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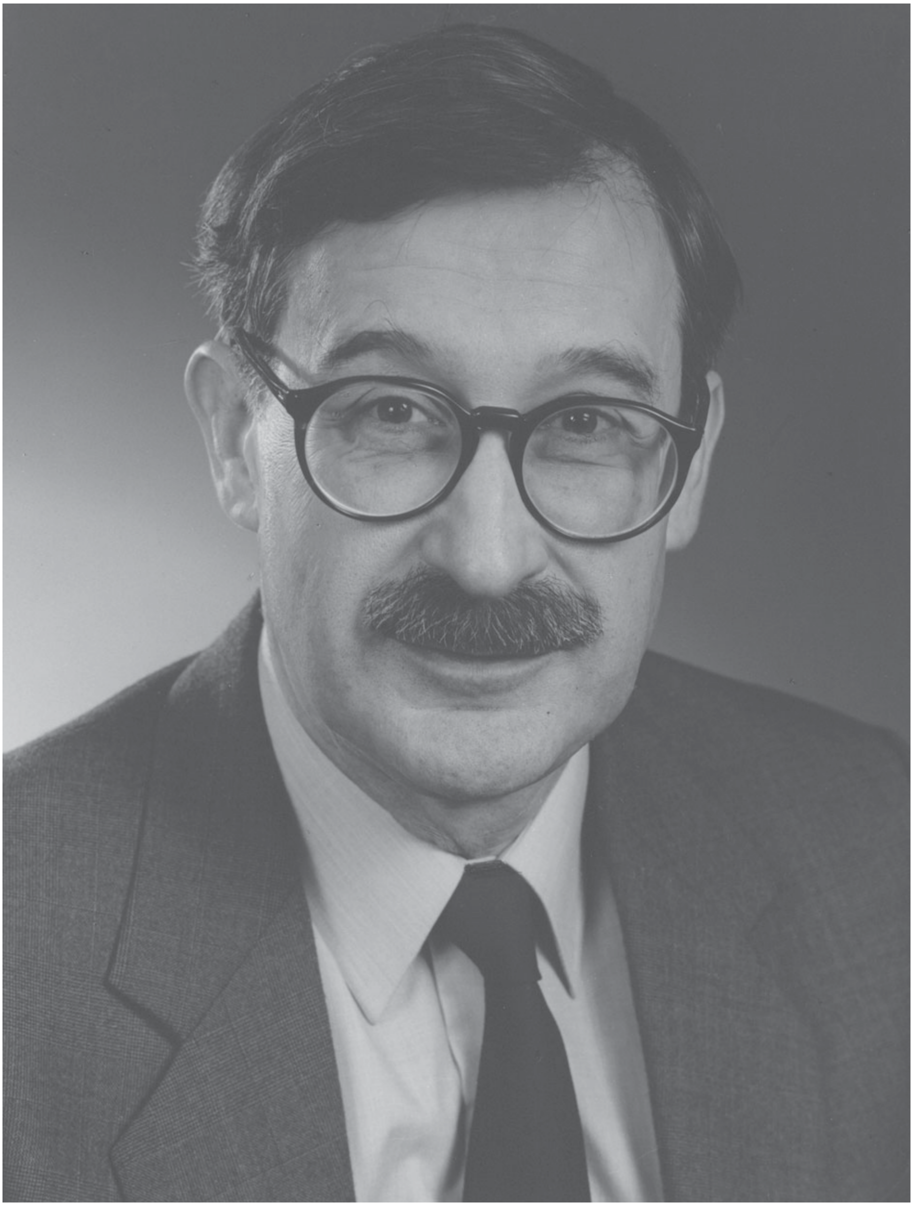

Ray Guillery

# RAINER WALTER GUILLERY

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Elected FRS 1983

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Rainer (Ray) Guillery was a remarkably productive neuroscientist and as such left an indelible mark on the field, both in terms of his direct contributions and also through his success at mentoring and nurturing young scholars who went on to successful careers of their own. Ray's work profoundly advanced our understanding of the related fields of development and thalamocortical functioning; his work was highly imaginative and insightful; and he was a cherished colleague and role model for his many former students and friends in the field. Ray's scholarly efforts were carried out on three continents. He trained initially in London and, after serving on the faculties at the Universities of Wisconsin and Chicago in the United States, he returned to England at the University of Oxford. After retiring from his Oxford post, he went back as a visiting scholar to the University of Wisconsin, and then moved to a post at the University of Marmara in Turkey, which is located in the Asian sector of Istanbul. He finally returned to Oxford in an emeritus capacity and remained there until his death.

## Family history

Ray was the most recent and important in a line of biomedical scholars. His father was an academic pathologist at a university in Greifswald, Pomerania. His mother was a technician working in the Charité Hospital in Berlin, where his father was in training and where they met. His paternal grandfather was an ophthalmologist with a serious research interest resulting in publications on the subject of visual acuity. As we follow the family tree, we learn that his paternal grandmother was Maria Deiters, who was the niece of Otto Deiters. Otto Deiters was an eminent neuroanatomist at the University of Bonn whose studies of the lateral vestibular nucleus were so influential that it is known as 'Deiters' nucleus'. His name is also associated

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with the 'Deiters' cells' that support outer hair cells in the cochlea of the inner ear. Ray became quite interested in his ancestral roots, especially the career of Otto Deiters, and he collaborated with Elisabeth Deiters, Otto's niece, to write a piece about Otto (10) and more recently with Vera Deiters, another descendant of Otto and distant relative to Ray (49).

## Childhood

### *Escaping Germany*

Ray was born on 28 August 1929 in Greifswald, Pomerania, where his father had a university appointment. Although his father was a German Catholic, his mother was a Russian Jewish immigrant to Germany, a fact that presages the drama to follow in Ray's upbringing in Germany.

Soon after his parents divorced in 1932, his mother moved with Ray and his older sister to Berlin, where he attended the Rudolf Steiner School, which he described as the only non-Fascist elementary school in Berlin. This lasted until 1938, the year of Ray's exodus from Germany. Although Ray's mother had converted to Quakerism, to the German authorities she (and Ray) remained Jewish. Perhaps fortunately, young Ray had little concept of what was going on in Nazi Germany at the time, particularly as it affected Jews, and so the events that soon occurred in rapid succession took him by surprise.

