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COMMENTARY

Harvey's Story

Anton Reiner

Department of Anatomy and Neurobiology, The University of Tennessee Health Science Center, Memphis, Tennessee, USA

Correspondence: Anton Reiner (areiner@uthsc.edu)

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ABSTRACT

Harvey Jules Karten passed away on July 15, 2024. With his passing, the world lost a remarkable and energetic man who had made major contributions to neuroscience, in particular, resetting our understanding of the evolution of the forebrain and the evolution of intelligence. He left behind a legion of loyal colleagues with whom he had collaborated and shared ideas, students he had inspired and trained, and non-neuroscientist friends he had made in the passionate pursuit of his hobbies—sailing, skiing, and hiking.

Harvey Jules Karten passed away on the morning of July 15, 2024 at his home in Del Mar, California, with his loving family gathered for his final days. He had suffered a massive cerebral hemorrhage 3 weeks prior and had been passing in and out of awareness since then. Two days earlier, on July 13th, he was briefly alert, and his family took him into the backyard, in a wheelchair, to celebrate his 89th birthday. The day was clear and peaceful. On the patio, surrounded by palm trees and lush plantings, everyone ate chocolate mousse, one of his favorites, and Harvey smiled as they all sang "Happy Birthday." With his passing, the world lost a remarkable and energetic man who had made major contributions to neuroscience, in particular, resetting our understanding of the evolution of the forebrain and the evolution of intelligence. He left behind a legion of loyal colleagues with whom he had collaborated and shared ideas, students he had inspired and trained, and non-neuroscientist friends he had made in the passionate pursuit of his hobbies—sailing, skiing, and hiking.

1 | Family Background and Childhood—1935–1951

Harvey was born on July 13, 1935 in the Bronx, New York City, and lived his first years on the Grand Concourse in a neighborhood of European Jewish immigrants. His parents, Ernest Karten and Esther Wacks Karten, had separately immigrated to the United States in the mid-1920s from a small town in Galicia called Molodechno, then part of Poland but now in Belarus and called Maladzyechna. As typical of eastern European Jews living in the Western part of the Russian Empire (a region called the Pale of Settlement), the Karten and Wacks families experienced harsh poverty and government-sanctioned anti-Semitism that motivated Ernest and Esther, and many others like them, to emigrate. Ernest and Esther met and married in New York City and lived in the Bronx for the first years of their marriage. They had a daughter, Deborah in 1929, and the family moved to Jersey City, New Jersey in the late 1930s. Ernest became a shopkeeper and went into the candy store business, first in Jersey City, and then later in nearby Bayonne, New Jersey. The candy store business was never lucrative, however, and the family needed to work long hours to survive economically, with Esther taking on seamstress work to help. As an adult, Harvey often said, with regret, that his mother worked 364 days a year and that the family ate dinner together only once a year, on the first night of Passover. When Harvey reached school age, he was sent to attend and board at an elite private Jewish school (termed a Yeshiva) on the Lower East Side of Manhattan, called The Rabbi Jacob Joseph (RJJ) School, where the students studied a rigorous Talmudic curriculum. Harvey was not fond of the narrowness of the curriculum, did poorly, and his father had to haggle with the administration to keep Harvey enrolled. Sadly, the family believed that Harvey's sister did not merit the same investment in education, because she was a girl. Although it was a financial strain to send Harvey to a private school, the family wanted to provide Harvey with an opportunity to succeed in America, and they saw education as the path to that goal. For high school, Harvey attended Yeshiva University's Preparatory School for Boys, also known as the Manhattan Talmudical Academy (MTA), located in Washington Heights in northern Manhattan, again as a boarder.

Harvey's parents experienced economic duress throughout the Great Depression. Because the candy store was never especially successful, they kept it open 7 days a week, requiring that they work on the Sabbath, which they found very distressing. Although Ernest and Esther had left behind the pogroms and violence they had endured as youth in Europe, anti-Semitism was widespread in the United States. For example, Harvey attended Jewish Yeshivas rather than any of the other private schools in New York City, because they would never have admitted a poor Jewish boy like him. Moreover, the Karten family store was often vandalized on Halloween, Easter, Christmas, and Jewish Holidays. As if that were not bad enough, on one occasion when Harvey had come home to Jersey City for the weekend, he was stabbed in the chest with scissors by Italian-American gang members because he was Jewish, and on another occasion, his head was grazed by a shot from a gang member zipgun. Overriding all of this during the World War II was the realization that family members who had remained in Poland were being murdered in the Nazi concentration camps. Harvey felt a need to make something of himself in America, both because of his parents' sacrifices for him, and for the sake of family abroad whose opportunities were being snuffed out.

The high school Harvey attended, the MTA, is a renowned orthodox Jewish private school, with many alumni who distinguished themselves in science and the humanities. The MTA combined religious education with excellent education in science and mathematics. Many years later Harvey noted that one of the teachers, Mr. Samuel Greitzer, affectionately called "Doc" by his many admiring students, changed his life by introducing him to the rigors and wonders of mathematics. Mr. Greitzer, in fact, went on to a notable career in academia and math education and became the founding chairman of the committee running the US Mathematical Olympiad. Except for his classes with Mr. Greitzer, however, Harvey did poorly in most of his subjects. In particular, he did not care for the religion courses, which required memorizing long text passages. Again, Ernest Karten had to intervene and cajole administrators to keep Harvey enrolled. As incongruous as it may now seem based on Harvey's eventual scientific accomplishments, he needed a private tutor to help him finish high school. Harvey's disenchantment with much of his education led him to often skip class and instead go to the American Museum of Natural History, where he absorbed the lessons of the museum about the wonders of nature. He found the bird exhibits of particular appeal, which seems prophetic given his later contributions to the understanding of avian brain organization. He also dabbled in electronics and avidly read the unsold Science Illustrated magazines that his mother brought him from the candy store. He additionally developed an interest in classical music by listening to the Metropolitan Opera Saturday Matinee radio broadcast and eventually learned to read music and play the flute. Notably, beginning in his early school years, Harvey was sent to an overnight summer camp in the Catskills called Camp Mechaneh. Harvey enjoyed camp life and there discovered his love of the great outdoors, a commodity in limited supply in Jersey City and Manhattan.

2 | College, Medical School and Residency—1951–1961

After just barely graduating from high school, Harvey was admitted in 1951 to Yeshiva University, a private Orthodox Jewish university in New York City. Harvey lived with his sister and an ever-changing set of roommates, in a small house near Pelham Parkway in the Bronx, which, despite the family poverty, their mother had managed to buy. He graduated with a B.A. in chemistry in spring of 1955 and by then had been admitted to the inaugural class of the Albert Einstein School of Medicine. The school opened its doors that fall with 53 students in the first class, and it was not yet accredited. Although Harvey had considered graduate school in chemistry, he chose medical school for several reasons. First, Ph.D. programs in chemistry were few, and graduate schools had strict quotas for admitting Jews. Second, Harvey felt the weight of family obligations, and becoming a physician seemed a better way to fulfill that obligation than becoming a Ph.D. with an uncertain future. Harvey's parents were immensely proud when he was accepted to the Albert Einstein School of Medicine, even if that choice was the consequence of Jewish quotas limiting his options at other medical schools. The Albert Einstein School of Medicine, in fact, had been created to help train Jewish physicians during this period when the quota system made it difficult for Jews to gain admittance to other medical schools. Harvey continued to live with his sister and various roommates in the house their mother had purchased. During his Yeshiva and Einstein years, Harvey often went on outings with friends and with the Appalachian Mountain and Sierra Clubs, developing skills in and a fondness for skiing. Although Harvey enjoyed the medical school courses, particularly neurophysiology, he still struggled to get good grades. Moreover, he found the weight of family expectations and the competition with other students to be an unpleasant aspect of his medical school experience.

