



The History of Neuroscience in  
Autobiography  
Volume 1

Edited by Larry R. Squire  
Published by Society for Neuroscience  
ISBN: 0-12-660301-4

Irving T. Diamond  
pp. 158–176

[https://doi.org/10.1016/S1874-6055\(98\)80007-8](https://doi.org/10.1016/S1874-6055(98)80007-8)



# *Irving T. Diamond*

**BORN:**

Chicago, Illinois  
September 17, 1922

**EDUCATION:**

University of Chicago, B.A., 1943  
University of Chicago, Ph.D. (Psychology, with W.D. Neff,  
1953)

**APPOINTMENTS:**

University of Chicago (1948)  
Duke University (1958)  
Professor of Neurobiology, Duke University (1988)

**HONORS AND AWARDS:**

James B. Duke Professor, Duke University (1971)  
National Academy of Sciences USA (1982)  
Distinguished Scientific Contribution Award, American  
Psychological Association (1988)  
William James Fellow, American Psychological Society  
(1989)

*Irving Diamond pioneered the anatomical and functional study of auditory cortex, and carried out fundamental studies of the organization of sensory and association cortex, thalamocortical pathways, and the superior colliculus.*

# Irving T. Diamond\*

I enrolled in a Chicago high school (Hyde Park, 1934) not far from the University of Chicago. At Hyde Park, the faculty and students were considered above average and I recall classes in differential calculus and college-level chemistry. Foreign languages were hardly touched, certainly not by me; I think I studied Latin for a year at most.

My parents were eager to see me choose the University of Chicago, which was taken to be the best university in the Western world, matched only by Oxford and Cambridge. I entered in 1938 and was serious about and excited by all or most of the classes. Teachers—such as Anton Carlson, the Swedish physiologist—were thrilling and often amusing. I remember Carlson picking up a beaker of urine and, after taking a sip, insisting it was just a glass of water—the point being that urine is as benign as a glass of water. Heinrich Kluver, Ralph Gerard, Sewell Wright, and Anton Carlson were all my teachers and members of the National Academy of Sciences. Each one was a specialist in either neurology, physiology, or genetics. Robert Maynard Hutchins, the president of the University, was tall and handsome, as well as charming and witty. He was unwilling to spend money to recruit top football candidates. All Chicago players were devoted to academic life. I remember that one year Chicago remained scoreless in an 80-point loss to Michigan at Stagg Field. I believe it was shortly thereafter that intercollegiate football was dropped at Chicago.

I was pleased by the camaraderie of fellow students, and was even a member of a fraternity. I recall many social events such as dances with white ties and tails. The shock of World War II led to a new and different climate. I was just 19 on Pearl Harbor Day; most of the males and some females enlisted, but we were permitted another year at the university.

In 1946 I was released from Army service, and returned to the University of Chicago. The atmosphere had changed completely—at least that was how I saw it, but perhaps I had changed. I became acquainted with the dean of humanities, a well-known philosopher, Richard McKeon. I enrolled in his courses and read, in English, the works of Aristotle, such as *Ethics*, the *Politics*, and *De Anima*. This experience, in turn, led to an acquaintance with “the great books.”

\*I thank Bill Hall for discussions about this chapter. Our collaboration over the last 30 years has been very important to me.

In 1948, well before I qualified for the Ph.D. degree, I was presented with the modest title of assistant instructor in the college of biology, with a salary of \$2,400 for the year. I was not alone in teaching the original papers from scientists such as Harvey (1628), Darwin (1859), Mendel (1865), Bernard (1877), and Sherrington (1906). Once a week I joined a small group of three or four other instructors for the purpose of improving our teaching. We would discuss the major papers in evolution, genetics, ecology, physiology, and anatomy, and we learned more about teaching undergraduates. We agreed to lecture occasionally to the students but, for the most part, our goal was to ask crucial questions of the class. For example: "How did Harvey identify the transport of blood from arteries to veins? From the right ventricle to the lungs? From the left ventricle to the aorta?" "Why did Mendel use the ratio of 3 to 1 when, in fact, the number of two distinct lines (for example, red and white, or round and angular) was 2.98 to 1?" (The answer to this question, of course, is that in the F<sub>2</sub> generation the genotypes could be viewed as 1/4 A:1/2 Aa:1/4 a. Mendel did not use double letter notation such as AA:Aa:aa.)

Darwin's basic principles were given a poetic description:

The entangled bank clothed with many plants of many kinds, with birds singing on bushes, with various insects fluttering about, with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other and so dependent on each other, have all been produced by the laws of growth, reproduction, external conditions of life, use and disuse, and a ratio of increases so high as to lead to a struggle for life (Darwin, 1859).

Darwin's concepts of inheritance, variation, and selection were his way to explain evolution. We also read how his effort to deal with gemmules as the mechanism in heredity fell short of the chromosome.

