receives signals from LMAN by N-methyl-D-aspartate (NMDA) receptors and from HVC by non-NMDA glutamate receptors. His project was the first extensive *in vitro* and intracellular study of the song system in my laboratory and in the birdsong field. This was his idea, because I did not know what NMDA was. His work started a new NMDA cottage industry in the birdsong community.

Mark Gurney was another adventurous student. The Nottebohm laboratory and we independently discovered sexual dimorphism in the song system of the zebra finch. I had this conversation with Mark Gurney who said "These gender differences may be genetic." I responded, "Genetics is molecular biology." He said, "You are right." He did the simplest experiment by injecting sex hormones into developing zebra finch eggs and newly hatched chicks. Mark found that estrogen masculinized the female song system. These birds sang when treated with testosterone in adulthood. Why estrogen instead of androgen? The brain (of rodents and birds) contains an enzyme that converts testosterone from the gonads into estrogen, which induces masculine differentiation in some areas of the brain. After Mark left, Gene Akutagawa and I took over the hormone project. Using radioactive markers to identify neurons, we showed that the neurons that migrated into RA (one of the brain song control areas) were born on the 7th day of incubation. These neurons are large and equal in size in both sexes on the first day of hatching. However, they undergo gradual atrophy and ultimately die in the female RA, whereas they grow in size in the male. We further showed that exogenous estrogen could prevent the atrophy and death of these marked neurons. There was a gradient of estrogen action; the earlier it was injected, the more effective it was in preventing cell atrophy and death. Today, estrogen is thought to be good for postmenopausal women not only for the maintenance of normal physiological conditions but also for preventing the death of their brain cells, although some experts disagree on this point. Who would have thought of a link between women's health and songbirds?

Mark Gurney and Larry Katz were good buddies when they were exploring something new. One day they set up the necessary gear to do intracellular recordings in HVC (another brain song control area) of a zebra finch. I told them to clap hands to see if neurons responded to sound. To their great surprise, they saw responses in HVC. I showed them how to use auditory instruments and measure sound levels. At any rate, they wrote up a simple

report. It was flatly rejected twice as an artifact, although it was eventually published. Another student, Jim McCasland, was recording multiunits (many neurons with a single electrode) in the HVC of behaving canaries. I told him to play canary song. He found that neurons responded much better to the song of a bird of the same breed than to the song of another breed of canary. Jim also showed that HVC neurons did not respond to playback of the bird's own song, while the canary was singing and immediately after the end of song. These preliminary findings were exciting, because the presence of auditory responses within the vocal control pathway suggested a possible link between the auditory and vocal control systems. Former postdoctoral fellows Marc Schmidt and Teresa Nick who joined me much later continue their work on the related problems of song selectivity and gating in zebra finches.

The discovery of neurons selective for the bird's own song was exciting, because they might represent the song template. I wanted to know what features of song these neurons were detecting. This study required analysis and synthesis of sounds. The song of zebra finches was too complex for analysis and synthesis at that time. I suggested to Dan Margoliash to undertake this project with white-crowned sparrows with simple tonal song, because Dan was the only student who could use computers. His results clearly showed the importance of both syllable structure and sequence. Separate groups of HVC neurons project to RA and X. When Allison Doupe joined my group as a postdoctoral fellow, she decided to check for auditory responses in the anterior forebrain pathway. She found selectivity for the bird's own song (BOS) in LMAN and X. Furthermore, she showed that injections of a local anesthetic to HVC abolished auditory responses in X and RA, suggesting that these nuclei received their song-selective property from HVC.

