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# COLIN BRIAN BLAKEMORE

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# INTRODUCTION

Colin Blakemore was a giant of neuroscience, whose direct research contributions shaped our modern knowledge of vision and the senses, as well as neural development, plasticity, and degeneration. His early work revealed that manipulation of the sensory environment exerts a profound influence on the growing nervous system, establishing that the activation of nerve cells is directly linked to the successful maintenance of these cells' connections with the rest of the brain. These and many later findings set the scene for understanding that the computational functions of the brain are the outcome of adaptive processes, which continue through adult life in many cases. Publicly, Colin's distinctive voice was well known in broadcast media, notably being the youngest ever presenter of the BBC Reith lectures at the age of 32. Colin became a regular communicator of the rapidly growing field of neuroscience and an effective advocate for the scientific understanding of our brains, bodies and mental life. He unflinchingly undertook the role of justifying the need for animal research to play its part in the development of science and medical treatment, even though this sometimes brought vilification, and even threats. Colin held many public-facing roles for scientific bodies, of which the most significant was his time as Chief Executive of the Medical Research Council. More personally, Colin's role as a mentor will always be remembered by his students, who valued more than anything Colin's remarkable ability to pause all his other activities and focus in on their scientific work and future careers.

Colin Blakemore

**Early life and education**

Colin Blakemore was born during the second world war at a military hospital in Stratford-upon-Avon, Warwickshire on 1 June 1944. Colin was the only child of Beryl Blakemore (née Smith) and Norman Blakemore. The family lived in Coventry, but his mother was taken to a military hospital in Stratford-upon-Avon to give birth, because of the bombing in Coventry. The family lived in a rented terrace house in the working-class district of Radford in Coventry. At the time, Beryl was a member of the Women's Land Army in England and Norman was in the Royal Air Force. Colin's father became a TV repair man after the war. Growing up in the war-damaged City of Coventry, it was evident early on that Colin was destined for great things, earning a place at King Henry VIII School Coventry, but always remaining quite grounded. The attitude of 'make do and mend' never left him from his childhood.

Having a TV set at home enabled Colin to watch David Attenborough's Zoo Quest programmes, and he developed a huge passion for natural history and science. He read Darwin's '*On the Origin of Species',* sitting in the local second-hand bookstore, because he could not afford to purchase the book. Colin attended the local primary school but, when he performed well above the average for his age, his parents scraped together the funds to send him from the age of seven to the fee-paying junior section of King Henry VIII School. He excelled in science, art, and sports. Passing the 11-plus exam entitled him to free secondary education in the senior school. Colin won a state scholarship to study medical sciences at Corpus Christi College, Cambridge, gained a BA degree (first-class honours) in Medical Sciences in 1965.

Blakemore had a duodenal ulcer during his teens, and a second in his third year at university, requiring a gastrectomy that removed half of his stomach. He almost died from bleeding caused by the ulcers. These conditions did not stop him from excelling in sport at school and at university and later, he had lifelong interest in fitness and sport, especially long-distance running. He completed 18 marathons and won the veterans' section for the British team at the Athens Centenary Marathon in 1996.

It was also at school, at the age of fifteen, that Colin would meet his future wife, Andrée Washbourne, at a concert at the Hippodrome, and a few years later, Colin and Andrée were engaged. Colin and Andrée married on the 28th August, 1965, honeymooned

on the RMS Queen Elizabeth and then flew from New York to San Francisco. This marked the beginning of a lifetime of interest in travel and absorption of ideas from other cultures California in the sixties was 'a blast', wrote Colin, and they returned to Berkeley, where Colin was supported by a Harkness Fellowship to complete a PhD in Physiological Optics in 1968 under the supervision of Horace Barlow, FRS 1969. Colin had life-long admiration for Horace and they continued to discuss science until Barlow's death in 2020 (Figure 1).

**Figure 1.** Colin Blakemore with Horace Barlow on Colin's 70th Birthday celebration symposium at St John's College, Oxford. Photograph by Zoltán Molnár. (Online version in colour)

**Cambridge**

After his PhD, Colin returned to Cambridge University for 11 years as a Demonstrator, Lecturer in Physiology, Director of Medical Studies (Downing College), and Royal Society Locke Research Fellow. Back in Cambridge, initially Colin and Andrée lived in a flat in the city, but then moved to a cottage in Milton. In 1974, their first daughter, Sarah-Jayne was born, two years later, Sophie, and then in 1979 Jessica, shortly before the move to Oxford. Even having children did dampen the love of travelling, as Colin wrote:

*I was on sabbatical leave, and we went to Keio University in Tokyo for 3 or 4 months. Sarah was with us - just 2 months old. I had a Chinese post-doc in my lab in Cambridge, and he managed to engineer a visit to China on the way back. I was one of the first Western scientists to visit China. We went to Shanghai and Beijing. We felt like aliens, pushing Sarah around the streets in a pram, surrounded by a crowd of Red Guards, as well as ordinary people.*

In Cambridge and later in Oxford, Colin was an unstinting and superb undergraduate teacher, who taught generations of medical and biomedical science students. He was a superb communicator, who really relished lecturing to undergraduates – and in return they loved, and remembered, his lectures. Even while he was head of department at Oxford, he had the most contact hours for teaching of anybody in Physiology, often giving several lectures in different topics to medical and biomedical students during the same day. Professor Ian Thompson mentions an illustration of Colin's dedication and determination. Around the time Colin was being headhunted for Head of the MRC, he was summoned at short notice to London. He had been scheduled to give two BM lectures that day, so he asked Ian, in advance, if he could do the first (supported by his slides and handouts): Colin would "definitely be back for the second lecture". Ian completed the first and was relaxing with a coffee, when Colin's PA found Ian: Colin was delayed, could Ian also do the second? Ian proceeded, but about halfway through, the lecture room doors burst open and Colin entered, determined to recapture his lecture and his audience.

**Figure 2.** Blakemore Family (from left to right – Sarah-Jayne, Colin, Andrée, Jessica & Sophie) on the occasion of Jessica Blakemore's wedding. Photograph supplied by Sarah-Jayne Blakemore. (Online version in colour)

**Move to Oxford**

In 1979, at 35 years old, Colin was appointed Waynflete Professor of Physiology at Oxford University in association with a Professorial Fellowship with Magdalen College: he was the youngest ever to be appointed to this post. When he showed up for his first faculty meeting at Oxford, George Radda FRS---not recognising the young-looking Professor---told him that "student representatives are not required for these items". Colin held the Waynflete chair for 28 years until 2007, making him the longest standing Waynflete Professor ever. During his tenure at Oxford, he greatly enhanced the reputation of the University Laboratory of Physiology (now called Department of Physiology, Anatomy and Genetics), attracting many eminent visitors to Oxford, and established new areas of research for the university. He transformed the department, which became a magnet for aspiring young neuroscientists as well as for visiting senior academics. He established a culture of openness and enterprise, building with resources from outside grants and fellowships, and was unstinting in his support and generosity towards the people he recruited. Another aspect of this generosity is that he only joined as co-author on publications for which he had made a serious practical

contribution. If he had acted as many others do, his stellar list of publications would be even longer.

**Research Achievements**

Colin's research pursued the theme of visual, auditory and somatosensory perception, mechanisms of neural plasticity, investigating disorders of brain development that might lead to cognitive disorders such as autism and dyslexia. His research identified sensitive periods of early development when brain plasticity is enhanced and his work defined mechanisms by which devastating conditions can be delayed, such as brain pathology in Huntington's disease. He pursued the consequences of his research into the clinical environment, translational research as it would be called today, but also clearly articulated that the new understanding of neuroscience would influence fields far outside science and medicine. Colin's colleagues and collaborators had very diverse backgrounds, ranging from psychophysics, computation, systems and cellular physiology, anatomy, imaging, and molecular biology. This diversity is reflected in the participants of his 70$^{th}$ birthday celebration symposium (Figure 3).