Not every great biologist need be a poet like Darwin. We taught the work of Claude Bernard, who in 1877 identified the significance of the liver—to retain sugar and to transport blood in the portal vein. We also read the works of Walter S. Sutton and Edward Murray East. Sutton recognized the brilliance of Mendel's principles of hereditary units, and from these developed his concepts of cell division, germ cells, and cytology. He determined that the chromosome group of pre-synaptic germ cells was made up of two equivalent chromosomes, one paternal and one maternal. East recognized that the continuous variation that he found in corn hybrids could be explained in Mendelian terms. He crossed 8-rowed corn (that is, corn with ears having eight rows of kernels) with 20-rowed corn and produced a hybrid having 14 rows per ear (F<sub>1</sub>). Then he showed that with self-fertilization of the F<sub>1</sub> population, there is a new population, F<sub>2</sub>, that includes corn of 8, 10, 12, 14, 16,

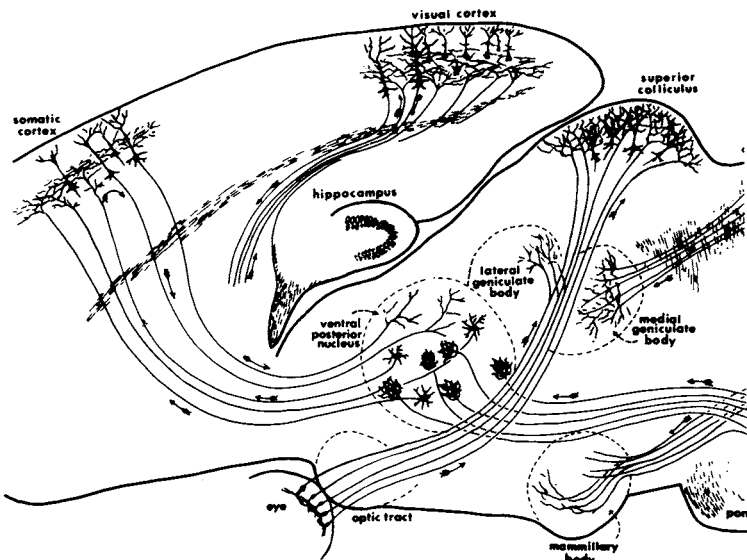
18, and 20 rows of kernels per ear. The F2 population follows a normal frequency distribution—that is, the 14-rowed corn occurs most frequently.

In each case, the achievements of these great biologists could only be fully appreciated by reading their original works.

## My Introduction to the Thalamus and Cortex

Although I began teaching college students with trepidation, experience ultimately led to confidence, but something was still missing. I needed to become a scientist; just reading about the great scientists was not sufficient. I required a Ph.D. thesis, and a warm friendship with W.D. Neff led to his supervision. Dewey Neff had already found his niche at the University of Chicago and had developed methods to train cats to jump over a barrier when there was a change in pitch or sound location (Neff et al., 1956). He was devoted to the auditory cortex and was attempting to identify its subdivisions. I was a helping partner in these efforts, concentrating on the brain and especially the cortex and thalamus.

At the turn of the century, the Spanish genius Santiago Ramón y Cajal drew countless pictures of the cortex and traced sensory pathways to it (see Figure 1). In England, Campbell wrote a long and detailed description of the visual cortex (1905). In 1910, George Elliot-Smith gave a series of lectures on the evolution of the cortex. His first principle was clear: “The key to understanding the cortex depends on an intensive study of the thalamus.” Some 20 years later, W.E. LeGros Clark—a friend of Smith’s—offered a similar principle: “The neocortex depends entirely on the thalamus for sensory information.”



**Figure 1.** Sensory pathways to the neocortex as drawn in the spirit of Cajal and published in his 1906 Nobel Prize lecture. Note three sensory pathways.

LeGros Clark's 1932b paper begins with a long paragraph and then turns to classifying distinctive features in the various thalamic nuclei. I quote the beginning:

With the solitary exception of olfactory impulses, all sensory impulses which are destined to reach the cerebral cortex have first to be filtered through the mass of grey matter which is found in the walls of the third ventricle. From the thalamus such impulses are projected on to the cortex by thalamo-cortical fibres, and their mode of distribution to topographical cortical areas is no doubt determined in large part by the spatial relationship of the thalamic nuclei from which these fibres arise. This fundamental fact has been emphasized by Cajal and Elliot-Smith and rests on the observation that projection fibres take the most direct and shortest route from the thalamic centres to the cortex. . . . The neocortex must depend entirely on the thalamus for the precise nature of sensory material that it receives indirectly from peripheral receptors.

In his 1932b monograph, LeGros Clark classified distinctive features in the various nuclei of the dorsal thalamus. The sensory relay nuclei are the most prominent and especially striking in "primitive" (LeGros Clark's term) mammals. The three primitive species discussed by LeGros Clark are the common shrew (*Sorex*), the hedgehog (*Erinaceus*), and the Virginia opossum (*Didelphis*). The three prominent sensory nuclei constitute what LeGros Clark called "the lower level": the ventral posterior nucleus (VP), the lateral geniculate nucleus (GL), and the medial geniculate nucleus (GM). The "upper level" comprises the lateral group and the mediodorsal nucleus. LeGros Clark recognized that in primates, even in prosimian primates such as the lemurs, the upper level of the thalamus had become larger than the sensory relay nuclei.

In the early 1950s, I recognized a giant in the field of neuroanatomy, Jerzy Rose. Rose teamed with Clinton Woolsey in the late 1940s, and they were a perfect pair, first at Johns Hopkins University and later at the University of Wisconsin. Rose's experiments with Woolsey (1949) relied on two methods, each supporting the other: (1) retrograde degeneration in the thalamus after restricted cortical lesions; and (2) evoked potentials in the auditory, visual, and somatic areas of the cortex. The borders of maps using the evoked potentials in sensory areas were meticulously precise, and when small lesions were made, degeneration was identified, as expected, in the lateral geniculate nucleus, the medial geniculate nucleus, and the ventral posterior nucleus—the three "extrinsic" nuclei.

