Jon Howard Kaas

Born:

Fargo, North Dakota
September 13, 1937

Education:

Northland College, Ashland, WI, BA (1959)
Duke University, Durham, NC, PhD (1965)

Appointments:

Postdoctoral Fellow, University of Wisconsin, Laboratory of Neurophysiology (1965–1968)
Assistant Professor, University of Wisconsin (1968–1972)
Associate Professor of Psychology, Vanderbilt University (1972–1978)
Visiting Scientist, University of California at San Francisco (1975 Summer)
Professor, Vanderbilt University (1978–2001)
Visiting Scientist, The Neurosciences Institute, New York (1982 Summer)
Visiting Scientist, Department of Physiology and Pharmacology, University of Queensland, Australia (1984 Summer)
Kennedy Center, Senior Fellow and Investigator, Vanderbilt University (1987–present)
Centennial Professor of Psychology, Vanderbilt University (1987–2011)
Distinguished Professor of Psychology, Vanderbilt University (2001–present)
Distinguished Visiting Professor, International Institute of Neuroscience, Natal, Brazil (2011)
Gertrude Conaway Professor, Vanderbilt University (2011–present)

Honors and Awards (Selected):

Krieg Cortical Discoverer Award, Cajal Club, 1980
The Earl Sutherland Prize for Achievement in Research, awarded by Vanderbilt University, 1985
Javits Neuroscience Investigator Award, 1987
Elected Fellow, American Association for the Advancement of Science, 1991
American Psychological Association Distinguished Scientific Contribution Award, 1994
Elected Member, International Neuropsychology Symposium, 1994
Elected Member, La Jolla Group for Explaining the Origin of Humans, 1998
Fellowship, Center for Advanced Study in the Behavioral Sciences, Stanford University, 1999–2000
Elected Member, National Academy of Sciences, 2000
Elected Fellow, American Academy of Arts and Sciences, 2001
Elected Member, Society of Experimental Psychologists, 2001
Karl Spencer Lashley Award, American Philosophical Society, 2006
Elected Associate, Neurosciences Research Program, The Neurosciences Institute, San Diego, 2009
Excellence in Graduate Mentoring Award, Vanderbilt University, 2009
Distinguished Visiting Professor, International Institute of Neuroscience, Natal, Brazil, 2011
George A. Miller Prize in Cognitive Neuroscience, Cognitive Neuroscience Society, 2014
Palay Award, Journal of Comparative Neurology, award by Wiley Publishing, 2014
Honorary Life Member, J. B. Johnson Club for Evolutionary Neuroscience, 2014

Jon Kaas is known for his comparative studies of the organizations of sensory and motor systems, especially in primates. A major interest has been in deducing the likely organization of the forebrain in early mammals, and how this organization has been altered in many ways in extant mammals. Other research efforts have been on how sensory and motor systems respond to injury and sensory loss. Contrary to early views, this research has demonstrated the remarkable plasticity of mature nervous systems.

Jon Howard Kaas

Introduction

Looking back on my career, I feel that my path was very unlikely and that I was extremely lucky. Quite simply, my background does not suggest an academic career. My parents came from large families that had limited means. My mother was from North Dakota and my father from northern Wisconsin. After he finished high school, my father received training and became a store manager, so we were somewhat better off, and this made a difference. I was born in Fargo, North Dakota, and after moving around a bit, we settled in a small town in northern Wisconsin (Spooner) but soon moved seven miles out of town, on the beautiful Namekagon River (now a National Wild River). This resulted in my grade school education being in a two-room school with no running water, and the same teacher for four years. Class sizes ranged from two to seven. At age 13, I was bused back to Spooner for high school, where I found support from a wonderful chemistry teacher, and enjoyed history class, which was well taught and interesting. But at home I was isolated, and read a lot in a somewhat random and unsupervised manner that somehow included Darwin, Poe, and Freud. To my surprise, Darwin's *Origin of the Species* had never been checked out from the school library, and was certainly unavailable elsewhere. No one I knew ever talked about any of these three. For religious reasons, my father clearly disapproved when he saw me reading Darwin, but he did nothing to stop me.

After graduation from high school, I briefly held a job on local road construction, and then at the local creamery, first cleaning pipes, and then, because of my high school chemistry, testing milk. Soon thereafter, while enjoying myself in a local tavern, although still only 17, I met a student from the nearest college, Northland College, some 80 miles north on Lake Superior. He suggested that I should attend Northland and that it wasn't too late to apply and be admitted for the fall semester. He thought, with my high school record, I would likely get a scholarship to cover most of the expenses. This proved to be true, and at the end of summer, I found myself at Northland, at the time a college of only 250 students, in a small dorm room with two other new students who soon became my close friends. While I continued to work some weekends and then in the summer, my parents were able to help me with fifty dollars per month and sometimes the use of a car. At Northland, teaching, as in high school, was uneven, but I had good-to-very-good classes in chemistry, physics, and math. I was most impressed with a new professor from New York, who took special interest in his students. He invited us

to his home to discuss readings and took some of us on field trips, including to the annual meeting for Midwest Sociological Society. For one of his classes, we were expected to do original research and this requirement made an impression on me. In my final semester, the rather young president of this small college offered a class in abnormal psychology. For a class paper, I combined two of my high school interests and tried to interpret the symbolic meanings of poems and stories of Edgar Alan Poe. With more experience, I would have thought it foolish and presumptuous to attempt such an effort, but the school president was impressed, and suggested that I should go to graduate school. He offered to help me and provided a strong letter of recommendation. This was way past the assumed deadline for graduate school applications, but he said not to worry, and soon I had offers in psychology from roughly six to seven universities. I wanted to work with Harry Harlow at the University of Wisconsin, and at first that seemed possible, but he was on leave, and he didn't take any students. I was told this by the acting director of graduate admissions at Wisconsin, who was a visiting professor from Duke. I answered that I would take my second choice of graduate school, and go to Duke. He said, "I'll see you there."

The Duke offer was impressive in that it was in a new interdisciplinary program funded by NSF in the Anatomical and Physiological Bases of Behavior. This program seemed so different from my background and interests in social psychology that it strongly appealed to me. On arriving at Duke on a very hot August day, I soon found that I was in way over my head. The new program meant that I and the other three students in the program would take basically all of the courses of first-year medical school, and, for me at least, most of the classes for first-year psychology students. When the lab instructor for gross anatomy found out how little I knew, compared to the well-prepared medical students, he quietly told me "you're never going to make it." But I did, and that year of medical school classes was very good for me and sometimes fun.

The most important thing that happened to me in graduate school was taking a first-year class with Irving Diamond. The class consisted of a series of assigned readings that the other students in the NSF program and I would discuss with Diamond in his office. This fit well with my habit of reading more about each topic from related papers, and Diamond was impressed enough to ask me to join his lab. I was too shy at that stage to have asked him myself (see autobiography, Diamond 1996). Diamond was a new faculty member just arrived from the University of Chicago, where he was known for his ablation-behavior studies of auditory cortex with Dewey Neff. I greatly appreciated my opportunity to work with Diamond, as he stressed understanding over rote learning and he asked questions like "why do you think the authors of a paper wrote the Introduction as they did?" He taught us to focus on the major contributions of published papers (why was this paper important) rather than weakness. He encouraged me to make

up for my weak background in biology by taking graduate classes in genetics and comparative physiology. As a result, I was lucky to have taken a class with a fantastic comparative physiologist, Knut Schmidt-Nielson (see Schmidt-Nielsen 1984), an experience that influenced my subsequent research greatly. Importantly, Diamond treated those of us in the laboratory as members of a family. I always knew I had his support. When I joined his laboratory, he told me that my thesis would be published in the *Journal of Neurophysiology*, and I would go on to the best of laboratories for my postdoc and training. Both predictions came to be true. While I was a graduate student with Diamond, I first worked on studies of the somatosensory system without much progress, and then I turned to do a thesis on the role of the corpus callosum in auditory behavior for my PhD (Kaas et al. 1967). This would not be considered adequate progress today.

During this time, I was very impressed with Bruce Masterton, who had joined the lab as an older student who left his position in mathematics to become a graduate student in psychology. Bruce completed his PhD with a series of brilliant studies on the roles of parts of the auditory system in sound localization and other behavior, and left for a faculty position at Vanderbilt, my present university. I also became close friends with two other graduate student members of the laboratory, Bill Hall and Herb Killackey, who later became collaborators. The focus of the Diamond laboratory had changed while I was a student from studies on the auditory system of cats to comparative studies of brain organization. This new direction greatly influenced my goals for the future.

My Years at the University of Wisconsin

After finishing my PhD, Diamond's strong recommendation got me accepted as a postdoctoral fellow in the Laboratory of Neurophysiology at the University of Wisconsin, headed by Clinton Woolsey. Woolsey was internationally known for his comparative studies of cortical and thalamic organization. He had moved from the Johns Hopkins University School of Medicine to forge his own laboratory, independent from any department, at the University of Wisconsin. He attracted an outstanding cast of faculty, some promoted after training in the laboratory (Robert Benjamin, Joseph Hind, Wally Welker, and John Brugge), and Jerzy Rose recruited from Johns Hopkins. Under the leadership of Jerzy Rose, the Wisconsin auditory facility and group was widely recognized as the best for studying the neurophysiology of the auditory system. I had planned to continue working on the auditory system, with a comparative approach across species. However, on my arrival Woolsey told me that the laboratory had enough fellows working on the auditory system and that I should work on the visual system; more specifically on the organization of visual cortex in cats. Since no one else in the laboratory was working on the visual system, and Woolsey had

published a paper on visual areas I and II in rabbits, he would help me. (At this time and for sometime afterward, Roman numerals were used to denote early visual, somatosensory, and auditory areas.)

