LAWRENCE WEISKRANTZ
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Larry Waite

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INTRODUCTION

Lawrence (Larry) Weiskrantz, widely recognized as one of the world’s leading researchers in cognitive neuroscience, was professor and head of the Department of Experimental Psychology at the University of Oxford from 1967 until his retirement in 1993. Under his leadership, the department became, and continues to be, one of the world’s leading centres for research in cognitive neuroscience. While at Oxford, he led a series of ground-breaking neuropsychological studies of residual cognitive and behavioural processing in patients with amnesia and cortical blindness. It was his demonstration of residual, but unconscious, visually-driven behaviour in patients who were clinically blind from damage to primary visual cortex that is his greatest legacy. He coined the now familiar term ‘Blindsight’ to refer to this remarkable ability. This work established Larry as a leader in research on unconscious processing, showing that operations from the control of action to high-level cognitive functions can unfold without conscious awareness. Because of his pioneering work, the study of the neural substrates of unconscious cognitive processes is now an essential and prominent part of the cognitive neuroscience enterprise worldwide.

* E-mail: mgoodale@uwo.ca
Larry’s father, Benjamin Weiskrantz, emigrated from Ukraine to America in 1913 at the age of 23. Benjamin, unlike his older siblings, who were largely uneducated, had attended a leading school, or ‘gymnasium’, in Ostrag, one of the oldest cities in Ukraine. Having a classical education proved to be an enormous advantage when Benjamin arrived in Philadelphia. He was admitted almost immediately into Temple University Medical School. After graduating with his medical degree, he remained on staff at Temple until 1929 and then went into private practice.

Larry’s mother, Rose Rifkin, also came to America from Ukraine, but as a young child of six with her parents. Benjamin and Rose met and married in Philadelphia. They had two children, Larry and his older sister, Charlot. Sadly, only a few years later, in 1932, Larry’s father died of kidney failure, leaving Rose to cope with Larry and Charlot entirely on her own. She decided that the only option was to arrange for Larry to be admitted into an orphanage. After much research, she settled on Girard College (figure 1), founded in 1833 as part of the legacy of Stephen Girard (1750–1831), a wealthy Franco-American merchant banker. Girard envisaged the college as a residential school for ‘poor, white, male orphans’. An orphan, according to Girard, was someone who was ‘fatherless’ and Larry was certainly that. The college had a strong academic record and was, by Stephen Girard’s decree, free from religious inculcation. Rose applied for admission on Larry’s behalf and he was admitted. According to Larry, this was a wise decision—and for him a life-changing event. More details about Girard College, and Larry’s life, can be found in the online supplementary material.

The curriculum at Girard was rigorous and broad. Larry excelled in academic courses and, in addition, was instructed in carpentry, machine-shop operations, shorthand, accounting, automobile maintenance and a host of other practical subjects. Larry flourished in the camaraderie that is often found in institutions like Girard and developed a certain self-sufficiency that comes from not living at home. In 1942, he graduated at the top of his class and at 17 was the class valedictorian.

Although his high-school education had officially ended, Girard College permitted Larry and other boys who were not yet 18 to stay on an extra year and take college level courses taught by staff from nearby universities. Larry decided that he enjoyed scholarship enough to contemplate continuing his studies at university. At the same time, he wanted to stay in the Philadelphia area and took it upon himself to apply to every college in eastern Pennsylvania that he could find listed in the Girard library. To his astonishment and delight, he was accepted on a working scholarship to Swarthmore College, which required him to work a few hours a week as a busboy in the cafeteria and later on as a technical assistant in the physics department, helping to set up practical classes.

At the time, according to Larry, he had no idea how lucky he was. Swarthmore was (and still is) one of the leading liberal arts colleges in the US. Founded in 1864 by Quakers, it had a formidable scholarly reputation and boasted many well-known figures in science and the arts. Larry, who was given a year’s university credit for the courses he had taken in his final year at Girard, found himself swept up in the intellectual life at Swarthmore, which was tempered by its tolerant Quaker heritage. He decided to major in physics, a subject that had interested him at Girard, and one that appealed to his fascination with gadgets and experimentation. As it turned out, physics at the university level was not as engaging as he thought it was going to be. Moreover, his concentration was not helped by the fact that many of his classmates were
young women; Swarthmore was a pioneer in co-education. More importantly, it was 1943 and he and other young men about to turn 18 were waiting to be called up to serve in the war that was still raging in Europe and the Pacific. He did not have to wait long. A short time after registering for the draft he was called up.

Larry was not sent to the front line, but ended up serving in the US Army Air Force as a cryptographic technician, learning how to operate various coding devices. He was shipped to Suez and then, after a brief interlude in Egypt where he had time to explore Cairo and the pyramids at Giza, was flown to Tehran where he spent many weeks coding and decoding messages. By then, the war in Europe had all but ended and he was ordered to a base in Bahrain, and then Saudi Arabia, before ending his stint in the Middle East in Cairo, where he was promoted to sergeant and put in charge of the code room at the airbase. At the war’s end, Larry and his company were flown to Casablanca where they embarked on a troop ship for home.