**Figure 3.** Group photo of Colin Blakemore's 70th Birthday celebration symposium at St John's College, Oxford. (Online version in colour)

**Visual perception of space and shape.**

Colin's initial influences in neuroscience were rooted in Cambridge of the 1960s where a fusion of different research traditions had been effected. Richard Gregory pursued the idea that perception was driven by internal models of the external world, an extension of Helmholtz's concept of unconscious inference in perception. At the same time, Kenneth Craik's writings on control systems and cognitive science and the achievements of Edgar (Lord) Adrian in sensory physiology promoted the view that brain mechanisms corresponding to these internal models were waiting to be discovered. It was into this territory, combined with a healthy dose of cybernetics and information theory, that Colin stepped as a medical student.

Colin's initial undergraduate encounter with Richard Gregory fixed one lifelong influence. Colin relates that he posed a question on perception to Gregory and immediately

received the suggestion of going to the lab to try something out experimentally. Colin was clearly hooked by this approach and thereafter encouraged it in all his dealings with colleagues and students. Colin was generous with both his time and his resources to develop the work of others and passionately believed in the empirical approach to settling issues.

Colin acknowledged the huge influence on his view of neuroscience from the papers of David Hubel ForMemRS 1982 and Torsten Wiesel ForMemRS 1982. In their extensive 1962 paper, they used microelectrode recording in anaesthetized cats to show that single nerve cells in the visual cortex responded to optical stimuli in highly specific ways. Unlike cells within the retina of the eye, these cortical nerve cells responded to the orientation of visual contours, being strongly active for some orientations and not at all for others. The nerve cells also showed extensive evidence of integration of visual information from the left and right eyes to make binocular responses. In doing so, the same orientation preference was observed for left and right eye inputs. Most spectacularly, the visual cortex seemed to be organized anatomically with respect to the inputs from the left and right eyes and the orientations preferred by the nerve cells. A small region of the visual cortex seemed to act as a visual analysis machine, being ready to respond to all the possible combinations of visual contours that might arrive with a small region of the visual field. Colin wrote later, *"Suddenly, the previously imponderable question of how the cerebral cortex works began to look tractable. Microelectrode recording in anaesthetised animals offered a way of listening in to the conversation within the brain."* (Blakemore, 2005)

At Berkeley in California, Colin began work on many aspects of binocular vision but the paper that is most celebrated is the discovery of neurons in the primary visual cortex of the cat that are sensitive to binocular depth. This work was prompted by the arrival of Jack Pettigrew (FRS 1987) from Sydney, who had worked on binocular physiology in Peter Bishop's lab. The resulting collaborative paper (Barlow et al., 1967) was a landmark step in understanding the physiology of three-dimensional perception.  from Barlow, Blakemore and Pettigrew (Figures 4, 5). Discovering neurons that could support perceptual function so early in cortical processing challenged much of the contemporary thinking. The discovery went hand-in-hand with Béla Julesz's demonstrations of depth from random-dot stereogram figures, where depth emerges from local point-to-point matching of dots

between left and right eyes, and the paper (Barlow et al., 1967) provided the physiological mechanism for this computational process.

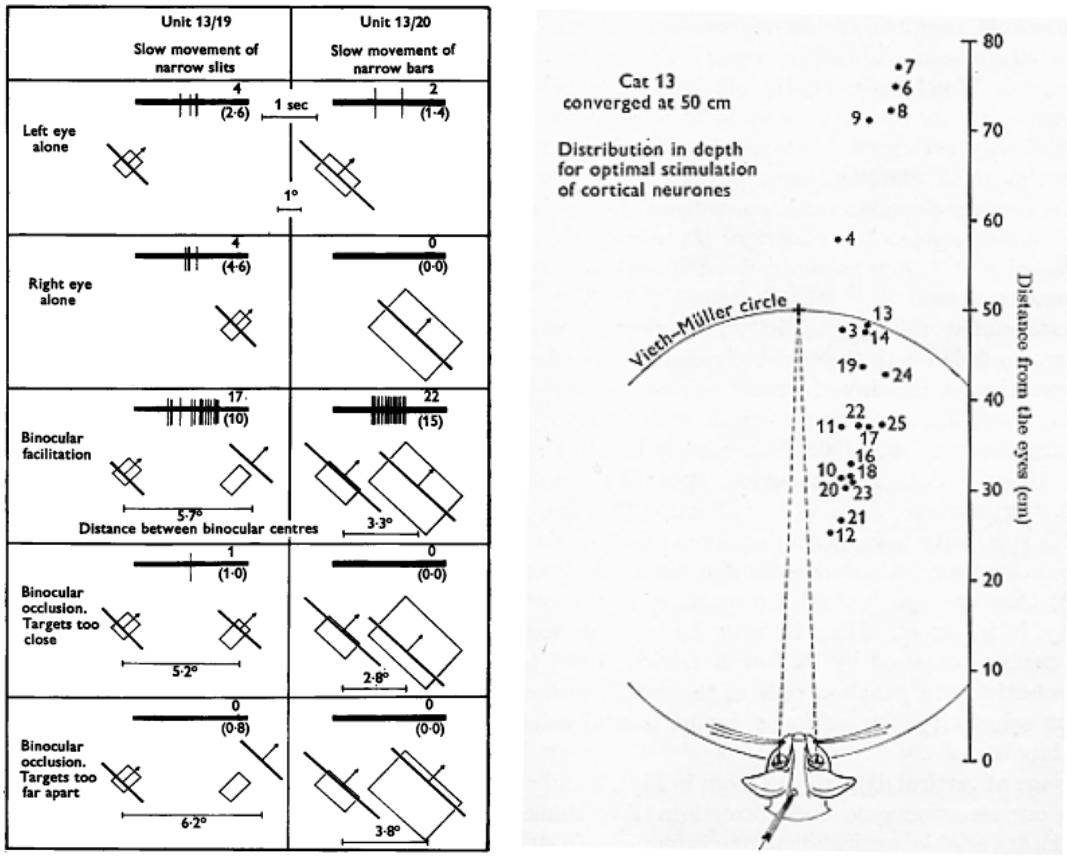


**Figure 4A.** Responses of two individual cortical neurons (left and right columns) from the cat primary visual cortex. The neurons are orientation tuned as Hubel and Wiesel described. From top to bottom, response to stimulation in left eye alone, right eye alone and three types of simultaneous binocular stimulation. The binocular response is strongest at a particular spatial offset between the left and right stimuli. **B** Barlow, Blakemore and Pettigrew realised that this specificity allows the neuron to signal binocular depths when the cat is viewing with normal eye co-ordination. The cat's cortex is equipped with neurons suitable for detecting a range of binocular depths. Adopted from Barlow et al., (1967).