This change of direction led to years of work on trying to map visual cortex in cats. Immediately, it became apparent that the earlier method used by Woolsey, that of flashing light from a row of bulbs into the visual field while recording evoked potentials from the surface of the brain, did not provide a uniform stimulus. With the help of trainees in neurosurgery during their research rotation, we outfitted a standard visual field evaluation device from the ophthalmology clinic with a strobe light so that we could flash a small one-degree spot of light anywhere in the visual field of the experimental animal. We continued the tradition in the Woolsey lab of recording from electrodes placed on the surface of the brain, but now we could also average evoked responses to reduce noise with the help of a new innovation, a large but computationally limited LINK computer—a first-generation computer for use in the biological sciences. We collected a lot of data on the retinotopic organization of visual cortex in cats, and later in a prosimian primate (slow loris), but the methods provided only a gross view of visual cortex organization. Our only published paper, a summer project for a medical student, was on the retinotopic organization of the very large superior colliculus of ground squirrels. Subsequently, Woolsey presented our maps of visual cortex in cats in a review (Woolsey 1971), but I foolishly declined his offer to be coauthor as I felt that our resolution of the retinotopy of extrastriate cortex was not good enough to distinguish VII and VIII, although a good map of VI was obtained. A breakthrough in procedures occurred when my friend from graduate school days at Duke, Bill Hall, came to work with me for a month on visual cortex of a small mammal, the hedgehog. We soon realized that brain surface recordings provided results that were too crude to reveal retinotopy in the small hedgehog brain, and so we switched to microelectrodes, something that Wally Welker (see Welker autobiography, 2001) was using as he mapped somatosensory cortex in his laboratory across the hall. In addition, Vincente Montero, a member of the Woolsey neurophysiology lab with experience mapping visual cortex in rats, advised us on anesthetics and the use of a translucent plastic hemisphere to present stimuli in the visual field. The altered methods worked, and we obtained evidence of the existence of visual areas I and II in hedgehogs (Kaas et al. 1970). By this time, despite my poor publication record, I was promoted to assistant professor in the Woolsey laboratory at Wisconsin. This meant that I had my own small lab, in part of a room, where I could set up to map visual cortex. Now I could go on to map visual cortex in other mammals.

To start, I took a leave for one summer and returned to the Diamond lab at Duke, where I was able to map visual cortex in grey squirrels (Hall et al. 1971) and tree shrews (Kaas et al. 1972a) with microelectrodes and

a plastic hemisphere with my close friends, Bill Hall and Herb Killackey. At the same time, my wife, Judith, returned to Duke with me to finish her PhD thesis. While I was at Duke, John Allman had come to Wisconsin from the University of Chicago to work with Woolsey on a PhD project on the pulvinar. This relationship did not seem to be working, and on my return, Woolsey suggested that John and I work together. This was extremely fortunate for me, as I had, as of yet, no one else to work with, and John turned out to be an exceptionally talented researcher. We started with the visual cortex, since it was more accessible than the pulvinar, and used owl monkeys, as Woolsey had obtained a number of them from another laboratory. Soon we were joined by graduate student Ron Lane and by Fran Miezin who had a master's degree in engineering. Both were great additions, but at first John and I worked alone and at a pace that would be hard to ever do again. We produced a series of papers on visual cortex of owl monkeys, providing the first complete retinotopic maps in any primate of V1 (Allman and Kaas 1971a) and V2 (Allman and Kaas 1974a). Perhaps our most important discovery was that of a systematic, retinotopic representation of the contralateral visual field in cortex, displaced from V1 in the caudal part of the middle temporal gyrus of owl monkeys, an area we termed the middle temporal visual area, MT. We demonstrated that MT was histologically distinct due to its dense myelination and that its neurons responded well to moving visual stimuli (Allman and Kaas 1971b). The homologous area in the cortex of the superior temporal sulcus of macaque monkeys, known to get direct inputs from V1 (Kuypers et al. 1965), was subsequently called V5 by Semir Zeki (Zeki 1983). Zeki had spent a few months at Wisconsin with Ray Guillery during this time, where I got to know him. John and I mapped a number of other visual areas, including the dorsolateral area (DL; Allman and Kaas 1974b) that largely overlapped the macaque area Zeki called V4, the dorsomedial area (DM; Allman and Kaas 1975), and the medial area (M; Allman and Kaas 1976). We also mapped the retinotopic organization of the superior colliculus in squirrels and tree shrews (Lane et al. 1971), owl monkeys, galagos (Lane et al. 1973), and cats (Lane et al. 1974), providing clear evidence that the representations in primates were of the contralateral hemifield only, while other mammals had a complete representation of the contralateral eye. Following John's original interest, we mapped a lateral nucleus in the inferior pulvinar of owl monkeys (Allman et al. 1972). We also started recording from the optic tectum of seagulls with a graduate student from biology, but the graduate student soon left and we dropped, what could have been, a very interesting project.

While working with John on these various studies, I also started to collaborate with Ray Guillery, a professor in the Anatomy Department who was in an adjacent part of the building (see autobiography, Guillery 1998). Guillery was working on the effects of producing an imbalance in binocular competition in the developing visual system by rearing cats with reduced

vision in one eye. This led to us extending this model to the well-developed visual system of squirrels producing results very much like that reported for cat visual cortex. In addition, Guillery was using the newly emerging Nauta methods of revealing brain connections, and discovered that the projections of the retina to the lateral geniculate nucleus of Siamese cats were abnormal. Soon we were using anatomical and physiological methods to study abnormalities in the Siamese cat visual system that resulted from their misdirected retinal projections (e.g., Kaas and Guillery 1973), and extended these studies to include a white tiger (Guillery and Kaas 1973), and ultimately in an albino monkey (Guillery et al. 1984). As our results on Siamese cats differed somewhat from those of Hubel and Wiesel (1971) in Boston, Guillery proposed that we assume that two patterns of cortical organization exist, one for Midwestern Siamese cats, and one for Boston Siamese cats. This seemed to be a practical way of resolving the differences. Through Guillery, I got to work with two of his postdocs, John Harting from the Diamond lab at Duke, and Ken Sanderson from P.O. Bishop's lab in Australia. John remained at Wisconsin, and later became chair of the Anatomy Department. As for teaching at Wisconsin, I was only required to offer a seminar. I scheduled it for 10–12 Saturday morning to discourage attendance. When only one student showed up, Denis Steindler, I suggested playing basketball 10–12, followed by an hour of discussion in the Badger Tavern. He agreed, and it didn't hurt him too much, as he went on to a successful career in neuroscience. Later I had the opportunity to collaborate with him when he was a faculty member at the University of Tennessee Medical School in Memphis, Tennessee.

My situation at Wisconsin had been perfect for me as I was well funded through Woolsey's center grant and surrounded by great investigators. Woolsey's efforts had provided outstanding histological services, a shop person within the laboratory, equipment repair and service, a trained assistant for animal surgery, and fantastic illustration and photographic services. My now-comfortable environment at Wisconsin soon radically changed as a result of being invited to interview by the Department of Psychology at Vanderbilt University in Nashville, Tennessee.

Starting at Vanderbilt

Sometime after my former classmate Bruce Masterton left Vanderbilt for Florida State, and his replacement did not get tenure, Diamond suggested me for the vacant position at Vanderbilt and encouraged me to at least interview there. The interview was in May while the snow was piled high in Wisconsin, and it was spring in Nashville. An outdoor party with the faculty reminded me of how long the winter was in Wisconsin. After some negotiating, I received an offer that was raised to that of associate professor, but the real inducement was an offer of a research position for my wife at the

Vanderbilt University Kennedy Center. I didn't want to leave Wisconsin, but this was a great opportunity for positions for both my wife and me, and so we moved. I started my position in 1973. I had the remarkably low start-up funds of $15,000, and a few rooms abandoned by the departed investigator who didn't get tenure. As a parting gift, this investigator had the rooms painted purple. I quickly realized I wasn't in Kansas (Wisconsin) anymore and scrounged what I could in equipment. I spent half of the $15,000 on a microscope, and soon spent the rest to support a graduate student, Rick Lin, who came from the Diamond lab, and most important, he knew how to do histology. Jennette Norden, a graduate student at Vanderbilt, joined me for her PhD research. She later received many awards for her outstanding teaching of neuroanatomy at Vanderbilt Medical School. My attempts to get a vision grant from NIH failed, to my surprise, but I was rescued by NSF and, soon thereafter, by a second NSF grant on somatosensory cortex. By 1975, I got my vision grant from the National Eye Institute (NEI), and in 1980, my National Institute of Neurological Disorders and Stroke (NINDS) grant on the somatosensory system. I have retained both of these NIH grants to this day. Having this consistent funding has been very important in my being able to maintain a functional laboratory. Unfortunately, funding for neuroscience has become much less dependable.

Teaching at Vanderbilt

As research dominated my time while I was in the medical school at Wisconsin, my teaching role in psychology at Vanderbilt was quite an adjustment. I was assigned two courses per semester, which meant six hours in class per week, and this continued until I was well past the level of full professor. I taught Physiological Psychology, which I renamed Introduction to the Neurosciences, when students asked, "Where is the psychology?" I started to teach animal behavior, with no relevant background, and it became my most fun class. I was asked to coteach human sexuality with Leslie Smith, but soon found this was too difficult for me, while Leslie continues this popular course on her own.

The teaching did me a lot of good, as I was always stressed when giving public talks, and my nervous system adjusted as it couldn't be stressed that many times a week. Teaching also taught me to keep things simple and to not put too much in a lecture. However, I have not been completely successful. Recently, my daughter, Lisa, sent me a book *Don't Be Such a Scientist* (2009) by Randy Olson, which listed all the mistakes scientists commonly make when giving talks. I recognized that I made, or make, most of them.