Larry was able to return to Swarthmore under the Servicemen’s Readjustment Act of 1944 (the so-called GI Bill of Rights). Because of his disenchantment with physics (arising in part from the horrors of Hiroshima and Nagasaki), Larry decided to major in psychology with minors in philosophy and English literature, a combination of studies he hoped would provide him with some insights into human nature. He had already been exposed to some psychology courses at Swarthmore and he knew that he would get excellent instruction. Indeed, the Department of Psychology at Swarthmore had some of the leading lights in the field, including
Wolfgang Köhler, Hans Wallach and Solomon Asch, all well-known psychologists in the Gestalt tradition.\(^1\)

Again, Larry flourished at Swarthmore, where intellectual rigour was combined with a reflective and tolerant Quaker tradition. He became editor of the school newspaper, played the violin in the college orchestra and founded a student group opposing racism.

In 1949, Larry graduated with highest honours from Swarthmore and began to make plans to take up graduate work at Harvard. Then another opportunity presented itself. He was selected as the recipient of a new scholarship awarded by a Mr Catherwood that would allow him to undertake academic activity of his own choosing, even abroad. Because some of Larry’s classmates and friends had elected to go to Oxford, Larry decided to use the Catherwood scholarship for a year’s personal study at the then Institute of Experimental Psychology at Oxford. He wrote to George Humphrey, the first professor of psychology at Oxford, and to his delight was accepted.

The Oxford Institute of Experimental Psychology, which had been founded only two years earlier in 1947, was housed in what used to be an old school building on Banbury Road. Although there were only a few students, graduate and undergraduate, Larry found the intellectual atmosphere invigorating. He discovered that he was eligible for graduate studies at Oxford and that members of the Allied Forces with war service could be excused from one year of university residence. He had already begun work on a research project that he had devised to extend the understanding of figural after-effects, a phenomenon in the Gestalt tradition he had learned about from Köhler and Wallach at Swarthmore. This project formed the subject of his graduate thesis. He was examined by viva voce by George Drew and Oliver Zangwill (FRS 1977), and received his graduate degree (initially a BSc but later changed to an MSc when Oxford abandoned the BSc). He published the results of the thesis in the *Quarterly Journal of Experimental Psychology* in 1950—his first publication (1)*.

After his successful year at Oxford, Larry returned to the US and entered the PhD programme at Harvard, in the Department of Experimental Psychology. He found himself drawn to what was then called ‘physiological psychology’, the study of the neural foundations of behaviour. His interest was further magnified when he was asked to teach an undergraduate course on the subject at nearby Tufts University—standing in for a faculty member who was ill. Around the same time, he learned from a friend that Karl Pribram had set up a non-human primate laboratory at a mental hospital in Hartford, Connecticut. Pribram, who was a skilled neurosurgeon, had given up clinical practice to devote himself to the study of the cerebral bases of behavioural and cognitive function in the macaque monkey. After visiting the laboratory, Larry managed to persuade the Harvard department and Pribram that he should conduct his thesis research in the Hartford laboratory. This move was a defining moment for Larry—one that led him to incorporate the non-human primate model into his research for the next 40 years and shaped the way in which he approached questions about behavioural and cognitive deficits and spared abilities in neurological patients.

Pribram and his group were challenging the then prevalent idea that the cerebral cortex worked largely as an undifferentiated whole, with little specialization beyond early sensory processing. By careful behavioural testing of monkeys with discrete brain lesions, the group

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1 The main tenet of Gestalt psychology is the idea that people tend to perceive objects as a whole and not simply as a sum of their parts. The word ‘Gestalt’ means ‘form’ in German.

* Numbers in this form refer to the bibliography at the end of the text.
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were able to demonstrate that there was in fact a great deal of specialization for cognitive functions, such as perception, memory and learning. For his thesis project, Larry decided (at Pribram’s urging) to investigate the possible role of damage to an ancient brain structure, the amygdala, in the emotional changes that accompany large lesions of the temporal lobe. The project worked out well and was eventually published (3).

The work that Larry had carried out with Pribram’s group easily satisfied his thesis requirement, but he was left with the hurdle of fulfilling the foreign language requirements for the Harvard PhD. He had to demonstrate modest proficiency in two other languages. He chose German and French. He passed his German exam easily but in order to prepare for the French exam, he elected to get some instruction. He took lessons from a young English woman, Barbara Edna Collins, whom he had met through a mutual friend. As he began to take his tutorials from Barbara, he found himself falling in love with her. Larry passed his French exam and was granted his PhD in 1953. A year later, he and Barbara were married.