Rose and Woolsey argued that a second class of nuclei, called "intrinsic," represented a higher functional level because they appeared to depend on projections from the extrinsic nuclei. The intrinsic nuclei include the pulvinar

nucleus and the lateral, posterior, and medio-dorsal nuclei; their projections to the cortex terminate in the association areas intercalated between the sensory areas. Rose and Woolsey demonstrated that in small, lower mammals like the rabbit, the area of the association cortex is much less than that of the sensory cortex. In primates, of course, the association areas have greatly expanded. This synopsis emerges in a 1949 paper by Rose and Woolsey.

A further step in Rose and Woolsey's inquiry was probably the result of an accidental reduction in anesthesia which increased the responsiveness of cortical neurons. They discovered that a second topographic sensory map is adjacent to each sensory area and is a mirror image of the first area. As a result, the nomenclature for cortical areas became SI and SII, AI and AII, and VI and VII. These "second" areas created a special problem. Do the extrinsic nuclei project only to AI, VI, and SI, or do they also project to AII, VII, and SII? Rose and Woolsey found that isolated lesions in the second auditory area (AII) of the cat produced degeneration neither in the medial geniculate nucleus nor in any other thalamic nucleus. Small lesions in the second visual area (VII) also failed to produce thalamic degeneration. This finding could mean that there is some sparse projection from an extrinsic nucleus or a collateral projection from an intrinsic nucleus. Larger lesions showed that the intrinsic nuclei—for example, the pulvinar nucleus—project to the regions intercalated between the sensory areas. In a rabbit, the strips intercalated between visual and auditory areas or auditory and somatic areas are narrow; the strips are larger in the cat and larger still in the monkey. The result is that an extensive area of the cortex in the primate is devoted to the pulvinar nucleus.

In addition to extrinsic and intrinsic nuclei, another region of the dorsal thalamus remained that, Rose and Woolsey insisted, did not project to the neocortex at all, let alone to the entire neocortex. That region consists of the midline and intralaminar nuclei. However, Moruzzi and Magoun (1949), using a new and quite effective method—stimulation of the reticular formation—speculated that the reticular formation influenced the neocortex by means of a relay in the intralaminar and midline nuclei. Ironically, the two papers (Rose and Woolsey's, and Moruzzi and Magoun's) were published back to back in the first volume of the *Journal of Electroencephalography and Clinical Neurophysiology* (1949).

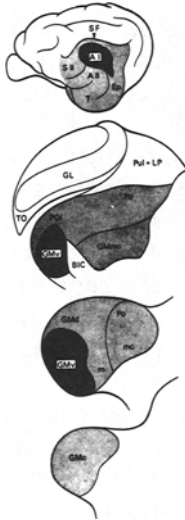
## The Auditory Thalamus and Cortex in the Cat

In the 1950s Neff and I focused on AI and AII in the cat and expected that removal of these subdivisions would handicap auditory discriminations, just as removal of VI and VII apparently destroyed visual discrimination. After several years of training cats to discriminate changes in pitch or temporal patterns of pitch or location of sound, we concluded that ablation of AI and AII did not result in permanent deficits (Butler et al., 1957; Diamond and Neff, 1957). However, significant behavioral deficits appeared if the lesion



extended caudally to the posterior ectosylvian gyrus (Ep) and ventrally to the rhinal fissure, thus including the insular-temporal areas. The results indicated that auditory information could reach the cortex through pathways in addition to the well-recognized pathway to the primary auditory area.

It was natural to look at the thalamus to explain the differences between the behavioral effects of ablating AI alone and ablating both AI and the extensive belt around AI—that is, Ep, AII, the insular area, and the temporal area. The time was right for me to learn histology—microscopic anatomy. I sectioned the brains of several cats and stained each section with Cresyl violet, looking for degeneration of cells. I sought advice from Jerzy Rose, and he invited me to take a train from Chicago to Baltimore to visit. I was surprised to spend the night in his home. His wife, who was born and trained in Europe (and a member of the faculty in a women's college), prepared a wonderful dinner and we had a pleasant evening. The next morning Jerzy looked at the stained sections. His response was: "Do you want me to be nice, or should I tell the truth?" And he made his point: "It is the poorest Nissl stain I have ever seen." His eyes twinkled, and in that second I knew Jerzy Rose. With an excellent histologist like him helping me, the following findings were made: with small lesions in AI, small patches of degeneration would be located in the rostral half of the principal division of the medial geniculate nucleus, now called GMv; with all of AI ablated, GMv showed severe degeneration; after large lesions of AII, the insular and temporal areas, and ventral Ep, GMv is spared, but degeneration covers the caudal medial geniculate nucleus (GMc) and the magnocellular medial geniculate nucleus (GMmc) (Figure 2) (Diamond et al., 1958).



**Figure 2.** Summary diagram showing that the ablation of AI (in black) leads to degeneration only to GMv.

In summary, the caudal division of the medial geniculate nucleus had the greatest amount of degeneration when the lesion was close to the rhinal fissure and behind the pseudosylvian gyrus. A comparison of GMv to GMmc is striking: GMv projects topographically just to AI, whereas GMmc projects all over the auditory field from the middle suprasylvian to the rhinal fissure. The extensive projections of the medial geniculate to areas well beyond the borders of AI and AII led me to question for the first time the fundamental distinction between sensory and association cortex—the “association cortex” was also a target of sensory relay nuclei in the thalamus.