In the autumn of 1938, Ray's mother was warned that Jewish passports were soon to be confiscated, and so she set in action a series of events that led to a lightning escape. Ray knew nothing of this until he came home from school one day to find their bags packed for travel, which immediately ensued. But it was complicated, and involved a breaking up of the family. Ray's sister had already reached safety at a Quaker boarding school in the Netherlands. His mother, via help from an English friend, travelled to London, where a job awaited her. Other family friends assisted Ray's escape to Switzerland.

The day of Ray's escape was understandably hectic. He was the last of his family to leave Berlin and was accompanied by a non-Jewish friend of his grandmother. The major concern was crossing the border into Switzerland. Ray's passport had a large J (for Jude) stamped on it, but it was covered by a cross, apparently to recognize his father's Catholic heritage, and no one quite knew what the border guards would make of it. Ray and his chaperone boarded the train in Berlin in the evening, and it reached the Swiss border the next morning. The border guards effectively ignored Ray, and he passed through without a hitch. It was probably as well that Ray had little appreciation for the drama of the episode and instead was entranced by the beauty of the Swiss Alps that he gazed upon during the border crossing.

Ray spent several months at a boarding school in Switzerland, and in early 1939 joined his sister at the Dutch boarding school. He and his sister then travelled to London for the summer vacation to visit their mother. They were scheduled to return to their school in the Netherlands on 3 September 1939, but England declared war on Germany on that day, an event that obliterated their travel plans. This probably saved Ray's life again, as well as his sister's, because had they been in the Netherlands at the start of the war, they likely would have perished in a concentration camp. We are all very fortunate that Ray managed to survive these early threats to his very existence, and it makes one wonder how many potentially brilliant scientists, artists and political leaders were stolen from civilization.

Figure 1. Ray in Oxford, 1943.

## *Growing up in England*

After a brief stay in London, Ray moved to Oxford (figure 1). It was common to move children from urban centres to safer locations, and many British families in rural settings took in such children. Ray was relatively unfortunate, because he was housed in a rather stark and unappealing boys' home in Oxford. His sister, however, boarded with the family of Wilfrid Le Gros Clark, an eminent neuroanatomist and then Dr Lee's Professor of Anatomy at Oxford. This allowed Ray, through his sister, to spend many thoroughly enjoyed visits, including most holidays, with the Le Gros Clarks. Eventually, Ray developed a connection with Le Gros Clark himself, which undoubtedly shaped Ray's ultimate career choice.

Ray's schooling at this time did not herald an academic life. He was enrolled in Sibford School in the Cotswolds, a school that did not expect its pupils to advance to university. In fact, teachers there viewed Ray as a future carpenter, and his education was especially deficient in mathematics and science. He left at 16. However, his mother had a strong ambition for him to become a doctor and thus strongly supported a university education for him. Ray therefore followed his tenure at Sibford School by enrolling in a grammar school, with the goal of spending the next two years making up various deficiencies so that he could qualify for admission to university. He did well and scored sufficiently high on examinations to be awarded a scholarship from University College London (UCL).

## University student life

Ray enrolled in UCL to study medicine. He took immediately to the new subject matter, particularly the anatomy and histology courses that opened his mind to new worlds of knowledge. The high level academic environment, unlimited access to biomedical books through well stocked libraries, exposure to teachers who were scientific giants (J. Z. Young and Bernard Katz among them) plus an array of visiting luminaries (among the neuroscientists: Roger Sperry, Lorenté de No and Heinrich Kluver) introduced him to a new intellectual world offering him a new perspective on career options.

During the summer after his first year, Ray earned some money working as a ward orderly in a London hospital. This experience soured for him a career as a medical doctor, a career that he saw as one that requires dealing with the public to provide routine, relatively mindless advice. This did not suit him: he sought more of a mental challenge, less routine and more independence. He realized that a career as a biomedical scientist would fulfil his career ambitions, and so he entered the PhD programme in Anatomy at UCL.

Ironically, of all his classes at UCL, Ray felt that the worst taught was neuroanatomy. However, as he progressed through the requirements, he spent much time in tutorials presided over by J. Z. Young, restoring his enthusiasm for neuroanatomy. Young became his PhD mentor, and he wanted Ray to do his thesis research on the avian brain, but he gave Ray considerable independence, allowing him to choose quite a different thesis project. Ray searched for an anatomical project that went beyond the merely descriptive to incorporate a quantitative analysis leading to functional interpretation, an approach that served him well throughout his career. He started out measuring dendritic segments between branch points in a Golgi study of hypothalamic neurons, but that led nowhere as far as he was concerned, and so he soon switched to a project that involved counting the axons in the mamillothalamic tract. This provided the basis for quality publications and his PhD thesis.

At about this time, Ray re-established his association with Le Gros Clark at Oxford, partly because the Oxford group was also interested in the hypothalamus and fornix. Tom Powell was a member of that team, which was soon joined by Max Cowan, and Ray quickly established what was to become a longstanding friendship and collaboration with both Max and Tom.

When Ray finished his PhD in 1954, he was 24 years old and had a serious decision to make regarding his career path. Many advisors and family members urged him to complete his medical training, arguing that this would ensure a useful, productive career. However, to complete his clinical training would take an additional three years or so, and J. Z. Young urged him to forego such training, because it would interfere, perhaps fatally, with Ray's goal to become an academic brain scientist. Since this is what Ray really wanted, he took Young's advice against that of many others, and he never looked back.

## Family matters and professional positions

### *University College London*

Following his PhD, Ray stayed on as a faculty member in the Department of Anatomy at UCL (figure 2). He worked his way up from assistant lecturer to lecturer to reader. This was a new, liberating experience for Ray. For the first time, he felt independent, both in terms of finances as well as in terms of his work, because he was given free rein to do whatever research he liked and was provided with the modest means to do so in terms of space, equipment and supplies.