Caltech has a graduate program called Computation and Neural System (CNS). CNS students are bright. When these students appreciate biological problems, they can do excellent research. I was telling my group in one of our luncheon gatherings that I had heard about new methods of recording from neurons in vitro called "whole cell clamp." I told my group that it would be interesting to try the methods in vivo. No one said anything at that time, but Mike Lewicki, a former mathematics student from Carnegie Mellon, came to my office to ask if the methods would work in vivo. I said "why not?" He started right away. He read that he could count the number of bubbles to measure the tip diameter of a capillary electrode. Because this method was too crude for him, he took electrodes to a scanning electron microscope on campus. When he plotted the tip diameters measured with this method and those with the bubble method, he got a straight diagonal line. This episode impressed me very much, because I like students who go beyond my knowledge and ability. Then, we heard that an assistant professor elsewhere was doing in vivo whole cell clamping. Mike went to see the person and came back to tell me that their methods were similar. Mike turned out to be a very

good neurophysiologist. He showed that the sensitivity of HVC neurons to syllable sequences involved inhibition; for example, a neuron responded preferentially to syllable A followed by syllable B. The reverse order induced inhibition in the neuron. He developed a simple circuit model that detected specific syllable orders.

From my time in the Marler laboratory, one topic stuck in my mind. It is about designing experiments to test whether or not delayed auditory feedback affects song. I got some people interested in the subject at Caltech. I read that someone designed a theater in which the audience wore wireless headsets and listened to music. This alone is not new, but coils surrounding the theater transmitted the electrical signals. When I told Dan Margoliash about this story, he got interested and built a small version of this setup. He wore magnetic earphones and stuck his head in the coils he made. This was a short-lived project, because Dan heard no sounds! More recently another ambitious student took this topic seriously and got excellent results by different methods. Anthony Leonardo, another CNS student from Carnegie Mellon, was not only smart but also technically skilled. He built a computer-based system to detect song and play back its delayed versions. Although birds heard natural and delayed feedback, they gradually changed the probability of syllable sequences and also syllable structure in some cases. Remarkably, the original song gradually recovered after normal feedback was restored. One summer, he went to the Bell Telephone Laboratory to work with Michale Fee in designing and testing the now well-known microdrive for zebra finches. He assembled two microdrives for his use in our laboratory. He quickly figured out how to place electrodes in LMAN. Recording single neurons in the LMAN of singing birds would answer the most important question about its role in the feedback control of song. Anthony did not find any effects of delayed feedback on the firing patterns of LMAN neurons. Despite these advances the control of song by auditory feedback remains one of the most important issues in birdsong research.

Owl Research

I became interested in barn owls when I heard Roger Payne present his thesis work on prey capture by barn owls in the 1963 International Congress of Ethology in Leiden, the Netherlands. My associations with barn owls started shortly after I moved to Princeton in 1966. A nice university employee who was curious about my research perhaps spread the word that I was interested in barn owls. Before long a local bird watcher brought three nestling barn owls to my office. Another person made an arrangement for me to obtain mice for free from a big pharmaceutical company nearby. As soon as the owls could fly, I moved them to a large room in an old house on campus. The owls grew fast, but one of them died perhaps because of fighting. I installed a large nest box for the remaining two. One day the graduate

student who was interested in studying the owls found one of the owls incubating eggs. The owl pair reared one set of young twice a year in spite of seasonal changes in day length and temperature. It seemed that the breeding of the owls depended only on the availability of mice. I also found that male and female owls could be distinguished by the coloration of their facial and breast feathers, white males versus brownish females. This finding made it possible to set up breeding pairs, making all future laboratory studies of barn owls feasible. I advised several Princeton seniors to do their thesis projects with owls. Hand-reared owls became so tame that the students could use behavioral criteria for memorization and discrimination of sound signals. Anything that the students did or found was new and worthy of publication.

I shipped 21 home-bred owls from Princeton to Caltech a day or so before my own departure for the West. Jack Pettigrew and I started to work on the visual system of the owl immediately after my arrival, partly because my main soundproof chamber was not ready yet. He already had a computer-controlled system of visual stimulation and data collection. We studied the response properties of neurons in a forebrain area called the visual Wulst mainly because the area was readily accessible without major surgery. We did find several interesting response properties. Jack kept telling me that the Wulst cells were just like those in the visual cortex of the cat, for example, with respect to their sensitivity to stimulus orientation, binocular disparity, and direction of movement. He told me that a blind folded physiologist would not be able to tell whether he is recording neurons from the cat visual cortex or from the owl visual Wulst. At any rate, we published a couple of papers on this subject. My big sound chamber was completed after Jack and I worked together in his laboratories for about a year.

