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SPECIAL ISSUE EDITORIAL
Introduction to the special issue in honor of Ray Guillery

Carol A. Mason[1] and S. Murray Sherman[2]
[1]Departments of Pathology and Cell Biology, Neuroscience, and Ophthalmology, Mortimer B. Zuckerman Mind Brain Behavior Institute, Columbia University, New York, NY, USA
[2]Department of Neurobiology, University of Chicago, Chicago, IL, USA

This issue of the *European Journal of Neuroscience* is dedicated to Rainer (Ray) Walter Guillery (28th August 1929—7th April 2017) (Fig. 1). Ray was an important, productive, and impactful 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. He was also a great friend, colleague, and mentor to many of us. His work on the development of the visual pathways and thalamocortical organization left us with a classic foundation and legacy for these important areas of neuroscience. More details about his life and career can be found in obituaries recently printed in this journal (Sherman *et al*., 2017) and elsewhere (Sherman, 2018), and in many of the articles in this special issue. Also, his CV is provided in Data S1.

The contributors to this issue represent an assortment of Ray's former colleagues, including his predoctoral and postdoctoral students, formal collaborators, and friends and associates. Each contributor was more than eager to contribute to this issue, such was the respect and admiration each holds for Ray. The papers follow no rigid configuration but instead include a range of manuscript types: remembrances, reviews, and original reports. Ray would have approved of this flexible and varied assemblage.

Ray was born in Berlin in 1929 to a Jewish mother and Catholic father, and his parents divorced when he was 3. Having been reared by a Jewish mother in Nazi Germany, it is remarkable that he survived to grace our lives and careers. In the fall of 1938, he had a rather dramatic escape to Switzerland and then England, and the escape meant travelling separately from his mother and sister. After a brief period, he settled in Oxford, boarding with a local family while his mother sought work in London. Interestingly, his sister also boarded in Oxford with the family of Wilfrid Le Gros Clark, an eminent neuroanatomist. Ray eventually came under Le Gros Clark's mentoring, which undoubtedly influenced Ray's choice of career.

Ray decided to study medicine at University College London (UCL), but soon decided that he preferred doing scientific research rather than treating patients, and he gravitated toward the study of the brain. Thus, he began a PhD program in Anatomy at UCL as a student of J.Z. Young. He did well enough as a PhD student to earn a teaching position at UCL starting in 1954, which offered a stimulating intellectual environment for a budding neuroscientist. His other chief accomplishment while at UCL was to meet his future wife (Margot Pepper), also a medical student. They married and parented three sons and a daughter.

In 1964, Ray and his family moved to the US, where he took up a new faculty position in Anatomy at the University of Wisconsin. It was during his time at Wisconsin that Ray established his career credentials, focusing on early visual development and thalamocortical relationships. One of us (SMS) while a graduate student in 1968 met Ray in Wisconsin, which started our lengthy collaboration; the other (CAM) joined Ray in 1976 at Wisconsin as a postdoctoral fellow. Ray was eventually recruited away to the University of Chicago in 1977 (taking CAM with him) to start the first neuroscience PhD program there. In 1984, he was recruited to Oxford University to become Chair of the Human Anatomy Department. The Dr. Lee's Professorship he held at Oxford was the same one that Le Gros Clark held when Ray first moved to Oxford as a boy.

In 1996, Ray reached the mandatory retirement age for England and was forced to step down as Departmental Chair and abandon his laboratory. However, he was far from done. Fortunately, John Harting, a close colleague of Ray's at the University of Wisconsin and Chair of Anatomy there at that time, offered Ray a Visiting Professorship back in Wisconsin. Ray quickly and enthusiastically accepted and was able to continue his research career. This phase lasted for 6 years, after which time Ray was ready to abandon an active research presence, although he continued to be fully engaged in scholarly activities and published a number of theoretical and review articles. However, no longer tethered to a laboratory, he decided to move closer to his daughter (Jane), who had converted to Islam and was living in Istanbul with her husband. Ray joined her there in 2002, having accepted a position as Professor at Marmara University. Although he thoroughly enjoyed his role as mentor to young Turkish neuroscientists at Marmara University and was much beloved by them, he never felt at home in Istanbul, largely because he felt uncomfortable in the culture there (Fig. 2).

Thus, in 2006 he returned to Oxford University as an Honorary Emeritus Research Fellow in the Medical Research Council Anatomical Neuropharmacology Unit and then the Brian Network Dynamics Unit. He occupied this position until his death. He very much enjoyed this last phase of his career and life because of the colleagues in the Unit who gladly accepted him and provided constant scholarly intercourse.

Ray left behind a remarkable legacy not just of scientific accomplishments but also of close friends, colleagues, and mentees. We consider ourselves most fortunate to be counted in all three categories. We trust that this special edition does credit to his legacy.

Correspondence: C. A. Mason, and S. M. Sherman, as above.
E-mails: cam4@columbia.edu, msherman@bsd.chicago.edu

FIG. 1. Ray Guillery.

