

William Russell Levick (1931–2022)[†]

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ABSTRACT

William R. Levick was one of Australia's most distinguished neuroscientists, making fundamental contributions to our understanding of the neural circuitry of the retina and the visual pathways. Levick's mastery of the extracellular, single-unit recording technology of his era elucidated the visual function of parallel networks of mammalian retinal neurons, each network transmitting via the optic nerve a unique rendering of the retinal image formed by the eye's optical system. His physiological analysis revealed the presence of complex processing at the earliest stages of the visual pathway, thus overturning the prevailing view that complex visual analysis begins in the brain. His best-known example is the discovery of a class of retinal ganglion cells that detect moving objects and identify their direction of motion in the visual environment. Another pioneering line of investigation revealed the irreducible fluctuations of light quanta as a fundamental limit to visual sensitivity and the reliable encoding of visual information by retinal neurons. Levick's legacy as a consummate experimental physiologist rests on his attention to detail, mastery of medical physiology needed for maintenance of first-class animal preparations, innovative resourcefulness in creating custom laboratory apparatus, and sheer intellect for the design, conduct, and assessment of experiments.

Keywords: direction selectivity, mammalian eyes, neurophysiology, orientation selectivity, parallel pathways, quantum fluctuations, retina, vision.

Early life in Australia

William (Bill) Levick was born on 5 December 1931 in Sydney, New South Wales (NSW), Australia. His father Russell Levick was born at Taree, NSW, and his mother Elsie (née Nance) was born at Kempsey, NSW. His father's family was long established in Australia, his grandfather having been a builder and carpenter in the rural Manning River district. Bill's father, the eldest of five brothers, became an accountant in Sydney, and the others became a farmer, a bank manager, a school teacher, and an architect. Bill's mother was the eldest of the three children of the Nance family. Her father was a seafarer born in the Isles of Scilly, UK, and her mother was the youngest daughter in a large family long-established on the central coast of NSW. Bill's maternal grandfather, although without special educational qualifications, was a powerful influence in fostering budding talents of curiosity and learning in his grandson.

Bill's recollection of his childhood years was that of a protected, frugal environment in the aftermath of the Great Depression and throughout World War 2 (1939–45). His father was a very authoritarian figure, and mother a very determined but sentimental individualist. His maternal grandparents, who lived close by, provided a very supportive, cushioning environment amid much sibling rivalry with his younger brother. Bill's public school education was greatly affected by the occurrence of Perthes' disease (*osteochondritis juvenalis*) of his right hip joint. Treatment by immobilisation in a long-leg hip spica for three months necessitated enrolment in correspondence school, followed by twelve

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months' use of crutches, which prevented his participation in sport. His secondary education was at Sydney Boy's High School, where he graduated 'Dux of School' (1948) and 'Top of State in Physics' in the NSW Leaving Certificate Examination (with high distinction in five other subjects). He was also the Australian National Schoolboy Chess Champion of 1949.

University education

Bill was strongly influenced towards a career in scientific research by high school chemistry master L. A. Bassar, who recommended his enrolment in the Faculty of Medicine at the University of Sydney. Again Bill excelled, taking first place in the three-year medical course (1949–51), with prizes for general proficiency and the Grafton Elliot-Smith prize in anatomy. This was followed by two years in the Faculty of Science (1952–3), where he earned a BSc degree with first class honours, won the University Medal in physiology (1953), and also earned an MSc degree (1954). He then returned to the Faculty of Clinical Medicine (1954–6), where, in the final year, he took first class honours and the University Medal with prizes in medicine, surgery, obstetrics and psychiatry. He was awarded the MD and BS degrees in medicine in 1957.

Not surprisingly, Bill's academic performance established an enviable reputation among his fellow students. Dr Jeffrey Clyde in Canberra recalls:

My first meeting with Bill was as a third yr med student when he was demonstrator for our physiology classes. We had heard of his great intellect and were in awe of him. We found him to be disarmingly modest, easy to talk to, always with a twinkle in his eye and a great sense of humour—indeed his uproarious laugh was known as the Levickian guffaw! For years when we would meet, the irreverent but very warm greeting would be 'hung-ho, old cock!' He had the typical Aussie contempt for pretence and elitism—for example after visiting Pompeii he was heard to say 'why do they fuss about this place—it is all busted and wrecked'. Socially, Bill was always a winner—his explosive laughter and rather bawdy sense of humour ensured his popularity everywhere. He was the darling of a number of young women—one of whom was known to serenade him from the street below his bedroom window at Bondi.

Career development

Following his formal education in medicine, Bill was appointed junior resident medical officer (1957) and then senior resident medical officer (1958) at the Royal Prince Alfred Hospital in Sydney. He then returned to the Faculty of Science to study mathematics as an additional subject,

finishing Mathematics I with high distinction (1959) and Mathematics II (1960). A defining moment in Bill's career occurred when he met Peter O. Bishop (FRS 1977), who supervised Bill's first research project, on saltatory conduction in single nerve fibres (Bishop and Levick 1956). Bishop strongly supported Bill throughout his research career in neurophysiology, starting at Sydney, then arranging an opportunity to work with Horace Barlow (FRS 1969) in Cambridge and Berkeley in the 1960s, a partnership that firmly established Bill's reputation for excellence on the world stage. Later, Bishop convinced Bill to return to his native Australia to take up a position as senior lecturer in physiology at the University of Sydney. Bishop's influence is best described in Bill's own words (Levick 1983):