Jack asked me what I was going to do. My original intent was to continue to analyze sound localization behavior by owls in a much more acoustically better defined environment than anything I had used before. Well, this idea ceased to occupy me after Jack and I had studied the visual Wulst cells. I naively thought that central auditory neurons might have spatial receptive fields like the visual cells. I also thought that these auditory cells might form a map of auditory space. There had been some reports of auditory neurons with spatial receptive fields, but systematic approaches to this question seemed lacking. Jack was more than enthusiastic about my ideas. He asked the legendary Herb Adams of Caltech to design and build devices and instruments necessary for this project. I do not know to this day who paid the bill, because I did not have any seed money or grant for this project. We wanted to move a small loudspeaker around an owl's head at a constant distance in the horizontal and vertical directions. Herb built a light semicircular rail along which the speaker could travel. Herb's "hoop" could be moved up and down either manually or electrically so that we could place the speaker anywhere around the owl's head.

My first postdoctoral fellow Eric Knudsen arrived around this time. Using this system, he and I quickly found auditory neurons that responded only when the speaker was in a particular area in space, that is, auditory receptive field. Although this finding was exciting, we did not find anything like a map. I did not realize that an auditory map was not expected, because unlike the visual system in which the sensory periphery, the retina, maps the visual field, the cochlea maps only sound frequencies. Because, as I pointed out earlier, auditory spatial receptive fields as such were already reported if sporadically, the value of our initial findings was limited. When Eric and I discussed what to do next, we agreed that we shift our focus to the midbrain auditory area. An exploration of the brain or earth without a map is precarious; we have to be lucky. We also could not afford to kill an owl for making a brain atlas, although we should have done it in retrospect. I cut a frozen owl brain along its midline with a band saw. Eric who had previously studied the midbrain auditory area of catfish could see the homologous area in the owl's brain. Somehow his measurements of depth and so forth on this specimen were useful enough to target the midbrain area.

We were lucky to insert an electrode into a midbrain area packed with auditory neurons with small spatial receptive fields. We named them "space-specific neurons." However, we could not go back to the same area without better landmarks on the skull or brain. When I was in Munich, I learned how to remove brain tissue by suction. I could expose the optic lobe of the owl by removing the overlying forebrain. Using surface blood vessels as landmarks, we probed the midbrain as systematically as we could. However, often the brain would start pulsating as I had seen in the cat. Also, any small damage to the surface of the exposed area would cause swelling, making it impossible to sample neurons at a fixed interval. The main problem in finding a map was the small number of neurons that we could sample during one penetration with a single electrode. Our electrodes were much too hard to make and too fragile. One day we were lucky enough to record some 16 neurons with the same electrode in the area that we subsequently named the "external nucleus" of the inferior colliculus. The loci and the sequences in which we encountered these neurons clearly indicated a map of auditory space as we depicted in the map we published. We published our papers describing auditory receptive fields and map in *Science*. The first of the papers was chosen as the best paper to appear in *Science* in 1977, and each of us received a medal from the American Association for the Advancement of Science (AAAS). Eric, Jack, and I were overjoyed, because it was our first award for writing a scientific paper.

Things around us started to change when laboratory computers appeared on the horizon. Jack's postdoctoral fellow Gary Blasdel set up and programmed computers for his laboratories. When Gary took part in one of our behavioral experiments, he programmed our first computer a PDP 11. After Eric's ascent to assistant professorship at Stanford, I was lucky enough to

get a new postdoctoral fellow, Andy Moiseff, who could not only program computers but also make digital instruments for auditory physiology. The subsequent arrival of computer-savvy graduate students Jamie Mazer, Larry Procter, Björn Christianson, and our first professional programmer, Chris Malek, modernized our stimulus delivery and data collection systems. Knowing the response properties of space-specific neurons, I wanted to investigate how their stimulus selectivity is created in the pathways leading to the site of the auditory space map. Our first step was to sample neurons in all brain areas leading from the cochlear nuclei (first brain auditory station) to the external nucleus of the inferior colliculus. We (including Moiseff, Sullivan, Terry Takahashi) obtained anatomical and physiological evidence suggesting the presence of two separate pathways leading to the external nucleus. One pathway deals with “time” leading to the creation of neuronal selectivity for the interaural time difference (ITD), and the other pathway deals with sound “level or intensity” leading to the creation of neuronal selectivity for the interaural intensity difference (IID). These discoveries led to studies of the mechanisms that give rise to the ITD and IID selectivity.