After graduation, Larry was content to continue working with Karl Pribram, albeit on soft money. Barbara was working as a teacher at the American School for the Deaf in West Hartford, close to the hospital where the Pribram laboratory was located. It all seemed settled. But then, as things tended to do in Larry’s life, another opportunity presented itself. He received a letter from the US National Academy of Sciences letting him know that he had secured a senior postdoctoral fellowship in physiological psychology, with support from the Carnegie Foundation. It was an attractive award, providing a generous stipend for a year’s research anywhere in the world. The possibility of returning to Oxford intrigued Larry—coupled with the opportunity of getting to know Barbara’s parents in England, whom he had yet to meet. Larry immediately wrote to Paul Glees, a leading anatomist based in the University of Oxford Department of Physiology, explaining that he would like to learn how to trace out the connections of the different nuclei in the amygdala. Glees agreed to take him on, and once more Larry, this time with his new wife, set off for a year in Oxford.

Larry and Barbara arrived in the UK. It all seemed perfect. But then Paul Glees let Larry know that he was spending the year in the States at the National Institutes of Health. Although this was initially a disappointment, Larry soon started some projects on his own, something that he was used to doing from his earlier days in Oxford. One of the projects, which looked at the effects of visual deprivation on retinal development in kittens, ended up being published in *Nature* (4). It definitely turned out to be a good year.

Just as Larry and Barbara were about to return to the US, their lives took another surprising turn. Larry was asked by Oliver Zangwill, who was then professor of psychology at University of Cambridge, if he would be willing to direct a new non-human primate research laboratory at Cambridge, one based on the Hartford laboratory developed by Pribram, at least for a couple of years. This presented Larry and Barbara with a difficult decision, but after some deliberation, they decided that Larry should take up the post.

After arriving in Cambridge, Larry and Barbara decided to take a chance on buying and living on a converted ex-working narrowboat, the *Phosphorus*, which they thought would provide cheap, and certainly unusual, accommodation for the two years or so they expected to spend in Cambridge (figure 2). In the end, they stayed in Cambridge for 11 years, spending most of that time living on the *Phosphorus* with a mooring opposite Jesus Green!

Larry and Barbara took the narrowboat on many trips along the canals and waterways of England, including a memorable trip from Cambridge to Oxford and back. The Oxford trip was only one of many adventures Larry and Barbara had on the *Phosphorus*, but with the
birth of their children, Conrad in 1963 and Julia in 1966, they eventually had to abandon the narrowboat for dry land.

During his 11 years at Cambridge, Larry had the opportunity to interact and collaborate with some of the leading researchers in brain and behaviour, particularly in vision, an emerging interest of his. These included Richard Gregory (FRS 1992), William Rushton (FRS 1948), Giles Brindley (FRS 1965) and Horace Barlow (FRS 1969). He also regularly met with researchers from the sub-department of animal behaviour at Madingley, headed by William Thorpe (FRS 1951). In fact, in the late 1950s and early 1960s, Zangwill and Thorpe organized a lively and well-attended discussion group for psychologists and biologists interested in behaviour, which was held in Thorpe’s rooms in Jesus College. Larry was an enthusiastic participant and later wrote a chapter for a book edited by Thorpe and Zangwill that emerged from these meetings (5). The chapter foreshadowed some of the issues associated with his highly influential work on spared visual abilities in monkeys and humans with damage to primary visual cortex.

Larry also accumulated a number of first-rate graduate students at Cambridge, including Alan Cowey (FRS 1988), Susan Iversen, Nicholas Humphrey, Paul Dean and Charles Gross. This was perhaps not surprising, because by all accounts he had a reputation of being an excellent supervisor. Alan Cowey wrote in his autobiography (2006) that Larry was the kind of supervisor who: ‘suggested rather than ordered, explained rather than pronounced, and had
an open-door policy with respect to his students. He was the best possible kind of supervisor for a young neuroscientist.’

Although Larry’s research programme was going well in Cambridge, he still had concerns about his financial security, particularly now that he had two children. He and Barbara were beginning to think about returning to the States. Oliver Zangwill wanted Larry to stay in the UK, but thought that the likelihood of a promotion to a readership and a permanent position at Cambridge was remote. So, he suggested instead that Larry consider applying for the vacant chair in psychology at Oxford. Larry, of course, was familiar with the Oxford department, and was not averse to the idea of returning there. After much ‘dithering’, as Larry put it, he sent off an application. A few days later, and perhaps not surprisingly, given how much Larry was respected, although he had not yet heard from Oxford, Cambridge came through with a readership. For Larry, this seemed ideal. He would now have a permanent position, an increased salary and, most importantly, freedom to devote a substantial portion of his time and energy to research. So, with that, he withdrew his application to Oxford and accepted the readership at Cambridge.

Things did not end there, however. Oxford wrote back to Larry, asking him to re-consider withdrawing his application and to accept the chair! A visit was arranged when he could look around the research facilities (including the plans for the new building on South Parks Road) and Magdalen College, to which the chair was attached. Larry was impressed with both and, after some discussion with Barbara and his colleagues at Cambridge, decided to accept the position. It was hard to turn down such a prestigious position, particularly when he had a real chance to shape the direction of research in psychology at Oxford.