I was headed into a surgical career but for some timely words of wisdom from the 'master of subtlety'. 'Why be a little fish in the big pond of medicine', said he, 'when you could be a big fish in the little pond of research?' How could he have imagined an appeal to vanity might work whereas an appeal to logic might not? Of course, there was a good deal more substance to the appeal in terms of the opportunities for research and it was also a happier time for research in Australia generally. The freedom of the training environment Peter Bishop created at Sydney was breathtaking: you could really learn the art of making things work on your own. It may not have been the fastest way to learn, but the experience is coded indelibly. He, now the 'master of strategy', also steered me imperceptibly into another kind of experience at Cambridge. Here, the magic of physiological investigation was woven with Meccano sets, mirrors, aircraft glue and imagination. The seeming flimsiness was more apparent than real, since this style of work subsequently survived a transatlantic transplantation to the uniquely heady environment on the eastern side of San Francisco Bay where research was conducted as a business as well as a pleasure. Later, with the bravado of youth, I flew in the face of the Australian custodians of my Fellowship in order to stay on at Berkeley, but again it was the shrewd parting words of Peter Bishop that started a slow fuse culminating in my pilgrimage home only 2 years later. I joined him once more in a totally unexpected venture at that Mecca of Australian neurophysiology in Canberra. What an experience it has been! Only now after his retirement do I really appreciate the true qualities behind his success: he had that happy knack of spotting where help would be most effective and he would give it unstintingly. It was not so much the amount of help but the notion of giving a 'fair go' that generated the inspiration that always surrounded him.

In 1966, following the resignation of Nobel Laureate Sir John Eccles FRS, Bishop was appointed professor and head of the department of physiology in the John Curtin School

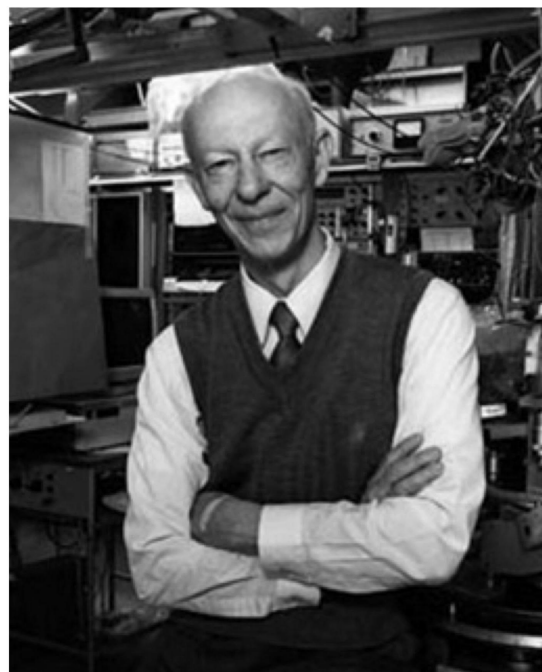


Fig. 1. Professor Bill Levick during his career at the Australian National University in Canberra in the 1970s (left) and in the 1980s (right). Photos provided by Rowland Taylor. Photo (left) is by Stephen Barry, used with permission of the Australian National University Archives (Australian National University Archives: Photographs of people at the Australian National University, ANUA 225–737, Dr William Russell Levick, 1982). Photo (right) is of unknown copyright.

of Medical Research (JCSMR) at the Australian National University in Canberra. As part of his move from Sydney, Bishop negotiated the appointment of Bill as professorial fellow (Fig. 1), thereby giving him the opportunity and resources to help build one of the premier visual neurophysiology centres in the world. One measure of their joint success was election to the Australian Academy of Science (Bishop in 1967 and Levick in 1973), and then to the Royal Society (Bishop in 1977 and Levick in 1982). But both would argue (Henry 1986) that their greatest success was attracting bright minds from around the world to join the effort to address the question of ‘How do we see?’. This scholarly army of research fellows, postdoctoral fellows and PhD students, with their fresh ideas and experimental muscle, were an essential ingredient for scientific advancement during the Bishop–Levick era at JCSMR (Vanev 2020).

Although Bill held a personal chair as professorial fellow, he did not seek administrative advancement into positions of power. For example, he did not seek status appointments such as head of department or influential administrative offices in the university’s central administration. Instead, he focused his attention entirely on laboratory science, mentoring junior colleagues, post-graduate students and visiting scholars (typically from overseas). Working closely with a small team of co-investigators, Bill was personally involved in all phases of research projects, teaching by example how to pursue excellence in scientific research. His publication philosophy was compellingly simple: get it right, then publish.

Directional selectivity of retinal ganglion cells

Vision is the process of gathering useful information about the environment from light entering the eyes. To survive, all animal species require visual information to help obtain food, to avoid becoming food for some predator, and to find a mate to perpetuate the species. These essential tasks involve not only a perceptual awareness of the environment, but also the appropriate motor responses guided by visual sensations. For example, one of nature’s simplest visual systems, the caudal photoreceptor of the crayfish, consists of a single light-sensitive cell that signals the ambient level of illumination to determine if its tail is in a dark hole (Welsh 1934). If not, the animal moves to find a place safe from predators. Cephalopods, by comparison, have eyes containing a single lens that focuses light entering the eye into an optical image on the surface of a primitive retina that consists entirely of a thin layer of light-sensitive cells (Young 1964). Each of these photoreceptors responds to the amount of light arriving from a particular visual direction, or place, in the environment and sends that message to the optic lobe of the animal’s brain without further processing.

Vertebrate eyes are vastly more complex, with a two-lens optical system, one fixed (the cornea) and the other adjustable (the crystalline lens), and an adjustable pupil (iris) to control the amount of light entering the eye. An internal muscle controls the shape of the crystalline lens as part of an auto-focus mechanism in the brain that uses signals gathered

from the retina to ensure the retinal image is well focused. Similarly, an auto-exposure circuit in the brain controls the iris muscle based on signals from the retina. The anatomical structure of the retina is also more complex, having evolved into a multi-layered tissue that separates the tasks of sensing light (by rod and cone photoreceptors) from informing the brain of relevant features of the environment (by ganglion cells via the optic nerve). Moreover, a layer of interneurons (bipolar cells) has evolved to relay signals from photoreceptors to ganglion cells using neural connections (synapses) located in synaptic layers before and after the interneurons. Other interneurons (horizontal and amacrine cells) transmit signals laterally to modulate the transmission of signals from receptors to the brain based on the local activity of neighbouring receptors. This five-layer retina (three containing cell bodies and two containing synapses where information is exchanged and modulated) is a neural pre-processing system that encodes the optical image of the environment before transmission to the brain via the optic nerve. To ensure survival of the species, this pre-processing stage must produce a 'neural image' of the environment that includes biologically useful information and, at the same time, eliminates distractions.