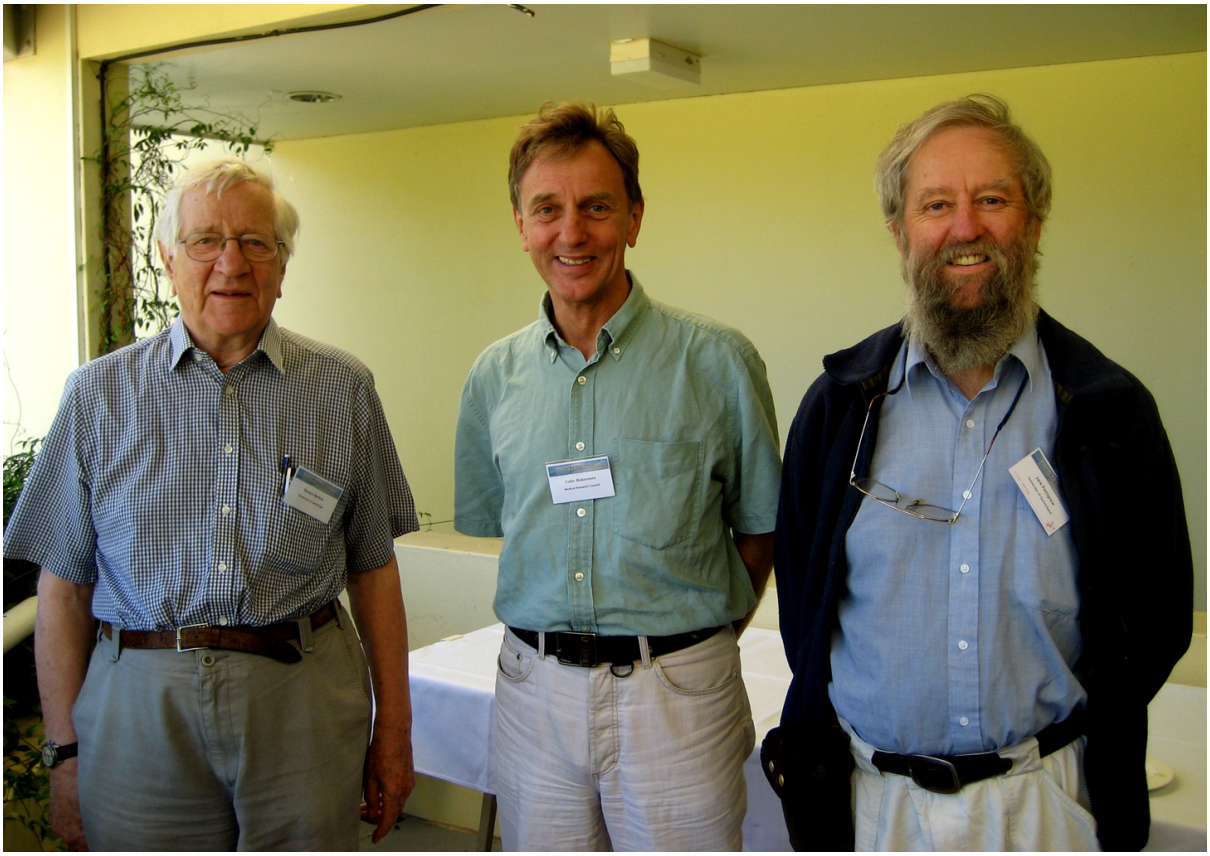

**Figure 5.** Horace Barlow FRS, Colin Blakemore FRS and Jack Pettigrew FRS in 2004, 37 years after the publication of their landmark study on 3D visual perception in 1967 (Barlow et al., 1967). Photo from Colin Blakemore's collection. (Online version is in colour)

On his return to Cambridge, Colin found that similar progress was being made with other aspects of early visual processing. This work coalesced into the proposal that early visual processing passes through a set of spatial and temporal filters that are selective for spatial frequency and orientation. One of the resulting landmark papers reported the selective adaptation of spatial frequency channels in human vision, as demonstrated by Colin with Fergus Campbell (Blakemore and Campbell, 1969). From this era of work, many of the modern developments of computer vision emerged. Colin rapidly established a visual neurophysiology lab in Cambridge and began a wide range of studies on the development and adult functions of the visual cortex.

**Early plasticity of visual system and clinical implications**

A central theme of Colin's research at this point was how environment, experience and learning shape the developing nervous system. At this stage in the research picture,

environment was regarded as a directly contrasting influence in development, distinct from inheritance and genetics. As Colin himself put it, this was "*a modern expression of the battle between nativism and empiricism in philosophy" (Blakemore 2005).* Eventually, this dichotomous thinking gave way to a view in which an important role for genetics is to build and specify a nervous system that is equipped with adaptive neural mechanisms that can benefit from environmental influence through plasticity and learning. In Colin's later view, these influences are all channelled through the ability of synaptic links between neurons to increase or decrease their strengths according to the timing and quantity of impulse activity in the pair of linked neurons.

Colin's earliest work concentrated on the developing visual system, particularly examining in detail how the properties of sensory neurons change during post-natal development when visual input can influence the activity and the growth of neurons. Colin studied initially how the two eyes' inputs to the visual cortex are co-ordinated. He did this by testing how the cat visual cortex responded to disturbance of binocular input, by blanking off the input from one eye, typically by surgically closing the lid of one eye. With no further intervention, the visual cortex became responsive only to signals from the eye with visual experience. Colin ingeniously demonstrated developmental plasticity by exposing first one and then the other eye to visual experience. He also pursued the consequences of developmental changes at the behavioural level, with a variety of tests of visual and visuo-motor function. This work was pursued in both cat and later in monkey (with Vital-Durand and Garey).

Colin pioneered work that demonstrated that the visual cortex adjusts itself during maturation to the nature of its visual experience. In visual cortex, neurons are selective for the orientation of lines and edges in the visual field, and the preferred orientations of different cells are distributed all around 'the clock'. Early visual experience can change this organization: kittens were exposed to visual environments that entirely consisted of high contrast black and white stripes either horizontal or vertical. This intervention changes the distribution of the orientation sensitivity of the visual cortical neurons (Blakemore and Cooper, 1970). Despite the initially sceptical response, these experiments subsequently received a robust reproduction in the hands of Sengpiel and colleagues (1999) (Figure 6).

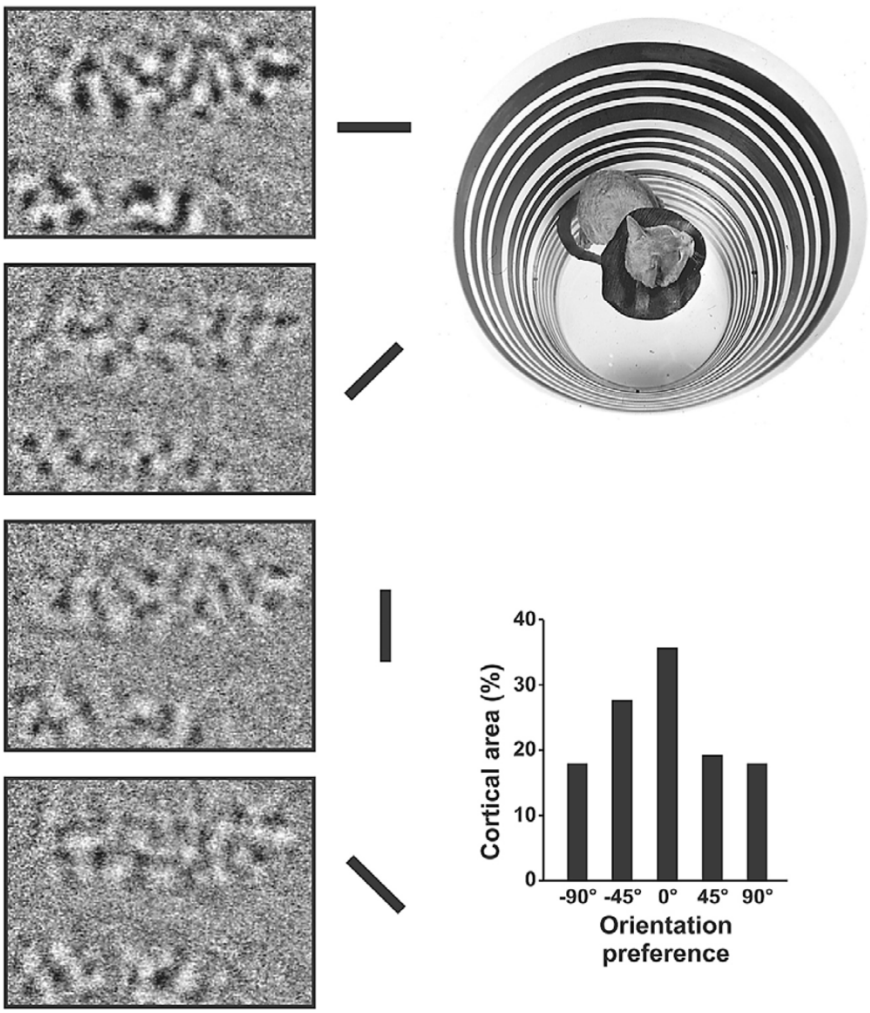


**Figure 6.** Optical imaging experiments by Sengpiel et al., (1999) to reveal the reorganisation of orientation columns in the cat visual cortex (V1) resulting from early selective exposure to contours of one orientation that was originally revealed with electrode recordings by Blakemore and Cooper (1970). The inset photograph shows a cat, wearing a ruff to restrict vision of its own body, standing on a glass platform in a large cylindrical chamber the internal walls of which were painted with high-contrast horizontal stripes. The cats in this study were exposed to the striped environment for a total of 75–120 hours between 2·5 and 6 weeks of age. Each image on the left shows a view, about 8 mm across, of V1 of the right hemisphere (at the top) and part of the left V1 (bottom left), in an anaesthetised cat. During the collection of each optical image, moving stripes were projected on to a screen in front of the cat's eyes, and the orientation of the stripes is indicated by the line segment next to each frame. Areas of neuronal activation appear dark. The regions of cortex responding to the horizontal stripes (the orientation experienced earlier in life) are larger than those

responding to other orientations. The histogram (bottom right) plots the cortical area devoted to the different orientations, zero being horizontal. Early exposure produces a substantial expansion in the size of columns devoted to the experienced orientation. Data from Sengpiel et al., 1999 and reproduced from Blakemore, 2005.