Early Research at Vanderbilt

At first, Rick Lin and I focused on anatomical studies of the connections of the visual system on monkeys, using the Nauta methods I learned

from Guillery. Then we added autoradiographic methods with the help of Vivien Casagrande, who had a PhD from the Diamond lab, and did a postdoc with Guillery at Wisconsin. I helped recruit Vivien for the Anatomy Department at Vanderbilt, and Vivien and I continue to collaborate on studies of the visual system. I also spent two summers at the University of California, San Francisco, studying auditory cortex with Mike Merzenich, as we had became close friends while both of us were postdocs in the Woolsey laboratory. This allowed me to learn about mapping auditory cortex, which paid off later, but also, and most importantly, to get Mike to come to Vanderbilt for a very productive year of collaborative research on the somatosensory system. As I had switched from auditory to visual system research in Woolsey's Laboratory, Mike had switched from his somatosensory background during his PhD with Vernon Mountcastle to auditory research at Wisconsin (see autobiography, Merzenich 2012). Thus, Mike was the leading collaborator for a series of studies on the organization of the somatosensory system in monkeys and then on the functional recovery of this system after sensory loss in mature monkeys.

I had wanted to expand my research program to include the somatosensory system, but needed to create a larger group of investigators. This started with the arrival of Rick Lin from Duke, and then Randy Nelson, a new graduate student with experience in the Diamond laboratory at Duke as an undergraduate. I was also very fortunate to be able to attract Dan Felleman to join the lab as a graduate student, as he had considerable experience as an undergraduate investigating the response properties of single neurons in the visual cortex of cats with Bob Emerson at the University of Rochester. In addition, I became the PhD thesis supervisor of Mriganka Sur, a gradate student in the Department of Electrical Engineering at Vanderbilt, through the help of a psychology professor, Bob Fox. Bob was very active in recruiting me to Vanderbilt and was a dependable supporter. Because I didn't have the funds, Bob supported Mriganka for me for a year. All these PhD students went on to complete postdocs in other laboratories and have productive research careers at major universities.

With graduate students like these, and Mike Merzenich joining us, how could we not become successful? We soon established that the traditional "S1" representation in primates consists of four complete representations of the contralateral body, one for each of the four classical architectonic areas of Brodmann: areas 3b, 3a, 1, and 2 (Merzenich et al. 1978; Kaas et al. 1979). On the basis of neuron response properties, and thalamic connections (e.g., Lin et al. 1979), we regarded area 3b as the primary tactile area, with areas 1 and 2 as higher levels of processing, and area 3a as the primary proprioceptive area. We were able to distinguish modular segregations of neurons responding to rapidly or slowly adapting cutaneous receptors in area 3b (Sur et al. 1981), determine quantitative features of the somatotopic representations in areas 3b and 1 (Sur et al. 1980), and described the

somatotopic organization of the ventroposterior nucleus in detail (Kaas et al. 1984). We also defined ventroposterior superior nucleus that relays proprioceptive information to areas 3a and 2, often by branches of the same neurons (Cusick et al. 1985). We mapped the somatotopy of area 3b or "S1 proper" in macaques, owl monkeys, squirrel monkeys, cebus monkeys, galagos, cats, grey squirrels, and tree shrews. We also mapped the somatotopy of area 2 in macaque monkeys and determined its connections (e.g., Pons and Kaas 1986). Much of this early research was made possible by the addition of Tim Pons as a graduate student, Preston Garraghty as a visiting graduate student, and Cassie Cusick as a postdoc from Ray Lund's lab.

In parallel with the above studies, we started a series of investigations of the responses of mature somatosensory system to sensory loss. We started by cutting the cutaneous median nerve to the thumb side of the glabrous skin of the hand, and tying the proximal end to prevent regeneration. This experiment was meant to be a control for studies on the regeneration of sensory nerves (cut nerves regenerate with errors, while a crushed nerve regenerates perfectly, as demonstrated with a postdoc, John Wall (Wall et al. 1983). However, when regeneration was prevented, our experiments revealed that the deprived cortical territories of the median nerve in areas 3b and 1 were reactivated by inputs from other parts of the hand over a period of weeks (Merzenich et al. 1983a, 1983b). This was at a time when it was widely believed that the organizations of sensory systems were mutable only during a narrow sensitive period of development. Our early experiments started us on a series of plasticity studies of the somatosensory system of adult primates that continue to this day. Also during this time period, additional experiments on the somatosensory system and studies of motor cortex were due to the arrival of Harry Gould after his PhD with Ford Ebner, and the help of Herb Killackey as visiting faculty. Sherre Florence joined us as a postdoc from Vivien Casagrande's lab. Sherre was instrumental in continuing the somatosensory plasticity studies, along with Preston Garraghty when he returned to my lab after postdoctoral research with Mriganka Sur at Yale and MIT. Mike Sesma came over from the Casagrande lab for a short period and produced a remarkable paper on area 17 projections in tree shrews (Sesma et al. 1984). Mike is now chief of the postdoctoral training branch at NIH.

Branching Out with a Second Wave of Co-investigators

I got to work with another group of investigators when Mike Huerta from the John Harting lab and graduate students Lynn Leuthke and Leah Krubitzer from Vanderbilt Speech and Hearing joined my lab. Rosalyn Weller was a new graduate student, and Iwona Stepniewska, an expert on motor cortex, came as a postdoc from the Nencki Institute in Poland (Iwona has now been with me for 25 years). Todd Preuss came as a postdoc with an interest in

brain evolution and frontal cortex from the Pat Goldman-Rakic lab at Yale, and Neeraj Jain, with a background in molecular biology, joined us from India. Patricia Gaspar came on leave for a short time from her research position in Paris, where she studied neural development. Additionally, Ken Catania, while working on his PhD with Glen Northcutt, came to investigate the somatosensory system of star-nosed moles, and he stayed on as a postdoc. Later additions were graduate students Carolyn Wu, Pamela Beck, Troy Hackett, Pei-Chun Fang, and David Lyon. Marcie Pospichal, a postdoc from another lab at Vanderbilt, headed experiments on visual cortex in cats.

From the many important contributions of this group, I will mention only a few. Harry Gould led our first efforts to use stimulating microelectrodes to map motor and premotor cortex in monkeys, and we were the first to conclude that the organization of the primary area, M1, has an overall crude somatotopy, but with regionally formed mosaics where adjoining sites evoke different, but related, movements (Gould et al. 1986; see Kaas 2012, on the possible significance of the "fractured" somatotopy). This was followed by a number of studies on the organization and connections of motor and premotor cortex in various primates and other mammals. Mike Heurta produced one of the best comparative studies of the connections of the frontal eye field across New and Old World monkeys (Heurta et al. 1987). In a series of comparative and developmental studies, Rosalyn Weller showed that 80 percent of the retinal ganglion cells that project to the parvocellular geniculate layer in primates selectively degenerate after lesions of primary visual cortex (e.g., Weller and Kaas 1989). This suggests that those ganglion cells have no axon terminals in other targets to sustain them, and, of course, they can play no role in the "blindsight" reported in humans with V1 lesions. With our studies of the connections of visual and somatosensory system, and the plasticity of the somatosensory system after injury continuing, we branched out to study the reactivations of visual cortex after lesions of the retina (Kaas et al. 1990) with the collaboration of Yuzo Chino, and auditory cortex after a hearing loss in adult monkeys (Schwaber et al. 1993). Thus, the organizations and functions of somatosensory, visual, and auditory systems are not fixed during development, but are capable of structural and functional modifications that may compensate, in part, for sensory loss. One reviewer of our paper on visual cortex reactivation argued that our results could not be correct, as the lack of plasticity of the mature visual system of mammals was well established. The paper was published anyway.

As a member of the laboratory, Ken Catania continued to describe the strange somatosensory system of the star-nosed mole (Catania et al. 1993; Catania and Kaas 1997), while moving on to study cortical organization in shrews, opossums, and hedgehogs (e.g., Catania et al. 1999). Ken has many other unique accomplishments, and he is now a chaired professor in the Biology Department at Vanderbilt. Leah Krubitzer discovered that the region of somatosensory cortex known classically as SII contains

two somatotopic representations, which we named S2 and PV (for parietal ventral), first in squirrels (Krubitzer et al. 1986) and then in other mammals, including monkeys (Krubitzer and Kaas 1990). In related experiments, Cassie Cusick discovered a new "ventral" somatosensory area (VS) in monkeys (Cusick et al. 1989). These newly discovered areas have now been described for humans.