Discovering which environmental features are preserved by the eye and which are eliminated, and how the retina accomplishes this selective filtering, was the central goal of Bill's scientific life. Like the sculptor who removes stone or wood to reveal an envisioned figure, Bill demonstrated empirically that the physiological process of extracting useful visual information from the retinal image is subtractive, using inhibitory synapses to eliminate features of the retinal image that are not useful for driving behaviour. The prime example, for which he is best known, is the asymmetric inhibitory neural mechanism that extracts the direction of moving objects from analysis of the retinal image.

Bill Levick was introduced to his life's quest by Horace Barlow at Cambridge. Prior to his arrival, Barlow had studied the visual behaviour of individual ganglion cells of the frog retina and found a variety of different types. Cells of a given type responded to characteristic 'trigger features' present in the retinal image and were blind to other features. Barlow's explanation for why such cells are important to the animal's survival would prove to be a major influence guiding Bill's career. Barlow said (Barlow 1953):

When feeding, [a frog's] attention is attracted by its prey, which it will approach, and finally strike at and swallow. Any small moving object will evoke this behaviour, and there is no indication of any form discrimination. In fact, 'on-off' units seem to possess the whole of the discriminatory mechanism needed to account for this rather simple behaviour. The receptive field of an 'on-off' unit would be nicely filled by the image of a fly at two-inch distance and it is difficult to avoid the conclusion that the 'on-off' units are matched to this stimulus and act as 'fly

detectors'. ... The retina is acting as a filter rejecting unwanted information and passing useful information.

Armed with his first-class medical qualifications, and thoroughly trained by Peter Bishop in the art and science of recording responses of single neurons in living mammals, Bill Levick was ideally suited for repeating Barlow's experiments in mammals. In a series of experiments conducted in Cambridge and Berkeley, Levick, Barlow and collaborators systematically explored the visual requirements to elicit vigorous responses from ganglion cells of the rabbit retina (Barlow and others 1964). Later, they worked extensively with the cat eye (Cleland and others 1971; Cleland and Levick 1974a, 1974b), with an occasional reunion with the rabbit (Vaney and others 1981; He and others 1998), thereby discovering an even greater diversity of trigger features than reported in the frog. From these experiments it became clear that the analysis of sensory information is carried much further in two synaptic layers of the retina than was commonly supposed.

The most dramatic example of highly specific trigger features was found in the so-called 'directionally selective' ganglion cells. These neurons respond strongly to an object moving across the neuron's receptive field in a certain 'preferred' direction, but respond only weakly or not at all to motion of the same object in the opposite ('null') direction (Barlow and others 1964; Barlow and Levick 1965). It was immaterial whether the object was brighter or darker than the surrounding area, which indicated that the sign of stimulus contrast was a 'blind feature' of these directionally selective cells. Which portion of a cell's receptive field was traversed by a moving object was also immaterial, as shown in Fig. 2. Directional selectivity was the same regardless of whether a spot of light moved through the top, middle or bottom of the receptive field, which proved that the directionally selective property is distributed over the entire receptive field. A video recording of Bill demonstrating directional behaviour in ganglion cells of the rabbit retina is provided as electronic supplementary material.

Additional experiments designed to reveal the physiological mechanism responsible for such complex behaviour led to a model in which synaptic inhibition played a crucial role in sculpting response properties of sensory cells. This classic 1965 paper (Barlow and Levick 1965) has been cited 2000 times.

The critical question raised by these observations was how to suppress a neural response to an object moving in the null direction when a vigorous response is elicited by the same object moving in the opposite direction. An important clue emerged from the observation that, when movement of the object in the null direction is halted, a burst of neural impulses occurs when the movement resumes. This suggested a hypothesis for directional selectivity: continuous movement in the null direction generates a wave of inhibition that propagates in the null direction at a slightly faster

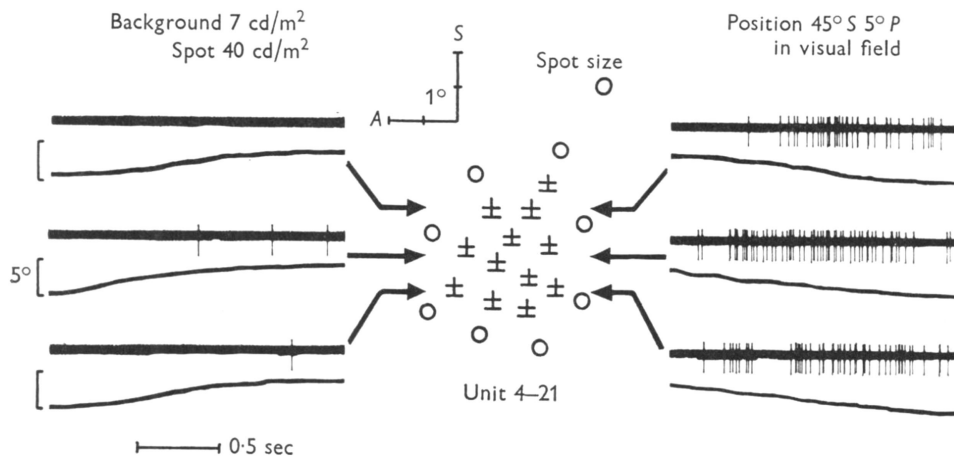


Fig. 2. Demonstration of directional selectivity in a retinal ganglion cell of the rabbit retina. From Barlow and Levick (1969a), used with permission from John Wiley and Sons.

rate than the excitatory response to the same stimulus. This wave of inhibition quashes, or ‘vetoes’, the excitatory wave that follows. Halting the object’s motion allows the inhibitory wave to decay so that when motion is resumed there is no obstacle to the cell’s excitatory response. If this hypothesis is correct, then motion itself is not strictly needed to demonstrate directional selectivity. A temporal sequence of flashing two stationary spots of light should elicit an excitatory response when the sequence mimics motion in the preferred direction but no response when the sequence mimics motion in the null direction. That prediction was confirmed, thereby supporting Barlow and Levick’s mechanistic hypothesis.