Closely related to Colin's fundamental research was the clinical observation that one out of ten persons has weak or non-existent binocular depth vision. The work with experimental animals therefore also had a clinical inspiration, since the experimental interventions mirrored the loss of vision in one eye often arising in human infants and manifest as the clinical condition of amblyopia. This is sometimes obvious but also sometimes only exposed with specific tests that require binocular depth vision. Colin's research sought to understand why some children acquire a a condition of asymmetric refraction between the two eyes (anisometropia) or squint during infancy. In this case, the inputs that the brain receives from each eye do not match; children then develop profoundly impaired vision in one eye, a condition known as amblyopia. The animal experiments on the developing visual system suggested that patching the eyes of affected children briefly during an early critical period of development could establish new visual pathways and improve their vision.

One of Colin's last publications (Huang et al., 2022) concerned a randomised clinical trial in children to establish treatment for amblyopia based on more recent understanding of the rules of synaptic plasticity. Rather than simply blocking input from the fellow eye in order to let the amblyopic eye strengthen its connectivity with the cortex, this approach sought to improve the influence of the amblyopic eye under binocular stimulation. They tested the hypothesis that repeated asynchronous stimulation of the two eyes, in which the weaker amblyopic eye receives stimulation slightly ahead in time of corresponding stimulation to the fellow eye, might induce synaptic plasticity and rebalance input. The results suggested that the influence of asynchronous binocular treatment is potentially 50 times more efficient than patching. This most recent work builds on accumulated insights from animal studies that have had a huge influence on corresponding studies of human visual development and clinical ophthalmology. Many of Colin's most prominent awards and honours cited this area of his work as the basis for recognition.

**Assembly of neuronal circuits and their plasticity**

Colin was also engaged with the fundamental question of how neuronal circuits adaptively adjust as they start to process sensory input and how they undergo plastic changes in response to changed environmental influences. Colin wrote in 2005: *"[The] capacity for the environment to have a beneficial influence on the development of the brain must itself depend on genetic mechanisms. The emergence of genes that enable neural activity to have an organising effect on neurons, was a transcendent step in evolution—a genetic mechanism that empowered the brain to acquire new information from the environment, and hence to break out of the information straitjacket of the genetic code."* (Blakemore, 2005)

At later stages of his career, Colin extended his sensory development and plasticity work to rodent models. The barrel field of the somatosensory cortical area, S1, proved to be particularly useful. This area receives patterned input from the rodent's whiskers. This nerve pathway delivers a strict correspondence between the peripheral sensory organs and cortical architecture (Woolsey and Van der Loos, 1970). Nerve fibres leave the whiskers and make a connection in a mid-brain structure called the thalamus. A second set of nerve fibres leaves the thalamus, carrying signals from each individual whisker in a clear pattern, related to peripheral topography. As these thalamic fibres grow into the cerebral cortex during the first days of postnatal development they initially form a homogeneous plexus within the input layer of the cortex, but they then segregate into a pattern that corresponds precisely to the peripheral arrangement of the whiskers. The cortical targets of these projections are also homogeneously distributed at birth, but then get displaced towards the edges of the thalamocortical clusters and form septa.

Each wall-plus-plexus is called a "barrel" (Figure 7A, B). Colin recognised the power of mouse genetics for defining the cellular and molecular mechanisms of thalamocortical interactions (Molnár and Blakemore, 1995; Molnár et al., 1998). An important outcome was the identification of genes involved in enabling nerve cells to modify their connections in response to the flow of nerve impulses through them (Hannan et al., 2001).

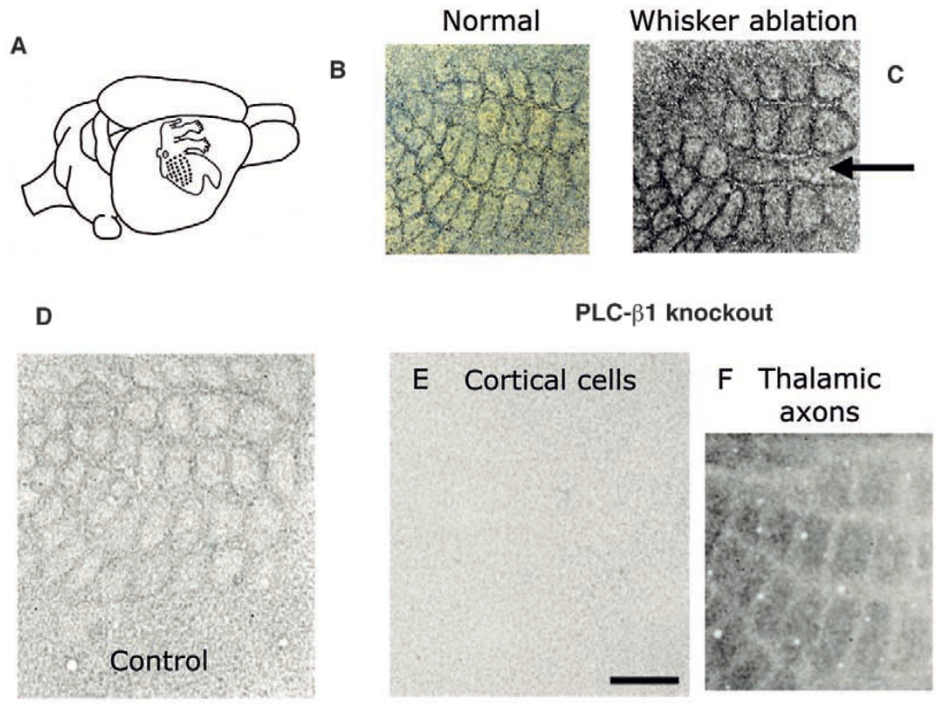


**Figure 7.** The "barrel field" of the primary somatosensory cortex of the rodent is an excellent model system to identify molecular and cellular mechanisms of activity-dependent plasticity of sensory areas. A: The somatic sensory cortex in the adult mouse has a large area dedicated for the representation of the sensory innervation of the whiskers. B: On a tangential section through the region where thalamic axons terminate (layer 4), Nissl staining reveals layer 4 cell bodies that are organised into densely packed walls of the "barrels". Each barrel corresponds to a single whisker on the opposite face of the mouse. Nerve terminals from each whisker arrive in the cell-sparse halo in the middle of each barrel. C: If a row of whiskers is removed within the first few postnatal days, the corresponding set of barrels fails to develop normally (arrow) but if this ablation is later, no such changes occur. D, E and F: Formation of cortical barrels is affected by genetic knockout of mGluR5-phospholipase C-β1 (PLC–β1). D shows barrels in normal one week old cortex; E shows absence of normal barrels with PLC–β1 knockout; F shows that normal pattern of nerve terminals from the thalamus persists even though no barrels are formed among the cortical nerve cells. All images from one-week-old mouse, scale bar=100um. Original data from Hannan et al., (2001).