## A Change in Life

In December of 1957 my wife and I traded the snow and sleet of Chicago for a vacation among the orange and palm trees of Beverly Hills, California. I had just begun sunbathing in the garden of my wife's grandmother's home when I received a telegram from the University of Chicago Board of Trustees: I had been promoted to “associate professor with indefinite tenure.” I recognized the honor but, nevertheless, I had been thinking of leaving Chicago and Duke University had recently offered me a position. I had scarcely heard of Duke University at the time and was not even aware that Duke was in the state of North Carolina. I visited Duke twice and decided against moving to a town with just two sites for bed and breakfast: one downtown hotel and a Howard Johnson's Motor Inn. However, with Duke's promise of tenure and new opportunities for science and collaboration, I was finally persuaded to make the move.

Besides transferring equipment, the most significant part of the move was transferring my former Chicago students, John Jane, Bruce Masterton, and John Utley. Masterton and Jane took on a number of projects, including the function of tectum for attention to auditory stimuli, the effects of auditory cortex ablation, and the role of auditory structures such as the superior olive and lateral lemniscus in sound localization. Utley worked hard on the analysis of retrograde thalamic degeneration after cortical lesions in the opossum (Diamond and Utley, 1963).

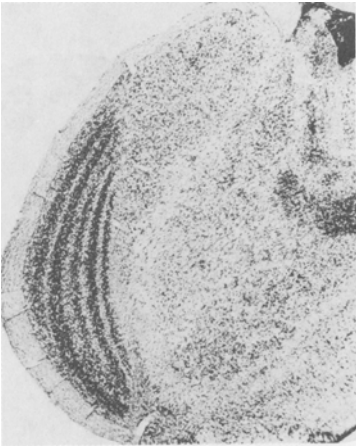
Bill Hall was finishing an undergraduate degree and joined our team, developing skills at an exponential rate. When Jon Kaas appeared from the northern border of Wisconsin he was quite shy to the point of being almost speechless. However, his skills and scientific judgment developed at a great rate and remain a power. The hedgehog became the central species of study inasmuch as its neocortex is small and primitive. Hall and Kaas concentrated on the visual cortex. Removal of the entire striate cortex of the hedgehog failed to produce complete degeneration of the lateral geniculate nucleus and, indeed, it showed only moderate degeneration. To produce severe degeneration in the lateral geniculate nucleus it was nec-

essary to ablate both the striate cortex and the surrounding belt of cortex. The belt could be named VII, the striate VI. The lateral posterior nucleus clearly projects to both VI and VII, and only when both are destroyed does the lateral posterior nucleus show severe degeneration.

A new phase began at Duke with the arrival of the tree shrew. The next section will identify a group of students with both post- and predoctoral degrees who initiated the study of this remarkable species: Vivien Casagrande, John Harting, Herb Killackey, and Marvin Snyder.

### The Visual Thalamus in the Tree Shrew

When LeGros Clark served in the British Army in Burma, Malaya, and Siam, he could hardly escape the jungles and especially could not escape the tree shrew. I believe he communicated regularly with Elliot-Smith, chairman at University College of London, and both agreed that the *Tupaia* brain was primate-like, albeit primitive. I saw many of LeGros Clark's slides in Oxford, and I was aware of the striking appearance of the striate cortex and the lamination of the lateral geniculate nucleus of the shrew (Figures 3a and 3b).



**Figure 3a.** Photomicrograph showing the lateral geniculate body and the pulvinar nucleus in *Tupaia glis*.

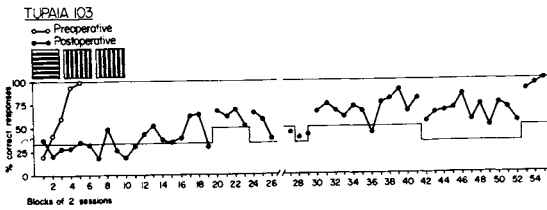
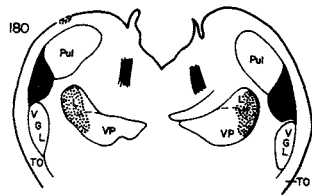
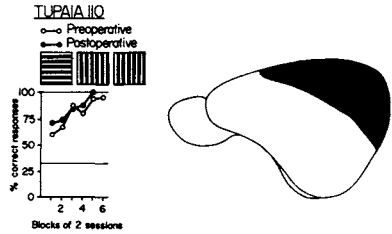
**Figure 3b.** Photomicrograph of the striate and extrastriate cortex in *Tupaia glis*.



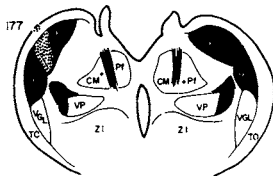
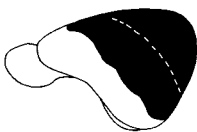
LeGros Clark was no longer chairman of Anatomy but still had a position at Oxford when I was there on sabbatical in 1964 to 1965. We had lunch about once every other week in his office. What a fine man! He knew I had worked with the hedgehog and opossum. He also included the tree shrew in our discussions. His first paper about this species was "The Thalamus of *Tupaia*" in 1929.