More than thirty years would pass before the elusive anatomical location of the neural synapses responsible for directional selectivity was found in the dendritic trees of these neurons (Taylor and others 2000). Another twenty years later, the long-sought evidence of directionally selective neural circuits in the primate retina were eventually discovered (Kim and others 2022; Wang and others 2023), thus confirming Bill’s evolutionary view that all vertebrate retinas are constructed from the same basic template, with the major differences between species being a matter of emphasis appropriate for the animal’s environment and lifestyle.

Levick and Barlow’s pioneering work on directional selectivity is one of the most influential papers in visual physiology, inspiring hundreds of subsequent studies in various fields (Fig. 3). One such study examined the statistical distribution of preferred directions from a large sample of directionally selective ganglion cells responsible for detecting motion at various places in the rabbit’s visual field (Oyster and Barlow 1967). Most preferred directions fell into four cardinal directions—up, down, left and right—which are the same directions of image motion produced by eye rotation when each of the four extraocular muscles is separately activated. This is no mere coincidence; it suggests a simple way for an animal to prevent motion blur in the retinal image of a moving object. Rotating the eye to stabilise the image of a moving object could be achieved by a coordinated



Fig. 3. Bill Levick in his laboratory demonstrating the visual behaviour of retinal ganglion cells to school children during the annual open day at John Curtin School of Medical Research, Australian National University, Canberra. Photo by Larry Thibos, -1980.

activation of the four extraocular muscles based on the retinal responses to the components of object motion in the four cardinal directions.

Limits to visual sensitivity and the constraints on the reliable encoding of visual information

Levick and Barlow’s discovery of inhibitory neural mechanisms capable of extracting from the retinal image the presence and direction of moving objects coincided with their observation of randomness in the train of nerve impulses carried by individual fibres of the optic nerve under light-adapted conditions (Barlow and Levick 1969b) and also in the dark (Bishop and others 1964). These observations posed a fundamental question: how is it possible for the retina to reliably encode important trigger features of the retinal image when individual ganglion cells respond randomly even in the absence of light stimulation? Although a

firm theoretical basis for approaching this question had already been laid (Shannon 1949; Tanner and Swets 1954), empirical evidence was needed to implicate the retina as that stage of the visual pathway where noise limits signal reliability, as had been suggested earlier (Barlow 1956). First in Cambridge, then in Berkeley, Barlow and Levick showed how the detection of light by individual ganglion cells can be formulated as a classic problem of detecting signals in the presence of noise. The irregular discharge of nerve impulses in the absence of a visual target represents noise, and the extra nerve impulses generated by a target represent the signal (Barlow and Levick 1969a; Levick 1973).

Employing the theory of signal detection as a mathematical framework for experimental design and results analysis, Barlow and Levick showed that the detection of a flash of light depended primarily on the number of extra impulses generated by the target (the 'signal') relative to variance in the maintained discharge (the 'noise'). This conclusion heightened the significance of their earlier finding that the noise factor is largely independent of the background level of illumination thanks to neural mechanisms of adaptation. Thus the number of extra impulses required for visual detection is largely independent of the background. In their own words, 'What the retina has done is to "normalize" the changing input and present it in standardized form at the output. This must be what the neural mechanisms of adaptation are all about' (Barlow and Levick 1969a). Pushing this line of inquiry to study the maximum visual sensitivity achievable by an individual neuron, the team of Barlow, Levick and Yoon showed that for ganglion cells of the fully dark-adapted cat retina, only two or three quanta of light at the cornea are required to elicit an average of one extra nerve impulse (Barlow and others 1971). They estimated that only 15–50% of photons incident on the cornea are likely absorbed by rod photoreceptors, and of course, only one rod can absorb a given photon. The startling implication of their experimental results was that every photon absorbed by a rod generates at least one extra nerve impulse in every ganglion cell connected functionally to that rod. That conclusion provided the physiological evidence needed to understand how it is conceivable for a human observer to detect a flash of light when as few as seven photons are absorbed (Hecht and others 1942).

That early work of Levick and Barlow indicated that fluctuations in the number of quanta contained in any given flash of light represent an irreducible source of variability that is responsible, at least in part, for the failure of ganglion cells to perform visual tasks without error. To pursue that line of thinking, Bill and colleagues undertook further experiments to explore the extent to which response variability can be attributed to the unavoidable variability of quantal absorptions (Levick and others 1983). Some theoretical predictions of the quantum fluctuation hypothesis were not verified empirically, which led to a consideration

of intrinsic noise, that is, a retinal source of random events that are additional to, and independent of, the events originating from quantal absorptions. This biological source of noise, dubbed 'scotons' (the elementary particles of 'dark light' caused by spontaneous isomerisation of opsin molecules), consists of events that are indistinguishable from photo-isomerisations due to the absorption of light. Quantitative analysis indicated that ganglion cells behave as if these two sources of variability were independent and additive, with total variance equally divided between internal (scoton) and external (photon) sources of quantum fluctuations (Thibos and Levick 1990).