Mouse mutants demonstrated that the periphery-related patterning of the thalamocortical axons and the patterning of the layer 4 neurons into barrels depend on both pre- and post-synaptic mechanisms (Hannan et al., 2001; Erzurumlu and Kind, 2001; Barnett et al, 2005). The presynaptic mechanisms enable the thalamocortical projections to develop patterns matching the

periphery, whereas postsynaptic receptor mediated signal transduction is required to cause the migration of cortical, layer 4 neurons out of the halo to establishment of the septa.

**How do cortical areas emerge?**

Taken as a whole, the adult cerebral cortex in mammals is a continuous sheet, divided into many distinct areas. Although each area has six layers of cortical nerve cells from the surface down to the axon fibres of the white matter, the number of cortical nerve cells in each layer differs markedly from one area to another. These differences reflect different computational functions of those areas. Colin was very interested in the mechanisms that generates specialisation of these neocortical areas. At what stage of development do differences among areas emerge and are these differences predetermined or induced by the environment?

The initial axonal projections from the thalamus to the cortex are topographically organised but grow to reach the future neocortex before the peak production of new cortical neurons (Rakic, 1988) and before any specialisation of the cortical layers (Molnár and Blakemore, 1995; Molnár et al., 1998a,b,c). Nerve cells grow out from the primordial thalamus as an ordered bundle at an early stage, even before the thalamic projection nerve cells segregate into distinct nuclei and as immature cortical neurons have only just started to arrive where the future neocortex is forming at the so-called cortical pre-plate. As the early thalamocortical projections approach the pre-plate, nerve cells that will eventually signal back from cortex to thalamus are encountered. These pairs of nerve cells from different origins join to proceed to advance to their respective future targets. This “handshake” between the two sets of fibres from different origins is thought to play an important role in the subsequent guidance of thalamic fibres towards the appropriate region of cortex (Molnár and Blakemore, 1995).

**Plasticity at all times: from the earliest thalamocortical interactions to adult disease states**

To study the earliest thalamocortical interactions that mediate specialisation into cortical areas, Blakemore’s laboratory developed new *in vitro* co-culturing techniques. By taking

living brain tissue from different anatomical locations and at different stages of development, Molnár and Blakemore (1990,1999) revealed a cascade of interactions between cortex and thalamus. At certain stages of development, molecular signals encouraging growth of nerves are produced but later on other signals bring this growth to a halt. A change in the size or proportions of the thalamus or of the cortex leads to compensatory changes in the mapping between thalamus and cortex, an idea first advanced by Guillery and Stelzner (1970).

To test the idea of autoregulation between thalamus and cortex required a model where these earliest stages can be manipulated by removal of part of the developing cortical sheet before arrival of thalamic fibres. Marsupials provide this opportunity (Molnár et al, 1998c). The result was clear. Removal of part of the cortex results in a map of sensory areas in which the entire bundle of thalamic axons is compressed onto a much-diminished cortical area. Equally important, the thalamus was uniformly reduced in size. The thalamus regulated its outgoing neuronal projection to fill the cortical space available and, in turn, was itself regulated by the size available at the cortical target.

Noting the importance of structured neural activity in early development of the brain, Blakemore also began to study whether similar neural activity might have beneficial effects in neurodegenerative disorders (see Spires and Hannan, 2005). For example, the Huntington's disease, which is single-gene dominant, causes severe degeneration of the corpus striatum and the cortex surrounding it, with consequent enlargement of the ventricles. These neurodegenerative conditions were thought to follow an inevitable decline if the gene mutation was present. Blakemore's group studied a transgenic mouse model of Huntington's disease and found that enrichment of the sensory environment can delay the onset of motor signs (van Dellen et al, 2000; Spires et al, 2004). This intervention also delayed the manifestation of the molecular cascade responsible for disease progression. These studies suggested new options for therapeutic or preventive approaches to this devastating condition. This work triggered interest in addressing other neurodegenerative conditions, such as Alzheimer's and Parkinson's disease, from this perspective, to explore the benefits of environmental enrichment in preventing or delaying onset and progression of these diseases (Spires and Hannan, 2005).

**Consciousness is an epiphenomenon**

Throughout his career, Colin was very interested in large-scale questions posed by neuroscience. He addressed these at an early stage in the Reith lectures on the "*Mechanics of Mind*". Colin's knowledge of psychology, philosophy, biology, chemistry, and physics put him into a unique position to launch testable hypotheses on consciousness from many different angles. He studied illusions, perceptual ambiguity, such as the one related to binocular rivalry, and described those signals within the cortex correlated directly with perceptual shifts (Sengpiel and Blakemore, 1994; Andrews et al, 2004).

Colin debated and exchanged correspondence with many other scientists and philosophers on the nature of consciousness. At the time much of this debate was engaged with the question of whether there are neural correlates of conscious experience, which Crick and Koch had defined as "the minimum neuronal mechanisms jointly sufficient for any one specific conscious experience" (see Koch et al, 2016).

As Colin himself puts it, *"It is clear that most of what the brain is doing at any time is not within the domain of awareness. Some crucial decision making, such as the control of the heart and the gut, never bothers the conscious mind. Other functions - such as the control of breathing—rarely do. More significant, we are unaware of much of the detail of sensory analysis and motor control: we have no subjective experience of the pre-processing in sense organs or the intricate choice of motor units for any particular movement. Our awareness is a constantly shifting. ….Even among those parts of neural processing that can enter conscious experience, most are excluded most of the time. The process of attention sweeps across the landscape of candidates for consciousness, selecting at any one time only a tiny amount of information to display on the screen of awareness."* (Blakemore 2005).

There are elements to this account that are intriguing from present-day perspective. Here, the issue of consciousness is taken to be closely aligned to the question of awareness. Whilst acknowledging that there are other aspects of consciousness over and above awareness, Colin points out that the operation of the selection filter is a fundamental aspect

of consciousness that is captured by studying awareness. Colin was also acutely aware of the information-processing heritage of his earlier training. He identifies that this presents a key issue: the quality of information processing by the brain is not improved or enhanced when we become aware of something. . This led Colin to the following, slightly unsettling, thought*: "Although it is often assumed that the mechanisms of consciousness must have evolved…[but] consciousness itself cannot have evolved by Darwinian selection. The underlying neural mechanism, which happens to produce consciousness, is the phenotype that has been selected by evolution. Being conscious is an epiphenomenon."* (Blakemore 2005).

Colin here poses the question of exactly what evolutionary forces may have driven the emergence of conscious awareness and concludes that the one thing that cannot have driven this emergence is consciousness itself. The logic of this is cleanly expressed. It is similar to the point made repeatedly about the neurophysiological explanations of certain visual illusions, such as the simultaneous tilt illusion (Blakemore and Tobin, 1972). The neurophysiology must come first, so it is erroneous to suppose that the neurophysiology is organized so as to deliver the psychologically-experienced illusion. Rather, the illusion arises inescapably from the neurophysiological mechanisms; similarly so, for consciousness. Selection pressures during evolution must work on the physiology and anatomy of the brain and body. There is no causal path that could allow genetics and natural selection to exert a direct influence on thoughts and consciousness. Darwinian selection can shape the emergence of brain mechanisms that coincidentally enable conscious perception, but the selection pressures are acting upon genes that control the properties and development of brain cells.

**Science communicator**

It is impossible to understand Colin's career without appreciating his early commitment to science communication. For Colin, this was not an additional activity to be overlaid on scientific studies. Rather it was an integral part of them. The constant activity of public engagement shaped his own scientific studies and his style of writing his own scientific papers. Colin's drive to achieve transparency in science communication was not

universally appreciated. His sheer fluency and intense activity could make colleagues feel uncomfortable, particularly if this caused them to reflect on their own shortcomings in this area.