This issue

Eighteen articles are included in this special issue. Many of them are remembrances of Ray as mentor and role model, with reference to his lively discussion and debate over the issues that fascinated him. Three remembrances were contributed by his trainees: Anthony LaMantia (2019) and Chris Walsh (2019), who were students during Ray's last period until 1985 in the US at the University of Chicago, and one of us (CAM) (Mason, 2019), who was his postdoctoral fellow during this time (see above). This latter article is the most unusual, because the reminiscences are blended with Ray's own story of how he discovered a path to albinism through his serendipitous finding of aberrations in the path from eye to brain in the Siamese cat. The remaining articles are written by close associates and colleagues who all readily agreed to write a piece for this special issue.

The articles are divided into two broad categories. The first alludes to Ray's forging a path using genetic models to understand the development of 'normal' brain circuitry. Anthony LaMantia presents a lyrical acknowledgement and so does Chris Walsh, each describing Ray's influence on their own work on olfactory system and forebrain development, and on human cortical malformations, respectively. These authors and Jeremy Taylor (2019) cite Ray's work on the albino and his influence on their thinking. I (CAM), too, elaborate on Ray's elucidation of the albino – the genetics of pigment formation and the associated abnormalities of retino-thalamo-cortical pathways – and propose a developmental basis for these connectivity abnormalities, with the albino mouse as a model. And Chris Walsh takes Ray's belief of the complex relationship between genotype and physiology of cerebral cortical circuits to new heights, explaining the interplay of genes and circuitry in normal and perturbed human cortical development.

The second swathe of papers focuses on retinogeniculate, intrathalamic, thalamocortical, and corticothalamic connectivity, which was Ray's main interest at the end of his career.

One of us (SMS; Sherman, 2019) writes about his early days of collaboration, since 1968, to the time of Ray's death. This enduring collaboration, resulting in numerous theoretical and review papers and chapters plus three monographs, fostered new ideas about thalamocortical circuitry.

Martha Bickford (2019) pinpoints two of Ray's papers on Golgi preparations of the cat LGN (Guillery, 1966) and ultrastructure of the synaptic interconnections in the laminae of the LGN (Guillery, 1969), as contributing a solid foundation for countless studies of connectivity in the thalamus and beyond.

Chinfei Chen (Hong *et al*., 2019) takes up this theme and demonstrates that axon arbors from the same class of retinal ganglion cells exhibit quite different arbor structure depending on the region in the LGN they innervate, supporting the long-standing view that targets can influence morphology of their afferents.

Zoltan Molnár (2019) describes intracortical and thalamic arousal of cortical areas emanating from Layer 6b, dubbed by Ray as 'a layer with no known function', connections that Molnar proposes are involved in higher cortical function.

Filiz Onat *et al*. (2019) give a loving account of Ray's mentoring and support during his time in Turkey. Ray, at the microscope, noticed in their retrograde fills of cortical pyramidal cells in layer 5, corticofugal axons extending to the ventral anterior and ventral lateral nuclei of the thalamus, but not the ventral posteromedial regions. This article epitomizes Ray's insight into anatomy and connectivity and especially the significance of branching axons and their sphere of influence.

Kathy Rockland (2019), an early pioneer of cortical layer analysis and single-axon morphology, reveals that corticothalamic axon arbors from layer 5 have a low degree of convergence onto targets compared with corticothalamic terminations from layer 6, which are highly convergent.

Two papers describe the development of connections between thalamus and cortex. Bill Guido's laboratory (Sokhadze *et al*., 2019) analyzes postnatal development of cholinergic input to the mouse thalamic reticular nucleus, to show that corticothalamic projections form well after the laying down of retinofugal circuits, and that non-visual circuits precede visual inputs. Andy King (Lohse *et al*., 2019) parses the auditory system of ferrets, a model also familiar to Ray to understand the role of early sensory experience and plasticity in the mature nervous system, on the corticothalamic feedback in the perception of complex sounds, and corticocollicular projection neurons in accommodating altered auditory spatial cues.

Jeff Hawkins (2019) writes from the theoretician's point of view, one who was deeply affected by Ray's thinking. Jeff sings the praises of Ray's 1995 paper (Guillery, 1995), presaging that corticofugal cells in layer 6 project modulatory inputs to the thalamus, whereas those in layer 5 serve as the initiation of cortico-thalamocortical circuitry to pass information between cortical areas in parallel with direct corticocortical projections.

Jon Kaas and colleagues (Baldwin *et al*., 2019) present an evolutionary analysis of corticotectal projections, with a view of how inputs from different sensory modalities, including auditory, higher order somatosensory and other cortical regions in grey squirrels, are more akin to tree shrews and primates in that they lack inputs from primary somatosensory and motor cortex. He concludes that this animal resembles species with visual rather than tactile-based navigation. This study is reminiscent of the work Vivien Casagrande and Jon Kaas did while working with Ray, engendering the use of multiple species to acquire an evolutionary face to their studies. The second study by Jon Kaas (Cerkevich & Kaas, 2019), again applies a comparative anatomical analysis to the projections from cortical area 1, a non-primary somatosensory area in the primate squirrel monkey, with anterior parietal cortex receiving tactile information. They thus relate this connectivity to new and old world macaque monkeys.