Through mutual friends, Ray met his future wife, Margot Pepper, whom he married in 1954. At the time, he was a new assistant lecturer in anatomy at UCL and she was a medical student at St Mary's Hospital. She finished her medical training and went on to enjoy a long career as a physician. Ray and Margot extended their family with the births of four children during his stay at UCL: Peter John Guillery, born on 6 January 1957, is currently an architectural historian living in London; Nigel Robert (known as Edward) Guillery, born on 18 June 1958, is a paediatric nephrologist living in Portland, Oregon; Richard Philip (Phil) Guillery, born on 25 March 1960, works for sustainable forestry as a director at the Forest Stewardship Council, and lives in Colorado; and Jane Louise Guillery, born on 20 September 1963 and now Jane Kandur, is a teacher and translator living in Istanbul.

After six years on the faculty at UCL, Ray was entitled to a sabbatical leave. His colleague, Tom Powell, had just returned from a sabbatical spent at Johns Hopkins University in Baltimore, Maryland, that was deemed quite successful. This encouraged Ray to follow suit by finding the right situation, preferably in the United States. Tom suggested to Ray that he work with Jerzy Rose at the University of Wisconsin, a suggestion that Ray enthusiastically accepted. To finance the project, Ray successfully applied for a Rockefeller Travelling Fellowship. Accordingly, he moved the whole family to Madison, Wisconsin, for the academic year of 1960–61.

Whereas Ray felt the year was unsuccessful as far as his own experiments were concerned, the time was enormously productive both in terms of its effect on his thinking about future research problems and by leading to his forming relationships with prominent American neuroscientists of the day. These included leading figures at Wisconsin, such as Jerzy Rose and Clinton Woolsey, and also colleagues met on visits to their laboratories, including Sandy Palay, Ted Bullock, Walle Nauta and Vernon Mountcastle. The year in Madison energized Ray when he returned to London to follow up on research topics gleaned from his experience. The experience also created a very favourable impression of research in the United States, one that eventually led to his spending much of his career there.

After the Guillerys returned to London, Ray settled back into a routine he enjoyed as an independent investigator. Soon after his return, Le Gros Clark offered him a faculty post at Oxford University. Ray was quite tempted, but both because he and his family were happy in London and also because the offer perversely involved a pay cut, Ray turned it down. In doing so, he reflected on what his future career path might be, and was influenced to consider offers elsewhere. Margot was also thinking seriously about her medical career, and both she and Ray felt that there was more opportunity for each in the United States. He received several

Figure 2. Ray as a lecturer, University College London, 1955.

offers from the United States and chose to accept one from the University of Wisconsin, which would represent a sort of homecoming for the Guillerys.

*University of Wisconsin, first part*

And so, in 1964, the family moved to Madison, Wisconsin, where Ray took up a new position of Associate Professor of Anatomy. He felt that the environment in Madison was particularly conducive to his career development and enjoyed a remarkable period of productivity and influence in the field. In fact, Ray regarded this time in Madison as the most scientifically productive of his entire career. It is during this period that he began research for which he gained considerable recognition: he initiated comprehensive anatomical work on the organization of the cat's lateral geniculate nucleus; he discovered the anomalies of central visual pathways associated with albinism; and he helped confirm and enhance the concept of a critical period in early development of visual pathways based on binocular competition.

Ray was now being seen in the field as a leader on the rise with an especially compelling and insightful research programme. As a result, numerous new job opportunities beckoned, causing Ray and Margot to consider their career options, which at the time were beginning to feel limited in scope in Madison. Ray became more and more committed to a feeling that his research programme was much better served by developing a local environment in which he would have many colleagues with whom to interact and exchange ideas. In other words, Ray embraced the sense that neuroscience was a field about to explode in importance and scope, and he wanted to develop the field further at the University of Wisconsin. However, his attempts to attract support for this idea from the local leadership, and particularly the Medical School Dean, fell mostly on deaf ears.

## *University of Chicago*

This made him more receptive to the right sort of offer from elsewhere. The University of Chicago called. The initial offer of the Chair of the Anatomy Department was rejected by Ray, because the faculty therein expressed little enthusiasm for Ray's ideas of developing neuroscience. But the Dean (Dan Tosteson) wanted Ray and supported neuroscience, and so he made a second offer: a position in the Department of Pharmacological and Physiological Science plus that of the founding Chair of the Committee on Neurobiology, a new organization at the University of Chicago responsible for developing its first PhD programme in neuroscience, one that is university-wide and still flourishes. And so Ray moved to Chicago with his family in 1977 (figure 3). Ray relished this opportunity to provide a leadership role in developing neuroscience at the University of Chicago, a development that arguably started with his appointment and continues to this day. The move also benefited Margot's career, because she was able to complete her dermatology residency at the University of Chicago and joined their staff in dermatology thereafter. Ray told me later that, of all his university appointments, all at elite institutions, he felt most at home academically with the University of Chicago. He particularly appreciated the high and uncompromising academic standards of the institution, a rare example of a university in the United States that gave up big time football (in 1946), because the football programme competed with and threatened the academic goals of the university.

Thus, Ray was quite happy at Chicago and supposed he would spend the rest of his career there. However, out of the blue was delivered the possibility of becoming head of a major department, Human Anatomy, at the University of Oxford. This came about when Tom Powell, his friend and colleague and a member of that department, encouraged Ray to apply for the vacancy. Ray and Margot, being British, had always thought they would want to retire in England, and the idea of moving there in order to settle in before retirement appealed to them. Also, the University of Oxford always had a particularly strong appeal for Ray, and the proffered position, Dr Lee's Professor of Anatomy, is the same that Le Gros Clark once held. This move involved a significant salary decrease, but Ray and Margot calculated that they could accept this, largely because their financial responsibility for their children's education was nearly at an end. So, he threw his hat in the ring. The position was first offered to Gordon Shepherd, who declined, and then to Ray, who accepted and did not feel slighted at being the second choice.