Upon completing medical school in 1959, Harvey chose a 1-year internship in psychiatry in Salt Lake City, Utah, his specialty area during medical school. The decision to pursue training in Salt Lake City was motivated by his desire to be near the mountains and farther away from family pressures and orthodox Jewish cultural expectations. His summer camp stints as a young boy had allowed him to discover his love of the mountains, which was further developed by overnight hiking and skiing trips as a teen and young adult. In Salt Lake City, however, Harvey felt overworked and underpaid, and he thought that the hospitals were poorly equipped. He did not have enough money for clothes, rent, or food. Although he was not certain that he was well suited

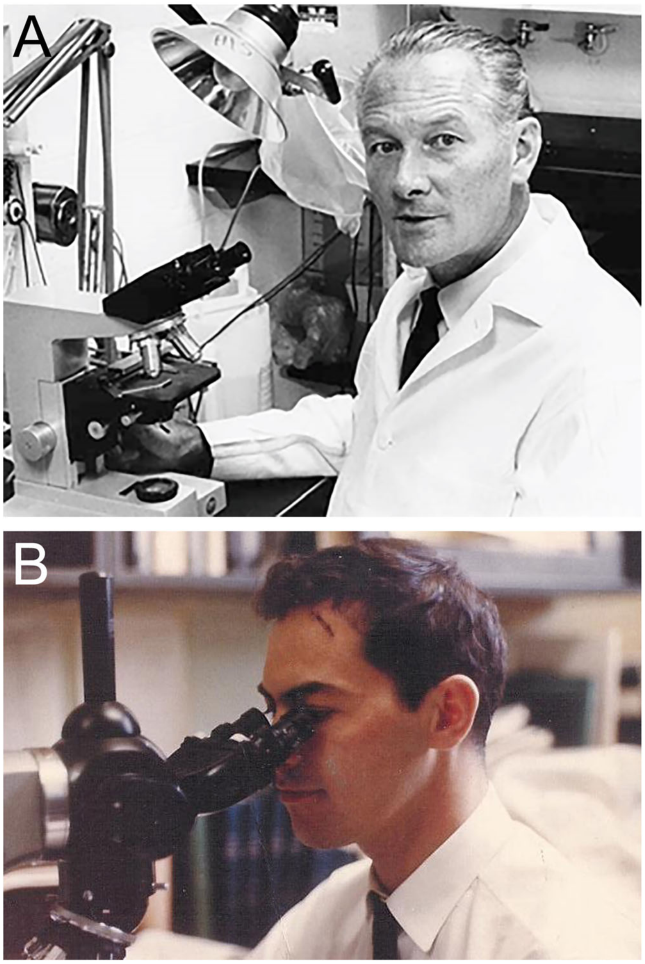

FIGURE 1 | (Image A) Walle Nauta at the microscope during his MIT days (from www.ernst-poeppel.com). (Image B) Harvey at the microscope during his medical school days.

to the profession of psychiatry, he completed his internship in 1960 and began what was intended to be a 2-year residency in psychiatry at the University of Colorado Psychopathic Hospital. This was the point at which the conflict between his not-yet-fully-formed love of science and his sense of family obligation to pursue medicine came to a head. Although his residency allowed him to remain close to the mountains and made it possible for him to go skiing frequently, he again found the work tedious and burdensome, and he became yet more convinced that he was a poor fit for psychiatry. He did not enjoy any aspect of his residency. He did not find his interactions with patients rewarding, and he did not enjoy his relationships with his attending or chief residents. Despite his misgivings about medicine as a career, he had persevered out of a sense of duty to the financial sacrifices of his parents on his behalf, a sense of guilt that his sister had been denied similar opportunities for his sake, and the need to not squander opportunity denied his European relatives lost in the Holocaust. But his dissatisfaction with medicine had finally become too much. During his first year, Harvey applied for and was awarded a Public Health Service Training Grant in Psychiatry from the National Institutes of Health (NIH) to work with famed neuroanatomist Walle Nauta (Figure 1A) at the Walter Reed Army Institute of Research in Washington, DC.

3 | Training in Neuroscience Research With Walle Nauta at Walter Reed—1961–1965

When Harvey was awarded the training grant, his supervisors allowed him to temporarily suspend his residency thinking the research experience would better prepare him to be a psychiatrist. Although Harvey was expected to return to finish his psychiatry residency, the allure of neuroscience and his emergent talent for it assured he never did. In 1961, despite the strong disapproval of his parents, Harvey began what was supposed to be an 18-month research position. Having recently broken his ankle badly while skiing in Colorado (which eventually required surgery to repair), Harvey arrived at Walter Reed on crutches. He was given a microscope to sit down at (fortunately) and some slides of cat brain sections to examine, and he was transfixed by the beauty of the brain. He spent the next 8-h peering through the oculars at the slides, studying the connections of a white matter region called the fields of Forel (Figure 1B). Harvey realized that there was so much to learn about the brain, and he felt unleashed by the opportunity to reveal the unknown. Harvey was to remain at Walter Reed until 1965, making discoveries during that 4-year time period that began to establish his scientific legacy. To the end, however, his parents never understood what he did as a neuroscientist and were always disappointed that he did not open a private practice in Manhattan and become a rich doctor.

Harvey arrived in Walle Nauta's laboratory at a particularly fortunate time in the history of neuroscience. The field of neuroanatomy had largely been static for decades because nearly everything meaningful that could be done with the available methods of staining neurons and their fibers had been done. The cytoarchitectural features of brain in diverse species had been characterized, but few of the major connections between brain regions had been determined. Thus, firm and detailed information about overall brain connectivity was lacking. Without such information, understanding brain function was simply not possible. Into this breach stepped Walle Nauta. Walle was born in the Dutch East Indies and trained as a physician at Leiden University in the Netherlands, completing his training in 1942, just as the Nazis invaded. The perseverance and heroism of Walle and his wife Ellie during World War II make a remarkable tale unto itself (https://nap.nationalacademies.org/read/11807/chapter/16), but for the current narrative what is important is that Walle took a lectureship at the University of Zurich after the war. There he realized that his goal of elucidating hypothalamic function required knowing the connections among its many cell groups. As a means for obtaining this information was lacking, Walle set about developing a suitable technique. His method relied on silver staining to detect degenerating axons and terminals that originated from a given brain region after that region was destroyed. Although the Nauta method had forerunners in the reduced silver staining methods of Bielschowsky and Cajal, degenerating and normal axons could not be readily distinguished from one another using the prior approaches. By meticulous trial and error, Nauta and Paul Gygax, a doctoral student in organic chemistry at the Swiss Federal Institute of Technology, developed the Nauta-Gygax method, which selectively stained degenerating axons (Nauta and Gygax 1951). With this development, Nauta went from obscurity to being sought after and was recruited by David Rioch to the Department of Neurophysiology in the Research Division of Neuropsychiatry at Walter Reed in 1952. The Nauta-Gygax method was a major enabler of the rise of modern neuroscience and attracted many eventual luminaries to Walter Reed who sought to learn this powerful new method. Harvey too had heard of the remarkable method Nauta had developed and on that basis had written his NIH application to train with him. Joining Harvey in the Nauta lab was Sven Ebbesson (who became a highly regarded and prolific comparative neuroanatomist). Numerous other researchers in the Department of Neurophysiology were collaborating with Nauta at the time, including Boyd Campbell (who in his subsequent career contributed to understanding the principles of brain evolution), Ford Ebner (who subsequently contributed to understanding brain plasticity), and William Mehler (who made prominent early discoveries on basal ganglia connectivity). Further enriching the environment in the Department of Neurophysiology were Robert Galambos (a prominent figure in understanding auditory brain function) and David Hubel (who went on to win a Nobel prize with Torsten Wiesel for research on cortical visual function). Other noteworthy researchers at Walter Reed during Harvey's time there were Elliot Valenstein, an experimental psychologist and chief of the Neuropsychology section, and Joseph Brady, a pioneer in behavioral pharmacology and head of the Department of Experimental Psychology.

Nauta was a thoughtful and caring mentor, who sought to advance the careers of his trainees. So that his students and collaborators received full recognition, Nauta would commonly not be a coauthor on their studies, regardless of his own contributions. In Harvey's case, Nauta also wanted him to develop his own research program. Recognizing that many other researchers were already working on the cat brain, Nauta suggested that avian neurobiology was a wide-open area for study. The 1936 three-volume series, *The Comparative Anatomy of the Nervous System of Vertebrates, Including Man* by Ariëns-Kappers, Huber, and Crosby (1936), had characterized the organization and presumed connectivity of the avian brain, but Nauta thought much more might be discoverable using the Nauta-Gygax method. Nauta also realized that Harvey's study of avian brain organization might proceed better if he collaborated with someone who had experience in working with birds and in behavioral techniques. It thus came about that Joseph Brady, who had learned of Harvey from his conversations with Nauta, played match-maker and introduced Harvey to a young newly-minted Ph.D. member of his group, William (Bill) Hodos, whose prior work had been in the brain role in motivation in diverse species. In Bill Hodos, a Jewish boy from Brooklyn, Harvey found a kindred spirit and began a friendship that lasted a lifetime, sharing love of life, family, and science, and bad schoolboy jokes. They came to have pet names for one another, Bill addressing Harvey as Reb Hillel, and Harvey addressing Bill as Reb Velvel. Reb is Yiddish shorthand for Rabbi, their salutation thus being a reference to their shared background as Yeshiva students in New York City.