Parallel processing of the retinal image: a physiological solution to the information bottleneck of the optic nerve

Receptive fields are the windows through which the brain experiences the visual world. Ganglion cell receptive fields are particularly significant because of the great narrowing of the visual communication channel imposed by the optic nerve: there are far fewer nerve fibres than photoreceptors. It is to be expected, therefore, that image-processing operations performed by a ganglion cell's receptive field are the outcome of evolutionary strategies for compressing the neural image of a visual scene. Since the principles underlying the design of the visual system may well have received their severest test at the optic nerve bottleneck, it was here that Bill and his colleagues concentrated their attention. The central idea to emerge from that effort was that different functional classes of retinal ganglion cells represent orthogonal information channels, each acting as a filter to process the retinal image with unique spatial, temporal, spectral and adaptive characteristics as required by different target nuclei in the brain responsible for performing specific visual functions (Cleland and Levick 1974a, 1974b; Vaney and others 1981; Levick and Thibos 1983; Thibos and Levick 1983).

An unexpected discovery arising from this latter series of experiments was a response bias favouring stimuli oriented in a radial direction, that is, parallel to a line joining the cell's location to the area centralis (Levick and Thibos 1980). This observation was surprising because orientation selectivity had previously been considered a property that emerged first in visual cortical neurons of the brain. The new results redirected attention to retinal morphology, that quickly revealed a corresponding radial elongation of dendritic fields of ganglion cells in cats (Leventhal and Schall 1983), monkeys (Schall and others 1986) and humans (Rodieck and others 1985). Assuming the mechanism responsible for this elongation of dendritic fields also increases the radial spacing between fields, then this mechanism provides an explanation for the bias in spatial acuity in human peripheral vision for radially oriented gratings (Wilkinson and others 2016).

In his historical examination of the foundations of visual neuroscience in Australia, [Vaney \(2020\)](#) placed the work of Bill and colleagues in context:

The whole range of visual neuroscience from photoreception to psychophysics has been pursued in Australian laboratories but, arguably, the most distinctive contribution of Australian visual neuroscientists has been in the area of parallel processing in the visual system. The foundation for this research was the careful characterization of the unexpected diversity of RGC types in the mammalian retina undertaken in the 1960s and 1970s by Barlow and Levick, Rodieck and Stone, Cleland and Levick, and Stone and Fukuda. A key insight had been provided by the contemporary demonstration of Christina Enroth-Cugell and John Robson that Stephen Kuffler's concentrically organized RGCs could be divided into X-cells and Y-cells, depending on whether the RGCs gave linear or nonlinear responses to flickering stimuli. What the Australian School excelled at was showing how the information from different types of RGCs was processed in higher visual centers. This involved careful studies analyzing the functional projections from the retina through different layers of the LGN to visual cortical areas, and the projections to a dozen distinct subcortical visual centers. The picture that emerged from these studies was that visual processing is highly parallel, with precisely ordered functional channels that are dictated by the afferent RGCs, and which feed into parallel cortical and subcortical visual pathways. These discoveries overturned the prevailing view that the visual system is ordered hierarchically.

In his summary of work in the Canberra years ([Levick 2001](#)), Bill explained that the concept of parallel channels within the optic nerve is a key feature of the visual pathway from photoreceptors to the brain:

The initial processing of visual information occurs in the retina, a complex laminated structure of rod and cone photoreceptors, interneurons and retinal ganglion cells (RGCs). The axons of ganglion cells, via the optic nerve, the optic decussation and the optic tract, synapse with neurons in the lateral geniculate nucleus (LGN), the axons of which project via the optic radiation to regions of the cerebral cortex concerned with vision. The very essence of organization in the central nervous system resides in the patterns of interconnections made by individual neurons at different functional levels. Since the late 19th century such patterns have been inferred indirectly, and often incorrectly, from morphological studies. For example, in the LGN, the main link between retina and visual cortex, it was known that individual LGN neurons were studded with thousands of synapses. This had led to the belief that the LGN was a major centre of integrative activity. An entirely different picture emerged from a neurophysiological attack on the issue

carried out by William Levick, Brian Cleland and Mark Dubin in 1971. By making simultaneous single-cell recordings from an LGN neurone and a succession of RGCs, it was established that essentially every output impulse from the former was attributable to an incoming impulse from one (8% of dual recordings) or just a very small number (up to 5) of RGCs. In one stroke, the notion of massive convergence was swept aside. A large proportion of the thousands of synapses on an LGN neurone must be coming from only a single RGC or a very small number of them. This result attracted wide and persistent attention because it provided much-needed linkages between methodologically different fields of retinal morphology, neurophysiology, and visual psychophysics. What the multiple classes of ganglion cells are doing is supplying a multi-dimensional analysis of the visual scene to higher centres via an inherently parallel visual pathway.

Although the concept of parallel channels in the optic nerve was inherent in the well established grouping of optic nerve fibres in cats into three classes based on conduction velocity of nerve impulse ([Bishop and Clare 1955](#)), a systematic functional classification based on visual and morphological characteristics required a good deal more work by many research groups ([Levick 1981](#); [Levick and Thibos 1983](#)).

Scientific reputation

Bill Levick's scientific reputation as a consummate experimental neurophysiologist rested on his attention to detail, mastery of medical physiology needed for maintenance of first-class animal preparations, innovative resourcefulness in creating custom laboratory apparatus and sheer intellect for the design, conduct, and assessment of experiments. Prior to Bill's leaving Berkeley for Canberra, one of us (Thibos) was told that Bill was the type of careful investigator who, upon selecting a calibrated spectacle lens from a clinical set of trial lenses, would still measure its power to be sure the lens was not mislabelled or out-of-tolerance. As Visiting Professor Theodore Cohn, also from University of California, Berkeley, remarked during his sabbatical leave at Canberra, 'The only thing Bill leaves to chance is the arrival of photons'. The veracity of that statement is demonstrated by the following anecdote recalled by Larry Thibos at Bill's Festschrift in 1997:

