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# Peter Orlebar Bishop 1917–2012

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Peter Orlebar Bishop was an Australian neurophysiologist renowned for his ingenious quantitative approach to study of the mammalian visual system and great ability to attract a large number of talented people to visual research. Peter's research was based on specially designed, precise instrumentation and data quantification applied mainly to analysis of the response properties of single neurones in the principal dorsal thalamic visual relay nucleus, the dorsal lateral geniculate nucleus (LGNd) and the primary visual cortex. This quantitative bent was evident throughout Bishop's entire research career: starting with the design and construction of innovative DC amplifiers; through to his quantitative analysis of optics—'schematic eye' for the cat, which rivaled Gullstrand's schematic eye for humans; to creating and demonstrating validity of the concept of 'projection lines' in the representation of contralateral visual field in different cellular layers of the LGNd of mammals with frontally positioned eyes and discovery of a very substantial binocular input to single LGNd neurones. The engineering approach of Peter was probably at its heuristic peak when it revealed many details of binocular interactions at the level of single neurones in the primary visual cortex—the interactions that appear to underpin overall mechanisms underlying stereopsis, the high precision binocular depth sense.

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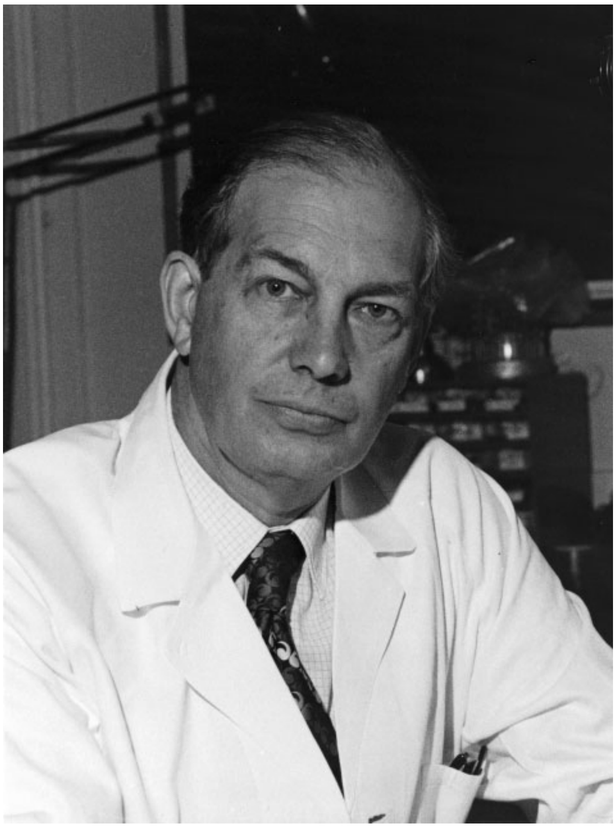
## Early Life

Peter Bishop was born in the Australian rural city of Tamworth in 1917.[1] His mother, Mildred Bishop (née Vidal), showed substantial interest not only in the emotional wellbeing, but also in the intellectual 'drives' of her children—three sons and two daughters. Her second born son, Peter, while attending the state primary and high schools in Armidale showed keen interest in mathematics and basic physics and wanted to be an engineer.[2] Those interests were probably the main underpinning of a close friendship with his contemporary, John Warcup Cornforth who, many years later (1975), was awarded the Nobel Prize in Chemistry 'for his work on the stereochemistry of enzyme-catalyzed reactions.[3] Peter's father, Ernest, had a secure job as a government surveyor for the district of Armidale in northern NSW, and his instruments may have had a subliminal effect on Peter's passion for the construction of precise instrumentation, particularly involving optics. Recognizing Peter's intellectual abilities and drive, his mother suggested preparation for entry to medical school. Despite Ernest's steady job, the family budget was tight. Nevertheless, the money was found and Peter, aged 14, was sent to a prestigious boarding school, the Barker College in Hornsby on the outskirts of Sydney, about 400 km south-east of Armidale. As Peter points out in his 1996 autobiography,[4] at the height of the depression, there were only 78 pupils in a school that in better times would enrol more than a thousand students. In addition to excelling in mathematics and physics, Peter was a very popular footballer, and finally a Dux, achievements that became enshrined in the school's honour board. Apart from studying the normal high-school curriculum, Peter's mind was concentrated on competition for the Exhibition Scholarship (later called Commonwealth Scholarship), one that paid for tuition at university. In 1934, in the second attempt at the yearly examination, Peter succeeded and in 1935 enrolled in the Medical School at the University of Sydney.