After the papers by Casagrande, Glendenning, Harting, Killackey, and Snyder, the tree shrew became our laboratory's central topic of study. We reasoned that if the cortex of the tree shrew fit the traditional view of sensory and association cortex, the lateral geniculate nucleus would project only to the striate cortices, and the pulvinar nucleus would project only to the association areas between VII and the auditory field. The surprising result was the ability of the tree shrew to discriminate between different patterns and different colors after complete removal of the striate cortex; the completeness of the lesion was verified by the complete degeneration of the lateral geniculate nucleus! Only when the rest of the occipital cortex (areas 18 and 19) plus the temporal cortex were ablated in addition to area 17 was the tree shrew unable to discriminate between upright and inverted triangles (Figures 4a and 4b) (Snyder et al., 1966; Snyder and Diamond, 1968).

**Figure 4a.** Learning curves for the tree shrew before and after complete removal of the striate cortex.



**Figure 4b.** Failure to attain visual discriminations after ablation of both the striate and temporal cortex.



After long and tedious training, some vision remained as indicated by better than chance discrimination between horizontal and vertical stripes. As a result of these huge cortical lesions, the pulvinar nucleus was severely degenerated in addition to the lateral geniculate nucleus. The results immediately showed that the pulvinar nucleus does not depend solely on fibers from the lateral geniculate. This conclusion convinced us that the pulvinar nucleus is not intrinsic, and that some part of the visual brain stem must be a source of a visual pathway to the pulvinar nucleus (Diamond and Hall, 1969). These results were reminiscent of earlier ones from the auditory cortex in the cat. It followed that much of the cortex between the primary visual and auditory areas of the tree shrew was the target of a visual pathway and should be classified as sensory rather than association cortex, according to the traditional definition.

A good starting point was the tecto-thalamic pathway projections that had been identified in lower vertebrates. In 1966, use of the Nauta method allowed tracing fibers from the tectum to the nucleus rotundus in birds (Karten and Revzin, 1966). In tree shrews, small lesions were made in the superficial layers of the superior colliculus, which revealed a strong projection to the pulvinar nucleus (Harting et al., 1973a,b). The well-established pathway from the optic nerve to the superficial superior colliculus (SC) explained the role of the pulvinar nucleus and the temporal cortex in the tree shrew's vision; it also seemed likely that at least some part of the pulvinar nucleus in all mammals receives visual impulses from the superior colliculus (Diamond, 1973, 1982).

Whereas the two pathways from the retina, one to the lateral geniculate nucleus and the other to the superior colliculus, forced a major revision of our view of cortical organization, further experiments in *Tupaia* have subsequently revealed increased complexity. First, the pulvinar is not the only target of a superior colliculus projection. Two of the six geniculate layers are also destinations of superior colliculus fibers. These two layers, 3 and 6, have smaller cells and project above layer IV in the striate cortex. The lateral geniculate layer 3 is particularly striking as its projection reaches cortical layer I. Two methods support this finding: anterograde transport by the Nauta method shows that the lateral geniculate projects strongly to layer I of the striate cortex and retrograde transport after applying horseradish peroxidase (HRP) on the surface of the striate cortex labeled cells in lateral geniculate layer 3 (Carey et al., 1979a,b). The conclusion was clear that the simple distinction between sensory and association areas fell far short of accounting for the multiple pathways through which the visual system influences the cortex.

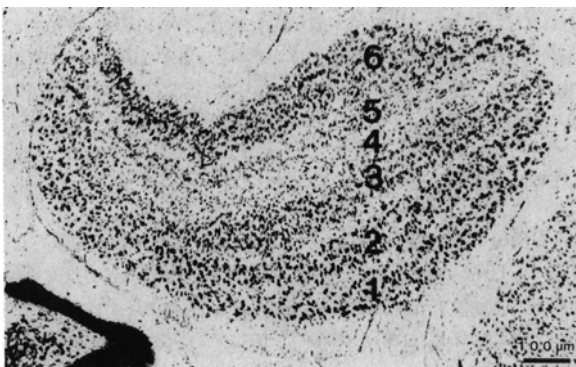
## Visual Pathways and Fiber Size: Cat and Galago

Just 10 years after Rose and Woolsey's 1949 paper, George Bishop (1959) proposed a new way of explaining the significance of fiber size. The prevailing view was initiated by studies of Gasser and Erlanger (1929), who showed that fiber size was a function of modality or submodality; large fibers convey touch

and small fibers pain. Later, Bishop (1959) turned to the visual system and was convinced that only the large fibers of the optic tract reach the lateral geniculate nucleus in the cat. The small fibers of the optic tract project instead to the tectum, and this seems to hold for all vertebrates. Bishop then made his major point that fiber size differences are a reflection of stages in the evolution of sensory pathways. Newer, large fibers bypass the older centers in the brain stem. In contrast, older, small fibers synapse step-by-step through the brain stem. Bishop showed that C fibers in the lateral columns project to the reticular formation and, with further synapses, the pathway continues to the intralaminar nuclei. This proposal is compatible with that of Giuseppe Moruzzi and Horace Magoun, who had inferred a diffuse projection from intralaminar nuclei to the superficial layers of the entire cortex. Their stimulation of the reticular formation had the important result of a change from sleep to a waking state. However, Bishop took an alternative, but not necessarily contradictory, view: the diffuse projection from the intralaminar nuclei to the cortex produces the experience of burning pain characteristic of C fibers.