We placed much emphasis on the most important part of the time processing pathway. This part consists of axonal delay lines provided by the axons of neurons in magnocellular nucleus (the first brain auditory station) and coincidence detectors provided by neurons of nucleus laminaris (the second station). The laminaris turned out to be a very difficult site to investigate, because holding single neurons was hard. Using evoked potentials, Sullivan and I observed a map of ITDs in each frequency band in the nucleus laminaris. Later, Catherine Carr and I not only managed to record single laminaris neurons to confirm the existence of ITD maps but also figured out the neuronal circuits underlying the coding of ITD. This set of circuits resembles the famous model proposed by Lloyd Jeffress in 1948. My group has published papers to show how our findings are consistent with this model. Our exploratory study of the IID processing pathway identified the first binaural station called VLVp in the anterior part of the hindbrain. Manley, Köppl, and later Adolphs found how this station encodes IID. VLVp neurons receive excitatory input from the contralateral nucleus angularis (first brain station of the intensity processing pathway) and inhibitory input from the contralateral VLVp, and the degree of inhibition varies systematically to form a map of IID's.

The space-specific neurons require combinations of ITD and IID. This fact indicates that the time and intensity pathways converge on single neurons. The convergence of the two pathways occurs first in each frequency band in a midbrain area called the “lateral shell” of the central nucleus of the inferior colliculus. Different frequency bands converge on each single neuron in the next area called “external nucleus” where the map of auditory space resides. Next I wanted to know how the requirement for the ITD and IID combination is created. I advised Jose Luis Peña that he might try

intracellular recording of cells in the external nucleus to see how postsynaptic potentials change with combinations of ITD and IID. When I casually showed the data to Partha P. Mitra, a physicist, he said that multiplication of postsynaptic potentials for ITD and IID would account for the combination sensitivity. We proved him right by carrying out mathematical analyses with the help of Fabrizio Gabiani who was a postdoctoral fellow in the laboratory of my colleague Gilles Laurent.

The results of all these efforts eventually led to the formulation of an outline of signal processing in which major events leading to the genesis of the stimulus selectivity of space-specific neurons were identified. I am proud of this accomplishment, because few other vertebrate sensory systems are understood at this level. A notable exception is the work of Walter Heiligenberg and his associates. Walter had come to the laboratory of Ted Bullock in San Diego a couple of years before my move to Pasadena. I saw Walter and his wife Zsuzsa often at their home in Del Mar. Walter was killed in a plane accident, and Zsuzsa died of cancer. I still think of them all the time. The jamming avoidance of electric fish *Eigenmannia* was the subject of his research. This species emits low frequency sinusoidal electrical signals for navigation in muddy waters. The fish raises or lowers its signal frequency in response to frequency differences between it and other individuals in the vicinity. This response is called the "Jamming Avoidance Response." Unlike our owl project, Walter went from the peripheral sensory organs to high-order areas in the brain to figure out how the fish determines which way it should change its frequency. The decision to lower or raise the fish's own frequency involves separate time and amplitude pathways, and their convergence in the mid-brain as in the owl. Just as the owl's space map area, the highest area in the fish contains single neurons that respond selectively to the sign of frequency differences between the two fish. I have published essays comparing the owl and electric fish algorithms. This experience has convinced me that there should be some universal rules by which complex sensory signals are processed by the brain.