Our Studies of the Auditory System

I always felt that there was much we could learn by studying the auditory system in parallel with our studies of the visual and somatosensory systems. I had started working on auditory cortex with my PhD thesis, continued with a study with Ralph Beital, completed while I was at Wisconsin, but only published 20 years later when Ralph came back to neuroscience (Beital and Kaas 1993). Additionally, I had helped map auditory cortex in squirrels and tree shrews with Mike Merzenich in San Francisco. The opportunity to do more finally came when Lynn Leuthke (Huerta) from the Speech and Hearing Department at Vanderbilt wanted to do her PhD thesis with me on auditory cortex. This got us started on studies of auditory cortex organization and connections in squirrels (Leuthke et al. 1988) and marmosets (Leuthke et al. 1989). Lynn married Mike Huerta, and both ended up in administrative positions at NIH. The studies continued with the arrival of Anne Morel, after a PhD in auditory physiology in Switzerland and a postdoc on the organization and connection of the auditory thalamus in cats with Tom Imig in Kansas. We were able to use microelectrode mapping methods to define subdivisions of auditory cortex and then determine their connections in owl monkeys (Morel and Kaas 1992) and then, with the help of Preston Garraghty, in macaque monkeys (Morel et al. 1993). Anne and I applied for an NIH grant to continue these studies, and it was awarded. But before it could start, Anne received an offer of a research position in Switzerland that was too good to turn down, and our joint research plans and the grant funding were abandoned. Fortunately, Troy Hackett, another graduate student from the Speech and Hearing Department, wanted to do his PhD with me, and we subsequently picked up where Morel and I had left off. We studied the connections of the third level of auditory cortex in macaques, the region we defined as the parabelt, with the belt and core areas (Hackett et al. 1998). Troy continued with related anatomical studies, including comparative studies of auditory core areas in macaque monkeys, chimpanzees, and humans (Hackett et al. 2001). We proposed a general model for auditory cortex organization and connections in primates (Kaas and Hackett 2000) that became widely accepted. Troy has stayed at Vanderbilt, becoming a professor in the Speech and Hearing Department, and has become the foremost authority on the anatomical organization of the auditory system in primates. I continue to value his advice and experience, as Troy continues

his research at Vanderbilt. Corrie Camalier, a recent graduate student who helped develop single unit recording from auditory cortex in macaques with Troy, also wrote a nice review with me (Camalier and Kaas 2011). Corrie moved on to auditory research at NIH as a postdoc.

Studies of the Response Properties of Single Neurons in Somatosensory Cortex

My experience with quantitatively characterizing the properties of single neurons was initially limited to those conducted on MT and V1 of owl monkeys with Dan Felleman (Felleman and Kaas 1984). Dan truly amazed me as he constructed a motor-driven mechanical system for projecting visual stimuli on a screen, rotating the image, and moving it about, all under the control of a primitive PDP-8 computer. Later, I was encouraged to do more studies of neuron responses by Miguel Nicolelis, who convinced me of the value of using chronically embedded microelectrode arrays to study the processing of somatosensory information across cortical areas in monkeys (Nicolelis et al. 1998). Miguel has become a close friend, and he helped and advised me in many ways. With his guidance, I continued the chronic recording studies with Neeraj Jain and Hui-Xin Qi (e.g., Jain et al. 2001). Hui-Xin finished her PhD in Switzerland on motor cortex of monkeys, and came to me as a postdoc in 1996. She has stayed with me ever since, while gradually taking over our program on the organization and plasticity of the somatosensory system in primates. Hui-Xin convinced me that we should continue our single neuron recording studies by using the 100-electrode Utah array that was used for the visual cortex of cats in the nearby laboratory of A. B. Bonds. With the help of a very talented graduate student, now a postdoc, Jamie Reed, we were able to demonstrate that neurons in primary somatosensory cortex (area 3b) of monkeys integrate information from all over the hand, while having small excitatory receptive fields on only small parts of the hand (e.g., Reed et al. 2010). We also showed that this integration of information included that from stimuli on both hands (Reed et al. 2011), even though there are very few direct corpus callosal connections in the hand representation of area 3b. More recently, we have used this multielectrode approach to study the response properties of neurons in area 3b of monkeys after behavioral recovery from a sensory loss of the dorsal column branches of tactile afferents from the hand. The return of nearly normal response properties to reactivated cortical neuron representation suggests that these reactivated neurons play a critical role in the behavioral recovery of hand use (Qi et al. 2014). We are currently investigating potential anatomical sources of this reactivation with the help of Chia-Chi Liao, an outstanding postdoc from the National Taiwan University (Liao et al. 2015). The evidence suggests that the preservation of even a few of the normal connections can be very important, as they become potentiated and activate

larger populations of neurons. In addition, new connections appear to play a role in the reactivation (see Kaas and Bowes 2014). As part of her PhD thesis with me, Charnese Bowes demonstrated that treatment of a brainstem nucleus with an enzyme, after a sensory loss, promoted the growth of new connections and the reactivation of somatosensory cortex (Bowes et al. 2012).

Counting Neurons and Other Cells in Brains

At a neuroscience meeting in Natal, Brazil, in 2004, and again at the Society for Neuroscience meeting in 2004, I met a most remarkable woman from Brazil at her posters. Suzana Herculano-Houzel had invented a more productive way of counting the numbers of neurons and other cells in any brain or part of brain by homogenizing the tissue and counting cell nuclei from samples (the isotropic fractionator method; Herculano-Houzel and Lent 2005). The great advantage of her new method was that accurate estimates of neuron numbers in any structure could be rapidly obtained (see Herculano-Houzel et al. 2015 for an evaluation of methods). By determining the numbers of neurons in rodent brains of different sizes, Suzana showed that neuron-packing densities were not maintained with increases in brain size, so that the larger brains of larger rodents had fewer neurons than expected from brain size. We decided to collaborate on counting from primate brains of different sizes, and found that primate brains do maintain neuron packing densities with increasing brain sizes (Herculano-Houzel et al. 2007). Thus, to the extent that neuron numbers reflect brain functions, primates have an increasing advantage over rodents (and other mammals) as brain sizes increase. Given the astonishing lack of reliable information on neuron numbers for brain structures across the many animal taxa, and the effectiveness of these new methods, there has been an explosion of efforts from several groups to obtain new data on neuron numbers in brains and brain parts. Christine Collins, who had worked with me on the visual system as a postdoc and research assistant professor for a number of years, took over this part of our program for neuron and cell counting, and developed an automated method of counting using flow cytometry (Collins et al. 2010). Nicole Young, a postdoc from Canada, joined us and was responsible for an important study showing that the motor cortex of baboons with spontaneous epilepsy had lost a large proportion of their neurons in motor cortex (Young et al. 2013). Many of our studies have depended greatly on Suzana, and we continue to work together. Her PhD student, Mariana Gabi, has recently joined my lab as this work continues with the help of graduate students Dan Miller and Emily Rockoff. Our studies indicate that neuron packing densities vary greatly across the cortical sheet in all primates, being low in some areas such as primary motor cortex, where average neuron size is high, and very high in primary visual cortex, where small layer 4 neurons

dominate. In brief, neuron packing densities relate to average neuron size, and these anatomical specializations reflect the specializations of different cortical areas for different functions.

Studies of Networks for Action-Specific Behaviors in Parietal-Frontal Cortex in Primates

A number of years ago, I was treated to an amazing demonstration of brain function while I was visiting the laboratory of Mike Graziano at Princeton University. Mike had a microelectrode in motor cortex of an awake, somewhat bored macaque monkey, and every time he delivered a half second train of electrical pulses via the microelectrode to motor cortex, the monkey calmly brought its hand to its mouth. Mike discovered that motor and premotor cortex have subdivisions where action-specific, ethnologically relevant movements could be reliably evoked by electrical stimulations long enough ($\sim$ 0.5 sec) to complete the movement (for details, see Graziano 2009). I realized that this type of stimulation could be a powerful tool, and introduced it to my lab in studies lead by Iwona Stepniewska, who had worked with me before on motor systems, visual cortex, and the pulvinar. We started our studies on galagos, a small prosimian primate, in which we were studying frontoparietal connections (Fang et al. 2005). We soon found that we could study the functionally related cortical subdivisions we called domains, in anesthetized as well as awake primates. In prosimian galagos, we discovered that as many as eight domains existed in motor cortex, again in premotor cortex, and a third time in posterior parietal cortex (Stepniewska et al. 2005). Domains included those for grasping, reaching, hand-to-mouth, head or body defense, running, face aggressive, and looking. Functionally matched domains across the three critical regions were serially interconnected, and the evoked motor behavior was dependent on the contributions of primary motor cortex. Omar Gharbawie, a postdoc from Canada, joined these efforts, and we extended our studies to New World monkeys and then macaque monkeys (for a review, see Kaas and Stepniewska 2015). Omar focused his studies on macaque monkeys and recently moved to become an assistant professor at the University of Pittsburgh.

While our studies revealed major similarities in the organization of posterior parietal cortex and frontoparietal networks across the prosimian, New World monkeys, and Old World monkey branches of primate evolution, the elaboration of posterior parietal cortex and these frontoparietal circuits was not seen in tree shrews (Remple et al. 2007), a close relative of primates. Thus, a major expansion and involvement of posterior parietal cortex in motor behavior evolved in the ancestors of early primates but not in the close relatives of primates (Kaas and Stepniewska 2015).

It may seem unusual to study neural networks that relate to specific behaviors with electrical stimulation, but this approach gives us a higher

level of control over the outputs of these networks as we alter them in various ways. For example, we have determined the effects of complex patterns of movement of selectively deactivating parts of the network with muscimol (Stepniewska et al. 2014) or with cortical cooling (with Dylan Cook and Leah Krubitzer) while electrically stimulating other parts of the network. Our studies continue, and they give me the opportunity to continue to collaborate with two of my former PhD students, Leah Krubitzer and David Lyon.

Optical Imaging of Cortical Responses

I have benefited greatly through collaborations with other faculty members at Vanderbilt, including former members of my lab after they became faculty (Troy Hackett and Ken Catania), but especially Vivien Casagrande, as we have worked together on many projects, and Anna Roe, a major addition to the faculty of my department. Anna finished her PhD at MIT with one of my first PhD students, Mriganka Sur. Vivien started the optical imaging research at Vanderbilt. This method of visualizing cortical activity was well suited to studies in our usual experimental primates, galagos, owl monkeys, and squirrel monkeys, as these primates have few cortical fissures so that more cortical regions of interest are exposed for study. Thus, we were able to image functionally related activity in visual area MT (e.g., Xu et al. 2004) and other visual areas, as well as somatosensory cortex. With the arrival of Anna Roe as a new faculty member, such experiments continued in her lab, with the help of Peter Kaskan (Kaskan et al. 2009), a talented graduate student. With the help of other graduate students, Reuben Fan and Mary Baldwin, we used optical imaging to demonstrate the location and retinotopy of dorsal V3 along the rostral border of V2 in galagos (Fan et al. 2012). Other experiments involved imaging MT after lesions of visual cortex to reveal a prominent loss of visually evoked activity, ocular dominance columns in primary visual cortex, and patterns of cortical activity evoked by focal microstimulation of cortical sites.