I was one of those fortunate few who had an opportunity to experience life as a visual neurophysiologist with Bill Levick as my primary mentor, in my case for 8 wonderful years at the Australian National University in Canberra (1975–83). Bill was a master of extracellular recordings of individual retinal ganglion cells and optic nerve fibers. It was painstaking work to methodically characterize the visual behaviour, axonal conduction velocity, and central projection of large populations of individual cells necessary

to develop the modern concept of parallel visual pathways. Yet that was how it was accomplished, one cell at a time, by dedicated scientists like Bill Levick and his contemporaries. In those days, Principal Investigators at the John Curtin School of Medical Research at ANU were expected to devote themselves full-time to experimental work, with generous institutional support eliminating the need to teach or apply for external grants. As a young post-doc, I benefitted greatly from that extraordinary environment because it meant that I had Bill's full attention as a mentor and luminary for all of our laboratory experiments. Bill taught me the empirical methodology of mammalian neuroscience, how to think about the link between structure & function, and how to envision neural processing of the retinal image by intermingled populations of retinal neurons with specialized features needed for the visual tasks they support. That experience shaped my entire career as an educator and vision scientist. The scientific culture of Bill's lab was on full display when my former mentor at Berkeley, Prof. Ted Cohn, arrived at ANU to spend his sabbatical leave. Ted's goal was to test the predictions of quantum fluctuation theory for light detection (tests he had performed previously on frogs for his PhD dissertation) in a mammalian species, the domestic cat. This experiment necessitated total dark adaptation of the experimental animal, as well as the experimental scientists. Bill's lab was well suited for these conditions, with multiple facilities for controlling environmental light. The windows could be fully covered with black, light-tight shades which, just to be sure, were shrouded in drapes made of heavy, black felt covered with additional black fabric, the edges of which were glued permanently to the walls to avoid light leaks. The same type of drapes covered the multiple racks of analog electronic equipment (filters, amplifiers, oscilloscopes, etc.), all of which had pilot lights or glowing vacuum tubes that would have interfered with the experiments if allowed to escape into the room.

To further shield the animal's eye against possible stray light, Bill had invented a device he called 'the octopus', which was a sheet of black felt with a small hole in the center. Centered on the hole, and firmly attached to the felt, was a calibrated artificial pupil made of metal painted black. Surrounding this artificial pupil, the felt had been cut into long radial strips, rather like the tentacles of an octopus. After mounting the pupil directly in front of the animal's eye, these strips were carefully wrapped around the cat's head so as to block all possible light paths (other than through the artificial pupil) into the cat's eye by any remnants of stray light that may have escaped the other precautions. Then, just to be absolutely certain that the animal was protected against errant rays of light, the entire animal table (~2 m in diameter) was completely entombed by additional black drapes. As a final precaution against the possible intrusion of sunlight into the lab, data collection didn't begin until after

nightfall. Given these extensive experimental precautions, and a prolonged period of dark adaptation, even the most skeptical experimenter was convinced that the maintained discharge of isolated retinal ganglion cells was not due to photons—there weren't any. The only other possible stimulus was 'dark-light', 'eigengrau', 'photooffs', i.e. 'scotons', the elementary particles of darkness. At the conclusion of our experiments, Levick took the lead in writing up the manuscript for publication, longhand, using a fountain pen freshly filled with indelible black ink. Bill was an old-school scientist who believed in thinking before writing, so his handwritten draft was nearly perfect when finished. Nevertheless, upon review prior to handing the manuscript to the typist, Bill did occasionally notice an inappropriate word or phrase that needed correction. His technique was neatly straightforward: he pulled from his drawer a pair of scissors, forceps, a mm rule, and a sheet of blank, self-adhering labels. He measured the length and width needed for an appropriate label, cut it to size, used the forceps to place it carefully over the offending words, and then penned in the replacement, again with black indelible ink. When the completed manuscript was finally posted to the journal, the experimenters began the long wait for an editorial decision. In those days, airmail was too expensive for academic manuscripts so the package traveled by slow boat, both ways, across the Pacific Ocean. Months later, long after Ted's sabbatical had ended and he had returned to Berkeley, the much anticipated review arrived in Canberra. The reviewer gave faint praise for our 'work on a minor issue that might be of interest to a few specialists in the field'. The reviewer did have one technical concern, however, asking 'Did the authors consider the possibility of stray light affecting their results?'

Aiming always for the definitive experiment, Bill's professional life was a long, joyful immersion in a fascinating, scientific sea of empirical facts, compelling ideas and lasting insights. At the same time, his idiosyncrasies were often a source of amusement to his workmates, who gathered daily for lunch in the office of department head, Professor Peter Bishop. As Austin Hughes recalled (Hughes 1986):

There must be a mysterious ingredient which made the famous Lunch Table function. How otherwise could certain of his colleagues have stood the strain of watching Bill Levick fold his sandwich wrapper around the remains of a blackened banana on some 3700 working days? I suspect it was Peter Bishop's magic phrase 'changing the subject' or, when I was speaking, 'seriously now' which maintained a semblance of law and order.

On other occasions Bill would, when conversation lagged, pose questions such as 'Would it be possible to drill a hole through a teacup so small that a photon could not pass through?'. Or a similarly unfathomable query, this time on

an astronomical scale: 'Is there a line-of-sight from this lunch table to the end of the Universe that does not intersect a star?' We could but shake our heads in wonder at the man's thought processes, and wait for Professor Bishop to change the subject!

At Bill's retirement Festschrift in 1997, Horace Barlow noted that every scientist needs a Bill Levick to tell them where they are wrong, without fear or favour. In any discussion with Bill, there was always a good chance that, at some stage, Bill would say 'there is a bit of a wrinkle to that'—and he would then proceed to modify or even demolish your conclusions. Many years later, at Bill's funeral, David Vaney said:

Such moments are remembered long after the details of the science have started to recede. We remember Bill as an unfailingly polite gentleman who embodied the values of the 1950s in which he had developed from a young undergraduate to a skilled doctor. We remember Bill for his big-hearted warm greetings, even on his 90th Birthday (5 December, 2021) when he was fading away. We remember Bill as a brilliant scientist.