Echolocation in Birds

Jack Pettigrew and I worked very hard in the laboratory, but we also needed time off to move from indoor to outdoor adventures. In late November 1976, I organized an expedition to Colombia, South America to study oilbirds (*Steatornis caripensis*), which use echo-location for obstacle avoidance and nest site recognition in deep and completely dark caves. I obtained a grant from the National Geographic Society for the Columbian expedition and recruited experts on avian brain, (Sven Ebbesson, Harvey Karten), echolocation (Nobuo Suga), and Jack Pettigrew. Rodolfo Llinás who is originally from Bogota helped us with local arrangements including establishing contact

with the U. S. Embassy to have someone who could help us with customs clearance. However, Jack and I caused a big problem by sending a couple of boxes containing instruments by a separate flight. When we told the Embassy Liaison that those boxes were coming in another flight, he said "oh no," meaning that he would not be able to arrange their safe passage through the customs. While we were waiting for the resolution of the problem, we assembled whatever we had in a hospital laboratory, which Rodolfo secured for us. One day Jack and I rented a car to go to one of the oilbirds caves. We were really impressed by their habitat and behavior.

A few days after our trip to the cave, the U.S. Embassy wanted to give us some information about Columbia. Because most members of my expedition did not want to bother with this invitation, Nobuo Suga and I, who were not even U.S. citizens, went to the Embassy. We were shown a large map of the country in which many places were marked with some symbols. The attending official told us that those markings indicated the sites of guerilla activities by various groups. One of the areas was close to the cave Jack and I visited! On the whole, we lost too much time to do any serious experiments in the laboratory. As Jack and I were walking to the airport terminal where we were to board a plane for Los Angeles, an official approached and took Jack away, because Jack was conspicuous with his beard, long hair, and short pants. Jack returned after a few minutes. We wrote off Columbia after these experiences.

I saved enough grant money to stage two more expeditions to continue the oilbird project. In November, 1977 Jack and I went to Trinidad after I had carefully arranged our safe passage through the customs and a permit to catch oilbirds. I also learned about the well known oilbird cave and the old research station (William Beebe Tropical Research Station) where we could set up our neurophysiological laboratory. The research subject was vision this time, partly because we were curious to know whether oilbirds' brain visual areas contain neuron types that respond to the same stimuli to which the owl's Wulst neurons respond. This topic was also relevant to the controversy that was going on between Hubel and Wiesel on one hand and Blakemore, Pettigrew, and Barlow on the other with regard to the innateness of neuronal responses to stimulus orientation and the direction of movement. Jack and I went to the deepest and totally dark part of the cave to collect oilbird chicks from their nests. We carried them in a completely dark box back to the laboratory. We recorded neurons in their visual Wulst as we had done before with owls. We used the types of stimuli that were used for the study of the cat's cortical neurons. Jack was amazed to find neuron types that responded to stimuli that also drove those of the cat's visual cortex. He had to admit that these types of neurons do not need any visual experience to develop their preference for orientation and the direction of movement. He said "It's innate," the word he had never uttered before.

Pleased with the outcome of the vision research, I staged another expedition to Trinidad in May 1978, this time with Eric Knudsen to study hearing in oilbirds. Eric and I did field experiments in which we put up a two dimensional array of discs of different diameters across the flight path in the cave to see the smallest disc they could detect by echolocation. We used an infrared search light and an infrared telescope to watch the birds. We also recorded auditory responses in the forebrain auditory area and the cochlea of anesthetized birds to determine their auditory threshold for different frequencies. We learned that the oilbird's ear was most sensitive to 2 kHz and that its highest audible frequency is no higher than 8 kHz, although the clicks they emit during echolocation contain frequencies as high as 15 kHz.