The first issue for Harvey and Bill to resolve was which pathways to trace and which avian species to employ. Pigeons were the standard model in those days for avian behavioral research and studying ascending sensory pathways seemed straightforward and fundamental. Given that it was already established that the avian midbrain tectum received direct visual input from the retina, they began by determining the target of the ascending tectal projections to the thalamus. Harvey and Bill, together with an electrophysiologist colleague, Alan Revzin, showed using the Nauta-Gygax method and brain recording methods that the tectum had a major projection to a prominent round nucleus in the thalamus aptly called nucleus rotundus (Karten and Revzin 1966), and that nucleus rotundus projected to a circumscribed nucleus in the telencephalon then called the ectostriatum (Figure 2A) (Revzin and Karten 1967; Karten and Hodos 1970) but now called the entopallium for reasons that will be explained later. By using behavioral approaches and with Bill taking the lead, Harvey and Bill further showed that lesions that destroyed either rotundus or ectostriatum impaired visual discrimination (Hodos and Karten 1966, 1970). During this time, Harvey also traced the ascending auditory pathways, finding that the ascending projection from auditory midbrain (the inferior colliculus) ended in a circumscribed rounded thalamic nucleus called ovoidalis (Karten 1967), which then itself projected to a crescent shaped field in the telencephalon called Field L (Karten 1968). These types of studies required accurate placement of electrodes for recording or for making lesions in the brain, and to make this possible, Harvey and Bill first had to create a stereotaxic atlas of the pigeon brain. The atlas they created (Karten and Hodos 1967) not only facilitated their research studies but also summarized and formalized what was known about the organization and nomenclature of the avian brain at that time.

Harvey's and Bill's discoveries, however, posed a problem for what was then the conventional understanding of avian brain organization. Both the ectostriatum and Field L are enclosed in a larger telencephalic field that was called the neostriatum at that time (now called the nidopallium). Lying above the neostriatum is another field then called the hyperstriatum ventrale (now called the mesopallium) and lying above that a series of additional fields then with hyperstriatum in their name (these also collectively called the Wulst). Because they are the constituents of a large dorsal territory that bulges into the lateral ventricle, the regions then called the hyperstriatum ventrale and neostriatum are together referred to as the dorsal ventricular ridge (DVR). The canonical interpretation at that time, as presented in Ariëns-Kappers, Huber, and Crosby (1936), was that the avian and mammalian telencephalons were fundamentally different. In particular, although the mammalian telencephalon was recognized to consist of a nonlaminated core region (called the basal ganglia) and a surrounding laminated region (called the neocortex), the avian telencephalon was considered to consist almost exclusively of a hypertrophied basal ganglia, hence the presence of the root "-striatum" in many telencephalic regional names. This neuroanatomical interpretation was in concordance with the prevalent mammocentric view that mammals exhibit flexible intelligent behavior, whereas birds exhibit only stereotyped behavior, with neocortex considered necessary for intelligent behavior and the basal ganglia thought to be the seat of stereotyped behavioral routines. These notions were the underpinning of the triune brain concept of MacLean (1990), and his promulgation of that concept served to make these ideas yet more widespread. The notion that birds were intellectually limited "birdbrains" was, however, a strange concept for science to hold, given that it was juxtaposed to the centuries-old belief that owls are wise and the common observation, as enshrined by Aesop in one of his fables, that crows are clever. In any case, Harvey and Bill recognized that ectostriatum and Field L were anatomically similar to regions of neocortex in that they received sensory

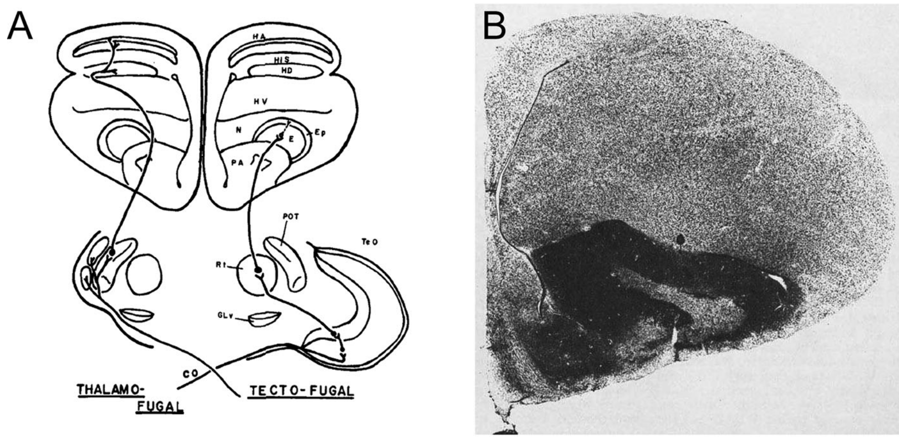

FIGURE 2 | (Image A) Schematic drawing, showing the ascending thalamofugal pathway to the Wulst on the left side of the brain and the ascending tectofugal pathway to the ectostriatum (now called entopallium) on the right side of the brain. (Image B) Photomicrograph of a coronal section through the pigeon telencephalon stained for AchE, showing the limited extent of the avian basal ganglia. CO, optic chiasm; E, Ectostriatum; Ep, peri-ectostriatal belt; GLv, ventral geniculate nucleus; HA, hyperstriatum accessorium; HD, hyperstriatum dorsale; HIS, hyperstriatum intercalatus suprema; HV, hyperstriatum ventrale; PA, paleostriatum augmentatum; POT, principal optic nucleus of thalamus; Rt, nucleus rotundus; TeO, optic tectum. *Source:* (A) From Figure 4 in Harvey's *1969 Annals of the New York Academy of Sciences* study. (B) From Figure 2 in Karten and Dubbeldam (1973).

thalamic input and that ectostriatum participated in sensory information processing, and likely Field L did as well. Of course, it was possible that ectostriatum and Field L were specialized parts of avian basal ganglia, and their resemblance to neocortical areas deceiving. The emergence of methods for characterizing brain regions by their unique neurochemistry, however, soon belied this possibility. Other researchers (Koelle 1954; Dahlström and Fuxe 1965) showed that the striatal part of the basal ganglia in mammals was rich in the enzyme acetylcholinesterase and in terminals containing dopamine. When Harvey applied these methods to pigeon telencephalon, he found that only a ventral territory below the DVR was enriched in acetylcholinesterase and dopaminergic terminals (Figure 2B) (Karten and Dubbeldam 1973). Harvey concluded that the avian basal ganglia occupied no greater proportion of the telencephalon than they did in mammals, and the DVR lying above the true avian basal ganglia was akin to mammalian neocortex in connectivity, function, and neurochemistry.

4 | Harvey at Massachusetts Institute of Technology (MIT)—1965–1974

The studies described above, started in the early 1960s, took years to complete and publish, but the findings enabled Harvey to obtain NIH grants to support his salary and the ongoing research. In 1964, Nauta was recruited to the Department of Psychology at MIT by its head, Hans Lukas Teuber, and became Professor of Neuroanatomy. Harvey moved to MIT in 1965 and was joined by Lennart Heimer, who during his MIT time improved on the Nauta-Gygax method, with a technique known as the Fink–Heimer method (Fink and Heimer 1967). The three shared contiguous lab space, to facilitate their interactions. Before the move, however, important life events occurred for Harvey—he met and married Elizabeth Bunim (Figure 3). Elizabeth's father, Joseph Bunim, was the head of the National Institute of Arthritis and Metabolic Diseases at NIH, and Harvey was introduced to Elizabeth by a friend who happened to work with Joseph Bunim.

FIGURE 3 | Harvey and Elizabeth in 1964.

She was a graduate of the Beth Israel Hospital School of Nursing in Boston, and during their courtship, Harvey would often visit her while she was yet in Boston. Harvey and Elizabeth married on March 22, 1964 in B'nai Israel Synagogue in Washington, DC, as announced in the New York Times, and went on to have three sons, Joseph in 1965, Seth in 1966, and Daniel in 1969.