The Organization of the Pulvinar Complex in Mammals

I have been interested in the visual pulvinar since my early mapping studies of part of the inferior pulvinar with John Allman (Allman et al. 1972). In primates, the pulvinar has been historically divided into inferior, lateral, and medial "nuclei." A breakthrough in my understanding came early in my career at Vanderbilt when my graduate student, Rick Lin, provided clear evidence in owl monkeys that the traditional inferior pulvinar contained at least three separate nuclei, including IPp, or posterior division of the inferior pulvinar, projecting to temporal cortex; a medial division, IPm, projecting to MT; and a large central division, IPc (Lin and Kaas 1979). IPp and IPc received dense inputs from the superior colliculus. Cassie Cusick, after

she left my lab for a faculty position at Tulane (e.g., Gutierrez et al. 1995), and Iwona Stepniewska (e.g., Stepniewska and Kaas 1997) further defined the subdivisions of the pulvinar complex on the basis of striking histochemical differences and patterns of cortical and subcortical connections. The results led us to subdivide the large IPc subdivision into central lateral and central medial nuclei of the inferior pulvinar, IPcl and IPcm. We have summarized our views on pulvinar organization across New and Old World monkeys and proposed that the large nucleus of the inferior pulvinar, IPcl, and large ventrolateral nucleus of the lateral pulvinar, PIvl, are connectionally related to early visual areas V1, V2, and V3, and they largely contribute to the ventral stream of cortical processing. The three remaining nuclei of the inferior pulvinar, IPp, IPm, and IPcm, all have connections with the MT complex of visual areas, which contributes to the dorsal stream of visual processing (Kaas and Lyon 2007). Most recently, graduate students Pooja Balaram and Mary Baldwin (now postdocs at Harvard and University of California, Davis) further studied pulvinar organization in prosimian galagos, and a range of nonprimate mammals, in an effort to identify homologous nuclei across mammals and suggest how the pulvinar complex in primates evolved (e.g., Baldwin et al. 2013). Relevant studies by other members of the lab that contributed to our present understanding include an early study on pulvinar connections to VI in galagos by Laura Symonds (Symonds and Kaas 1978), my early study of pulvinar connections in squirrels with Bill Hall and Irving Diamond (Kaas et al. 1972b), and David Lyon's description of pulvinar organization in tree shrews (Lyon et al. 2003).

Studies of Cortical Chemoarchitecture

When I started in the field of neuroscience, there were only a few ways to determine how brains are functionally organized or anatomically connected. To anatomically recognize subdivisions of the cortex and thalamus, we largely depended on the traditional Nissl and myelin stains (e.g., Kaas et al. 1972b). A friend from my time at Wisconsin, Margret Wong-Riley, later introduced us to the useful cytochrome oxidase methods (Wong-Riley 1979). Now there is a vast array of powerful methods that more clearly reveal subdivisions of the brain of functional significance. Many graduate students, postdocs, and faculty collaborators helped bring these newer methods into common use in the laboratory. To mention a few, Todd Preuss (now faculty at Emory) and Iwona Stepniewska initiated our early histochemical studies, including those involving ape and human brains (Preuss et al. 1999). Fabrizio Strata, as a postdoc from Italy, described the chemoarchitecture of the somatosensory brainstem (Strata et al. 2003). Peiyan Wong, an amazingly efficient and productive graduate student from Singapore via Oxford University, really brought our studies of chemoarchitecture to a high level (e.g., Wong and Kaas 2010). Pooja Balaram, a highly productive graduate

student, introduced the use of differential levels of expression of vesicular glutamate transporters to define subdivisions of the brain and suggest functions (e.g., Balaram et al. 2013). Toru Takahata, a postdoc from the Yamamori lab in Japan, introduced us to the power of using visual deprivation to alter the express of "early genes" in the visual system (e.g., Takahata et al. 2009). Currently, a project with Carl Zilles in Germany will allow us to further understand the organization in cortex of galagos by using receptor-binding procedures.

Other Important Contributors at Vanderbilt

I have been and remain fortunate to have outstanding individuals help me run the laboratory. When I arrived at Vanderbilt, a highly motivated undergraduate, Gay Spease, decided that she would manage the laboratory, organize our weekly volleyball game, and do histology. She did all this very well, but soon left for medical school, where I am sure she had great success. Other lab manager–histologists followed, but I was very lucky when Judy Ives transferred from the Medical School to become my histologist, and later hired Laura Trice to help her. Both of these wonderful and invaluable woman have been responsible for the high quality of our histology, training graduate students and postdocs in histochemistry, and making new additions to the lab feel welcome. While Judy Ives retired some years ago, Laura continues to do a great job. Many undergraduates have helped on research projects in the lab. Most have gone on to medical school, with a few to graduate school. Recently, Christina Cerkevich and Mary Baldwin finished PhDs in the lab, after starting in the lab as undergraduates. Mary is a talented illustrator and as such greatly improved our papers. In addition, as a former athlete on the Vanderbilt Track Team, she was one I could count on to share my interests in sports. Pooja Balaram, a Vanderbilt undergraduate, trained in another lab and then joined my lab for graduate school. Finally, MD/PhD student Mark Burish was such an asset to everyone, as he so willingly helped conduct their research. Mark's father had been chair of my department, and later Vanderbilt provost, and he was both very effective and well liked. Clearly Mark reflected his father's best traits.

International Schools and Exciting Meetings

Perhaps the most important conference for my development was the Symposium on Basic Thalamic Structure and Function in Brooklyn, New York, in 1971. A number of major investigators were invited, including my former PhD supervisor, Irving Diamond. As I was still just a postdoc in the Woolsey laboratory, I wasn't invited at first, but Diamond insisted that I was an expert on the lateral geniculate nucleus (a major exaggeration) and eventually I was invited. The talks at the symposium were published in the

new journal, *Brain Behavior and Evolution*, and my paper with John Allman and Ray Guillery (Kaas et al. 1972c) recently became a "Citation Classic" in that journal (Kaas 2015). My experience at the Brooklyn meeting made me more confident, and I was eager to participate in such symposia again. The next opportunity came quickly at a symposium on Developmental Aspects of Vision in 1972, where I went as a substitute for Ray Guillery, who couldn't attend. The highlight of the meeting, for me, was a great talk by Colin Blakemore. It was easy to see, even at this early stage, that Colin would be very successful. We continued to interact over the years, and a friendship has developed. Meetings in other exciting places included an interesting conference on comparative aspects of brain organization held in Caracas, Venezuela, in 1974, which was organized in part by Sven Ebbensson, now another longtime friend. Mike Gazzaniga invited me to fantastic meetings in Barcelona and Venice. The Venice meeting featured Stephen Jay Gould taking us to the Basilica of San Marco to explain his concept of the role of repurposed structures, like the spandrels of the Basilica, in evolution (Gould and Lewontin 1979).

In 1986 I was fortunate to be invited to be a lecturer in a course on the organization and development of brains at the International Center for Theoretical Physics in Trieste, Italy, and I returned in subsequent years four times as an organizer, and I helped some of these students come to labs in the United States. The two- to four-week courses were a great success and provided interaction with advanced students from all over the world, including students from "third world countries." I interacted with investigators from Cuba, and I then met with one of them again when I was a lecturer in a two-week IBRO workshop in Cuba in 2007. I was able to help some of the students in Trieste come to labs in the United States and one of them, Velayudhan Rema from India, came to work with Ford Ebner at Vanderbilt. Rema soon convinced me to add her boyfriend (now her husband), Neeraj Jain, to my lab as a postdoc. Both are now back in India, where Neeraj has become a productive, highly respected neuroscientist. In Trieste, an Italian PhD student, Fabrizio Strata, generously provided his car for my wife to use during our time there. It was the smallest car I have ever been in. Barbara became so used to the Italian style of driving, that she became impatient with the slow pace of Nashville drivers for months after our return. Fabrizio also introduced us to a tradition that takes place in the hills around Trieste, where in early fall the local farmers serve their new wine with local cheeses and breads in an outdoor setting in their vineyards. Later, Fabrizio came to work with me as a postdoc. A good friend, Mathew Diamond, the son of my PhD mentor, Irving Diamond, and a very successful neuroscientist in Trieste, organized subsequent sessions of the course. I have also been a lecturer, and sometimes co-organizer, of courses in Lausanne, Switzerland; the Karolinska Institute in Stockholm (thanks to G. Grant); several cities in Germany; Naples Italy, Barcelona Spain, and the Summer Institute in

Cognitive Neuroscience in Santa Barbara and Lake Tahoe. All these occasions resulted in great interactions with students and other faculty, and an appreciation of other cultures.

While traveling to participate in conferences and international meetings in a number of countries, I was able to develop special ties with investigators in some of these countries early in my career. One such place was Berlin, Germany, at a Dahlem Workshop in 1977 (Kaas 1977), well before the Berlin Wall came down. A special tour was arranged to visit the great Pergamon Museum in East Berlin. This workshop was special in that we formed groups that were required to come up with a summary of agreements over a topic of concern. I was able to attend two subsequent Berlin meetings, and other meetings in Germany.