This was most evident in ethical debates on animal experimentation. There were clearly some medical and scientific colleagues who did not want to take the personal risks associated with speaking publicly on this issue. There were also those who took the view that transparency was unhelpful. Their attitude to this area of research might be summed up the quip, often misattributed to Bismarck, that making laws is like making sausages because it is better not to know what went on in the process. Colin was deeply antipathetic to this position. For him, this view was not just irrational but truly irresponsible. The fact that so many universities and research institutes now subscribe to a Concordat on transparency in animal research is a measurable outcome of Colin's early engagement with this issue.

The intensity of the debates over animal research often overshadowed Colin's other activities in public engagement. Colin was a frequent broadcaster on radio and television. In 1976, Colin gave the BBC Radio 4 Reith Lectures 'Mechanics of the Mind' and remains to date the youngest person ever to deliver these lectures, covering the neuroscience of sleep, language, consciousness, and mental illness. He went on to present and contribute to hundreds of radio and television broadcasts. In 1988 Colin presented a 13-part TV series, *The Mind Machine*, on BBC Two accompanied with a popular book. He also wrote articles and opinion columns for national newspapers, and other books for the public include *Mechanics of the Mind*, for which he won the Phi Beta Kappa Award in Science*, Images and Understanding*, *Mindwaves*, *Gender and Society,* and *The Oxford Companion to the Body*. He received several awards for science communication, including the Royal Society's Michael Faraday Medal, as "one of Britain's most influential communicators of science".

**Animal testing and animal rights**

Building on his view that scientists have a duty to explain their science to the public, Colin publicly defended use of animals in research, when there are no alternative methods and the benefits of the research really outweigh the harms inevitably incurred when using animals (Blakemore and Davidson, 2006). This public-facing stance led to personal threats to him and his family. Colin and his family suffered considerably because of his public stance on animal research. Colin's view of the duty to explain was not simply motivated by the spirit of scientific inquiry. It was rooted in compassion and a desire to bring healing to humans who suffered.

Without compromising his position, Colin sought to debate the ethics and practice of animal research with those who were publicly opposed to it. To discuss issues relating to animal experimentation, together with Les Ward of the anti-vivisection group Advocates for Animals, Colin co-founded a bipartisan think tank called the Boyd Group in 1992. Colin was at various stages chair of the Coalition for Medical Progress, the Research Defence Society and Understanding Animal Research, the last of these being an organisation launched in 2008 and devoted to making the public case for responsible use of animals in research. Colin was a huge advocate of 3Rs - replacement, reduction, and refinement— to minimize the welfare costs to animals used in research whenever it was possible (Blakemore et al., 2012).

"Colin was unusual in being such an eminent scientist who valued and befriended science press officers" wrote Fiona Fox (Fox, 2020). When the media reported that his knighthood had been blocked because of his outspoken support for vivisection, Fiona relates that Colin went on [the BBC Radio 4 programme] *Today*, threatening to resign as head of MRC unless the government publicly stated its support for animal research, which it duly did. Fiona Fox immediately called his head of press to congratulate her on a bold and audacious media strategy. There was a pause on the line before she confessed, she had no idea Colin was doing it. Colin had of course been speaking to journalists for years before professional science press officers came along and he wasn't a fan of prepared media 'lines', favouring an approach where scientists answer questions openly and truthfully.

**Public engagement**

Colin was not simply a science populariser. The purpose of his public engagement was neither to enthuse those who are already 'Science interested', nor to enhance the position of science itself. The aims were to better inform the wider public, enhance the quality of national discourse, and to encourage a scientifically literate electorate to demand evidence-based policies. Colin's view was that public engagement is necessary to earn public trust. As head of the MRC, he made media work part of the grant conditions – a game-changing move, which saw public engagement gradually recognised as part of what it means to do good science.

Colin's expertise helped to shape public policy in many areas. He was a member of the Independent Expert Group on Mobile Phones (the Stewart Committee) in 1999–2000 and was an advisor to the Police Federation and the Home Office on the safety of telecommunications systems. Among his government advisory roles, he was a member of the UK Drug Policy Commission. In 2007, with Professor David Nutt and others, he co-authored a provocative letter to the Lancet assessing the harms of legal and illegal substances, including alcohol and tobacco, and arguing that policy should be based on level of harm (Nutt et al., 2007). Colin was a member of the Longevity Science Advisory Panel of Legal & General, and he served on the European Advisory Board of Princeton University Press.

Colin played a major part, with Nicholas Wald and others, in the adoption of a new UK-wide policy to add folate to wheat flour to provide a baseline of protection against spina bifida in early pregnancies (Wald et al., 2020). In 1991, the report of the Medical Research Council (MRC) Vitamin Study, a randomised trial, had shown that a large proportion of neural tube defects can be prevented by increasing folic acid intake immediately prior to pregnancy and in the early stages of pregnancy. Even though over 80 other countries had introduced mandatory fortification of flour with folic acid without adverse effect, there was a reluctance in the UK to follow the advice of its scientists. The article with Nicholas Wald and others helped to change the policy in the UK of adding folic acid to flour to make this very significant step in preventing neural tube closure defects in the UK. It is estimated that adoption of this policy reduces around 200 neural tube defects each year – around 20% of the annual UK total.

At his death, Fiona Fox (2022) pointed out that the word used more than any other about Colin was brave. "*Maybe we highlight that because it's a trait we find hard to emulate. As a community we often feel fearful and cautious. Surely if we publicly criticise government - we will lose our ability to influence things on the inside. Surely if we speak out on toxic issues we will be harassed or cancelled. Surely if we appear on the media a lot our science will be dismissed. Colin proved that none of that has to be true. You can be brave and outspoken while still wielding influence and respected for your science."*

**Building a scientific community**

In addition to being head of a large and very active research group and university department, Colin shaped neuroscience in Oxford as the founding director of the James S. McDonnell and Medical Research Council Centre for Cognitive Neuroscience at the University of Oxford. He served as president of the Physiological Society, and as president and chair of the British Association for the Advancement of Science, now the British Science Association. In 1981, he became a founding member of the World Cultural Council.

Colin had a huge impact on British science by engaging with the public and with distinguished scientific organisations. He held several influential positions, including serving as President of the Biosciences Federation (now the Society of Biology), the British Neuroscience Association and The Physiological Society, and as President and Chairman of the British Association for the Advancement of Science (now the British Science Association). When Colin was appointed chief executive of the Medical Research Council, the government-funding body that operates medical research institutes and distributes grants, there had been public criticism of its operations in the UK Parliament. There was a concern that the funding body was losing the trust of both experimental and clinician scientists. Colin immediately reinstated the research project grant as a unit of funding, which had been abandoned as a mode of funding under his predecessor. Colin regarded the research process as essentially requiring a means of stimulating and supporting innovation by individual research groups in the UK. Without single project grants, that innovation was stifled. Colin's tenure at the MRC became adversely affected by the controversy over the

future of the National Institute for Medical Research (NIMR) at Mill Hill, which was only resolved in 2015 when NIMR fused with the new Crick Institute in central London. As so often with public policy in the UK, many difficult issues surrounding this Institute had been repeatedly deferred until decisions could no longer be avoided.

After his stint as Chief Executive of the Medical Research Council from 2003 until 2007, Colin returned to Oxford to continue as Professor of Neuroscience and Supernumerary Fellow at Magdalen College until his 'retirement' in 2012. Colin was then appointed to a newly created Professorship of Neuroscience & Philosophy at the School of Advanced Study, University of London, where he directed the Centre for the Study of the Senses. He held an honorary professorship at the University of Warwick, and a professorship at Duke-NUS Graduate Medical School in Singapore, where he was chairman and then external scientific advisor to the Neuroscience Research Partnership.

Colin subsequently held other professorial positions, including the Yeung Kin Man Professor of Neuroscience and senior fellow of the Hong Kong Institute for Advanced Study at City University of Hong Kong, whilst maintaining links with Oxford, continuing both his own neuroscience research and his many other services to science and medical research. He was finally knighted in 2014, some years after the earlier scandal over this honour. Colin diplomatically stated that he was "surprised and delighted".