By the late 1960s, Harvey recognized that the DVR contained subregions organized into separate nuclear groups that were akin to the layers of specific cortical regions and had interconnections that were akin to those between layers of neocortex. Field L, for example, was like Layer 4 of primary auditory cortex, as they both receive auditory thalamic input. Field L then projected to a nearby DVR region akin to Layers 2 and 3 of primary auditory cortex, which in turn projected to a region like Layers 5 and 6 of primary auditory cortex. Thus, the connectivity and function of DVR was like that of neocortex, although its architecture was nuclear and deceptively more similar to that of striatum. This discovery upended the traditional view (e.g., Ariëns-Kappers, Huber, and Crosby) that the lateral wall of the ancestral amniote telencephalon had mainly consisted of basal ganglia, with mammals adding a neocortex during their evolution, but reptiles and then birds progressively expanding the basal ganglia. Harvey realized and in various talks at meetings and informal presentations came to espouse the view that Wulst and DVR were similar in function and were evolutionarily related to neocortex. This made Harvey something of a heretic in the field. Elizabeth Crosby was alive at this time and an influential member of the American Association of Anatomists (AAA). When Harvey applied for membership to the AAA in the mid-1960s, as all neuroanatomists did before the Society for Neuroscience existed, his application was turned down. Whether it was Crosby's influence, as Harvey suspected, or the fact that, as a lapsed psychiatry resident, he had insufficiently demonstrated his anatomical mettle is uncertain. In any case, Harvey was accepted into the AAA upon reapplication and was awarded its C.J. Herrick award as the outstanding young comparative neuroanatomist in 1968. In 1969, Harvey published a study in the Annals of the New York Academy of Sciences in which he presented his evidence that DVR and Wulst in birds contain the same neuron types as mammalian neocortex and show the same connectivity patterns as layer-specific cell types do in neocortex, despite being organized into separate nuclei rather than into separate layers (Karten 1969). This conclusion shifted the paradigm on the organization and function of the avian telencephalon and set the stage for a large body of subsequent work further detailing comparisons between avian DVR and Wulst on one hand and neocortex on the other. A second study with Nauta reprised these ideas (Nauta and Karten 1970). In the two studies, Harvey also sought to explain how the differences between avian telencephalic and mammalian telencephalic organization arose, speculating that some alteration during mammalian development caused the neuron types that occupy the DVR and Wulst in birds to migrate into the neocortex in mammals. This speculative part of Harvey's formulation remains more controversial.

During his time with Nauta, Harvey transitioned from being a research neophyte uncertain of his future to someone who had found a profession that fit perfectly with his persona. He established himself as an accomplished brain scientist who had profoundly altered the field and begun to influence new generations of neuroscientists. For example, Harvey's findings in pigeons formed the basis for the work of Ford Ebner and his post-doctoral fellow Bill Hall on thalamo-telencephalic projections in turtles (Hall and Ebner 1970) and research by Mike Pritz on thalamo-telencephalic projections in caiman (Pritz 1974a, 1974b, 1975). Their studies showed that forebrain organization in reptiles was much like what Harvey had discovered in pigeons, and that the reptilian DVR too was not part of the basal ganglia. Mike Pritz, who has remained a productive comparative neuroanatomist, while also having had a lengthy career as a neurosurgeon, noted that what struck him most about Harvey at that time was that "he had an encyclopedic knowledge not only of avian neurobiology but also that of mammals and other vertebrates." Ann Butler, who later published a comparative neuroanatomy textbook with Bill Hodos (Butler and Hodos 2005) recalled a meeting on the thalamus at City University of New York (CUNY), Brooklyn in June 1971, at which Harvey gave a presentation on his findings of the restriction of the avian striatum to the ventral telencephalon and his findings on visual and auditory pathways to the Wulst and DVR. Ann had just completed her Ph.D. training with Glenn Northcutt, in which she had studied the dorsal thalamus and visual pathways in iguanas and begun her first year of postdoctoral work with Ford Ebner, who had been recruited to Brown University after his stint at Walter Reed. At this point in her career, she was already intent on focusing on the evolution of the forebrain, particularly the dorsal thalamus, and Ford took Ann and other lab members to the meeting due to its relevance to their interests. Ann regarded the findings that Harvey presented as pivotal breakthroughs in the field, which helped to affirm that her own chosen research direction would be productive and rewarding. Although the proceedings of the meeting were to be published in the journal Brain, Behavior, and Evolution, Ann noted with some regret that Harvey's study was not forthcoming. In his eagerness to move forward and discover what was new, Harvey sometimes lagged in publishing what was no longer so new.

In any case, Harvey was now ready to be a mentor himself. His first graduate student at MIT was Len Maler, who sought to apply a mathematical approach to the operation of the brain, and had decided that the lateral line system of weakly electric fish would be a suitable model of sensory processing. This was very far afield from Harvey's ongoing research, but Harvey's eagerness to expand his own thinking and Len's interest led him to be receptive. Len recalls, "He bought me a few aquaria, fish and supplies and was incredibly supportive and helpful as I learned to do surgery, perfusions and the Fink-Heimer technique. We got it all working and Harvey's enthusiasm and continued mentoring were absolutely essential." A second graduate student, Tom Finger, soon followed, who also was interested in fish neurobiology. Harvey took both Len and Tom with him in 1972 on a 6-month sabbatical to work with Ted Bullock, a pioneering neuroethologist who was already studying electroreception in fish, at the Scripps Institution of Oceanography in La Jolla, California. There, Len examined the central projections of the mechanoreceptive anterior lateral line nerve and the electroreceptive posterior lateral line nerve in gymnotid fish, and Tom worked in a complementary fashion on the central projections of mechanoreceptive and electroreceptive lateral line nerves in bullhead catfish, as well as on olfactory and gustatory projections in catfish. Harvey also proved to be a far better editor than composer of manuscripts, and Len noted that Harvey's incisiveness helped him hone his professional writing skills (Maler, Finger, and Karten 1974). Both Len and Tom went on to become successful and accomplished neuroscientists, and Tom became a lifelong close friend and supporter. Another important aspect of the stay in San Diego was that the locale provided a rich scientific environment, as well as a relaxing setting that was appealing to Harvey, in no small part because California did not share the Jewish and WASP expectations of East Coast culture.

During his time at MIT, Harvey continued his enthusiasm for skiing by frequent trips to nearby skiing venues. Lennart Heimer accompanied Harvey on some of these occasions, which was very eye-opening for Harvey, who considered himself an expert skier, as Lennart had been a member of the Swedish national team. During one early such outing, before Harvey knew of Lennart's prowess, he warned Lennart that Lennart would likely have a hard time keeping up with Harvey and his friends. When Harvey reached the bottom of the slope, he found Lennart already there waiting nonchalantly. As he approached,

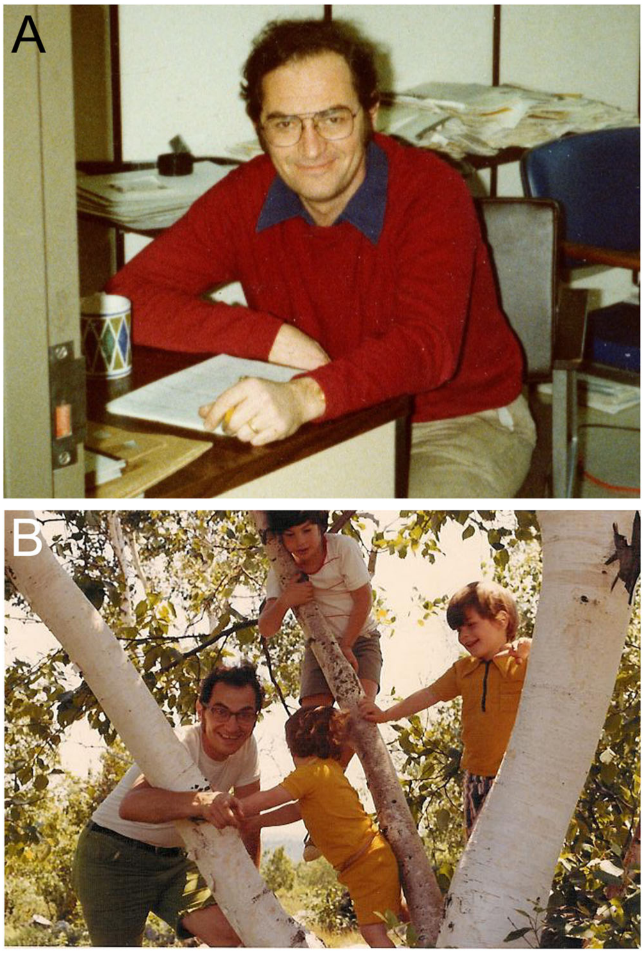

FIGURE 4 | (Image A) Harvey at Nick Brecha's desk at SUNY, editing a manuscript in 1980. (Image B) Harvey and his boys climbing a tree, clockwise from Harvey—Joseph, Seth and Daniel.