Of course, Larry did some negotiating before he took the job. He wanted to continue his work on non-human primates, and thus, before the new building was finished, he needed assurance that there would be temporary but serviceable facilities for such work in the current building, as well as access to the surgical facilities in the Department of Physiology. He requested that more academic, administrative and technical posts be made available as psychology expanded in the new building. He also felt that it was important to have an honours psychology programme that would run in parallel with, but independently from, the ‘traditional’ PPP (philosophy, physiology and psychology) programme at Oxford. His negotiations were (largely) successful and he agreed to take up the chair in the academic year of 1967–68.

The Institute of Experimental Psychology’s temporary housing was at 1 South Parks Road, close to where the new building, which was to be shared between psychology and zoology, was being erected. It was an old three-storey Victorian building, with Larry’s office located in a corner on the top floor. I remember the building well because I joined Larry’s research team in 1969 as a postdoctoral fellow, with a newly-minted PhD from the University of Western Ontario in Canada.

In the two years I spent at Oxford, I had many opportunities to discuss science with Larry, most of which took place in his tiny top-floor office. Our discussions were always stimulating, for me at least. Although Larry often challenged my ideas, he was always supportive and encouraging. Moreover, he had a sly sense of humour, and loved wordplay. As a consequence, conversations with him were marked not only with insightful comments on research but with unexpected puns (some of them real ‘groaners’) and other verbal pranks.

Although the foundations for the new building at South Parks Road and St Cross Road were already being dug in 1967, the year Larry arrived in Oxford, it wasn’t ready
for occupation until 1970. That year, Larry and most of the members of the Institute of Experimental Psychology moved into the building—and at the same time the Institute became the Department of Experimental Psychology. After spending so many years in the small (and totally inadequate) house at 1 South Parks Road, Larry and his departmental colleagues were delighted with the new space. In addition to new non-human primate facilities, human laboratories and office space, there were wide corridors and lots of open space for getting together for tea and coffee. There were initially some tensions that Larry had to deal with between the psychology and zoology departments with respect to parking, furnishings and shared space, but, in general, relations between the two departments were cordial and often productive with respect to scientific collaborations.

Under Larry’s watch, the Department of Experimental Psychology at Oxford became one of the leading psychology departments in the world, particularly in the field of cognitive neuroscience. He had brought Alan Cowey, Edmund Rolls and Nicholas Humphrey with him from Cambridge, and over subsequent years recruited Richard Passingham (FRS 2009), Donald Broadbent (FRS 1968; who sadly passed on shortly after moving to Oxford) and David Gaffan. He even persuaded Jerome Bruner, a leading developmental psychologist, to leave Harvard and take up the Watts Chair in Experimental Psychology. Other notable researchers in the department were Patrick Rabbit, Jeffery Gray, Anne Triesman (FRS 1989), Michael Argyle, Brian Rogers and Peter Bryant (FRS 1991). It was indeed a formidable array of scientists—and Oxford’s reputation in experimental psychology, particularly cognitive neuroscience, continues today.

Larry also had success on other fronts. With the encouragement of the Organisation for Economic Co-operation and Development (OECD), who were interested in expanding neuroscience meetings in Europe, he spearheaded a committee aimed at exploring the possibility of creating an association of scientists interested in the relationship between brain mechanisms and behaviour. After some enthusiastic discussion and consultation with other researchers across Europe, a new society was formed in 1968, the European Brain and Behaviour Society, known more familiarly as EBBS. Larry became its first president and the first meeting of EBBS was held in Marseilles in 1969. EBBS continues to be a flourishing enterprise and celebrated its fiftieth anniversary in 2018, the year that Larry died.

Larry was also a force in the Oxford community. One accomplishment he was particularly proud of was the creation of a cycle path that allows one to cycle from Marston and Headington to South Parks Road, and from there to other university buildings and the city centre, thereby avoiding the busy roads in central Oxford. Navigating the bureaucracy and handling the always sensitive town and gown relations were not easy tasks, but with the help of his supporters, both from the City of Oxford as well as from the university, Larry’s vision prevailed—although it must be said that it took fully 17 years from the initial submission in 1974 to the opening in 1991. Larry’s persistence and eventual success led one supporter to suggest that the path be called The Wise Way in Larry’s honour—a proposal that sadly did not come to pass.