There is another bird species called "cave swiftlet" (*Collocalia fuciphaga*) that uses echolocation for navigation in caves. In September 1980, I went to Chillagoe, Australia with a group of bat researchers including Don Griffin, Roderick Suthers, Jim Simmons, and local participants Jack Pettigrew and Roger Cole. I was much impressed to see Rod Suthers record tracheal air flows in a tethered swiftlet. I told him that he could use the same method in singing birds, and he later did just that to discover many interesting facts about song production. Chillagoe is an old mining town in northern Queensland. In Southeastern Asia, cave swiftlets provide nests for Chinese bird nest soup. Fortunately, their nests are protected in Australia. These birds are tiny compared with the crow-sized oilbirds. We saw many of them flying over their nesting caves in the day time unlike oilbirds that come out of their caves only at night. They begin to emit echolocation calls when they approach the entrance of their home caves. Three of us set up our gear in the same motel room where we slept. The temporary laboratory was better equipped than my home laboratories. We used neurophysiological methods to determine their auditory threshold. We showed for the first time that the frequency range of hearing in cave swiftlets did not include ultrasound frequencies.

My Other Activities

Academic High Society

My introduction to academic high society began in 1975 when I was invited to join a discussion group called the Neuroscience Research Program (NRP) led by Francis O. "Frank" Schmitt of MIT. This group included not only neuroscientists but also people from other fields such as Manfred Eigen. I did not know why a relatively young (42) person like me was invited to a group of famous senior scientists like Walle Nauta, Ted Bullock, David Hubel, Seymour Kety, and Vernon Mountcastle. The members met twice a year in Boston. The NRP organized other meetings and symposia in addition. I met practically all leading U.S. and foreign neuroscientists at the NRP.

In fact, many of them are contributing to the present volume! Individual encounters seemed to remove the potential barriers due to age and status. I learned a lot more from private conversations with my senior colleagues than from formal lectures. As Frank was slowing down, the NRP moved to the Rockefeller University and thence to San Diego with Gerald Edelman as the new director.

Creation of a Scientific Society

In 1981, I attended a conference on vertebrate neuroethology in Kassel, Germany. Ted Bullock, who was one of my heroes, rounded up several people during this meeting to discuss the possibility of organizing an international society for neuroethology including vertebrate and invertebrates researchers. There was a division between these two groups of neuroethologists. For example, the late Graham Hoyle ranked invertebrate researchers like himself in “A” class and vertebrate researchers like me in “B” class. His criterion for the A class was the cellular level of analysis with identifiable neurons, which few vertebrate researchers could achieve. Ted who worked on both invertebrates and vertebrates emphasized the need to bring the two groups together. He asked me to contact potential members around the world. It took me about 2 years to collect enough names, because I was writing letters and waiting for replies. I still have a vast number of letters I sent and received during the above period. After I completed this phase of organization, I suggested to Ted the possibility of organizing the first international congress of neuroethology in Tokyo, because my good friend Kiyoshi Aoki of Sophia University in Tokyo offered to raise funds for the congress. Aoki graduated from Hokkaido University a couple of years after me. He told me that the rich father of one of his graduate students would support the congress, if funds from government sources were unavailable. Aoki single-handedly raised funds and took care of all logistic aspects of the congress. Ted and I made a list of potential plenary speakers including Edward Evarts, Eric Kandel, Seymour Kety, and other big names, even though some of them were not bona fide neuroethologists, because they were not studying the neural mechanisms of natural behaviors. When I asked Ted how we should make the final list of speakers, he said that we the committee of two could decide by voting! Thus, I learned a new form of democracy, and the first congress was held in 1986. Aoki later told me that Japanese participants were much impressed by the final list of speakers. They wondered how a young chap like Aoki could attract such foreign luminaries, reflecting the Japanese hierarchical system I mentioned before. I succeeded Ted as president to consolidate the society and prepare for the next congress in 1989 in Berlin. The eighth congress was held in Vancouver this past summer (2007). I am pleased to see the fruit of our early efforts.