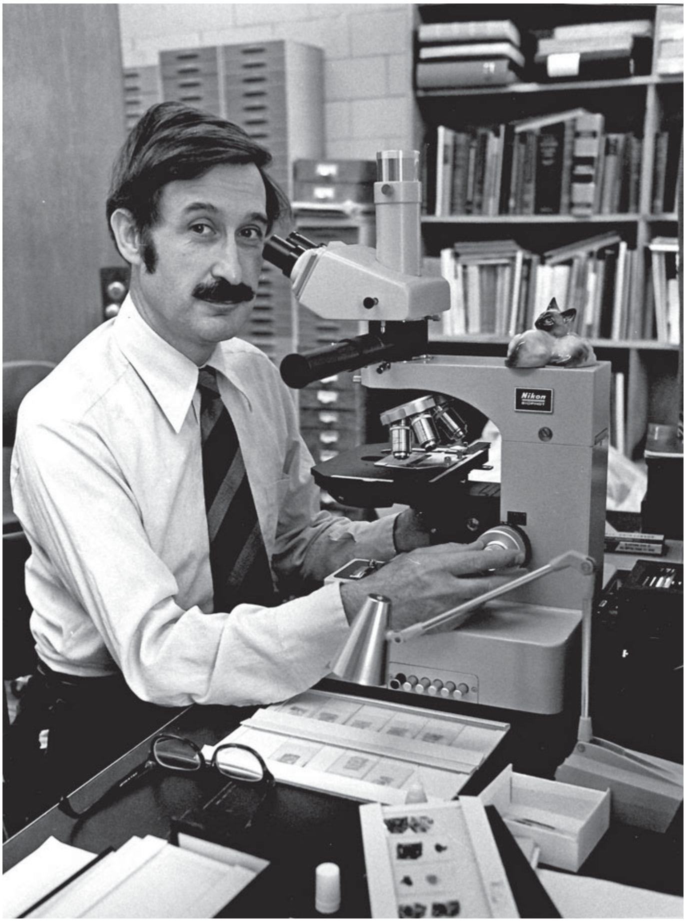

Figure 3. Ray at the University of Chicago, 1977.

## *Oxford University, first part*

Ray's move to Oxford came in 1984 and included a position as Fellow of Hertford College (figure 4). As head of the department, Ray encountered a number of administrative problems he had not bargained for, problems that had a decidedly negative influence on his time in Oxford. He inherited a department with internal strife, particularly between the technical staff and department administrator.

Another frustration for Ray involved the tension between the colleges and science departments at the University of Oxford. The 38 colleges that make up the University operate as a loose confederation, and they vary widely in wealth, stature, and age. Students generally apply to a specific college for admission to the University, and their education consists of a mixture of both conventional classes run by the academic departments of the University, and tutorials run by their individual college. This means that the college faculty has to cater for all of its students and therefore is organized for breadth of knowledge rather than depth. Most faculty positions are owned by a specific college, which created a problem for Ray in his

Figure 4. Ray as Head of Human Anatomy, University of Oxford, 1992. (Online version in colour.)

efforts to improve his department through faculty recruiting. When identifying candidates, the Department and colleges were typically at odds, because the college required individuals who had to spend considerable time on tutorials and numerous other college duties. Conflict arose, because the demands of the colleges left insufficient time and energy to build and sustain an active and productive research programme. Further exacerbating the problem for Ray was that he did not much care for college life, and so he had rather little to do with his appointment at Hertford College.

However, in spite of his frustrations as head of department, Ray did enjoy his time at Oxford. He revelled in the academic and cultural life it afforded beyond college life, and his research programme continued to be a source of pleasure and pride for him. He was also asked to be the founding editor of the *European Journal of Neuroscience*, which he carried out successfully, developing it into a major scientific journal.

One unfortunate outcome of the move to Oxford was personal. Margot had been promised, as part of the move, an attractive clinical position, a promise that was not kept. She suffered professionally and felt that there was no future for her career in Oxford. This led to a separation, and eventually a divorce, as Margot moved back to Madison, Wisconsin, to resume her career there.

*University of Wisconsin, second part and 'retirement'*

In 1996, Ray reached the age of mandatory retirement. I put the 'retirement' in the title of this section in quotes because Ray's continued scientific activity and productivity belied the usual sense of retirement. Ray was far from done and briefly fretted about his situation. Just then, he received an offer from John Harting, then Chair of Anatomy at the University of Wisconsin, to return to his old department as Visiting Professor and Senior Scientist. Ray quickly and enthusiastically accepted. He was given a well-equipped laboratory and proceeded with experimental work in collaboration with various colleagues there.

In 2001, Peter Spear, a neuroscientist and close colleague of Ray's, returned as Provost to the University of Wisconsin. Previously, he had been a long-time faculty member at the university, but had spent the last few years as Dean of the College of Arts and Sciences at the University of Colorado. Peter had always wanted to see neuroscience further developed at the university, and he felt as Provost, and with Ray's help, this could now be accomplished. However, both Ray and Peter were frustrated by bickering among the neuroscience faculty regarding what direction the new development should take and who should lead it. As a result, no progress was made.

Ray's attempts to continue his research programme were hampered by his inability to retain funding from the National Institutes of Health (NIH). In my opinion, this reflected a bias on the part of NIH grant reviewers against neuroanatomy, an unwise and counterproductive development that stranded Ray and other classically trained neuroanatomists. Eventually, this led Ray to forego laboratory research and concentrate instead on producing review papers and manuscripts. In a sense, this freed him geographically, because he felt he could contribute in this manner from any location, thereby contributing to his relocation to Istanbul.

*Istanbul*

At this point in his life, family held increased importance for Ray. His daughter, Jane, had married a Turk, converted to Islam and moved with her husband to Istanbul. Ray thought it would be nice to continue his career near his daughter, and so he moved to Istanbul in 2006 as a visiting professor in the Anatomy Department of Marmara University. In that capacity, he encountered several young faculty members struggling to develop respectable careers as neuroscientists, and he committed to a role as their mentor. He loved that role, and by all accounts these younger faculty members adored Ray and blossomed under his tutelage. The success of this venture remains to be determined. His role as mentor at Marmara University is specifically, but also more generally, aptly described in a piece written by his daughter, Jane, published in an Istanbul paper, the *Daily Sabah*, on 12 May 2017:

> Ray Guillery was first and foremost a mentor. He knew how to teach. He would lead his students to a certain point, and then leave them floundering, knowing that they would swim in the end. One of his former postgraduate students, now an eminent scientist in the United States, said the following about him: 'You always taught me how much fun science could be. . . . the combination of science, humor and scholarship . . . I had never seen anything like that before.' He goes on 'You always helped me find my own answers to the tough questions.'
>
> The same sentiments were echoed at Marmara University. There were many tears when talking about Professor Guillery. Not only was he a great scientist; according to the people gathered there he was a kind, generous, caring teacher and a man with ethics and integrity. He was always willing to help them with experimental procedure and to go over any scientific paper.