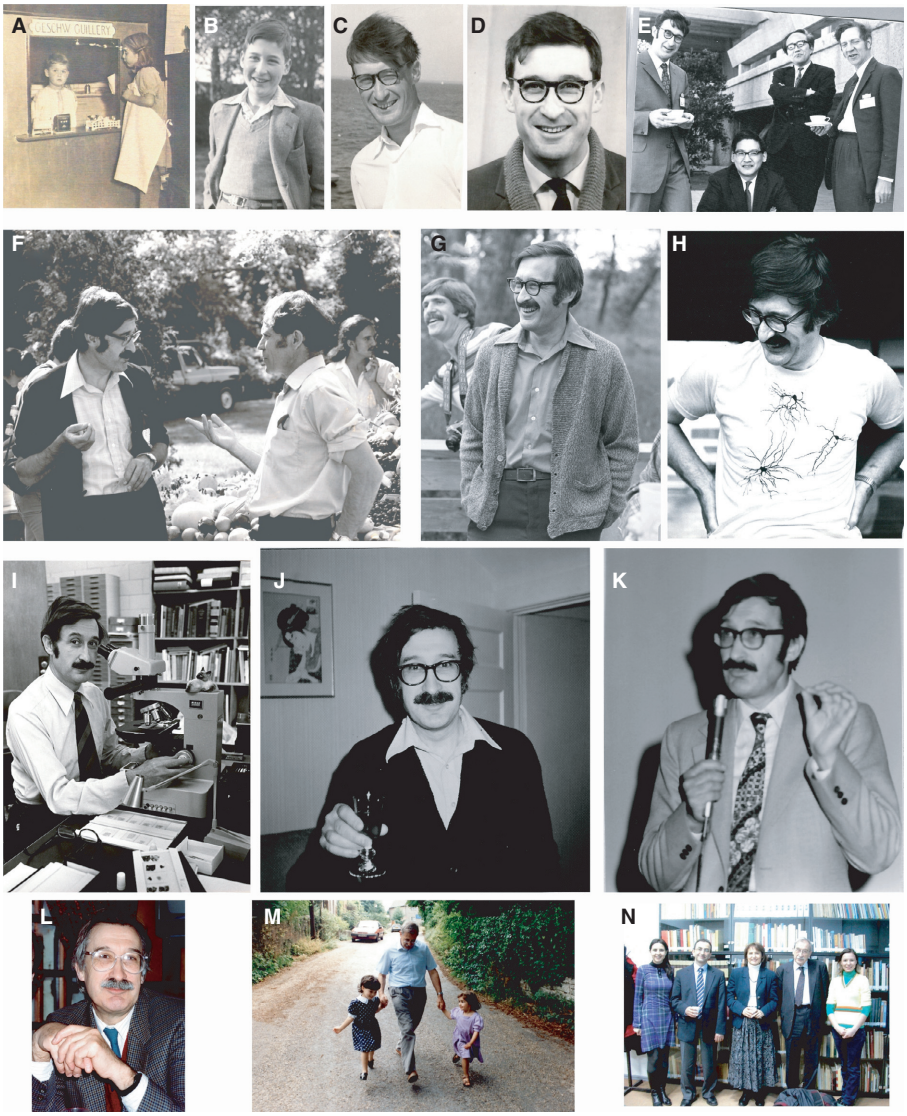

FIG. 2. Ray through the years. A: 1933. With sister Evamaria (Ria). B: 1943. C: 1955. D: 1964. E: 1970. With Horace Barlow on the right and two colleagues; taken in Japan. F: 1976. With Torsten Wiesel. G: 1977 at the University of Wisconsin. H: Leaving Madison for Chicago. Ray's t-shirt depicts the three types of cat LGN cell he identified via Golgi staining. I: 1977. At the University of Chicago. J: 1978. K: 1978. L: 1992. M: 1995. With grand-daughters Zehra and Harriet at Oxford University. N: 2010. With colleagues at Marmara University in Istanbul.

Two articles give depth to Ray's ideas that sensory and motor signals are widely broadcast and inextricably linked. Anna Mitchell was a colleague at Oxford until the end, and she discusses the functional role of the rhesus macaque monkey's parvocellular nucleus of the mediodorsal thalamus in learning, memory and cognitive control (Chakraborty *et al*., 2019). Mriganka Sur (Huda *et al*., 2019) elucidates how sensorimotor transformations involve cortical and subcortical circuits that create internal models as a substrate for action.

Marty Usrey (Alitto *et al*., 2019) provides an update of his earlier work on recordings in anesthetized cats to understand information flow and where features first appear in retina and LGN. These paired recordings of retina and geniculate cells, then geniculate output to layer 4 of visual cortex, highlight the relationship between the time course and strength of retinogeniculate interactions and their dependence on stimulus contrast.

Taken together the scope of these papers, which reflect major advances in neuroscience, owe a great debt to Ray's influence. They well serve to illustrate his impact on the field. Ray will be sorely missed as a colleague, mentor, role model, and friend.

Supporting Information

Additional supporting information can be found in the online version of this article:
Data S1. Ray Guillery.

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