Prizes

The number of monetary prizes given to scientists seems to have been increasing in recent years especially in United States. It is refreshing to know that people of means support arts and sciences. Prizes always took me by surprise, that is, I had neither worked toward them nor expected them. Thus, I do not know if prizes motivate scientists to work harder and more creatively. Nevertheless, I admit that recognition by respected members of my field is important and encouraging to me. I would like to record here my most extraordinary experience in connection with the receipt of the 1990 International Prize for Biology, which was established in 1985 in honor of the Showa emperor of Japan who was a biologist. As I was being taxied from my hotel to the Japan Academy building in Tokyo, I saw empty streets with policemen standing at various corners, because the streets were on the route that the imperial limousine was taking to the Academy. I could not believe that I caused such massive public measures, even if they were done for the imperial procession. As soon as I arrived at the Academy, I was given a long minute-by-minute list of events that would occur during the day. The quality of the paper used for this list was something I had never seen before. It looked like a modern version of an ancient scroll. The first item was a private audience with the emperor (son of the Showa emperor) and the empress in a small room. The imperial couple came in silently without any guards or servants. We greeted and exchanged a few words. She asked me about my mother. After this brief encounter, we separately went to a large auditorium where I received the prize. On the podium, the imperial couple sat in the middle surrounded by some dignitaries such as the minister of education and the president of the academy. The audience included many university presidents, representatives from foreign embassies, my friends (by invitation), and press people. I walked to the assigned post in front of the imperial couple and faced the audience to deliver a short speech in English. I felt a bit uncomfortable to turn my back toward the imperial couple, because this was not allowed in the old days when the emperor was God. After the prize ceremony, the guests lined up behind me to greet the imperial couple. I deeply bowed in front of the couple, and they bowed lightly according to the Japanese custom, while my friend Rüdiger Wehner (University of Zürich) coming behind me shook hands with the couple. Moreover, he told me that he chatted with the empress about her youthful experience in Switzerland. When Seymour Benzer received the prize some year later, his boys hugged the empress! If I had done that, the scene would have been in all newspapers the following day.

The day after the event, someone, perhaps a reporter, phoned me to ask how I could accept the prize created in honor of the Showa emperor, a war criminal. I told him that I was selected not by the imperial department but by a committee of distinguished scientists. I know this because I served on

it a few years later. A similar protest was also staged at Kyoto University where there was a symposium in my honor following the Tokyo ceremony. I saw a few placards denouncing the Showa emperor but not me personally. When this emperor came to visit Kyoto shortly after the war ended, students from Kyoto University mobbed the imperial limousine chanting "war criminal." This incident was a front page sensation in all newspapers, because something like this had never happened before. A middle-aged teacher at our high school asked how many of us agreed with the rioters. I was the only pupil who supported the demonstration. The teacher asked "only one?" and chastised my conservative classmates. Although the emperor may have been deceived by his military advisors, the students wanted to remind the people of his possible culpability.

A few years later when I went to Japan, the imperial couple invited me to their temporary palace for a dinner. Fortunately, this time I was not alone but with my friend Kiyoshi Aoki who was familiar with the imperial court. His contact at the palace had asked him what I would prefer to eat, Western or Japanese. I opted for Japanese. Four of us dined in a little cozy room, and the food was Kaiseki, which usually consists of a sequence of small dishes. We were served many small dishes at once, spoiling the most important aspect of savoring Kaiseki. The imperial couple did not say a word about the dinner, making me wonder if they liked the food. Although they asked me questions slowly I could not find an appropriate moment to ask them a question. I do not think that they intentionally avoided questions from me. Perhaps they were trained to develop this skill by necessity. I would have asked how they liked their way of life. When a servant (I did not know his exact title) came to say "Time's up," the emperor asked for "10 more minutes?" The servant came back exactly after 10 minutes. I could not help feeling sorry for the couple, because they were not as free as I was. I liked them as individuals, particularly the charming empress who came from a rich commoner family. When newspaper articles about her mental state began to appear, I sent her a reel of tape containing the song of European nightingales, because she had expressed her interest in them in our previous encounter. She sent me a beautifully handwritten letter, telling me how much she appreciated them. On another occasion, I gave a private lecture on birdsong for their daughter who was interested in birds.