> But perhaps the most important lesson he taught the scientists at Marmara was the ability to say 'I don't know' to a question. To be honest about the limits of our knowledge, and then push those limits back.

Whereas he enjoyed his role as mentor, he never felt at home in Istanbul, partly because of the prevailing religious environment that made him feel a perpetual outsider and partly because he missed living in direct contact with leading neuroscientists. Ray felt the need to relocate. As seemed to be always the case with Ray, each time he experienced wanderlust, an attractive offer to move was made available. This one came from Oxford, again.

### *Oxford University, second part*

In 2010, Ray accepted an offer from Peter Somogyi, who headed the MRC Anatomical Neuropharmacology Unit at Oxford University, to become an Honorary Emeritus Research Fellow. Peter gave Ray a desk, computer and office space, plus the opportunity to interact with all of the bright, accomplished neuroscientists in the unit. This was another happy time for Ray. He thus spent his last days.

## Scientific accomplishments

Ray is chiefly known for his work on the structure, function and development of thalamus and thalamocortical relationships.

### *Early efforts at UCL*

When Ray started as a PhD student, he was a complete scientific novice, and this period for Ray did not involve an interest in the thalamus: that would come later. As noted above, his supervisor, J. Z. Young, gave Ray a pretty free hand, which at the beginning posed difficulties as Ray struggled to identify practical problems to form a thesis project. He avidly read the literature, and decided, somewhat against Young's early advice, that the hypothalamus represented an interesting structure that he wished to explore. He thus designed a neurohistological study involving the counting of neurons and axons related to the mamillary bodies, a part of the hypothalamus. This is an example of a study that involved no guiding hypothesis to be tested, and indeed Ray remained throughout his career a sceptic of the fashionable view that the only science worth doing involves testing of hypotheses.

His first publication (1), was a carefully executed, thoroughly documented, and thoughtfully presented analysis of numbers of mamillary body neurons plus mamillary tract axons, leading to a conclusion regarding the branching and terminations of the tract axons. Ray continued studying the hypothalamus, leading to several more publications (2, 3, 4), one of which (3) became a citation classic.

These initial studies were done at the light microscopic level, but Ray soon became enamoured with the possibilities in the new technology of electron microscopy. J. Z. Young foresaw the power and future of electron microscopy and invested in bringing the technology to UCL. His student was George Gray, a pioneer in using electron microscopy to classify synapses in the nervous system. Gray was a close colleague and friend to Ray and taught him how to use the electron microscope.

*Studies of the lateral geniculate nucleus*

Ray's detailed analysis of circuitry of the lateral geniculate nucleus in cats and monkeys early in his career really solidified his reputation as a first-rate neuroscientist. His interest in the subject can be traced to his early sabbatical at the University of Wisconsin with Jerzy Rose: Rose and Woolsey had described the concept of 'sustaining' thalamocortical projections, which came to be understood as thalamic relay cells projecting axons that branched to innervate multiple cortical areas. These evolving ideas drew Ray's interest to the thalamus, which he carried back to UCL.

Ray returned to find that the interest in electron microscopy at UCL Anatomy, which was building when he left for his sabbatical, had increased significantly, and so he immediately sought to master the new technique to explore his new interest in the thalamus generally and the lateral geniculate nucleus specifically. This led initially to a series of electron microscopic studies involving a rather eclectic group of subjects: the central nervous system of lizards (5), the mammalian spinal cord (6), the structure of dendritic spines (7), the ventral nerve cord of the leech (8) and degenerating axons in the spinal cord and mamillary bodies (11).

Soon Ray's interest refocused on the thalamus. A catalyst for this was the presence of two friends and collaborators at UCL also interested in the thalamus: Pete Ralston, whom Ray had met when both were at the University of Wisconsin, and Marc Colonnier. With Marc, Ray published his first detailed account of synaptic circuitry in the thalamus using the electron microscope, targeting the monkey lateral geniculate nucleus (9). In this study they classified synaptic terminal types and described large terminals onto geniculate cells that they determined were retinal in origin.

Ray then relocated to the University of Wisconsin, where he continued his research into thalamic circuitry, but now switched to the cat's lateral geniculate nucleus as his main model for study. He followed up his detailed electron microscopic study of the monkey's lateral geniculate nucleus with a back-to-back detailed account of the synaptic organization of the cat's lateral geniculate nucleus (13, 14). These provided the classic foundation for understanding basic circuitry of the thalamus, and to this day, nearly a half a century later, the cat's lateral geniculate nucleus remains the best understood thalamic nucleus in terms of circuitry, a status that can largely be traced to Ray's pioneering efforts. One of his chief contributions was clarifying the organization of the synaptic triad, a structure involving three synapses and common to the thalamus. For the lateral geniculate nucleus, the three synapses are: 1) a retinal terminal contacting a relay cell dendrite; 2) the same retinal terminal contacting a GABAergic, dendritic terminal from an interneuron; and 3) the same interneuron terminal contacting the same relay cell dendrite. Thus, the dendritic terminal of the interneuron is both presynaptic and postsynaptic.

These and other features of geniculate circuitry were being described concurrently and independently in the somatosensory thalamus, mainly by Pete Ralston at Wisconsin and Ted Jones with Tom Powell at Oxford University. As a result, Ray's description of the lateral geniculate nucleus came to be seen as a useful, first approximation model for all nuclei of the mammalian thalamus.

Ray published another classic paper on the cat's lateral geniculate nucleus, this one a classification of cell types based on Golgi impregnations (12). He described four cell classes: Classes 1 to 3 are located in the A laminae, and Class 4 in lamina B. Ray's 1966 classification was prescient, because it aligns with a later classification of physiologically defined cell types: Classes 1 and 2 proved to be Y and X relay cells, respectively; Class 3, the local interneuron;

and Class 4, the W cell. Ray later showed that lamina B is actually a set of separate laminae, which he renamed the C laminae (15); he further refined this in a study with his postdoctoral researcher, Terry Hickey (22). He then defined the organization of and retinal inputs to other parts of the cat's lateral geniculate nucleus: the medial interlaminar nucleus and geniculate wing (30).