Bishop identified still another path by recording visual impulses in the pulvinar nucleus. The impulses were produced by stimulating the optic tract but were delayed by a synapse, which Bishop attributed to a relay in the lateral geniculate nucleus. If visual input reached the pulvinar from a source inside the thalamus, the pulvinar would be intrinsic in Rose's sense of the term. As it turned out, the delay could be attributed to the superior colliculus, so the pulvinar is not intrinsic, but instead falls into Rose's extrinsic class. There still was a third class of thalamic nuclei according to Rose: those nuclei that are not relays in any sensory path and receive fibers only from the association cortex. This third class may include larger portions of the primate pulvinar and provide the basis for the higher level of thalamic processing envisioned by both LeGros Clark and Rose.

The role of cell size and fiber size became important in my laboratory as well. We found that the lateral geniculate of *Galago senegalensis* has three pairs of layers: magnocellular, parvocellular, and layers 4 and 5, with small pale cells (Figure 5) (Itoh et al., 1981; Diamond, 1993).



**Figure 5.** Photomicrograph of a frontal section of the lateral geniculate body of *Galago senegalensis*. Note the small cells filling layers 4 and 5.

The visual thalamus is not the only sensory relay to show a relation between fiber size and modality. Our laboratory demonstrated that cells of different sizes in the ventral posterior nucleus of the cat project to different layers of somatic cortex (Penny et al., 1982).

One might expect that there also would be a close correspondence in *Galago* between the sizes of afferent fibers in the optic tract and the sizes of the cells in the three lateral geniculate layers of a set. Large axons project to the pair of magnocellular layers, and small fibers project to the pair of layers with the small cells, layers 4 and 5. This small cell pair projects to the cortex above layer IV (Itoh et al., 1982).

I began this section with Bishop's rejection of modality as the significance of fiber size; instead, he regarded the larger fibers as phylogenetically more recent pathways that bypass older brain stem centers. Fiber size may turn out to have some relation to submodality after all. The information conveyed from the retina to the lateral geniculate layers 4 and 5 in *Galago* is surely not the same as that received in the big cell layers by large axons (Conley et al., 1987).

Summary: There have been advances in our understanding of thalamo-cortical organization as research methods have been refined and improved. The idea of intrinsic thalamic nuclei has given way to the discovery of multiple pathways from the retina and from both deep and superficial layers of the superior colliculus to the thalamus. The sizes of axons projecting to a thalamic nucleus are not uniform. On the contrary, large cells in the lateral geniculate receive large fibers and small cells receive small fibers. Large and small cells in a single thalamic nucleus send fibers to different layers of the cortex. The superior colliculus is important for understanding the organization of the thalamus and the cortex and, in particular, makes an important contribution to the visual pathways to the cortex. I have tried to show that my own research relied heavily on many major figures in neuroanatomy and neurophysiology and in the evolution and development of the thalamus: Ramón y Cajal, Campbell, Sherrington, Elliot-Smith, LeGros Clark, Rose, Woolsey, and Bishop. George Bishop and I made a promise to work together—he visited Durham and I St. Louis. I enjoyed his large farm house and the seemingly rural surroundings of his many acres. Fences and shrubs isolated him from the middle-class neighborhood that had sprung up around him. His laboratory was small, and he shared an office with his assistant. No one presented a more humble view of a science laboratory. When I said good-bye to George Bishop in St. Louis in 1971, he was elderly and quite ill. We both knew we would not see each other again.

## The Role of Universities—Inside and Outside the United States

Over the years I have had a chance to lecture at many universities and have learned much, especially when I have been invited to speak at academic institutions in foreign countries.

I begin by telling a moving experience that taught me the meaning of “chairman.” In 1970, I visited the Institute of Neurophysiology in Pisa. When the time came for my lecture, Dr. Giovanni Berlucchi introduced me first in Italian, then in English. I stood behind a large table in a traditional European auditorium, looking up at the steep rows of students and staff. To my surprise and disappointment, I could not find Professor Moruzzi, chairman of Physiology. Just as I began to talk, I heard some noises at the side of the auditorium. Some students were carrying in an ancient leather chair. Moruzzi followed them in, nodded to me, and sat down—in his chair! The meaning of a “chairman” finally took on significance. After the lecture, Moruzzi showed me his private library in his apartment above the laboratories of the institute. The books were bound in ancient white leather, one of which was the great treasure of an original edition of William Harvey.

In the fall of 1980, I was invited to lecture at the Sechenov Institute of Evolutionary Physiology in Leningrad. At that time, traveling to the USSR and lecturing to the Russian Academy of Science was not recommended by the U.S. State Department, but it was left up to me to decide whether to proceed. My wife accompanied me. Leningrad was dismal in many ways, but I felt the warmth and sincerity of my hosts, especially Dr. Margareta Belehova, who continued to write and send photographs long after I returned from this trip.