My Hobbies

I have been lucky, because I did not have to go far from my hobby to my scientific subjects. Playing with animals was my main hobby in my childhood. I now have only dogs. I have trained dogs to do tasks like tracking and searching. These tasks are easy from the trainer's point of view. When I started to train Border Collies for sheep herding a few years ago, I began to realize that my previous experience was not useful for this "sport." Most dog

trainers agree that sheep herding is the hardest dog sport, although it is not a sport for real sheep herders. My explanation for the difficulty is the interaction of three different species. Border Collies are selectively bred for sheep herding by enhancing obedience and certain aspects of predatory behavior such as circling prey. This means that the dog has his own way of dealing with sheep, and the shepherd has to shape these responses to his advantage. However, sheep also have instinctive responses to dogs. If shepherds do not know these responses, they cannot herd sheep with dogs. So, I now have to train my dogs to work not for me but with me. I like this, because I have to think hard and keep moving, good antidotes against physical and mental aging!

Acknowledgments

I would not be in this volume without the indefatigable efforts of my parents to help me get out of the unkind world in which they were destined to live. I thank the tax payers of Japan, Germany, and United States for their support of my training and research through fellowships and grants administered by respective governmental agencies. I am also grateful to individuals and groups that have given me prizes and grants for my work. I thank Jack Pettigrew whose encouragement and participation in the initial phase of the owl project was the key to my decision to look for auditory spatial receptive fields and map. My special thanks go to Peter Marler who played the most pivotal role in my development as a scientist.

I list below all the people who participated in my research projects because many of them are not mentioned in my research accounts above, which emphasize only the main stream of the events. I take this opportunity to thank all for their contributions.

Former Graduate Students

Princeton era (1967–1975)

Manley, Geoffrey A. (Professor Emeritus, Technical University of Munich, Germany)

Caltech era (1975–)

Owl Projects

Adolphs, Ralph (Professor, Humanities Division, Caltech)

Christianson, Björn (Postdoctoral fellow, University College London)

Egnor, Roian (Janelia Farm)

Mazer, James A. (Assistant Professor, Yale University)

Proctor, Larry (Amgen)

Birdsong Projects

Gahr, Manfred (Dept. Director, Max-Planck Institut für Ornithologie, Germany)

Gurney, Mark (PV, deCode-Genetics, Inc. Iceland)

†Katz, Lawrence (Professor, Duke University)
Köpl, Christine (Research Associate, University of Sydney)
Leonardo, Anthony (Group leader, Janelia Farm).
Lewicki, Michael (Associate Professor, Carnegie Mellon University)
Margoliash, Daniel (Professor, University of Chicago).
McCasland, James S. (Professor, Upstate Medical University)
Mooney, Richard (Professor, Duke University)
† deceased

Former Postdoctoral Fellows

Owl Projects

Albeck, Yuda (Israel)
Carr, Catherine E. (Professor, University of Maryland)
Fujita, Ichiro (Professor, Osaka University)
Funabiki, Kazuo (Research associate, Osaka Biosciences Institute)
Knudsen, Eric I. (Professor, Stanford University)
Moiseff, Andrew (Professor, University of Connecticut)
Mori, Koichi (Section chief, NRCD, Japan)
Peña, Jose Luis (Assistant Professor, Albert Einstein College of Medicine)
Saber, Kourosh (Associate Professor, UC Irvine)
Shanbhug, Sharad (Postdoctoral fellow, Albert Einstein College of Medicine)
Sullivan, Ted (Private enterprise)
Takahashi, Terry (Professor, University of Oregon)
Viete, Svenja (Veterinary practice, Los Angeles).
*Volman, Susan (Program Director, NIH/NIDA)
Wagner, Hermann (Professor, University of Aachen, Germany)

* worked on owl and songbird

Birdsong Projects

Doupe, Aïllson (Professor, University of California, San Francisco)
Funabiki, Yasuko (Research associate, Kyoto University)
Nick, Teresa (Assistant Professor, University of Minnesota)
Leppelsack, Hans (retired Professor, Technical University of Munich)
Perkel, David (Professor, University of Washington)
Schmidt, Marc (Associate Professor, University of Pennsylvania)
Striedter, Georg (Associate Professor, University of California, Irvine)
Vu, Eric (Research Associate, Barrow Neurological Institute)
Watanabe, Dai (Professor, Kyoto University)

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