### *Studies of albino animals*

During the course of Ray's studies of lamination in the cat's lateral geniculate nucleus, he noticed a curious anomaly. Peter Spear, Ray's colleague at the University of Wisconsin, told me how this played out in his own words:

> I admired Ray when I went to Wisconsin as a young assistant professor, and he became a role model for me. A story that made a big impression on me was his discovery of the Siamese cat visual-system abnormalities and their relation to albinism. He told me that he was simply looking at LGNs [lateral geniculate nuclei] in the microscope as part of an unrelated ongoing study, and noticed that one of them had a strange laminar pattern. I think many people would have shrugged and crossed it off as a 'weird cat'. But not Ray. He had careful records of each cat, and he went back to see what he could find out about that particular one. It was a Siamese. So, Ray went out to find additional Siamese cats to study and discovered that this was a consistent abnormality. He then went on to determine what caused this abnormality and how it was related to albinism in many different species. This whole sequence of events reflected Ray's genuine curiosity about the visual system, his carefulness and meticulous work, and his willingness and ability to use whatever approach was necessary to determine underlying mechanisms. He wanted to get the right answer, and the complete answer, to questions of interest, and he wasn't in a rush to do it.

The anomaly Peter referred to was a misrouting of axons in the optic tract such that many from the temporal retina, which normally project ipsilaterally onto lamina A1 of the lateral geniculate nucleus, instead cross to innervate geniculate lamina A1 on the wrong side (17). Ray would go on to show the relationship between this anomaly and the temperature-sensitive albinism that gives Siamese cats their beautiful coloration: no melanin forms in warmer parts of the body, but does so in cooler parts, like the tips of the tail and ears. This landmark discovery opened an entirely new field of research into the effects of albinism in the development of the central visual pathways, a field in which Ray became a major player but one that also attracted many other laboratories to join in.

Ray followed up his discovery in two ways. First, he established that the Siamese cat anomaly was due to its form of albinism and not due to some feline aberration. He showed that essentially the same misrouting of optic tract axons occurs with albino mutations in mice (32), rats (34), ferrets (17), tigers (20), minks (23), axolotls (27), wallabies (39), monkeys (30) and humans (25).

Second, and largely in collaboration with Jon Kaas, who was then his colleague at the University of Wisconsin, Ray embarked on a series of studies to define certain functional consequences of the misrouting of optic axons seen in Siamese cats. First, they mapped the lateral geniculate nucleus of these animals and found that the aberrant temporal retina input to layers A1 and C1 created a break in the orderly retinotopic map, and within this break was a segment showing a mirror image of the mapping seen in normal cats (18). They then shifted their focus to visual cortex (21). Curiously, they found two different effects of the retinal rerouting in cortex: in some Siamese cats, the abnormal segments of laminae A1 and C1 were suppressed in cortex so that these regions of visual field were mapped normally but represented only by the contralateral eye; in other cats, the whole retinotopic map in cortex is expanded to include the aberrant representations of laminae A1 and C1 appended to the normal map.

There is an interesting side note to this latter series of experiments that Ray and Jon pursued. Their original survey of cortical mapping in Siamese cats found only the first type of arrangement described above, in which the aberrant geniculocortical input is suppressed and which they referred to as the 'suppressing' version. However, at the same time, work done at Harvard University by David Hubel and Torsten Wiesel on Siamese cats described the other version, in which an extra anomalous map was created in visual cortex (Hubel & Wiesel 1971) and which Ray and Jon referred to as 'correcting'. This at first seemed like the beginning of a controversy, but then Ray and Jon continued their studies and found examples of the correcting version. Controversy resolved! Ray and Jon aptly named the version they first described as the 'Midwestern' Siamese cat, and the version described by Hubel and Wiesel as the 'Boston' version. These names stuck. Ray further pointed out that the Boston version showed a more sophisticated handling of the misrouted optic axons and that one should expect such from a Boston versus Midwestern solution.

Soon after Ray made his move to Chicago, his interest in albinism centred on why axons went the wrong way through the optic chiasm in albino animals. Here, he teamed up with Carol Mason, his postdoctoral fellow in Chicago, and they began to attack this question. This was a problem that Carol quite successfully carried with her as she developed her own independent research programme at Columbia University. Ray and Carol continued to collaborate and, with Jeremy Taylor, published a definitive review on the topic, which appeared just before Ray 'retired' (36).

### *Studies of development and plasticity*

Another line of research Ray is well known for is studies of development and plasticity, mostly involving the visual system as the model for experimentation. Mainly these studies involved observing the effects of perturbation of the developing visual system by the use of lesions or sensory deprivation.

### *Studies of binocular competition*

My personal favourite among Ray's research topics was his insightful studies of the developmental mechanism of binocular competition to guide formation and maintenance of connections in the central visual pathways. Earlier, Hubel and Wiesel had published their classic study on the effects of early visual deprivation on development of visual cortex (Wiesel & Hubel 1965): they reported that monocular deprivation (by lid suture) basically prevented the deprived eye from developing effective control of cortical neurons, whereas binocular deprivation allowed each eye to control cortex, albeit not normally. One explanation of the lesser effects of binocular deprivation was that it provided balanced deprivation of the two eyes and that normal development involved a competitive tussle between the eyes for control of central visual pathways; neither eye has a competitive advantage with binocular deprivation, leading to the less deleterious effects of this deprivation when measured by ocular control of cortical cells. This developmental mechanism came to be known as 'binocular competition'.

The problem at the time was that there were other plausible explanations for the difference in the effects of monocular (unbalanced) versus binocular (balanced) deprivation. Ray did a series of experiments to establish decisively that binocular competition indeed plays a major role in early development of the central visual pathways. First, he, along with Dennis Stelzner, his postdoctoral fellow, extended an earlier observation by Wiesel and Hubel that monocular deprivation causes cell shrinkage in deprived layers of the lateral geniculate nucleus (Wiesel & Hubel 1963). Ray and Dennis repeated the experiment and confirmed the cell shrinkage, but noted that it was limited to the part of the lateral geniculate nucleus in which the binocular part of the visual field is mapped (16). That is, each eye of a cat (or any other mammal) sees the same part of central visual field, known as the 'binocular segment', but there are 'monocular segments' at the extreme periphery seen only by the ipsilateral extreme nasal retina of each eye. Ray and Dennis observed that only the deprived binocular segment, but not the deprived monocular segment, showed shrinkage of geniculate cells. This provided strong evidence for the mechanism of binocular competition, because, by definition, deprived geniculate cells representing the monocular segment are not in competition for central connections (e.g. in the cortex) and thus can grow to normal size.