Other connections formed with investigators in Australia. It started with collaborations with Ken Sanderson while we were both at the University of Wisconsin and continued after he returned to Australia. To this day we stay in touch. My first trip to Australia was to give a talk at an international meeting in Sydney, in 1983, where I stayed in a cheap hotel to save money and discovered it was in a part of the city dominated by sailors and bars. After the meeting, I participated in a wonderful Festschrift for P.O. Bishop, where speakers were isolated on Lord Howe Island. Bishop, a leading visual neuroscientist, attracted postdocs from many countries, including Jean Bullier from France (after a PhD at Duke). There I also met Boydan Dreher, Horace Barlow, Jack Pettigrew, Jon Stone, Bob Rodieck, and Geoff Henry. I had other visits to Australia, but none better than a research stay with Jack Pettigrew to catch fruit bats, record from somatosensory cortex, see the Great Barrier Reef, and write a paper for *Nature* within a month (Calford et al. 1985). For the trip, I took my son, and Mike Huerta, a postdoc with me at the time, and we found it convenient to break up the long flights with a stopover in Hawaii on the way down, and in Tahiti on the way back. We were in Tahiti for Bastille Day and enjoyed a big celebration. Herb Killackey, there for other reasons, joined us.

Soon thereafter, Jean Bullier and Henry Kennedy organized a large international meeting on the visual system in Lyon, France, in 1986. It was fortunate for me that this was one of the first such meetings in France where talks could be in English. I have returned to Lyon, famous for its cuisine, many times, and remain close to Henry as a collaborator and friend. Other visits took me to Paris where my former collaborator, Patricia Gaspar, has become a leading neuroscientist. There have been many other great meetings in wonderful places that led to new relationships, such as those at the Wenner-Gren Center and the Karolinska Institute in Stockholm, the International Summer School in Amsterdam, meetings in Montreal, and the RIKEN center in Tokyo.

Two other places have special meaning for me. First, my interest in the organization of the brain in small-brained mammals led to an invitation

from Roca-Miranda, known for his work on the brains of South American opossums, to visit in Rio de Janeiro, which led to an NSF U.S.–Brazil Cooperative Research Grant. This led to more visits, including those to other cities in Brazil, and to research collaborations. An early collaborator was Joao Franca, and then other Brazilians unrelated to the original funding, especially Miguel Nicolelis and Suzana Heuculano-Houzel, but also Marcello Rosa after he moved to Australia. Another place of special importance to me is Taiwan. My first graduate student recruit at Vanderbilt was Rick Lin from Taiwan, and three subsequent graduate students or postdocs have been from Taiwan: Carolyn Wu, Pei-Chun Fang, and Chia-Chi Liao, all great contributors. Wu and Fang especially collected data that led to a better understanding of cortical organization in prosimian galagos. During visits to Taiwan, I witnessed two typhoons, and with Rick Lin, visited his father's family home (his father was a popular senator in the Taiwan government), and stayed at a beautiful lake in the mountains.

A Special Event

In 2000, I was elected to the National Academy of Sciences. This would be special for anyone, but for me it was the honor of having Mort Mishkin call and inform me of the award. Mishkin is a special hero of mine as he always interacted with me in a positive manner, and his laboratory at NIH produced so much of the research that interested me. Following this event, I received congratulations from two unexpected sources, my high school chemistry teacher, who actually remembered me, and my Northland College teacher in social psychology who meant so much to me.

While there have been other special events, I mention only one more here. For many years, I have had the privilege of serving on the editorial board of the *Journal of Comparative Neurology*, for a time as an associate editor. This has been a favorite journal of mine, where I have more published papers than anywhere else. One of the most outstanding editors of the journal was Sanford Palay. I enjoyed interacting with him, and receiving his detailed comments and corrections on my submitted papers. What an honor it was for me to have received the Sanford Palay Award from the *Journal of Comparative Neurology* and the Cajal Club in 2014.

What Has Been Accomplished?

With more than 50 years in research and many collaborations, what has been accomplished? I feel that our research has led to a much better understanding of the organization of sensory and motor systems in primates, especially at the cortical and thalamic levels. In addition, we have revealed much of the astonishing ability of these systems, in mature primates, to spontaneously recover from injuries and sensory loss. We are beginning to understand

how these reactivations and recoveries occur through the strengthening of weak pathways and the growth of new ones. Our focus is starting to move toward discovering and testing treatments that may promote recoveries (Bowes et al. 2012). These advances were made in conjunction with studies from many other laboratories, all aimed at the same broad goals. In addition, much of our research effort has been directed toward understanding differences and similarities in brain organization in mammals less commonly studied than the usual model species. This includes our research on opossums, tenrecs, shrews, tree shrews, seals, tarsiers and galagos, and other prosimian primates. Our studies of forebrain organization in prosimian galagos and tree shrews have been especially important to me as galagos represent a major branch of primate evolution, and tree shrews are closely related to primates and thereby provide insights on the emergence of primates. While there are difficulties in studying such mammals, and often with little in the published literature to guide us, the payoff is in finding out things that are unlikely to be produced by other laboratories. Thus, we are able to see more of what is possible in the evolution of nervous systems, and infer what the brains of extinct mammals were like (Kaas and Preuss 2014).

We were able to maintain our research on galagos for so long by maintaining a breeding colony. Important, related discoveries have been made with this primate by members of the Diamond laboratory, Vivien Casagrande at Vanderbilt, and Mary Carlson during her graduate student years and while she was faculty at Washington University in St. Louis. This shared interest led to many collaborations and research so that the general organization of the forebrain of galagos is fairly well known. It now appears that galagos have roughly 40 cortical areas that are shared with New World and Old World monkeys. Studies on galagos and a few other prosimians make it possible to say, with considerable certainty, that all primates have inherited a collection of visual and other cortical areas, including visual area MT, from a common ancestor. MT does not appear to exist in any extant nonprimate, so studies of MT's role in vision are possible in primates alone. While much can be learned from studies on brains much different than ours, comparative studies of brain organization have the potential of revealing what can and cannot be inferred about humans from studies on other species.

Epilogue

Things have worked out very well for me. My first wife, Judith, was a fellow graduate student, and she gave me two wonderful children, who decided early on not to be scientists. They provided me the continuing joy of six grandchildren. My second wife, Barbara Martin, works closely with me, and travels with me everywhere. She remains my closest friend. As I continue

to train graduate students and postdocs, I wonder about their future. Most of my earliest coworkers are now well-established, productive neuroscientists, or for some, highly effective teachers and administrators. Two former graduate students and postdocs, Leah Krubitzer and Ken Catania, stand out because they received the highly prestigious MacArthur Fellowship for their highly original research, and more important to me, they remain good friends. Sadly, two others, Tim Pons and Yvonne Rothemund, have died, and this continues to disturb me as I think of them. With both, I enjoyed many conversations, always with good humor that lifted my spirits.

The years of research have taught me to not hold any beliefs too dear. As one example, I initially held (with John Allman) that a number of visual areas in primates border V2, rather than a V3. Experiments by David Lyon convinced me with compelling evidence that all primates have a V3 (e.g., Lyon and Kaas 2002), and this long-held view (e.g., Zeki 1978) is widely accepted today. Yet, it is important to recognize that not all reported observations on visual cortex organization in primates fit nicely into that framework (Kaas et al. 2015), and that ultimately some further modifications of present views may prevail. Quite often, for any area of study, all available observations do not point in the same direction. Thus, we should be ready to change our minds about even our long-held views.

The opportunities I had, and those my early students had, seem less available now. The best undergraduates in my lab, about 10 per year, go to medical school. Graduate students at Vanderbilt and elsewhere ask, "What else can I do?" Now, it seems that the field requires the most dedicated and success is very uncertain. But I still feel that it is most important to do what you most want to do. Have a profession that is not work, but the most enjoyable hobby you can imagine. I live in Nashville, a center for the music industry, and I meet people all the time who are struggling to be part of that industry. Competition is intense, and many will not make it, but many persevere because that is what they want to do. An academic career can be fantastic, as you can be your own boss and largely do what you enjoy. If that is what you want to do, more than anything else, perseverance with talent still pays off. Failure is possible, and even likely, but give it a shot. For me, I still love what I do, I'm funded and have a lab with great co-workers, and my oldest granddaughter, Lili, is an undergraduate at Vanderbilt. Life has been good.

References

Allman JM, Kaas JH. Representation of the visual field in striate and adjoining cortex of the owl monkey *(Aotus trivirgatus)*. *Brain Res* 1971a;35:89–106.

Allman JM, Kaas JH. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res* 1971b;31:85–105.

Allman JM, Kaas JH. The organization of the second visual area (VII) in the owl monkey: A second-order transformation of the visual field. *Brain Res* 1974a;76:247–265.

Allman JM, Kaas JH. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). *Brain Res* 1974b;81:199–213.

Allman JM, Kaas JH. The dorsomedial cortical visual area: A third tier in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res* 1975;100:473–487.

Allman JM, Kaas JH. Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science* 1976;191:572–575.

Allman JM, Kaas JH, Lane RH, Miezin FM. A representation of the visual field in the inferior nucleus of the pulvinar in the owl monkey (*Aotus trivirgatus*). *Brain Res* 1972;40:291–302.

Balaram P, Hackett TA, Kaas JH. Differential expression of vesicular glutamate transporters 1 and 2 may identify distinct modes of glutamatergic transmission in the macaque visual system. *J Chem Neuranat* 2013;50–52:21–38.

Baldwin MKL, Balaram P, Kaas JH. Projections of the superior colliculus to the pulvinar in prosimian galagos (*Otolemur garnettii*) and VGLUT2 staining of the visual pulvinar. *J Comp Neurol* 2013;521:1664–1682.