My lectures required three hours because each of my sentences in English was followed by translation into Russian. My wife sat in the large audience of well over 200 people. At one intermission, she called my attention to someone who was sitting nearby—a physicist, Adolph Lev—who had spent time in the physiology department at Duke University. Adolph turned his head away from me and in a low voice gave me his telephone number. How could I find a telephone? There was no telephone in our hotel room because Soviet policy decreed that “guests” could not telephone. I suggested to the young KGB assistant, who was assigned to escort us everywhere, that he need not accompany my wife and me to the ballet that evening. Later, during the intermission, I walked alone to find a telephone booth. I had just one kopeck in my pocket. I telephoned and planned a way of meeting Adolph. One week later, it was pitch dark and cold when my wife and I left the hotel and walked six blocks to find Adolph waiting for us in an old automobile. He drove for an hour and stopped in front of his home in a 10-story building just two years old. The building was cracked, the elevator weak. In his flat the shades were drawn and his words to us were these: “They can’t make a fool of me.” The frustration of Dr. Lev was apparent. We could now, finally, discuss our lives as scientists openly without KGB monitoring or censure.

Another recollection from this trip was the darkness that fell early in the evening and lasted late into the morning. I would leave the hotel to



take a walk before breakfast and see lines of people two blocks long waiting to get into a shop; each person left the shop carrying one loaf of bread.

Two years after my Russian trip my wife and I visited China. This tour began in Hong Kong where the university was entirely devoted to English. Doctors Hwang and Wong helped prepare our visit there and Dr. Paul Poon, who spent a couple of years with Dewey Neff, arranged everything before and during our stay. The hotels had every luxury, the restaurants were excellent, and Rolls Royce automobiles were in abundance.

A short train trip from Hong Kong brought us to Guangzhou (Canton). During my lecture I sat at a large table covered with a white cloth, everyone wore open-necked white shirts, and tea was served throughout. Dinner was in Canton's oldest restaurant, where the service was superb. We left Canton by plane for Shanghai during a torrential rainstorm that came close to a typhoon. We were met at the airport by Professors T.P. Feng and H. Chang, along with other senior members of the two institutes they headed. Chang had spent several years in Washington D.C. He was optimistic about future plans for building a research facility in Shanghai. Feng was remarkable—old enough to have known Sir Charles Sherrington and Lord Adrian in England.

The research laboratory at the University in Peking (Beijing) focused on the physiology and psychophysics of vision. In addition to touring the Great Wall, we had considerable time to walk through the Forbidden City. A final experience was learning how the Chinese suffered during the Cultural Revolution. With stoicism, resignation, and even good humor, they related stories about sentences to hard labor, separation from families, seeing libraries pillaged and schools closed.

I have visited Japan, a complex place, several times. Japanese scientists have worked in my laboratory and one, Kazuo Itoh, was here for three years. I spent a year at Oxford in the 1960s and I have spent many summers in the Cotswolds since that time. Italy is a place of my close friends, Drs. G. Maachi in Rome, G. Berlucchi and M. Benvivoglio in Verona, R. Spreafico in Milan, and G. Rizzolatti in Parma. Several Italian scientists have also worked in my laboratory, Drs. G. Luppino, M. Matelli, and M. Molinari.

In May 1992, I discovered to my complete surprise a special issue of the *Journal of Comparative Neurology*. This issue had been published in my honor. The editor-in-chief was Sanford Palay and the contributors were my former students—Jeff Winer, Pete Casseday, Karen Glendenning, David Fitzpatrick, and others I have identified in the above text. An article by my youngest son, Mathew, a neurobiologist in Trieste, Italy, can also be found in this issue of the journal.

Finally, my laboratory at Duke University has had many rotations of students and postdoctoral fellows through the years. At a recent Society for Neuroscience meeting, a session was given in my honor. I went to the session without any notion of what was to follow, which turned out to be

presentations by Vivien Casagrande, John Harting, Jon Kaas, David Hubel, David Fitzpatrick, and Bill Hall. This event was the highest moment of my career. I was touched and delighted, as were my children who attended, Mathew, Nancy, and Thomas.

### Selected Publications

- Bernard C. Lectures in diabetes and animal glycogenesis. Paris: Bailliere, 1877.
- Bishop GH. The relation between nerve fiber size and sensory modality: phylogenetic implications of the afferent innervation of cortex. *J Nerv Ment Dis* 59; 128:89–114.
- Butler RA, Diamond IT, Neff WD. Role of auditory cortex in discrimination of changes in frequency. *J Neurophysiol* 1957;20:108–120.
- Campbell AW. Visuo-sensory and visuo-psychic areas (Chapter V). *Histological studies on the localization of cerebral function*. Cambridge: Cambridge University Press, 1905.
- Carey RG, Fitzpatrick D, Diamond IT. Layer I of striate cortex of *Tupaia glis* and *Galago senegalensis*: projections from thalamus and claustrum revealed by retrograde transport of horseradish peroxidase. *J Comp Neurol* 1979a;186:393–438.
- Carey RG, Fitzpatrick D, Diamond IT. Thalamic projections to layer I of striate cortex shown by retrograde transport of horseradish peroxidase. *Science* 1979b;203:556–559.
- Casagrande V, Harting JK, Hall WC, Diamond IT, Martin GF. Superior colliculus of the tree shrew: evidence for a structural and functional subdivision into superficial and deep layers. *Science* 1972;177:444–447.
- Conley M, Penny GR, Diamond IT. Terminations of individual optic tract fibers in the lateral geniculate nuclei of *Galago crassicaudatus* and *Tupaia belangeri*. *J Comp Neurol* 1987;256:71–87.
- Darwin C. The origin of species. (Originally published in 1859.) New York: Mentor Books, 1958.
- Diamond IT. The evolution of the tectal-pulvinar system in mammals: structure and behavioral studies of the visual system. *Symp Zool Soc Lond* 1973;33:205–233.
- Diamond IT. Changing views of the organization and evolution of the visual pathways. In: Morrison AR, Strick PL, eds. *Changing concepts of the nervous system*. New York: Academic Press, 1982;201–233.
- Diamond IT. Parallel pathways and fibre size. In: Minciacchi D, Molinari M, Macchi G, Jones EG, eds. *Thalamic networks for relay and modulation*. New York: Pergamon, 1993;3–15.
- Diamond IT, Hall WC. Evolution of neocortex. *Science* 1969;164:251–262.