The genesis of the study by Ray and Dennis reveals much about Ray's powers of observation. As he related to me, he had already understood that a test of binocular competition could be achieved by noting the effects in monocularly deprived animals on the deprived binocular segment of the central visual pathways, which should be maximally affected, versus the deprived monocular segment, which should be minimally affected. Since Wiesel and Hubel had published effects of monocular deprivation on sizes of geniculate cells, and since the lateral geniculate nucleus has well defined binocular and monocular segments, he wondered why they did not comment on this. Did they miss it or simply found no difference in effects? So, he went back to their paper; when he reread it, now several years after its publication, he found clear evidence for his hypothesis in Figure 1 of that paper (Wiesel & Hubel 1963), which was a photomicrograph of a section through the monocularly deprived cat's lateral geniculate nucleus. This figure clearly shows that the lateral extent of the deprived lamina A, which represents the monocular segment, seemed to have no cell shrinkage. Ray simply repeated the experiment, with Dennis Stelzner, and made the actual measurements of cell size separately in the binocular and monocular segments, leading to definitive evidence for binocular competition (16).

While this paper probably convinced most people of the validity of the concept of binocular competition, this was not enough for Ray. His rigorous approach allowed for other interpretations of the data, such as more peripheral parts of the visual world (i.e. the monocular segments) were simply less susceptible to the effects of deprivation, because acuity was so much poorer in these segments. And so he devised an ingenious experiment in which he created an artificial, *central*, monocular segment, which he called the 'critical segment', by placing a centrally located lesion in the nondeprived eye of monocularly deprived kittens. He repeated the approach of measuring geniculate cell sizes in these animals when they grew to maturity and indeed found that cell sizes were normal in both the natural monocular and critical segments (19). I think this convinced even Ray that binocular competition was real, but he still wanted more evidence.

It was at this point that I began my formal collaboration with Ray, although we had already established an active correspondence on neuroscience topics of mutual interest. This led to a series of studies of monocularly deprived cats with critical segments showing: that these cats could orient properly with their deprived eyes to objects in the monocular and critical segments, but seemed blind elsewhere; that the deprived eye could drive cells normally in visual cortex in the monocular and critical segments, but not elsewhere; and that there was no loss of geniculate Y cells in deprived monocular and critical segments, but such losses occurred in deprived binocular segments of the lateral geniculate nucleus (24, 26, 28).

### *Studies of the thalamic reticular nucleus*

Ray's last series of experiments focused on the organization of the thalamic reticular nucleus. This actually started with a significant but underappreciated paper he published with Vicente Montero during his first faculty stint at the University of Wisconsin (29). The importance was showing that the thalamic reticular nucleus is topographically organized, because dogma at the time suggested its connections were entirely diffuse. This transformed ideas about the functional properties of the thalamic reticular nucleus. However, Ray did not get back to studying the thalamic reticular nucleus until he made his move to Oxford. Working there largely with John Crabtree, a postdoctoral fellow, and Herb Killackey, who was on sabbatical leave from the University of California at Irvine, Ray further explored the topographic organization of the thalamic reticular nucleus. As often happened with Ray, although he played a major role in developing the experiments to probe topography in the thalamic reticular nucleus, he did not feel he made enough of an experimental contribution to add his name to the paper (Crabtree & Killackey 1989), but he did so on later efforts (33).

### *Theoretical contributions with me*

I first met Ray in 1968 when, as still a graduate student, I visited Wisconsin. We found immediately that we shared many common interests and biases in neuroscience, and from that first meeting until his death, we kept up a constant stream of communications: letters and phone calls at first, segueing into emails and Skype later on.

As noted above, we collaborated on experiments on the critical segment model in the 1970s. However, what really catalysed our further collaboration was a year-long sabbatical I spent with him in Oxford (1985–1986). We had intensive face-to-face discussions, mostly about thalamocortical organization. These often began as an unconventional notion by one of us that, if not dismissed immediately by the other, led to animated back-and-forths. Often, the end result was pointless, but, occasionally, this exercise led to the further development of a useful (to us) new concept. And for us it was all great fun (figure 5).

The three main concepts that emerged from this are: the classification of glutamatergic inputs into 'drivers' and 'modulators'; the classification of thalamic relays into 'first order' and 'higher order', with the latter being the relay in thalamo-cortico-cortical circuits; and the hypothesis that many and perhaps all driver inputs to thalamus carry an efference copy message. Such was the harmony of our thinking and the tortuous evolution of each concept that I honestly cannot remember which of us initiated each.

In any case, we followed up the sabbatical year with extensive emails furthering these discussions. At the time, we saw these as private and for our own amusement and edification. But at some point, we realized that it might be useful to start making these ideas public in the form of thought pieces. This ultimately led to 10 reviews or perspectives (37, 38, 41, 42, 43, 44, 45, 47, 48, 51) and three monographs (40, 46, 50).

*Drivers and modulators*: At the time we started this, in the late 1980s, the prevailing view of brain circuit function was that glutamatergic pathways carried the basic information from place to place, and other pathways (cholinergic, GABAergic, noradrenergic, etc.) served to modulate how that information was processed. It was an implicit notion that the glutamatergic

Figure 5. Ray and I in Chicago in front of the 'Bean', 2010. (Online version in colour.)

pathways operated in a sort of anatomical democracy, with the importance or impact of the input being monotonically related to its numbers of axons or synaptic terminals.

We struggled with this idea because of our growing knowledge of the lateral geniculate nucleus. We knew that geniculate relay cells receive two main glutamatergic inputs, one from retina and the other from layer 6 of visual cortex. We also knew that these inputs act very non-democratically, because whereas synapses from the cortical input outnumber retinal synapses on relay cells by roughly an order of a magnitude ∼50% versus ∼5% of all synapses with the remaining synapses arriving from local GABAergic cells and brainstem modulatory neurons that are cholinergic, noradrenergic, etc., it had been clear for decades that the retinal input was functionally dominant in terms of carrying information to geniculate cells for relay to cortex.