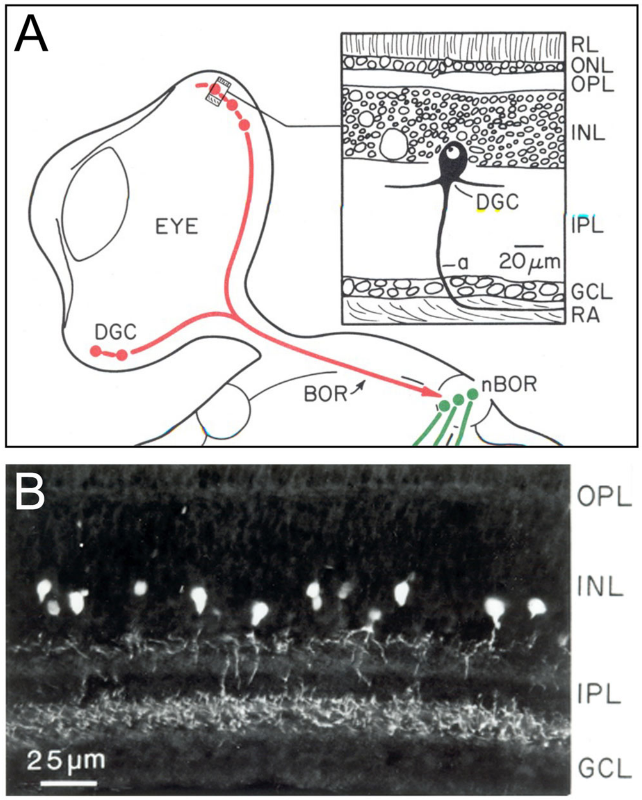

FIGURE 5 | (Image A) Schematic drawing showing a displaced ganglion cell (DGC) and its projection to the nucleus of the basal optic root (nBOR) in pigeon. (Image B) Enkephalinergic amacrine cells in the pigeon retina, labeled by immunofluorescence. *Source:* (A) This is a cropped version of Figure 38 in Brecha et al., 1980. (B) From Figure 26 in Brecha (1983). These images were generously provided by Nick Brecha.

Lennart innocently inquired, "Did you fall?" Harvey realized that he should henceforth not be misled by Lennart's unassuming manner. Harvey also added an additional hobby to his repertoire during his MIT time—sailing. Although he had sailed with others while at Walter Reed, he now started taking sailing lessons on the Charles River. He remained dedicated to the craft and became quite accomplished over the years, and this provided a further way for him to enjoy the great outdoors and the relaxation it provided with family and friends.

5 | Harvey at State University of New York (SUNY), Stony Brook—1974–1986

After he had spent 9 years at MIT, SUNY at Stony Brook (which was in the process of investing in their neuroscience program) made Harvey a substantial offer, with Harvey moving there in 1974 (Figure 4A). The location for Harvey and the family was ideal. They bought a home on an inlet of Long Island Sound, and they purchased small motorboats for outings into the Sound. They often rented a sailboat in the summer, and the family sailed up and along the East Coast between Long Island and Ipswich, Massachusetts on multi-week trips (Figure 4B). A graduate student, Nick Brecha, soon joined the lab, and then a second, David Katz. Harvey's reputation continued to grow, and he attracted a series of postdoctoral students during the late 1970s and early 1980s, including Steve Brauth, Steve Hunt, me (Tony Reiner), Gary Korte, Rodrigo Kuljis, Bill Eldred, Jon Erichsen, and Kent Keyser. Each of these went on to their own successful careers in neuroscience.

By the early 1970s, pathway tracing methods relying on axoplasmic transport had supplanted the Nauta-Gygax and Fink–Heimer methods. As revolutionary as the methods relying on detection of degenerating axons had been, they were now just a springboard for what followed—the autoradiographic detection of anterogradely transported radioactive amino acids and the chromogenic detection of retrogradely transported horseradish peroxidase after targeted brain injections. These new methods were easier to use and more powerful than the approaches Nauta had developed or inspired, and the Karten lab quickly switched over to their use. Harvey left considerations of brain evolution behind for the time and focused on underexplored aspects of visual system organization. The new work examined the cell type specific inputs and outputs of pigeon tectum initially, then branched out to studies of the connectivity and function of the accessory optic system (Figure 5A) (Brecha and Karten 1981), which in turn led to examining retinal cell types and circuitry (Figure 5B). The studies of retinal cell types were made possible by the quick embrace by the Karten lab of the newly developed methods for immunohistochemical labeling of neural tissue in the late 1970s. Nick, in particular (and later Kent Keyser), used this approach to document the amazing diversity among amacrine cells in the retinal inner nuclear layer, on the basis of differences in their neuropeptide content and in their morphology as revealed by the immunolabeling (Brecha, Karten, and Laverack 1979). Immunohistochemistry proved to be a tool for not only neuronal typology but also for circuit analysis. As neuropeptides commonly serve as neuromodulatory neurotransmitters, they are present both in neuronal cell bodies and in their synaptic terminals. Confirmation that a particular set of terminals arises from a particular set of neurons could be achieved by lesioning the putative neurons of origin or severing the tract containing the axons and examining if the terminals of interest were gone. This also was far simpler than the Nauta-Gygax or Fink–Heimer methods. Using these experimental tools, Jon Erichsen and I, together with an energetic graduate student from a different lab, Paul Gamlin, worked out the circuitry and function of the different parts of the nucleus of Edinger–Westphal in birds (Reiner et al. 1983). Steve Brauth and I began working on the connectivity and neurochemistry of the avian and reptilian basal ganglia (Reiner, Brauth, and Karten 1984), studies that reinforced the conclusions from Harvey's work at Walter Reed and MIT. Bill Eldred and Rodrigo Kuljis studied the neurochemistry of the frog and turtle visual systems (Eldred and Karten 1983; Kuljis and Karten 1983). It was a vibrant, collaborative, and innovative time in the lab, and Harvey was at the center of it all, providing input on new findings and making suggestions as to additional projects to pursue. Nick Brecha recalls: "Harvey was one-of-a-kind with a deep, probing and restless intellect, he was creative, insightful and with a boundless energy." Nick further noted Harvey's "constant stream of new ideas and approaches in pursuit of a better understanding of the nervous system", and that "His ability to infuse a high level of enthusiasm and confidence was infectious and exciting for all of us."

6 | Harvey's Lab at University of California at San Diego (UCSD)—1986–2006

In the middle of his time at SUNY, Harvey spent 1979–1980 as a visiting scientist at the Salk Institute in La Jolla. Nick, having remained on as a postdoctoral fellow after receiving his Ph.D. in 1978, oversaw the lab in Harvey's absence. Harvey's research activities at the Salk generated new ideas for his SUNY lab, and his time there convinced him that he yearned to live and work in the San Diego area. He was very pleased then to be recruited to the Department of Neurosciences of the UCSD and moved there with a number of lab members in 1986. At about the same time, UCSD also recruited Glenn Northcutt from the University of Michigan in Ann Arbor to the Neurobiology Unit of the Scripps Institution of Oceanography. Glenn is a prolific comparative neuroanatomist, now retired, with a particular interest in fish brain evolution and systematics. Harvey and Glenn published a study together on shark telencephalon neurochemistry in 1988 (Northcutt, Reiner, and Karten 1988), a topic on which their research interests aligned.

The move to UCSD for Harvey was both a lifestyle and a science choice. He had not fully enjoyed hiking and camping on the East Coast, as he found it too rainy and buggy, and now he was able to go hiking in the Sierra Nevada and Cascade Mountains on a regular basis with his sons, Joseph, Seth, and Daniel. Moreover, Harvey further devoted himself to his sailing passion, buying a 37-foot long sailboat, a Tayana 37, which he named the Night Heron, and joining the local yacht club. He also became a member of the Tayana Owners Group (TOG), a sailing club with about 2000 members, and later served as an administrator of its quarterly newsletter, TOG News. He took his family on many lengthy trips, including trips to Alaska and the Pacific Northwest. Harvey became an expert sailor, and a student of the art of sailing. Harvey often hiked, kayaked, and sailed with his colleague and friend Ed Rubel, a neurobiologist at the University of Washington in Seattle specializing in the avian auditory system. For many years, each summer included a backpacking or kayaking adventure. Despite their shared research interests, Ed says that they spoke minimally about science. Their trips together were about adventure and friendship, and a shared love of natural beauty. Ed recalls, "We talked about all the things close friends talk about; family, friends, goals and consequences, and where to make camp."