Larry retired in 1993, when he reached 67, the mandatory age for retirement at that time. He became professor emeritus as well as an emeritus fellow of Magdalen College, and continued his research essentially unabated, perhaps even more so after he was freed from administrative responsibilities.
As Larry would be the first to admit, much of his research was driven by unexpected findings that emerged from his experiments. A good example of this happened early in his career during the year he spent at Oxford on a Catherwood Scholarship, well before he completed his PhD at Harvard. While he was studying whether or not a figural after-effect would occur in a stroboscopic display after viewing a stationary adapting stimulus (1), he realized that he needed to carry out a control experiment in which participants simply imagined the black fixation point that had been used in the main experiment. To his surprise, he found that one of the participants later reported seeing a white square of roughly the same size (a negative after-image) that presumably had been induced by the black square she had imagined in her mind’s eye. This mentally induced after-image, like the normal after-image that is induced by looking at a bright light source, obeyed Emmert’s Law (Emmert 1881): the further the distance of the surface on which the after-image is ‘projected’, the larger it appears to be. All of this led to another publication in the same journal in the same year (2). This phenomenon had been noted by William James and similar cases were reported by Ian Oswald (1957), a young researcher who studied at Oxford shortly after Larry left. Larry’s work on the topic foreshadowed a large body of work showing that after-images are not simply driven by activity in the retina, but are modulated by a number of central processes (Kirschfeld 1999).

Larry’s work on the amygdala, which formed the basis of his PhD thesis at Harvard, was conducted at Karl Pribram’s lab at Hartford, Connecticut. The starting point for the work was the Klüver–Bucy syndrome, an interesting collection of symptoms that was observed by Heinrich Klüver and Paul Bucy after they carried out bilateral lesions of the temporal lobe in macaque monkeys in the 1930s (Klüver & Bucy 1937, 1939). The monkeys, who had been quite fearful and aggressive before the surgery (some extremely so), became quite tame and docile afterwards. In addition, the monkeys showed visual agnosia, an inability to recognize objects by sight, and also a profound memory deficit. Finally, the monkeys became hypersexual, attempting to engage in sexual activity when confronted with other monkeys of either sex, inanimate objects or even the animal technicians. Pribram and his younger colleague, Mortimer Mishkin, had already demonstrated a role for the temporal lobe in visual discrimination learning and memory, but the possible role of the temporal lobe in emotion and sexual behaviour was still unexplored. One structure that Pribram thought might be implicated was the amygdala, an ancient structure buried deep in the temporal lobe. He persuaded Larry that this might make a promising project for his PhD.

Larry, with Pribram’s help, made lesions of the amygdala in several monkeys. He found that these lesions, which spared much of the rest of the temporal lobe, increased tameness and reduced or eliminated previous fear responses. He also concluded that the monkeys had difficulty identifying reinforcing stimuli (3). This work still stands as a seminal study in demonstrating the role of the amygdala in the mediation of emotional behaviour, particularly fear.

Although Larry worked on a number of different research questions after his move to Cambridge, including the neural substrates of hearing and taste, more and more of his attention was shifting to the role of different areas of the cerebral cortex in visual perception. He and his graduate students began to explore the effects on visual perception of making discrete lesions in different areas in the cortical visual pathways in the macaque monkey from primary visual
cortex in the occipital lobe (where visual signals first enter the cerebral cortex) to higher-order visual areas in the temporal lobe.

One question that they addressed was one that had pre-occupied physiologists and psychologists from the late nineteenth century onwards: how much residual vision was present in the absence of primary visual cortex? According to some investigators pursuing this question, removal of the occipital lobes in monkeys caused permanent blindness whereas, according to others, animals with such lesions showed near-perfect vision (for an illuminating review of this early work, see (18)). Given that humans with such damage appeared to be essentially blind, the question was an important one. Together with Alan Cowey, one of his new graduate students at Cambridge, Larry carried out a study in which they made careful bilateral lesions of primary visual cortex in monkeys, with the damage centred as much as possible on the part of the occipital lobes responsible for central vision, which both monkeys and humans use when they look directly at a visual stimulus (7). Post-operatively, they found that the monkeys showed a profound decrease in their ability to detect the presence of a simple visual pattern. Moreover, the severity of the visual deficit corresponded with the completeness of the lesion in primary visual cortex, but, critically, the drop in visual performance was not absolute. The animals could still detect visual stimuli, even when the patterns were illuminated with rather dim light—and their ability to do this improved with training. Moreover, the affected region of visual space also contracted over time. In a separate set of experiments, in which Larry and Alan Cowey monitored where the monkeys were looking (using an innovative method for measuring eye position that Cowey had devised), they found essentially the same thing: monkeys continued to detect visual stimuli in parts of the visual field that would normally have been sub-served by the damaged region of primary visual cortex (6).