Colin was an international leader, and his legacy extends around the globe. His graduate students and collaborators were from all regions of the World. Colin first visited China in 1974, during the Cultural Revolution, and collaborated in research at the Institute of Biophysics of the Chinese Academy of Sciences in Beijing, in the late 1970s and early 1980s. His efforts to develop scientific relations between the United Kingdom and China were recognised in 2012 when he received the Friendship Award, the People's Republic of China's highest award for "foreign experts who have made outstanding contributions to the country's economic and social progress". In 2012 he was appointed a Master of the Beijing DeTao Masters Academy.

Colin was a patron of Humanists UK (formerly the British Humanist Association) and an Honorary Associate of the Rationalist Association and an honorary associate of the

National Secular Society. Colin believed that education starts from the earliest stages of school curriculum and the early experiences could have a very long-lasting effect on someone's beliefs. He was himself an atheist, although happy to attend ceremonies of religious worship. In 2002, together with Richard Dawkins; Roger Penrose, Lewis Wolpert and dozens of other distinguished British scientists, Colin wrote a letter to Tony Blair urging for a statutory requirement that creationism should not be taught in the national curriculum "as anything other than religious myths" and advocated for the teaching of Darwinian evolution to be introduced in primary school education. Colin was one of the signatories to a letter supporting a holiday on Charles Darwin's birthday, published in The Times on 12 February 2003, and sent to the Prime Minister and the Home Secretary.

Colin's insatiable curiosity applied to many fields, also including the visual arts. He was a long-time member of the Chelsea Arts Club and had a passionate interest in process of art production and loved talking to artists. Colin worked directly with both David Hockney and Patrick Hughes over the years, most recently when Colin was Director of the Centre for the Study of the Senses at the University of London's School of Advanced Study.

**Educator and mentor**

Despite Colin's very busy schedule, he performed most of his physiological and psychophysical experiments himself. He had exceptional manual skills, and his experimental techniques were hugely efficient and precise. He led by example and taught generations of neuroscientists who became inspired, influenced, and trained by Colin's activities and approach. A brief chat with him made one feel energised and enthusiastic about one's own work. Even after people had left his laboratory, he always showed great interest in his students' progress, being very proud if they made more advances.

Many of the graduate students and postdoctoral fellows from his laboratory remained collaborators and friends for decades (https://neurotree.org/neurotree/tree.php?pid=205). He created a culture of collaboration at every scale, and he put us in touch with the most qualified experts in the UK, Europe, Japan, US, and other parts of the world, to pursue collaborative work. He gave us a superb

example how to pass his legacy down to our students and hopefully to their students' students.

Colin was extremely supportive especially to many younger researchers. He quickly understood the major goals of their research areas and gave many useful suggestions that were absolutely on point. He was always a very active participant at scientific meetings, where he could spot contradictions immediately, gently teasing them out with a Socratic style of questioning.

Many year groups of medical and biomedical university students at Cambridge and Oxford grew up listening to his lectures, for which Colin consistently got the highest rating from medical students at Oxford for decades. He spoke about science with clarity, an easy elegance following tight and transparent logic. These exceptional qualities, evident from early stages of his career, made him much in demand for medical undergraduate and graduate teaching, and in print and broadcast media. Colin was deeply interested in history of neuroscience and his lectures were richly illustrated with historic concepts from Aristotle, Willis, Gall, Flourens, Gennari, Brodmann, Broca, Ferrier, Adrian, Sherrington, Holmes, and Penfield (see example in Colin's Harveian Oration, Blakemore, 2005).

**Personal legacy**

Colin was diagnosed with motor neurone disease in 2021. He returned from his post in Hong Kong to Oxford to be close to his family and receive excellent care from the specialised clinic at Oxford. His bravery, dignity and determination to resist the disease process to the end affected all of us profoundly – and yet, he also managed to retain a wry sense of humour about it. He was a proud man for whom appearance and style were always very important. Nonetheless, we also remember Colin for his rather wonderful and irreverent sense of humour, his love of Monty Python and not taking himself or life too seriously. Likely, this was how he was known by his grandchildren, Oscar, Charlie, Edee and Ayda, as Gaga. Colin never missed an opportunity to get dressed up for Christmas parties or Halloween, even as head of department!

Colin passed away peacefully at the age of 78 at Sobell House Hospice in Oxford on 27 June 2022, in the company of his daughters: Sarah-Jayne Blakemore FBA FMedSci

(Professor of Psychology and Cognitive Neuroscience at Cambridge), Jessica Blakemore, and Sophie Blakemore. Colin's wife, Andrée, had also passed away earlier the same year.

Colin combined in his character the spirit of enquiry together with that of compassion. At Colin's funeral, Terry Waite CBE: *'He championed reason against superstition, inquiry against authority. Above all, he said humans owed it to their nature to be curious, to inquire without inhibition.'* Colin will be dearly missed by his family, all his many friends, generations of medical and biomedical students, the entire scientific community, and others whose lives he touched. The Large Lecture Theatre in the Sherrington Building of the Department of Physiology, Anatomy and Genetics, University of Oxford has been renamed the Blakemore Lecture Theatre in recognition of the sustained and long-standing contribution of Colin as Waynflete Professor of Physiology and his time as an outstanding lecturer for generations of medical students and physiology students on the wonders of the brain.

**•MAJOR HONOURS, AWARDS, AND NAMED LECTURES**

list of the subject's most significant honours and awards

MEMBERSHIP OF ACADEMIES

- 1988 Member, Academia Rodinensis Pro Remediatione, Stockholm, Sweden
- 1990 Honorary Professor, China Academy of Management Science
- 1992 Fellow of the Royal Society (FRS)
- 1993 Foreign Member, Royal Netherlands Academy of Arts and Sciences
- 1995 Member, Academia Europaea (Academy of Europe) (MAE)
- 1998 Founder Fellow, Academy of Medical Sciences (FMedSci)
- 2005 Honorary Professor, Chinese Academy of Medical Sciences (Peking Union Medical College)
- 2007 Honorary Fellow, Indian Academy of Neurosciences
- 2008 Foreign Fellow, National Academy of Sciences, India
- 2009 Foreign Member, Chinese Academy of Engineering
- 2011 Member, European Academy of Sciences and Arts
- 2012 Member, DeTao Masters Academy, People's Republic of China
- 2017 Member, New York Academy of Science

AWARDS AND PRIZES

- 1972 Silver Award, British Medical Association Film Competition, for educational films
- 1973 Silver Award, Padua International Film Festival, for educational films

- 1974 Certificate of Educational Commendation, British Medical Association, for educational films
- 1974 - 1975 Leverhulme Fellowship
- 1975 Robert Bing Prize for Neurology and Neurophysiology (Swiss Academy of Medical Sciences)
- 1977 Copeman Medal for Scientific Research (Corpus Christi College, Cambridge)
- 1978 Richardson Cross Medal (South Western Ophthalmological Society)
- 1978 Man of the Year (Royal Association for Disability and Rehabilitation)
- 1978 Phi Beta Kappa Award in Science "for contribution to the literature of science" (Phi Beta Kappa)
- 1983 John Locke Medal (The Worshipful Society of Apothecaries)
- 1984 Prix du Docteur Robert Netter (Netter Prize) (Académie Nationale de Médecine, France), "for research on developmental disorders of vision"
- 1986 Cairns Memorial Medal (Cairns Memorial Fund)
- 1988 Norman McAlister Gregg Award in Medical Science (Royal Australian and New Zealand College of Ophthalmologists)
- 1989 Owen Aves Memorial Medal (Yorkshire Optical Society)
- 1989 Michael Faraday Prize and Medal (The Royal Society)
- 1989 Robert Doyne Medal (Oxford Ophthalmological Congress)
- 1990 GL Brown Prize (The Physiological Society)
- 1990 John P McGovern Science and Society Medal (Sigma Xi, Research Triangle Park, NC, USA)
- 1991 Montgomery Medal (Royal College of Surgeons in Ireland and the Irish Ophthalmological Society)
- 1992 Finalist for the Science pour l'Art Prize (Moët Hennessy/Louis Vuitton, Paris, France)
- 1993 Osler Memorial Medal (University of Oxford)
- 1993 Ellison-Cliffe Medal (Royal Society of Medicine)
- 1994 Charles F Prentice Award and Medal (American Academy of Optometry)
- 1995 Annual Review Prize (The Physiological Society)
- 1996 Alcon Research Institute Award "for research relevant to clinical ophthalmology" (Alcon Research Institute, Fort Worth, Texas)
- 1998 Memorial Medal of the Charles University, Prague, Czech Republic
- 2001 Alfred Meyer Award (British Neuropathological Society)
- 2001 Charter Award and Medal (Royal Society of Biology; formerly Institute of Biology)
- 2001 Baly Gold Medal (Royal College of Physicians)
- 2001 BNA Award for Outstanding Contribution to Neuroscience (British Neuroscience Association)
- 2001 Menzies Medal (The Menzies Foundation, Melbourne, Australia)