A full bibliography of Levick's published work may be found in the accompanying Supplementary Material S1.

Family life

Bill married Patricia Jane Lathwell on 14 August 1961 in Sydney, NSW, Australia. Patricia is the daughter of Henry and Edna Lathwell (née Kent), who emigrated to Australia from the United Kingdom in 1949. Bill and Trish had three children, Andrew (1962–86), Greg (1965–) and Cathy (1969–). Recollections by Greg and Cathy paint a loving picture of family life in the Levick home. As a father and grandfather, Bill displayed the same traits evident in his professional life as a research scientist. As Greg has recalled:

Dad was a gentle man in every sense of the word. He very rarely lost his temper. He believed in rational argument and in logic. When I was young he taught me how to reason and that has led me to being the man I am today. Dad taught me the basics of home maintenance like his dad taught him. I can change a washer in a tap, plane back a door which is out of true, thanks to Dad. When vandals pried out and destroyed my letterbox, Dad spent a day helping me concrete my new letterbox into the ground so it couldn't be pried out again. He was meticulous in all of his preparations, and taught me strict attention to detail. I remember thinking when I was young that Dad could have made a living as a handyman; it was only when I got older that I realized that he would not have made it: he'd have done one job a day, and while the results would have been absolutely perfect there'd have been no repeat customers due to how long he took.'

In her father's eulogy, Cathy said:

My Dad was exceptionally good with the little ones, in particular my son and daughter. He had impeccable patience and was always interested in all the simple games and interests of toddlers and young children. Dad would excel with the funny interactions which made the little ones laugh. He was young at heart. Dad was a unique teacher. During my high school years, I sometimes needed help with Physics or Chemistry. Whilst Dad was very capable of helping me, it was always a painstakingly slow process. He was a man of detail and first principles. My intention had always been to find a quick answer to my query, but an hour later, I would then have a much deeper understanding of the topic than I probably required.

Awards and recognition

1973 Fellow of the Australian Academy of Science
1977 Fellow of the Optical Society of America
1982 Fellow of the Royal Society

Supplementary material

Supplementary material is available [online](#).

References

- Barlow HB (1953) Summation and inhibition in the frog's retina. *Journal of Physiology* **119**, 69–88. doi:[10.1113/jphysiol.1953.sp004829](https://doi.org/10.1113/jphysiol.1953.sp004829)
- Barlow HB (1956) Retinal noise and absolute threshold. *Journal of the Optical Society of America* **46**, 634–639. doi:[10.1364/josa.46.000634](https://doi.org/10.1364/josa.46.000634)
- Barlow HB, Levick WR (1965) The mechanism of directionally selective units in rabbit's retina. *Journal of Physiology* **178**, 477–504. doi:[10.1113/jphysiol.1965.sp007638](https://doi.org/10.1113/jphysiol.1965.sp007638)
- Barlow HB, Levick WR (1969a) Three factors limiting the reliable detection of light by retinal ganglion cells of the cat. *Journal of Physiology* **200**(1), 1–24. doi:[10.1113/jphysiol.1969.sp008679](https://doi.org/10.1113/jphysiol.1969.sp008679)
- Barlow HB, Levick WR (1969b) Changes in the maintained discharge with adaptation level in the cat retina. *Journal of Physiology* **202**, 699–718. doi:[10.1113/jphysiol.1969.sp008836](https://doi.org/10.1113/jphysiol.1969.sp008836)
- Barlow HB, Hill RM, Levick WR (1964) Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. *Journal of Physiology* **173**(3), 377–407. doi:[10.1113/jphysiol.1964.sp007463](https://doi.org/10.1113/jphysiol.1964.sp007463)
- Barlow HB, Levick WR, Yoon M (1971) Responses to single quanta of light in retinal ganglion cells of the cat. *Vision Research* **11**(Suppl. 3), 87–101. doi:[10.1016/0042-6989\(71\)90033-2](https://doi.org/10.1016/0042-6989(71)90033-2)
- Bishop GH, Clare MH (1955) Organization and distribution of fibers in the optic tract of the cat. *Journal of Comparative Neurology* **103**, 269–304. doi:[10.1002/cne.901030204](https://doi.org/10.1002/cne.901030204)
- Bishop PO, Levick WR (1956) Saltatory conduction in single isolated and non-isolated myelinated nerve fibres. *Journal of Cellular and Comparative Physiology* **48**(1), 1–34. doi:[10.1002/jcp.1030480102](https://doi.org/10.1002/jcp.1030480102)
- Bishop PO, Levick WR, Williams WO (1964) Statistical analysis of the dark discharge of lateral geniculate neurones. *Journal of Physiology* **170**(3), 598–612. doi:[10.1113/jphysiol.1964.sp007352](https://doi.org/10.1113/jphysiol.1964.sp007352)