The spared visual abilities that were observed in the monkeys stood in sharp contrast to what is commonly observed in the clinic. Typically, humans with damage to primary visual cortex report seeing nothing in that part of their visual field that corresponds to their brain damage. Sometimes they might report seeing movement, when, for example, an open hand is moved rapidly back and forth in front of their eyes, or they might be able to detect the presence or absence of light. But they cannot see visual patterns, colour or shape. Even with more rigorous testing in the laboratory, people with damage to primary visual cortex seemed to have far less residual vision than monkeys with similar lesions. One of the most common explanations for this discrepancy at the time was that the neural circuits supporting cognitive, perceptual and motor abilities in humans have migrated over evolutionary time to the expanding cerebral cortex. This idea is often referred to as ‘encephalization of function’ (for an early discussion of this idea, see Marquis 1934). Vision, the argument goes, is no exception, so that visual processing in humans is more dependent on the cerebral cortex than it is in other animals, even monkeys, with much of the visual processing being mediated by neural circuitry in sub-cortical areas, such as the thalamus and the mid brain. Although it is certainly the case that there has been an enormous expansion of the cerebral cortex in humans, Larry did not believe that encephalization of function was the explanation for the clear difference between the apparent residual visual abilities of monkeys and humans following damage to primary visual cortex (5, 7). He argued that it had more to do with the way in which vision was assessed in the two species.

In the clinic, patients with damage to visual areas of their cerebral cortex are typically asked what they ‘see’ when they are presented with visual stimuli. This clearly cannot happen when monkeys are tested. Instead, monkeys are trained to detect or to discriminate between
visual stimuli for a juice or food reward. From the monkey’s point of view, whether it ‘sees’ the stimuli consciously or not does not matter. It is interested only in getting the reward. Thus, it might somehow be able to associate non-conscious visual signals or visually-driven signals from proprioception or even motor commands with one of the visual stimuli it was presented with, even though it doesn’t actually ‘see’ the stimulus. Larry speculated that if patients were tested in the same manner as monkeys perhaps they too would show evidence of residual but non-conscious visual processing. An opportunity to test this idea did not present itself until a decade later. But in the meantime, the idea of well-developed non-conscious processing in humans received support from an entirely different line of research that Larry had embarked upon.

After his move to Oxford in 1967, Larry began a long-term collaboration with Elizabeth Warrington (FRS 1986), who was based at the National Hospital for Neurology and Neurosurgery in London. The problem they decided to tackle was whether or not severely amnesic patients might show evidence of implicit (unconscious) learning even though they had no explicit (conscious) memory of ever having been exposed to the learning situation. Such patients, who most often have damage to the temporal lobes, cannot remember day-to-day events beyond a minute or two. They will deny, for example, having seen their doctor or nurses before and will show no recognition of them no matter how many times they meet them. Much of their memory for events before the brain damage or disease might also be disturbed, although very old memories may be recalled. Despite these profound disturbances in memory, their other cognitive skills are often relatively intact, provided they are tested in a way that does not put heavy demands on memory.

Earlier work by Brenda Milner (FRS 1979) at the Montreal Neurological Institute had shown that the famous patient HM, who showed a profound disturbance in his ability to form new memories, was able to learn motor skills, such as mirror drawing, even though every time he was presented with the task he was convinced that this was the first time he had seen it (Milner 1962). It was this kind of evidence for residual unconscious learning that led Larry and Elizabeth Warrington to explore whether or not densely amnesic patients (some of whom had damage to the anterior temporal lobe, like HM) would also show evidence of unconscious retention of high-level and meaningful stimuli such as pictures and words (8–10, 13). In some of their experiments, they first exposed the amnesic patients to a series of pictures (or lists of words in later experiments). Not surprisingly, when they were asked to recall the pictures or words they had been shown earlier, they performed poorly, recalling few or none of the stimuli. But when they were shown visually degraded or incomplete versions of pictures or words, they could identify those stimuli more quickly and accurately if they had been exposed to complete versions of them earlier. Again, they had no conscious memory of having seen them before. This paradigm, in which an earlier presentation of a stimulus, even if it cannot be recalled consciously, can improve recognition of that stimulus, is now called ‘priming’—and has become a standard tool for investigating unconscious learning and memory in laboratories around the world. The use of priming to reveal unconscious memory in densely amnesic patients resonated with Larry’s ideas about how to assess residual vision in humans with damage to primary visual cortex—and it turned out that an opportunity to test this possibility soon presented itself.

2 To treat his intractable epilepsy, HM had undergone bilateral excisions of the anterior temporal lobe (including the hippocampus, a structure now known to play a central role in memory).
Michael Sanders, a neuro-ophthalmologist at the National Hospital in London and a colleague of Elizabeth Warrington, had examined patient DB, who had undergone a unilateral excision of his right occipital cortex for an arteriovenous malformation. Remarkably, Sanders noticed that DB was able to reach out and grasp Sander’s hand in his blind field even though he reported not seeing it. This finding reminded Larry of the results of some ongoing work that Nick Humphrey, a young colleague of Larry’s, was carrying out at Oxford with a monkey (called Helen), who had bilateral occipital lesions. In a series of clever experiments, Humphrey had shown that Helen could look towards and pick up raisins and other small objects scattered on the floor, even though she appeared otherwise blind. These observations, together with a study published the year before by a group at MIT (Pöppel et al. 1973) showing that patients with occipital lesions could move their eyes to unseen targets in their blind field, led Larry and his colleagues at Queen’s Square to see if DB could in fact reach out and point towards targets in his blind field.