Through his TOG membership, Harvey became a source for sailing advice and suggestions for like-minded individuals, and he formed new lasting friendships among this community. One such individual was Bruce Pappas, an education consultant based in Minneapolis, Minnesota. In his later years, Harvey would visit him and they would sail Lake Superior in his boat Whisper, and Bruce would visit Harvey in San Diego. Bruce recalls, "We sailed. We went on long walks near his house and in the surrounding lagoons. He took wonderful pictures of birds. We ate well. We went out for dinners. We shopped together for food and cooked. We worked on his house. I looked forward to my annual visits (from snowy Minnesota). He adds, "…he had a very kind heart and welcomed me every time."

Kent Keyser moved with Harvey from SUNY to UCSD, and a new crew of postdoctoral fellows, including Thom Hughes, Toru Shimizu, Hillary Rodman, Onur Güntürkün, and Harald Luksch, joined the lab. All later went on to successful independent careers. Much of the research at UCSD, spearheaded by Kent and Thom, continued to focus on retinal organization and neurochemistry (Keyser et al. 1988). Hillary, Toru, and Onur worked on aspects of avian brain organization that harkened back to Harvey's research at Walter Reed and MIT, with Hillary and Onur working on forebrain visual system (Güntürkün and Karten 1991; Rodman and Karten 1995) and Toru, who obtained his Ph.D. with Bill Hodos, working on Wulst and DVR neurochemistry and connections (Shimizu and Karten 1990a). With Toru, Harvey wrote several studies expanding on his earlier ideas on neocortex evolution vis-à-vis avian brain organization (Karten and Shimizu 1989; Shimizu and Karten 1990b, 1991). Harald's work brought Harvey even closer to his initial interests and expanded on them. After Harald, who had carried out his Ph.D. work at the University of Köln in Germany on frog auditory system, initially contacted Harvey by email about postdoctoral work, Harvey outlined a research plan to study the morphology of a tectal neuron type in the avian tectofugal pathway with intracellular methods. Harald recalls that "Harvey sketched the problem and the putative outcome in such colorful and exciting words that I was immediately riveted by the subject. Coming from a physiology background, I also saw a computational angle in understanding the morphology." Because of their dendritic morphology, these tectal neurons were termed

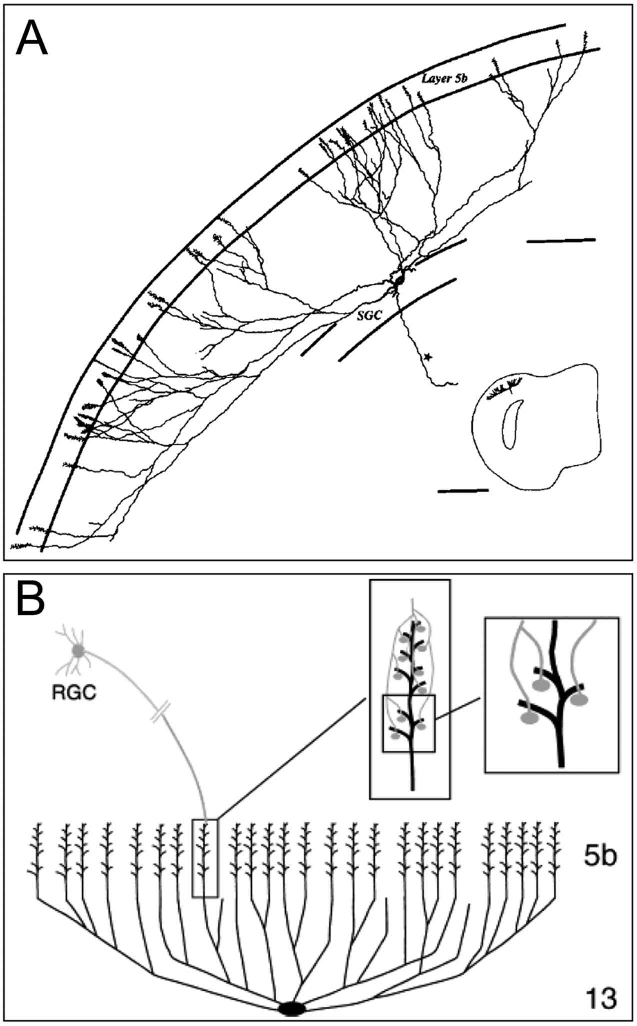

FIGURE 6 | (Image A) Reconstruction of a bottlebrush-type neuron, with a cell body in tectal layer 13 and bottlebrush dendritic endings in tectal layer 5b. The small outline drawing inset shows the location of the neuron and its expansive dendritic tree in the tectum. The scale equals 200 μm for the main drawing, and 2 mm for the inset. (Image B) Schematic drawing showing the idealized morphology of a bottlebrush tectal neuron and its confined input from a retinal ganglion cell (RGC) axon. A successive series of RGCs projects to a successive series of individual dendrites of a bottlebrush neuron, thereby making it possible for the neuron to compute the speed and direction of movement of small objects in the visual field. The insets show details of the presumed RGC input pattern. *Source:* (A) From Figure 4 in Luksch, Cox, and Karten (1998). (B) From Figure 14 in Luksch, Cox, and Karten (1998).

"bottle brush" neurons, and they projected specifically on nucleus rotundus. At UCSD, Harald and another German postdoctoral fellow, Ralf Wessel, who was working in the neurobiology laboratory of David Kleinfeld of the Department of Physics, detailed the morphology of these "bottle brush" neurons by intracellular fills (Figure 6A,B) (Luksch, Cox, and Karten 1998) and showed how "bottle brush" neurons can compute the direction and speed of small moving objects using time-delays in the visual responses in the different parts of their dendritic expanse (Luksch et al. 2001). The collaboration between the postdoctoral fellows also brought about a lasting collaboration and friendship between Harvey and David Kleinfeld.

The work Harald and Harvey had done on "bottle brush" cells showed that they project uniquely to nucleus rotundus in the thalamus, and they are one of the major tectal neuron types doing so. On the basis of his reading of the literature, Harvey had long suspected that the upper layers of mammalian superior colliculus, the homolog of avian tectum, contain neuron types that project to a mammalian homolog of nucleus rotundus in mammalian posterior pulvinar. With a graduate student, Dan Major, Harvey, and Harald later showed that "bottle brush" neurons are present in superficial superior colliculus in a highly visual mammal, the ground squirrel, and indeed project to posterior pulvinar (Major, Luksch, and Karten 2000). Harvey then reasoned that the morphology of "bottle brush" neurons in birds and mammals would not be so similar unless both they and their target had been inherited from the common stem amniote ancestor. Moreover, the tecto-thalamic circuit would not exist in the absence of a target in the telencephalon, and the similarity at the tectothalamic level would not have been preserved across phylogeny unless the telencephalic target had as well. Beltramo and Scanziani (2019) eventually identified the cortical area in receipt of caudal pulvinar input comparable to ectostriatum. As Harvey had shown in the early 1970s that an avian homolog of the mammalian geniculostriate visual system terminating in a part of the Wulst was akin to mammalian dorsal geniculate projection to primary visual cortex (Karten et al. 1973), the study by Beltramo and Scanziani confirmed that mammals also possessed a tectofugal pathway comparable to the avian one, as Harvey suspected all along.

During the late 1990s, developmental neurobiologists began to identify the genes that are critical to the regional differentiation of the brain during embryogenesis and to use in situ hybridization histochemistry to show the regional expression of those genes. The studies revealed that the telencephalon has two major parts, a lower part called the subpallium that largely becomes the basal ganglia, and an upper part called the pallium that largely becomes neocortex in mammals and Wulst and DVR in birds (Rubenstein et al. 1994). These findings emphatically supported the claims Harvey made about avian brain organization when he was at Walter Reed. Cliff Ragsdale at the University of Chicago and his graduate student Jennifer Dugas-Ford later showed (Dugas-Ford, Rowell, and Ragsdale 2012) that the different nuclear groups of Wulst and DVR Harvey had said were comparable to neurons in different layers of cortex did in fact possess the corresponding neurochemical signatures, thereby confirming the proposal Harvey had first made in his 1969 New York Academy of Sciences study.