- 2004 BioIndustry Association Award “for outstanding personal contribution to bioscience”
- 2004 Lord Crook Gold Medal (Worshipful Company of Spectacle Makers)
- 2005 Edinburgh Medal (City of Edinburgh)
- 2005 Science Educator Award (Society for Neuroscience)
- 2005 Harveian Oration (Royal College of Physicians)
- 2006 Kenneth Myer Medal (Howard Florey Institute, University of Melbourne, Australia)
- 2008 Finalist (with Sir Martin Evans and Sir David King) for the Morgan Stanley Great Briton of the Year Award
- 2009 James Bull Gold Medal (British Society of Neuroradiologists)
- 2010 Winner, Science documentaries, 2010 Festival de Film CinéGlobe, CERN, Geneva, Switzerland for The Man Who Stopped Smoking; documentary on the life of Sir Richard Doll, presented by Colin Blakemore; made for the BMJ (http://cineglobe.ch/2010/)
- 2010 Ferrier Prize & Lecture (The Royal Society)
- 2010 Ida Mann Medal (Oxford Eye Hospital)
- 2011 EXCEL Silver Award from Association Media and Publishing for the Society for Neuroscience Annual Report 2010, with illustrations from the Blakemore lab, Oxford
- 2012 Lord Brain Memorial Medal (Barts and The London School of Medicine and Dentistry)
- 2012 People’s Republic of China Friendship Award (China’s highest honour for foreigners)
- 2012 Ralph W Gerard Prize “for outstanding contributions to the field of neuroscience” (Society for Neuroscience)
- 2012 Chandaria Laureate (School of Advanced Study, University of London)
- 2013 Shortlisted for the Science Commentator Award (Editorial Intelligence)
- 2013 Kelvin Medal (Royal Philosophical Society of Glasgow)
- 2014 Member of the Berkeley Optometry Hall of Fame, University of California
- 2014 Member of the Science Council’s 100 Scientists (100 Leading UK Practising Scientists
- 2014 Knighthood in the Birthday Honours List for “contributions to scientific research, policy and outreach”
- 2014 Inaugural Award for Openness on Animal Research (Understanding Animal Research)
- 2015 Lennox K Black International Prize in Medicine (Thomas Jefferson University, Philadelphia)
- 2015 Elise and Walter A Haas International Award (University of California, Berkeley)
- 2018 President’s Research Medal (awarded quadrennially by The College of Optometrists)
- 2018 No 9 of the “30 Most Influential Neuroscientists Alive Today"
- 2020 Listed among “Top Longevity Scientists and Experts” in the Report on Longevity Industry in the UK (Aging Analytics Agency)

- Chair of the Selection Committee for The Brain Prize of Grete Lundbeck's European Brain Research Prize Foundation.

**ACKNOWLEDGEMENTS**

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**Figure and table captions**

**Figure 1.** Colin Blakemore with Horace Barlow on Colin's 70th Birthday celebration symposium at St John's College, Oxford. Photograph by Zoltán Molnár. (Online version in colour)

**Figure 2.** Blakemore Family (from left to right – Sarah-Jayne, Colin, Andrée , Jessica & Sophie) on the occasion of Jessica Blakemore's wedding. Photograph supplied by Sarah-Jayne Blakemore. (Online version in colour)

**Figure 3.** Group photo of Colin Blakemore's 70th Birthday celebration symposium at St John's College, Oxford. (Online version in colour)

**Figure 4.** responses of two individual cortical neurons (left and right columns) from the cat primary visual cortex, recorded by Barlow, Blakemore and Pettigrew. The neurons are orientation tuned as Hubel and Wiesel described. The panels from top to bottom show, in sequence, the response to stimulation in left eye alone, right eye alone and three forms of simultaneous binocular stimulation of left and right eyes. The binocular response is strongest at a particular spatial offset between the left and right stimuli. Barlow, Blakemore and Pettigrew realised that this specificity allows the neuron to signal binocular depths when the cat is viewing with normal eye co-ordination. Adopted from Barlow et al., (1967).

**Figure 5.** Horace Barlow FRS, Colin Blakemore FRS and Jack Pettigrew FRS in 2004, 37 years after the publication of their landmark study on 3D visual perception in 1967 (Barlow et al., 1967). Photo from Colin Blakemore's collection. (Online version is in colour)

**Figure 6.** Optical imaging experiments by Sengpiel et al., (1999) to reveal the reorganisation of orientation columns in the cat visual cortex (V1) resulting from early selective exposure to contours of one orientation that was originally revealed with electrode recordings by Blakemore and Cooper (1970). The inset photograph shows a cat, wearing a ruff to restrict vision of its own body, standing on a glass platform in a large cylindrical chamber the internal walls of which were painted with high-contrast horizontal stripes. The cats in this study were exposed to the striped environment for a total of 75–120 hours between 2·5 and 6 weeks of age. Each image on the left shows a view, about 8 mm across, of V1 of the right hemisphere (at the top) and part of the left V1 (bottom left), in an anaesthetised cat. During the collection of each optical image, moving stripes were projected on to a screen in front of the cat's eyes, and the orientation of the stripes is indicated by the line segment next to each frame. Areas of neuronal activation appear dark. Clearly, the regions of cortex responding to the horizontal stripes (the orientation experienced earlier in life) were much larger than those responding to other orientations. The histogram (bottom right) plots the cortical area devoted to the different orientations, zero being horizontal. Early exposure

produces a substantial expansion in the size of columns devoted to the experienced orientation. Data from Sengpiel et al., 1999 and reproduced from Blakemore, 2005.

**Figure 7.** The "barrel field" of the primary somatosensory cortex of the rodent has provided an excellent model system to identify molecular and cellular mechanisms of activity-dependent plasticity of sensory areas and provided strong evidence for the existence of sensitive or critical periods. A: The somatic sensory cortex in the adult mouse has a large area dedicated for the representation of the sensory innervation of the whiskers. B: On a tangential section through the region where thalamic axons terminate (layer 4), Nissl staining revealed layer 4 cell bodies that are organised into densely packed walls of the "barrels", also called septa, which form a pattern corresponding to the array of whiskers on the opposite face. Thalamic projections from single whiskers terminate in the cell-sparse halo in the middle of each barrel. C: If a row of whiskers is removed within the first few postnatal days, the corresponding set of barrels fails to develop normally (arrow) but if this ablation is later, no such changes occur. D: In a one-week-old mouse, the barrels have clearly formed, although the septa appear thicker. E: Similar preparation from a 1-week-old mouse with a null mutation of the gene for phospholipase C-1. The layer 4 cortical cells are distributed evenly because their migration to form the walls of the barrels has been disrupted. Scale bar=100um. F: Same as E but stained for metabolic enzyme cytochrome oxidase: this reveals that the thalamic axons segregate normally according to the peripheryrelated pattern, but they fail to impose a cytoarchitectonic pattern of layer 4 cells because of the lack of mGluR5-phospholipase C-1 pathways. From Blakemore 2005; Original data from Hannan et al., (2001).