As it turned out, DB behaved exactly like the monkey, Helen: when a target was briefly flashed in DB’s blind field, he was able to turn his head and eyes toward it and reach out and touch the location where it had appeared (11). Thus, not only did this confirm the earlier work by the MIT group, it also showed that when a more ‘natural’ response like reaching is used, rather than just a change in eye position, then the evidence for visual control of action in the absence of visual experience is even more convincing and extends further into the visual periphery (figure 3).
DB also offered an opportunity to test Larry’s idea that if residual vision in a human patient were assessed in the same way as it is in the monkey, then it might be possible to demonstrate detection and discrimination for patterns with different orientations (and patterns)—and even measure visual acuity, i.e. how fine a grating could be detected. To Larry’s delight (and amazement) that is exactly what happened. When DB was asked to simply guess which of two patterns was presented—rather than to report whether or not he ‘saw’ the stimuli—his performance, while not entirely normal, was well above chance, as was his visual acuity (11). At the same time, DB would claim that he was ‘just guessing’. It was the ability of individuals like DB to demonstrate visual abilities in the absence of conscious visual experience that led Larry (in his characteristic way) to call the residual abilities ‘Blindsight’, a name that has stuck and is now universally used to refer to the phenomenon (11, 12).

Not everyone, however, was convinced by Larry’s experiments. Some suggested, for example, that the above-chance performance was simply due to stray light stimulating that part of the retina projecting to intact primary visual cortex (e.g. Campion et al. 1983). Others suggested that the residual abilities were being mediated by spared ‘islands’ of intact vision within the blind field (Gazzaniga et al. 1994). These, and other critiques, have been put to rest by a large number of studies, many carried out by Larry and his colleagues, that have systematically eliminated possible counter-explanations. The stray light explanation, for example, has been handled by presenting visual stimuli in the so-called ‘blind spot’ that we all have in the visual field of each eye (14, 15). The blind spot corresponds to the optic disc where the fibres that make up the optic nerve leave the eye on their way to the brain. Of necessity, there are no photoreceptors in that tiny part of the retina. When Larry presented a small spot of light in DB’s blind spot, his guesses about whether or not the light was present were at chance. Yet when the spot of light was presented in neighbouring regions of his blind visual field, DB’s performance was well above chance. If stray light were the explanation, then his performance would be expected to be above chance for both blind spot and non-blind spot trials, yet that clearly was not the case. Of course, as expected, DB denied consciously seeing the spot of light on any of the trials. These and a multitude of other studies since the original report in 1974 have firmly established blindsight as a real phenomenon (11). Well after he had retired, for example, Larry and his colleagues showed that a patient, who exhibited complete cortical blindness after damage to both occipital lobes, was nevertheless able to negotiate obstacles that he reported not seeing as he walked from one end of a cluttered hallway to the other (19). Other patients have been shown to be able to discriminate between fearful, happy and neutral facial expressions that they report not seeing (e.g. (17); Striemer et al. 2019). This particular unconscious ability has been dubbed ‘affective blindsight’. The uncovering of this remarkable range of residual visual behaviours led Larry and others to make distinctions between different kinds of blindsight, based in part on the nature of the spared visual capacities and in part on the reported phenomenology of the patients (for a brief review of these distinctions, see Danckert et al. 2019).

At some level, it could be argued that the fact that a range of different visually driven behaviours survive damage to primary visual cortex is not that surprising; after all, the retina sends projections to a number of different sites in the brain, beyond those that reach primary visual cortex (for a review, see Milner & Goodale 2006). But even though many of these pathways were known to exist, until the work of Larry and his colleagues in the early 1970s, most investigators believed that humans were completely blind after damage to primary visual cortex and, at most, were capable of exhibiting only a few basic reflexes.
such as pupil dilation to a bright light. By testing humans in a way that did not demand conscious report, Larry revealed a whole panoply of spared, but unconscious visually driven behaviours—behaviours that are presumably mediated by the many pathways from the eye to the brain that bypass primary visual cortex. Since his pioneering work, labs around the world have replicated and expanded his demonstrations of residual vision after lesions of primary visual cortex and in many cases have identified the putative visual pathways mediating those spared behaviours (e.g. Ajina & Bridge 2018; Kinoshita et al. 2019; McFadyen et al. 2019).