The accumulation of evidence that Wulst and DVR are not constituents of the avian basal ganglia, and the increasing number of researchers working on Wulst and DVR function, began to create a nomenclatural problem. Much of the Wulst and DVR were still named with terms implying they were parts of the basal ganglia—typically having "-striatum" as the root part of their name. Mammal brain specialists reading the avian literature would typically be confused by this, especially in the case of "neostriatum"—a part of the avian pallium but also a term commonly used to refer to mammalian caudate and putamen. This confusion hindered the assimilation of avian brain findings into the broader neuroscience literature. Harvey and Bill Hodos were aware of this potential problem as they finalized their atlas, but there was not yet a clear reason for rejecting the 1936 terminology of Ariëns-Kappers, Huber, and Crosby, and no preferable alternative was available in any case. By the late 1990's, the time for an effort to change to a terminology without erroneous implications had finally arrived. This involved a multi-year open dialogue among avian brain researchers and culminated in a Nomenclature Forum at Duke University in summer of 2002, attended by 28 neuroscientists. The Forum was co-organized by Erich Jarvis, then at Duke but now at Rockefeller University, and me. Harvey and Bill provided their input but let the younger generation of scientists make the decisions. Although the process was not without contention, in the end, a recognized need to solve a problem plaguing the field united the researchers into choosing a mutually acceptable new terminology. In the new terminology, described in a publication in the Journal of Comparative Neurology (JCN) authored by the 28 participants (Reiner et al. 2004), obscure terms such as lobus parolfactorius were replaced by more readily understandable terms such as medial striatum (in this case), and misleading terms like neostriatum were replaced by descriptively correct and appropriate terms like nidopallium. In the end, the nomenclature revision was both a rejection of the erroneous terminology used by Ariëns-Kappers, Huber, and Crosby and a recognition that the work initiated by Hodos and Karten had led to uncovering those errors.

7 | Harvey as a Mentor and Colleague

Of his time with Harvey, Harald Luksch says, "Enthusiasm is what characterizes Harvey best in my mind—a profound and deep interest in, and enjoyment of cells, brains, people, arts and sailing (not necessarily always in this order). A typical day in the lab would have Harvey coming in late (but with a very fast pace), quickly peeking into every room (preferably those with a microscope). Having located someone who was inspecting tissue, he would ask his typical 'what have you got', followed by a 'let me have a look', and soon one was lectured first on the improvement of the image at whatever visual device one was sitting on, and then on the structure itself. If the results were sufficiently interesting, he would jump into explanations of the brain system, citing literature across many decades and referring to a zillion facts across the entire vertebrate kingdom." Harald goes on to say, "I learned from him that science should be fun—a somewhat different approach from the Germanic sincerity I had been brought up with. Harvey was emotional, witty, short tempered towards authorities, fun-loving, and always ready to laugh out loud." Harald later learned something more about Harvey. "How generous he was towards my background only became clear to me a decade later when I invited him to Germany; walking the cobblestones around the medieval cathedral of Aachen, he quietly remarked of how inconceivable it was that these were the same streets that the Shoah (i.e. Holocaust) happened." Harvey's roots were never far from his mind, and like his own mentor Nauta, he distinguished between those at fault and those not at fault.

It was not, however, just his own students Harvey inspired. He was generous of spirit, and always willing to engage and encourage fledgling neuroscientists. For example, Rich Mooney (Duke University) recalls, "I was lucky enough to first meet Harvey early in my doctoral training, as my advisor Mark Konishi and Harvey were close friends who shared a strong mutual interest in bird behavior and neuroanatomy. I say lucky because Harvey was immediately supportive of my interest in understanding the synaptic properties of the song system and, much to my surprise and delight, engaged me from the start as a colleague on equal footing. That is, kind of like a songbird tutor, he did not slow down or otherwise dumb things down for me and instead expected that I would closely follow his encyclopedic discourses on the avian brain. He balanced this inundation with remarkable reserves of patience as I asked one question after another to try to understand what he was telling me. Of course, with his great intellectual discipline and curiosity, Harvey continued to accrete more and more knowledge about comparative neuroanatomy, so I found myself in the same relative position to him—a mere neophyte—throughout my career. That he had a wicked sense of humor and great values strengthened our bond. Ultimately, he made it cool to ask how birds (and bird brains) do it!"

Similarly, Wayne Kuenzel (University of Arkansas) notes: "Over the 30 years of our phone calls and occasional visits to his lab and home addressing scientific issues, Dr. Karten became Harvey and a true friend. He critically reviewed the atlas of the chick brain that I and Manju Masson published 22 years later. The advice was always positive as well as frank. Harvey had such patience and understanding that I never hesitated to call him regarding any issue facing a faculty member in an academic environment. It clearly kept me going regarding pursuing the study of the complex neural systems of birds. Each time I visited his lab in San Diego I felt the excitement talking with his postdocs and graduate students." Wayne went on to say that he was "…so thankful that the area of avian neuroanatomy brought me to a person who was brilliant in that scientific field yet so modest about his noteworthy accomplishments."

8 | Approaching and Entering Retirement—2004–2024

Both Bill and Harvey were nearing 70 years of age and approaching retirement from active laboratory research in 2004. To honor their scientific achievements and thank them for their mentorship and friendship, Ann Butler, Toru Shimizu, and I (with Art Popper of the University of Maryland) organized a Festschrift on the University of Maryland campus that summer. Family, friends, students, and colleagues gathered to show their love and appreciation, with a day of talks and 2 days of meals and receptions (Figure 7A,B). The outpouring of affection and scientific regard was special for Harvey and Bill. Still, Harvey felt wistful about this and similar occasions, as they signified that much of life and career were behind him. He knew, however, that the recognition showed that what had transpired had been worthwhile. In 2005, Harvey received the Krieg Cortical Discoverer Award from the Cajal Club for his career contributions to the understanding of the cerebral cortex, further affirmation of the merits of his work.

By 2005–2006, Harvey had had enough of applying for grant funding to support his research, although he had been consistently successful in that regard since his first grant to work with Nauta. Even at this late stage of his career, though, his last postdoctoral fellow, Yuan Wang (currently at Florida State University), recalls of him, "He was so lively, full of energy and enthusiasm for

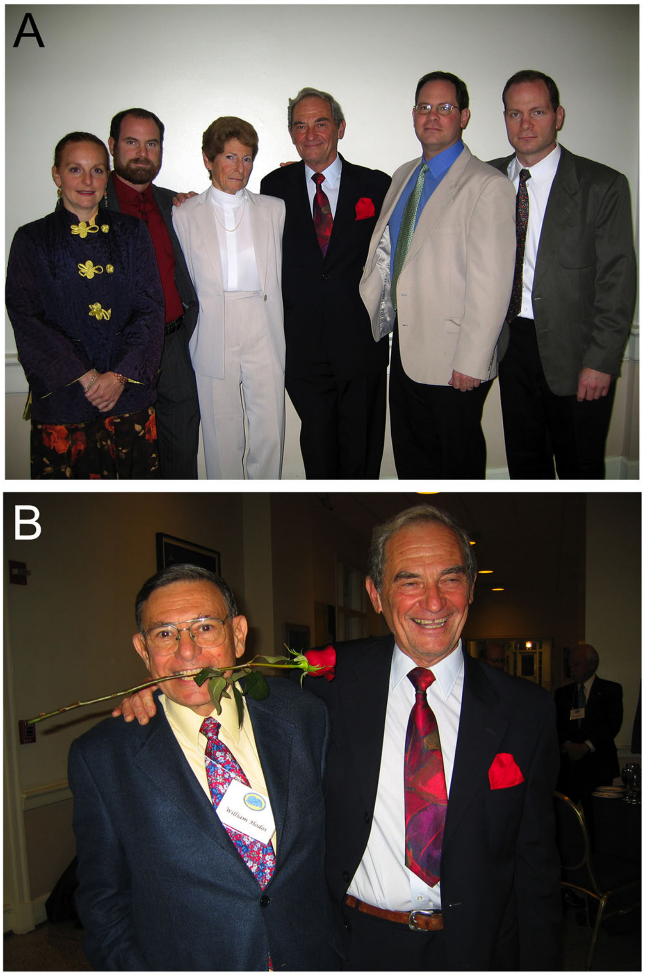

FIGURE 7 | (Image A) Harvey with his family at the 2004 Festschrift honoring him and Bill Hodos. From right to left, Seth, Joseph, Harvey, Elizabeth, Daniel, and Daniel's wife Marissa. (Image B) Photograph of Harvey and Bill enjoying the Festschrift.

science, nature, people, food, and life. Even when he was cursing about something (which he sometimes did), he appeared to be a wonder to me."