Beital RE, Kaas JH. Effects of bilateral and unilateral ablation of auditory cortex in cats on the unconditioned head orienting response to acoustic stimuli. *J Neurophysiol* 1993;70:351–369.

Bowes C, Massey JM, Burish M, Cerkevich C, Kaas JH. Chondroitinase ABC promotes selective reactivation of somatosensory cortex in squirrel monkeys after a cervical dorsal column lesion. *Proc Natl Acad Sci USA* 2012;109:2595–2600.

Calford, M.B., Graydon, M.L., Huerta, M.F., Kaas, J.H., and Pettigrew, J.D. Altered somatotopy in the brain of a flying mammal. *Nature* 1985;313:477–479.

Camalier CR, Kaas JH. Functional organization of primate auditory pathway and interactions with pathways of reward. In JA Gottfried, ed. *Neurobiology of Sensation and Reward, Chapter 9: Sound.* Boca Raton, FL: CRC Press, 2011.

Catania K, Kaas JH. The mole nose instructs the brain. *Somatosens Mot Res* 1997;14:56–58.

Catania K, Northcutt RG, Kaas JH, Beck PD. Nose stars and brain stripes. *Nature* 1993;Aug 5:364–493.

Catania KC, Lyon DC, Mock OB, Kaas JH. Cortical organization in shrews: evidence from five species. *J Comp Neurol* 1999;410:55–72.

Collins CE, Young NA, Flaherty DK, Airey DC, and Kaas JH. A rapid and reliable method of counting neurons and other cells in brain tissue: a comparison of flow cytometry and manual counting methods. *Front Neuroanat* 2010;4:1–6.

Cusick CG, Steindler DA, Kaas JH. Corticocortical and collateral thalamocortical connections of postcentral somatosensory cortical areas in squirrel monkeys: A double labeling study with wheat germ agglutinin (WGA) conjugated to horseradish peroxidase and radiolabeled WGA. *Somatosens Res* 1985;3:1–31.

Cusick CG, Wall JT, Felleman DJ, Kaas JH. Somatotopic organization of the lateral sulcus of owl monkeys: Area 3b, S-II, and a ventral somatosensory area. *J Comp Neurol* 1989;282:169–190.

Diamond IT, Irving T. Diamond autobiography. In LR Squire, ed. *The History of Neuroscience in Autobiography*, Vol. 1. San Diego: Academic Press, 1996;158–176.

Fan RH, Baldwin MK, Jermakowicz WJ, Casagrande VA, Kaas JH, Roe AW, Intrinsic signal optical imaging evidence for dorsal V3 in the prosimian galago (*Otolemur garnetti*). *J Comp Neurol* 2012;520:4254–4274.

Fang P-C, Stepniewska I, Kaas JH. Ipsilateral cortical connections of motor, premotor, frontal eye and posterior parietal fields in a prosimian primate, *Galago garnetti*. *J Comp Nuerol* 2005;490:305–333.

Felleman DJ, Kaas JH. Receptive field properties of neurons in the middle temporal visual area (MT) of owl monkeys. *J Neurophysiol* 1984;52:488–513.

Gould JH, III, Cusick, C.G., Pons TP, Kaas JH. The relationship of corpus callosum connections to electrical stimulation maps of motor, supplementary motor, and frontal eye fields in owl monkeys. *J Comp Neurol* 1986;247:297–325.

Gould SJ, Lewontin RC. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationists' programme. *Proc Royal Soc London*, Series B, 1979;205:581–598.

Graziano MSA. *The Intelligent Movement Machine.* New York: Oxford University Press, 2009.

Guillery RW. Ray Guillery autobiography. In LR Squire, ed. *The History of Neuroscience in Autobiography*, Vol. 2. San Diego: Academic Press, 1998;132–167.

Guillery RW, Kaas JH. Genetic abnormality of the visual pathways in a "white" tiger. *Science* 1973;180:1287–1289.

Guillery RW, Hickey RW, Kaas JH, Felleman DJ, DeBruyn EJ, Sparks DL. Abnormal central visual pathways in the brain of an albino green monkey (*Cercopihecus aethiops*). *J Comp Neurol* 1984;226:165–183.

Gutierrez C, Yaun A, Cusick CG. Neurochemical subdivisions of the inferior pulvinar in macaque monkeys. *J Comp Neurol* 1995;363:545–562.

Hackett TA, Preuss TM, Kaas JH. Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. *J Comp Neurol* 2001;441:197–222.

Hackett TA, Stepniewska I, Kaas JH. Subdivisions of auditory cortex and ipsilateral cortical connections of the parabelt auditory cortex in macaque monkeys. *J Comp Neurol* 1998;394:475–495

Hall WC, Kaas JH, Killackey H, Diamond IT. Cortical visual areas in grey squirrel (*Sciurus carolinensis*): a correlation between cortical evoked potential maps and architectonic subdivisions. *J Neurophysiol* 1971;34:437–452.

Herculano-Houzel S, Lent R. Isotropic fractionator: a simple, rapid method for the quantification of total cell and neuron numbers in the brain. *J Neurosci* 2005;25:2518–2521.

Herculano-Houzel S, Collins C, Wong P, Kaas JH. Cellular scaling rules for primate brains. *Proc Natl Acad Sci USA* 2007;104:3562–3567.

Herculano-Houzel S, Kaas JH, Miller D, Von Bartheld CS. How to count cells: the advantages and disadvantages of the isotropic fractionator compared with stereology. *Cell Tissue Research* 2015;360:29–42.

Hubel DH, Wiesel TN. Aberrant visual projections in the Siamese cat. *J Physiol* (London) 1971;218:33–62.

Huerta, MF, Krubitzer, LA and Kaas, JH. The frontal eye field as defined by intracortical microstimulation in squirrel monkeys, owl monkeys, and macaque monkeys. II. Cortical connections. *J Comp Neuro* 1987;265:332–361.

Jain N, Qi HX, Kaas JH. Long-term chronic multichannel recordings from sensorimotor cortex and thalamus of primates. *Prog Brain Res* 2001;130:63–72.

Kaas JH. Sensory representations in mammals. In GS Stent, ed. *Function and Formation of Neural Systems*. Berlin: Dahlem Konferenzen, 1977;65–80.

Kaas JH. Evolution of columns, modules, and domains in the neocortex of primates. *Proc Natl Acad Sci USA* 2012;109:10655–60.

Kaas JH. Principles of organization of the dorsal lateral geniculate nucleus. *Brain Behav Evol*; *Citation Classics*, 2015;85:137–138.

Kaas JH, Bowes C. Plasticity of sensory and motor systems after injury in mature primates. In Gazzaniga MS, Mangun GR, eds. *The Cognitive Neurosciences*, 5th ed. Cambridge, MA: MIT Press, 2014;103–118.

Kaas JH, Guillery RW. The transfer of abnormal visual field representations from the dorsal lateral geniculate nucleus to the visual cortex in Siamese cats. *Brain Res* 1973;59:61–95.

Kaas JH, Hackett TA. Subdivisions of auditory cortex and processing streams in primates. *Proc Natl Acad Sci USA* 2000;97:11793–11799.

Kaas JH, Lyon DC. Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res Rev* 2007;55:285–296.

Kaas JH, Preuss TM. Human brain evolution, Chapter 42. In LR Squire, ed. *Fundamental Neuroscience*, 4th ed. San Diego, CA: Elsevier Sciences/Academic Press, 2014;901–918.

Kaas JH, Stepniewska I. Evolution of posterior parietal cortex and parietal-frontal networks for specific actions in primates. *J Comp Neurol* 2015;epub ahead of print.

Kaas JH, Axelrod S, Diamond IT. An ablation study of the auditory cortex in the cat using binaural tonal patterns, *J Neurophysiol* 1967;30:710–724.

Kaas JH, Hall WC, Diamond IT. Cortical visual area I and II in the hedgehog: The relation between evoked potential maps and architectonic subdivisions. *J Neurophysiol* 1970;33:595–615.

Kaas JH, Hall WC, Killackey H, Diamond IT. Visual cortex of the tree shrew (*Tupaia glis*): architectonic subdivisions and representations of the visual field. *Brain Res* 1972a;42:491–496.

Kaas JH, Hall WC, Diamond IT. Visual cortex of the grey squirrel (*Sciurus carolinensis*): Architectonic subdivisions and connections from visual thalamus. *J Comp Neurol* 1972b;145:273–306.

Kaas JH, Guillery RW, Allman JM. Some principles of organization in the dorsal lateral geniculate nucleus. *Brain Behav Evol* 1972c;6:253–299.

Kaas JH, Nelson RJ, Sur M, Lin C-S, and Merzenich, MM. Multiple representations of the body within S-I of primates. *Science* 1979;204:521–523.

Kaas JH, Nelson RJ, Sur M, Dykes RW, Merzenich MM. The organization of the ventroposterior thalamus of the squirrel monkey, *Saimiri sciureus*. *J Comp Neurol* 1984;226:111–140.

Kaas JH, Krubitzer LA, Chino YM, Langston AL, Polley EH, Blair N. Reorganization of retinotopic cortical maps in adult mammals after lesions of the retina. *Science* 1990;248:229–231.

Kaas JH, Roe AW, Baldwin MKL, Lyon DC. Resolving the organization of the territory of the third visual area: A new proposal. Special Collection (Controversial Issues in Visual Cortex Mapping) *Vis Neurosci*, 2015;32:1–8.