One way to look at this is in terms of receptive field properties of the various neurons, because how a visual cell responds to sensory stimuli tells a great deal about the sort of information it might pass on to its postsynaptic targets. From this perspective, geniculate receptive fields, which are monocularly driven and exhibit the classic centre-surround configuration, are much like those of their retinal afferents and look nothing like those of the layer 6 cortical inputs, which tend to be binocularly driven with selectivity for orientation and direction of motion. This is reason enough to conclude that retinal inputs bring to geniculate cells the main information to be relayed. But what of the corticogeniculate input?

We floundered with this problem a bit until we noticed a paper from David McCormick's laboratory, which showed that, whereas retinal inputs to geniculate relay cells activate only ionotropic glutamate receptors (mostly AMPA and NMDA), cortical inputs additionally activate metabotropic glutamate receptors (McCormick & Von Krosigk 1992). This lit the proverbial light bulbs in our heads: perhaps there are systematic differences among different glutamatergic inputs, and a proper classification thereof would provide more insights into thalamic circuitry.

With this as a start, we combed the literature for relevant data and added some from my laboratory to come up with a new classification scheme for glutamatergic input, the defining parameters being a range of anatomical, pharmacological and physiological synaptic properties. This led to two clear types of glutamatergic input, first defined for thalamus and then extended to cortical circuitry. One type, which included retinogeniculate synapses, we called 'driver' because these provided strong postsynaptic activation, and this and other properties were consistent with these synapses being effective for transferring information to be relayed by thalamus. What of the other type? Key to our thinking was its activation of metabotropic receptors and relatively weak postsynaptic activation, which are features of classic modulator inputs, including cholinergic, noradrenergic, serotonergic and dopaminergic inputs. We therefore designated these glutamatergic inputs as 'modulator'. Classic modulatory inputs, however, tend to be diffusely organized and enact a global effect related to overall behavioural state, whereas the glutamatergic modulators we described are organized with a high degree of topography, allowing focal modulation as needed for such features as spatial attention, adaptation, etc.

The practical significance of the driver/modulator classification can be seen using the lateral geniculate nucleus as an example. For instance, if one simply considers the proportions of the glutamatergic inputs ($\sim$5% from retina versus $\sim$50% from cortex) with no understanding of the physiological relationships, the logical conclusions would be that cortical input represents the main source of information to be relayed back to cortex (a rather useless loop!) and that the small retinal input is of little significance.

*First and higher order relays*: The concept of first and higher order thalamic relays was initially based on the driver/modulator distinction. Our point was that a great deal can be learned about the function of a thalamic relay if its driver inputs can be identified among the many inputs a typical thalamic relay receives. Thus, the lateral geniculate nucleus can be defined as the relay of retinal input, the medial geniculate nucleus as the relay of inferior colliculus input, etc. The problem is that, for much of thalamus, the driving inputs had not been defined. For instance, the pulvinar and medial dorsal nucleus have well defined projections to cortex, but what were their driving inputs, or what information sources were they relaying to their cortical targets?

Ray wrote a brief thought piece that provided a plausible answer to these questions and laid out the basic argument for first and higher order thalamic nuclei (35). We followed up with a series of reviews and monographs, cited above, to add substance to this idea. The idea is that many thalamic relays receive their driving input from layer 5 of cortex. Thus, all relay cells receive a layer 6 input that is modulatory and organized mostly in a feedback manner, but some relay cells additionally receive a driving input from layer 5 that is organized in a feedforward manner. Those relays receiving a driving input from a subcortical source, like retinal input to the lateral geniculate nucleus, or medial lemniscal input to the ventral posterior nucleus, we called first order, and those receiving such input from layer 5 of cortex we called higher order.

This new concept of higher order relays provides a hitherto unappreciated function for most of thalamus by volume (e.g. the pulvinar or medial dorsal nucleus): these relays serve as a central station in cortico-thalamo-cortical, or transthalamic, pathways that subserve corticocortical communication. Furthermore, it seems that when two cortical areas are connected directly, they often and perhaps always have a parallel, transthalamic connection.

*Efference copies*: As we continued to ponder the identification of driving inputs to thalamus, we began to see a pattern dimly emerge as we brought together various unrelated bits and pieces from the literature. That is, the axons that carry driver input to thalamus, both first and higher order, often and perhaps always branch to innervate several extrathalamic targets. Once we noticed this pattern, we began arguing for different interpretations, as was our usual behaviour. We finally settled on a rather unusual but, we thought, plausible idea, as follows.

We first reasoned that one consequence of branching axons is that the same message, in terms of the pattern of action potentials, is carried down every branch to its different target neurons. This does not mean that every postsynaptic target of the various branches reacts the same, because synaptic properties likely differ, but we argued that the most efficient and error-free means of getting multiple copies of a message from one neuron to many is via branching axons. This, in turn, means that the message arriving at thalamus for relay is a copy of messages sent elsewhere. This led to the second point, because many of the extrathalamic targets of the branching driver inputs to thalamus appeared to us to be motor centres: bulbospinal centres such as the superior colliculus, red nucleus and brainstem reticular formation, and some of these axons proved to be pyramidal tract axons that also innervate the spinal cord directly. Thus, the motor message that emanates from a cortical area via these layer 5 cells, which represent the only avenue by which cortex can affect behaviour, is often copied to thalamus to relay to another cortical area up the appropriate hierarchy. In other words, the messages reaching thalamus for relay to cortex can in some sense be interpreted as copies of motor messages, and such a copy of a motor message is the definition of an efference copy. These ideas of efference copies being part of the message relayed through thalamus to cortex remain our most speculative suggestion, and it is too early to tell how much impact they will have.

### *Final contributions*

Ray pursued two independent projects towards the end of his life, one being his collaborations on Otto Deiters. The other, final, project was to put all of his thoughts about the brain into one place, resulting in *The Brain as a Tool* (52), a monograph published by Oxford University Press. There was drama at the end, because Ray sent back the final proofs of this book just days before his passing.

## Final thoughts

Ray's enormous contributions to the neuroscientific literature are well-documented and need no further elaboration here. What may be less appreciated is his contribution as a mentor and role model to the development of so many other successful scientists. I like to consider myself among them.

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