In late 2006, Yuan had finished her stint with him, and Harvey had indeed stopped applying for grants and his funded grants had ended. As medical schools are stingy about providing space to unfunded investigators, Harvey moved his laboratory into the Kleinfeld laboratory space in the Department of Physics. David Kleinfeld found Harvey's deep knowledge of brain organization and his keen intellect to be a valuable resource for his own work on whisking control in rodents as a model for sensory control of movement (Mercer et al. 2019). David also found that Harvey was a critical and well-appreciated mentor for David's students, as Harvey had been for his own. Harvey and David were good friends by now, and David enjoyed the daily discussions and kibitzing that accompanied Harvey's presence. David also had long learned that Harvey had his priorities, which were not necessarily those David might have expected. He recounts an episode in which he went to obtain Harvey's help photographing some histological samples, before Harvey had moved into David's space and still had his own lab and equipment. David recounts, "I asked if I could use his photomicroscope to take images. My request was met with a resounding 'no', a lesson on Koehler illumination, another on Bayer filters, and an admonition that no one was to touch his microscope." Just as Harvey had begun to take pictures, his cell phone rang. Harvey informed David that Larry Swanson, a well-known neuroanatomist at the University of Southern California, was on the line, they had important business to discuss, and he walked to the room next door for privacy. David continues, "Five minutes went by. Then ten. Fifteen. I walked over to listen in and caught a few words: 'spinnaker…jib…cleat'. After another five minutes, Harvey came back in the room, and said 'This is going to take a while—you know what you are doing—just take your picture'." David realized that a sailing discussion took priority over Harvey's previous, seemingly paramount, concerns about the care, and proper use of his microscope.

In addition to his collaboration with David, Harvey kept active in research in other ways. His knowledge was invaluable to a group at the University of Chile headed by Jorge Mpodozis working on avian brain organization, and there were frequent visits between Harvey and them (Fernández et al. 2020). He was also involved in the creation with the late Ted Jones (of the University of California, Davis) of the high-resolution digital brain atlases archived at Brainmaps.org (Jones, Stone, and Karten 2011). His technical expertise in computers, photography, and histology were invaluable in this regard. He also worked with Parth Mitra on similar types of endeavors (Karten et al. 2013; Mitra, Rosa, and Karten 2013; Chen et al. 2019).

In 2014, after Harvey had retired to Distinguished Professor Emeritus status at UCSD, his beloved wife Elizabeth died suddenly at their home in Del Mar. Bill Hodos phoned regularly to offer support and comfort. Sadly, Harvey's sister Deborah Karten Goldman died later that same year. When Bill's wife Nira passed away the following year, Harvey phoned Bill every day. Their schoolboy-like camaraderie helped them through their losses.

In 2015, Harvey received one of the most prestigious honors in science, election to the National Academy of Sciences. Prior to this, in 2008, he had been elected to membership in the American Academy of Arts and Sciences, another important honor recognizing his scientific work.

By 2015, Harvey was beginning to show a slight hand tremor, that he initially thought was benign, but was diagnosed as Parkinson's disease in 2018. Still, Harvey remained indefatigable. Medicines mitigated his tremor, and he kept on with research collaborations, correspondence with colleagues, and sailing. In April of the pandemic year 2020, Harvey sent me the following email to let me know how he was getting along. "I am holding up reasonably well to the social isolation. I get out to the bird marsh almost every other day, and manage to take a walk in the park behind my house every day. It's a large park, with most of it in undeveloped status with only dirt trails and lots of native shrubs. This is the peak of the wildflower season, and some of the flowers are less than 1 mm across (that's correct!). I usually take my camera along, and have been doing this 12 months a year for the past few years. As a result, I can compare the flowers through the course of a year. By late November, things are pretty arid, and only the hardiest of plants still are in flower. By early January, the first of the earliest plants start to flower, and with a decent rainy year (it was late

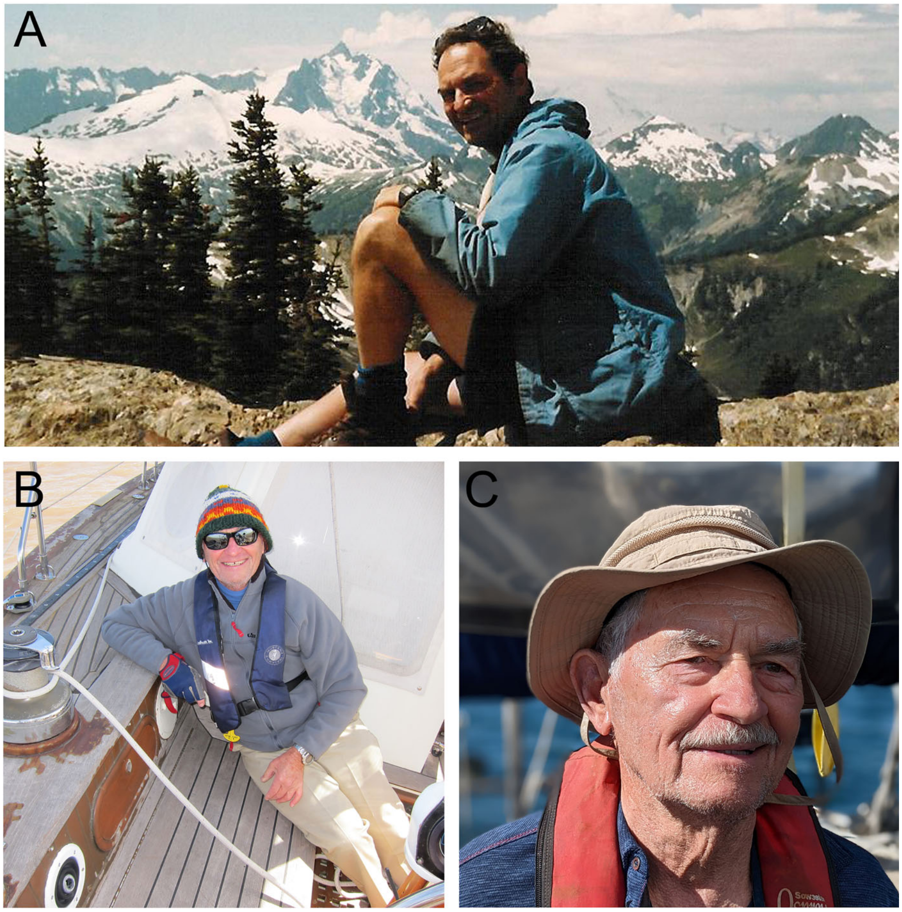

FIGURE 8 | (Image A) Harvey enjoying the view of the Cascade Mountains. (Image B) Harvey lounging on the sailboat of Bruce Pappas. (Image C) Harvey the sailor. *Source:* (B and C) Photographs courtesy of Bruce Pappas.

this year), by mid-March to early April (e.g., today) it is like a botanical garden of native desert plants. Every year I have to once again learn the names of even the most common of plants, though occasionally I surprise myself when I remember the name of some esoteric plant. I have gotten into serious bird photography—if by 'serious' you understand that it means that I have bought some outrageously expensive camera and very heavy telephoto lenses. It took a few years to learn how to take sharp pictures, especially given the limitations of my Parkinson's disease. The mixture of a fancy image stabilized camera, combined with L-DOPA, works wonders! I try to use a tripod when possible, a cable release so I don't have to touch the camera, and shutter speeds in excess of 1/1500th of a second. It's just an elaborate 'point and shoot' setup."

Harvey continued sailing his beloved Night Heron into his 88th year but finally had to sell it because his Parkinsonism had progressed to the point that he could no longer handle the boat. During his later years, he took satisfaction that the pejorative "birdbrain" had faded from everyday speech, due to the accretion of evidence that many types of birds, such as parrots and crows, possessed a pallium that is as neuron rich as neocortex in many mammals, including primates (Olkowicz et al. 2016; Ströckens et al. 2022), and that those neurons are organized into groups that are interconnected in a neocortex-like fashion (Herculano-Houzel 2020; Stacho et al. 2020). Harvey remained vital and mentally alert until his stroke. He lived a full life that engaged his abilities and passions, and he enriched science by his research and all who knew him by the person he was. Harvey may not have become the bigshot New York City doctor his parents hoped for, but he proved their investment in his education, early bumps notwithstanding, well worthwhile. To say the least (Figure 8).

Author Contributions

Anton Reiner wrote the text and created the figures.

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san diego April 30, 2015 (https://neuwritesd.org/2015/04/30/birds-brains-and-boats-the-harvey-karten-story); and *Walle J. H. Nauta* by Ted Jones in Biographical Memoirs: Volume 88, 2006 (https://nap.nationalacademies.org/read/11807/chapter/16). Note that in composing the above narrative, there are many research topics and colleagues that I have not mentioned, as Harvey's life and work were too richly detailed to include it all. A further glimpse of Harvey's life and many friends can be found at the following memorial site (https://www.forevermissed.com/harvey-j-karten/about).

Ethics Statement

This manuscript is a commentary and involves no primary animal research.

Consent

The author has nothing to report.

Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

This manuscript is a commentary and there are no primary data involved.

Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1002/cne.25685.

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