- Diamond IT, Neff WD. Ablation of temporal cortex and discrimination of auditory patterns. *J Neurophysiol* 1957;20:300–315.
- Diamond IT, Utley JD. Thalamic retrograde degeneration study of sensory cortex in opossum. *J Comp Neurol* 1963;120:129–160.
- Diamond IT, Chow KL, Neff WD. Degeneration of caudal medial geniculate body following cortical lesion ventral to auditory area II in the cat. *J Comp Neurol* 1958;109:349–362.
- Diamond IT, Fitzpatrick D, Conley M. A projection from the parabigeminal nucleus to the pulvinar nucleus in *Galago*. *J Comp Neurol* 1992;316:375–382.
- East EM. A Mendelian interpretation of variation that is apparently continuous. *The American Naturalist* 1910;44:65–82.
- Elliot-Smith G. Some problems relating to the evolution of the brain. *Lancet* 1910;1:1–6, 147–153, 221–227.
- Gasser HS, Erlanger J. The role of fiber size in the establishment of a nerve block by pressure or cocaine. *Am J Physiol* 1929;88:581–591.
- Harting JK, Hall WC, Diamond IT, Martin GF. Anterograde degeneration study of the superior colliculus in *Tupaia glis*: evidence for a subdivision between superficial and deep layers. *J Comp Neurol* 1973a;148:361–386.
- Harting JK, Diamond IT, Hall WC. Anterograde degeneration study of the cortical projections of the lateral geniculate and pulvinar nuclei in the tree shrew (*Tupaia glis*). *J Comp Neurol* 1973b;150:393–440.
- Harting JK, Glendenning KK, Diamond IT, Hall WC. Evolution of the primate visual system: anterograde degeneration studies of the tecto-pulvinar system. *Am J Phys Anthropol* 1973c;38:383–392.
- Harvey W. An anatomical disquisition on the motion of the heart and blood in animals. (Originally published in 1628; translated from Latin by Robert Willis.) New York: Dutton, 1908.
- Itoh K, Conley M, Diamond IT. Different distributions of large and small retinal ganglion cells in the cat after HRP injections of single layers of the lateral geniculate body and the superior colliculus. *Brain Res* 1981;207:147–152.
- Itoh K, Conley M, Diamond IT. Retinal ganglion cell projections to individual layers of the lateral geniculate body in *Galago crassicaudatus*. *J Comp Neurol* 1982;205:282–290.
- Karten HJ, Revzin AM. The afferent connections of the nucleus rotundus in the pigeon. *Brain Res* 1966;2:368–377.
- LeGros Clark WE. The thalamus of *Tupaia*. *J Anat* 1929;63:117–206.
- LeGros Clark WE. A morphological study of the lateral geniculate body. *Br J Ophthalmol* 1932a;16:264–284.
- LeGros Clark WE. The structure and connections of the thalamus. *Brain* 1932b; 55:406–470.
- LeGros Clark WE. The medial geniculate body and the nucleus isthmi. *J Anat* 1933;67:536–548.
- Mendel G. Experiments in plant hybridization. (Originally published in 1865.) Cambridge: Harvard University Press, 1960.

- Moruzzi G, Magoun HW. Brain stem reticular formation and activation of the EEG. *Electroencephalogr Clin Neurophysiol* 1949;1:455–473.
- Neff WD, Fisher JF, Diamond IT, Yela N. Role of auditory cortex requiring localization of sound in space. *J Neurophysiol* 1956;19:500–512.
- Penny GR, Itoh K, Diamond IT. Cells of different sizes in the ventral nuclei project to different layers of the somatic cortex in the cat. *Brain Res* 1982;252:55–65.
- Ramón y Cajal S. Comparative study of sensory areas, sensory pathways to the neocortex. *Clark University 1889–1899 decennial celebration*. Worcester, MA, 1899;311–382.
- Ramón y Cajal S. The structure and connections of neurons. Physiology or medicine: Nobel lectures including presentation speeches and laureates' biographies 1901–1921 (Nobel Foundation). (Originally published, 1906). New York: Elsevier, 1967.
- Rose JE, Woolsey CN. Organization of the mammalian thalamus and its relationships to the cerebral cortex. *Electroencephalogr Clin Neurophysiol* 1949;1:391–403.
- Sherrington, C. The integrative action of the nervous system. New York: Scribner's, 1906.
- Snyder M, Diamond IT. The organization and function of the visual cortex in the tree shrew. *Brain Behav Evol* 1968;1:244–288.
- Snyder M, Hall WC, Diamond IT. Vision in tree shrews (*Tupaia glis*) after removal of striate cortex. *Psychonomic Sci* 1966;6:243–244.
- Sutton W. The chromosomes in heredity. *Biol Bull* 1903;4:55–69.