The most notable feature of Larry’s work on both cortical blindness and amnesia has been his clear and convincing demonstration that many aspects of behaviour from simple actions to more complex cognitive processing can take place unconsciously. Of course, an important question flows from this: if so much can take place without consciousness, then why do we need consciousness at all? Larry tackled this and other vexing questions about the nature of consciousness in his well-known 1997 book, _Consciousness lost and found_ (16). As the title suggests, Larry developed his arguments about consciousness from his and others’ neuropsychological investigations of patients with brain damage, particularly those with damage to primary visual cortex, but in the book Larry goes well beyond this and examines arguments about the possible evolutionary origins of consciousness and why it might have evolved in the first place. These are not easy questions to answer, but
Larry’s ground-breaking work on blindsight and its implications for understanding the neural substrates of consciousness has provided a way forward.

Celebrations of Larry’s contributions to science

In 2006, on the occasion of Larry’s eightieth birthday, a festschrift was organized in his honour at City University in London by Arash Sahraie and John Barbur, close collaborators of Larry after his retirement (figure 4). The meeting was a great success both scientifically and socially, with a number of colleagues past and present in attendance. The talks and other related papers were later published in a special issue of *Neuropsychologia* in 2008; the editorial was a talk entitled ‘Surprises’ that Larry had given at the festschrift. In that talk, Larry reminisced about his scientific life and how he had always pursued an answer to the
unexpected or surprising finding, rather than accumulating knowledge about a foundational question in cognitive neuroscience (20).

Ten years later, in 2016, Marco Tamietto, another of Larry’s post-retirement collaborators, organized a workshop at the University of Torino in celebration of Larry’s ninetieth birthday. Again, this was a festive occasion that brought together many of Larry’s friends and colleagues in a suitably august setting, the home of the Accademia delle Scienze di Torino, a building dating back to the seventeenth century. And, again, Larry gave an inspiring talk about his academic life and scientific career (figure 5). In 2019, another special issue of *Neuropsychologia* was devoted to the talks given at the workshop as well as other papers related to Larry’s scientific contributions. Larry died on 18 January 2018, surrounded by friends and family, less than a year and half after the workshop in Torino.

Larry firmly believed, and I think he was correct, that he was lucky in life, both professionally and personally. In his unpublished autobiography, he wrote in typical Larry fashion: ‘It has been a good life—good students, colleagues, lovely family, in places of intellectual stimulation and congenial independence, with opportunities for flexing one’s research muscles. What more could one ask of Sir Endipity?’

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

| Year(s)       | Description                                                                 |
|---------------|-----------------------------------------------------------------------------|
| 1969–1970     | Inaugural President, European Brain and Behaviour Society                    |
| 1976          | Kenneth Craik Award, University of Cambridge                                |
| 1980          | Fellow of the Royal Society                                                 |
| 1980          | Sir Frederick Bartlett Memorial Lecturer, University of Cambridge           |
| 1987          | Member of the US National Academy of Sciences                              |
| 1987          | James Drever Memorial Lecturer, University of Aberdeen                      |
| 1988–1989     | Member of the Council of the Royal Society                                  |
| 1989          | Ferrier Lecturer, Royal Society                                             |
| 1990          | Member of the Academia Europaea                                            |
| 1990          | Hughlings Jackson Lecture / Gold Medallist, Royal Society of Medicine       |
| 1992          | William James Award, American Psychological Society                         |
| 1992–1999     | Honorary President of the European Society for Psychology and Philosophy    |
| 1996          | Donald O. Hebb Memorial Lecturer, Dalhousie University                      |
| 1997          | Harry Camp Memorial Lecturer, Stanford University                          |
| 1997          | Honorary Doctorate, University of Tilburg                                   |
| 1998          | Werner Heisenberg Lecturer, Bavarian Academy of Sciences / Siemens Foundation, Munich, Germany |
| 1999          | Herbert H. Reynolds Lecturer in History and Philosophy of Science, Baylor University |
| 1999–2018     | Honorary Member, European Brain and Behaviour Society                       |
| 2000          | Stephen Girard Award                                                       |
| 2001–2002     | President, Association for the Scientific Study of Consciousness           |
| 2002          | John P. McGovern Award Lecturer / Medallist, American Association for the Advancement of Science, Boston |
| 2002          | J. Z. Young Memorial Lecturer, University of Oxford                         |
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AUTHOR PROFILE

Professor Mel Goodale FRS

Mel Goodale completed his PhD in psychology at the University of Western Ontario, London, Ontario, Canada in 1969. He then spent two years as a postdoctoral fellow working with Larry Weiskrantz at the University of Oxford. Following his postdoctoral research at Oxford, Goodale accepted a position in the School of Psychology at the University of St Andrews in Scotland, where he began a lifelong collaboration with Professor David Milner. In 1977, he went back to Canada to take up a position at the University of Western Ontario, where he has remained ever since. His early work, in which he demonstrated that the visual control of action is functionally and neurally independent of conscious visual perception, laid the foundation for the Goodale–Milner ‘duplex’ account of high-level vision. Over the last two decades, he has carried out neuroimaging and psychophysical research that has refined and extended the two-visual-systems proposal. He was the founding director of the Brain and Mind Institute at Western, where he holds the Canada Research Chair in Visual Neuroscience.

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