Kaskan PM, Dillenburger, BC, Lu HD, Kaas JH, Roe AW. The organization of orientation-selective, luminance-change and binocular-preference domains in the second (V2) and third (V3) visual areas of New World of owl monkeys as revealed by intrinsic-signal optical imaging. *Cereb Cortex* 2009;19:1394–1407.

Krubitzer LA, Kaas JH. The organization and connections of somatosensory cortex in marmosets. *J Neurosci* 1990;10:952–974.

Krubitzer LA, Sesma MA, Kaas JH. Microelectrode maps, myeloarchitecture, and cortical connections of three somatotopically organized representations of the body surface in parietal cortex of squirrels. *J Comp Neurol* 1986;250:403–430.

Kuypers HGJM, Szwarcbart MK, Miskin M, Rosvold HE. Occipitotemporal corticocortical connections in the rhesus monkey. *Exp Neurol* 1965;11:245–262.

Lane RH, Allman JM, Kaas JH. Representation of the visual field in the superior colliculus of grey squirrel (*Sciurus carolinensis*) and the tree shrew (*Tupaia glis*). *Brain Res* 1971;26:277–292.

Lane RH, Allman JM, Kaas JH, Miezin FM. The visuotopic organization of the superior colliculus of the owl monkey (*Aotus trivirgatus)* and the bushbaby *(Galago senegalensis)*. *Brain Res* 1973;60:335–349.

Lane RH, Kaas JH, Allman JM. Visuotopic organization of the superior colliculus in normal and Siamese cats. *Brain Res* 1974;70:413–430.

Liao C-C, DiCarlo GE, Gharbawie OA, Qi H-X, Kaas JH. Spinal cord neuron inputs to the cuneate nucleus that partially survive dorsal column lesions: a pathway that could contribute to recovery after spinal cord injury. *J Comp Neurol* 2015;523:2138–2160.

Lin C-S, Kaas JH. The inferior pulvinar complex in owl monkeys: Architectonic subdivisions and patterns of input from the superior colliculus and subdivisions of visual cortex. *J Comp Neurol* 1979;187:655–678.

Lin C-S, Merzenich MM, Sur M, Kaas JH. Connections of areas 3b and 1 of the parietal somatosensory strip with the ventroposterior nucleus in the owl monkey (*Aotus trivirgatus*). *J Comp Neurol* 1979;185:355–372.

Leuthke LE, Krubitzer LA, Kaas JH. Cortical connections of electrophysiologically and architectonically defined subdivisions of auditory cortex in squirrels. *J Comp Neurol* 1988;268:181–203.

Leuthke LE, Krubitzer LA, Kaas JH. Connections of primary auditory cortex in the New World monkey, *Saguinus*. *J Comp Neurol* 1989;285:487–513.

Lyon DC, Kaas JH. Evidence for a modified V3 with dorsal and ventral halves in macaque monkeys. *Neuron* 2002;33:453–461.

Lyon DC, Jain N, Kaas J H. The visual pulvinar in tree shrews I. Multiple subdivisions revealed through acetylcholinesterase and Cat-301 chemoarchitecture. *J Comp Neurol* 2003;467:593–606.

Merzenich MM. Merzenich autobiography. In LR Squire, ed. *The History of Neuroscience in Autobiography*, Vol 7. San Diego: Academic Press, 2012;438–474.

Merzenich MM, Kaas JH, Sur M, Lin C-S. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in S-I in the owl monkey (*Aotus trivirgatus*). *J Comp Neurol* 1978;181:41–74.

Merzenich MM, Kaas JH, Wall JT, Nelson JR, Sur M, Felleman DJ. Topographic reorganization of somatosensory cortical areas 3b and 1 in adult monkeys following restricted deafferentation. *Neurosci* 1983a;8:33–55.

Merzenich MM, Kaas JH, Wall JT, Sur M, Nelson RJ, Felleman DJ. Progression of change following median nerve section in the cortical representation of the hand in areas 3b and 1 in adult owl and squirrel monkeys. *Neurosci* 1983b;10:639–665.

Morel A, Kaas JH. Subdivisions and connections of auditory cortex in owl monkeys. *J Comp Neurol* 1992;318:27–63.

Morel A, Garraghty PE, Kaas JH. Tonotopic organization, architectonic fields, and connections of auditory cortex in macaque monkeys. *J Comp Neurol* 1993;335:437–459.

Nicolelis MAL, Ghazanfar AA, Stambaugh CR, Ollvelra LMO, Laubach M, Chapin JK, Nelson RJ, Kaas JH. Simultaneous encoding of tactile information by three primate cortical areas. *Nature Neurosci* 1998;1:621–630.

Pons TP, Kaas JH. Corticocortical connections of areas 2, 1, and 5 of somatosensory cortex in macaque monkeys: A correlative anatomical and electrophysiological study. *J Comp Neurol* 1986;248:313–335.

Preuss TM, Qi H-X, Kaas JH. Distinctive compartmental organization of human primary visual cortex. *Proc Natl Acad Sci USA* 1999;96(20):11601–11606.

Qi H-X, Reed JL, Gharbawie OA, Burish MJ, Kaas JH. Cortical neuron response properties are related to lesion extent and behavioral recovery after sensory loss from spinal cord injury in monkeys. *J Neurosci* 2014;34:4345–4363.

Reed JL, Qi H-X, Zhou Z, Bernard MR, Burish MJ, Bonds AB, Kaas JH. Response properties of neurons in primary somatosensory cortex of owl monkeys reflect widespread spatiotemporal integration. *J Neurophysiol* 2010;103:2139–2157.

Reed JL, Qi H-X, Kaas JH. Spatiotemporal properties of neuron response suppression in owl monkey primary somatosensory cortex when stimuli are presented to both hands. *J Neurosci* 2011;31:3589–3601.

Remple MS, Reed JL, Stepniewska I, Lyon DC, Kaas JH. The organization of frontoparietal cortex in the tree shrew *(Tupaia belangeri)*: II. Connectional evidence for a frontal-posterior parietal network. *J Comp Neurol* 2007;501:121–149.

Schmidt-Nielsen K. Scaling, why is animal size so important? Cambridge, UK: Cambridge University Press, 1984.

Schwaber MK, Garraghty PE, Kaas JH. Neuroplasticity of the adult primate auditory cortex following cochlear hearing loss. *Am J Otology* 1993;14:252–258.

Sesma MA, Casagrande VA, Kaas JH. Cortical connections of area 17 in tree shrews. *J Comp Neurol* 1984;230:337–351.

Stepniewska I, Kaas JH. Architectonic subdivisions of the inferior pulvinar in New World and Old World monkeys. *Vis Neurosci* 1997;14:1043–1060.

Stepniewska I, Fang P-C, Kaas JH. Microstimulation reveals specialized subregions for different complex movements in posterior parietal cortex of prosimian galagos. *Proc Nat Acad Sci USA* 2005;102:4878–4883.

Stepniewska I, Gharbawie OA, Burish MJ, Kaas JH. Effects of muscimol inactivations of functional domains in motor, premotor and posterior parietal cortex on complex movements evoked by electrical stimulation. *J Neurophysiol* 2014;111:1100–1119.

Strata F, Cog JO, Kaas JH. The chemo-and somatotopic architecture of the galago cuneate and gracile nuclei. *Neurosci* 2003;116:831–850.

Sur M, Merzenich MM, Kaas JH. Some quantitative features of the body surface representations in areas 3b and 1 in owl monkeys: Magnification, receptive field area and hypercolumn size. *J Neurophysiol* 1980;80:295–311.

Sur M, Wall JT, Kaas JH. Modular segregation of functional cell classes within the postcentral somatosensory cortex of monkeys. *Science* 1981;212:1059–1061.

Symonds LL, Kaas JH. Connections of striate cortex in the prosimian (*Galago senagalensis*). *J Comp Neurol* 1978;181:477–512.

Takahata T, Higo N, Kaas JH, Yamamori T. Expression of immediate-early genes reveals functional compartments within ocular dominance columns after brief monocular inactivation. *Proc Natl Acad Sci USA* 2009;106:12151–12155.

Wall JT, Felleman, DJ, Kaas JH. Recovery of normal topography in the somatosensory cortex of monkeys after nerve crush and regeneration. *Science* 1983;221:771–773.

Welker W. Welker autobiography. In LR Squire, ed. *The History of Neuroscience in Autobiography*, Vol. 3. San Diego: Academic Press, 2001;502–545.

Weller RE, Kaas JH. Parameters affecting the loss of ganglion cells of the retina following ablations of striate cortex in primates. *Vis Neurosci* 1989;3:327–349.

Wong P, Kaas JH. Architectonic subdivisions of neocortex in the galago (*Otolemur garnetti*) *Anat Rec* 2010;293:1033–1069.

Wong-Riley MTT. Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome oxidase histochemistry. *Brain Res* 1979;171:11–28.

Woolsey CN. Comparative studies on cortical representation of vision. *Vis Res* (Suppl. 3) 1971;11:365–382.

Xu X, Collins CE, Kaskan PM, Khaytin I, Kaas JH, Casagrande VA. Optical imaging of visually evoked responses in prosimian primates reveals conserved features of the middle temporal visual area. *Proc Natl Acad Sci USA* 2004;101:2566–2571.

Young NA, Szabó CÁ, Phelix CF, Flaherty DK, Balaram P, Foust-Yeoman KB, Collins CE, Kaas JH. Epileptic baboons have lower numbers of neurons in specific areas of cortex. *Proc Natl Acad Sci USA* 2013;110:19107–19112.

Zeki S. The third visual complex of rhesus monkey pre-striate cortex. *J Physiol* 1978;277:245–272.

Zeki S. The distribution of wavelength and orientation selective cells in different areas of monkey visual cortex. *Proc Royal Soc London*, Series B, 1983;217:449–470.