- Cleland BG, Levick WR (1974a) Brisk and sluggish concentrically organized ganglion cells in the cat's retina. *Journal of Physiology* 240(2), 421–456. doi:10.1113/jphysiol.1974.sp010617
- Cleland BG, Levick WR (1974b) Properties of rarely encountered types of ganglion cells in the cat's retina and an overall classification. *Journal of Physiology* 240(2), 457–492. doi:10.1113/jphysiol.1974.sp010618
- Cleland BG, Dubin MW, Levick WR (1971) Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *Journal of Physiology* 217(2), 473–496. doi:10.1113/jphysiol.1971.sp009581
- He S, Levick WR, Vaney DI (1998) Distinguishing direction selectivity from orientation selectivity in the rabbit retina. *Visual Neuroscience* 15(3), 439–447. doi:10.1017/s0952523898153038
- Hecht S, Schlaer S, Pirenne MH (1942) Energy, quanta, and vision. *Journal of General Physiology* 25, 819–840. doi:10.1085/jgp.25.6.819
- Henry GH (1986) Peter Bishop—the Canberra years. In 'Visual Neuroscience'. (Eds JD Pettigrew, KJ Sanderson, WR Levick) pp. 434–437. (Cambridge University Press: Cambridge, UK)
- Hughes A (1986) Contributor's tribute to Peter Bishop. In 'Visual Neuroscience'. (Eds JD Pettigrew, KJ Sanderson, WR Levick) pp. 425–426. (Cambridge University Press: Cambridge, UK)
- Kim YJ, Peterson BB, Crook JD, Joo HR, Wu J, Puller C, Robinson FR, Gamlin PD, Yau K-W, Viana F, Troy JB, Smith RG, Packer OS, Detwiler PB, Dacey DM (2022) Origins of direction selectivity in the primate retina. *Nature Communications* 13, 2862. doi:10.1038/s41467-022-30405-5
- Leventhal AG, Schall JD (1983) Structural basis of orientation sensitivity of cat retinal ganglion cells. *Journal of Comparative Neurology* 220, 465–475. doi:10.1002/cne.902200408
- Levick WR (1973) Maintained discharge in the visual system and its role for information processing. In 'Handbook of Sensory Physiology. Vol. VII/3/3A'. (Ed. R Jung) pp. 575–598. (Springer: Berlin, Germany) doi:10.1007/978-3-642-65352-0_8
- Levick WR (1981) Development of ideas on the functional organization ganglion cells. In 'Advances in Physiological Sciences. Vol. 2'. (Eds J Szentagothai, J Hamori, M Palkovits) pp. 255–260. (Pergamon Press: Budapest, Hungary) doi:10.1016/B978-0-08-027371-6.50036-7
- Levick WR (1983) Contributor's tribute to Peter Bishop. In 'Visual neuroscience' (ed. J. D. Pettigrew, K. J. Sanderson & W. R. Levick), pp. 425–426. Cambridge, UK: Cambridge University Press.
- Levick WR (2001) Highlights of retinal research. In 'The John Curtin School of Medical Research: the First Fifty Years 1948–1998'. (Eds F Fenner, D Curtis) pp. 443–447. (Brolga Press: Gundaroo, NSW, Australia)
- Levick WR, Thibos LN (1980) Orientation bias of cat retinal ganglion cells. *Nature* 286, 389–390. doi:10.1038/286389a0
- Levick WR, Thibos LN (1983) Receptive fields of cat ganglion cells: classification and construction. In 'Progress in Retinal Research. Vol. 2'. (Eds N Osborne, G Chader) pp. 267–319. (Pergamon Press: Oxford, UK) doi:10.1016/0278-4327(83)90012-3
- Levick WR, Thibos LN, Cohn TE, Catanzaro D, Barlow HB (1983) Performance of cat retinal ganglion cells at low light levels. *Journal of General Physiology* 82(3), 405–426. doi:10.1085/jgp.82.3.405
- Oyster CW, Barlow HB (1967) Direction-selective units in rabbit retina: distribution of preferred directions. *Science* 155, 841–842. doi:10.1126/science.155.3764.841
- Rodieck RW, Binmoeller KF, Dineen J (1985) Parasol and midget ganglion cells of the human retina. *Journal of Comparative Neurology* 233, 115–132. doi:10.1002/cne.902330107
- Schall JD, Perry VH, Leventhal AG (1986) Retinal ganglion cell dendritic fields in Old-World monkeys are oriented radially. *Brain Research* 368, 18–23. doi:10.1016/0006-8993(86)91037-1
- Shannon CE (1949) Communication in the presence of noise. *Proceedings of the Institute of Radio Engineers* 37, 10–21. doi:10.1109/JRPROC.1949.232969
- Tanner WP, Swets JA (1954) A decision-making theory of visual detection. *Psychological Review* 61, 401–409. doi:10.1037/h0058700
- Taylor WR, He S, Levick WR, Vaney DI (2000) Dendritic computation of direction selectivity by retinal ganglion cells. *Science* 289, 2347–2350. doi:10.1126/science.289.5488.2347
- Thibos LN, Levick WR (1983) Spatial frequency characteristics of brisk and sluggish ganglion cells of the cat's retina. *Experimental Brain Research* 51, 16–22. doi:10.1007/BF00236798
- Thibos LN, Levick WR (1990) Quantum efficiency and performance of retinal ganglion cells. In 'Vision: Coding and Efficiency'. (Ed. C Blakemore) pp. 84–91. (Cambridge University Press: Cambridge, UK) doi:10.1017/CBO9780511626197.010
- Vaney DI (2020) The foundations of visual neuroscience in Australia. *Journal of Comparative Neurology* 528, 2792–2799. doi:10.1002/cne.24882
- Vaney DI, Levick WR, Thibos LN (1981) Rabbit retinal ganglion cells: receptive field classification and axonal conduction properties. *Experimental Brain Research* 44(1), 27–33. doi:10.1007/BF00238746
- Wang AYM, Kulkarni MM, McLaughlin AJ, Gayet J, Smith BE, Hauptschein M, McHugh CF, Yao YY, Puthussery T (2023) An on-type direction-selective ganglion cell in primate retina. *Nature* 623, 381–386. doi:10.1038/s41586-023-06659-4
- Welsh JH (1934) The caudal photoreceptor and responses of the crayfish to light. *Journal of Cellular and Comparative Physiology* 4, 379–388. doi:10.1002/jcp.1030040308
- Wilkinson MO, Anderson RS, Bradley A, Thibos LN (2016) Neural bandwidth of veridical perception across the visual field. *Journal of Vision* 16, 1. doi:10.1167/16.2.1
- Young JZ (1964) 'A Model of the Brain.' (Oxford University Press: Oxford, UK)

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