In the 1996 volume of the *History of Neuroscience in Autobiography* Peter reminisced:

> During the medical course, I was attracted to anatomy, particularly neuroanatomy. In the third year, I dissected a brain. I will never

> forget the fascination of actually holding a human brain in my hands and realizing that it once belonged to a person like myself with the same sorts of thoughts and feelings as I had. This experience had a tremendous impact on me, and from then on I never questioned that I would try to make a career in brain research.[5]

After qualifying in medicine in 1940, Peter was appointed a registrar of neurosurgery and psychiatry at the Royal Prince Alfred Hospital in Sydney. His hospital career was interrupted, however, by his service in the Australian Navy 1942–5 as a lieutenant surgeon. We do not know whether his love of engineering had any impact on his naval service in World War 2 on the cruiser *HMAS Adelaide* or the destroyer *HMAS Quiberon*. It appears, however, that during his naval service, Peter concentrated on his duties as a freshly baked lieutenant surgeon. Indeed, late in his life, when reminiscing about his naval service, Peter remembered the clash between himself, and the commander of the ship when it was stationary in the port of Mombasa in Kenya. Peter, a very junior lieutenant surgeon, suggested that two sailors suffering from acute piles should be assigned to light duties. The ship's commander did not accept the recommendation, so Peter complained to higher authorities and the vice-admiral in charge of the fleet resolved the issue in his favour.

## The Engineer of Visual Science: London and Sydney

In 1946, Peter, his wife Hilare (née Holmes) and their two young daughters Phillippa and Clare, moved to Oxford and later on to London. Peter started his scientific research career by building two high-gain DC amplifiers. The design was largely his own, although he got some help from a member of the biophysics unit at University College, Dr E. J. Harris, who was a qualified engineer. In the period of severe post-war scarcity, the choice of components was remarkably ingenious, while the details were sufficiently novel for the design to be published in a professional engineering journal. The performance of these amplifiers far exceeded the required performance for the electrophysiology taking place in the laboratory. Overall, Peter's early papers were concerned with the design of equipment rather than the collection and analysis of quantitative neurophysiological data, the activity for which he later became famous.

In 1950, Peter and his family returned to Sydney. As a National Health and Medical Research Council Fellow, Peter received a substantial equipment grant. The grant allowed him to build a large stock of electronic components, to construct DC amplifiers and establish a neurophysiological research group at the Department of Surgery of Sydney University. In 1951, he was appointed to a senior lectureship in the Department of Physiology. Peter's first research team consisted of several BSc (Med) students Jim McLeod, David Jeremy and Bill R. Levick, and MD candidate Jim Lance, who each later developed a distinguished career in neurology or visual neuroscience. They first investigated repetitive firing in the dorsal lateral geniculate nucleus (LGNd) of the cat, and the nature of synaptic potentials associated with synaptic transmission of optic nerve/tract signals in it.[6] Following in the footsteps of two prominent American neurophysiologists, George H. Bishop and J. L. O'Leary,[7] they attempted to correlate distinct conduction velocity groupings in the optic nerve of the cat with segregation of optic nerve fibres according to their diameters.[8]

Peter was promoted to the readership (research professor) in physiology in 1954 and in the following year, after the retirement of Frank Cotton,[9] he was appointed Professor of Physiology. The first task of the newly appointed professor was to develop and run a large number of physiology courses. In the period 1955–61 at the University of Sydney, 1500 students a year were taking physiology in various courses in the faculties of dentistry, medicine, science and veterinary science. Despite the huge teaching load, Peter was able to establish within the department the renowned 'Brain Research Unit', the name of which was engraved in gold leaf on a door in a picturesque sandstone archway at the University's Old Medical School. Within this unit Peter created an extraordinary research environment in which the quantitative approach and protection from intrusive bureaucracy nurtured the careers of young brain researchers. It is surely no accident that several outstanding visual neuroscientists such as William (Bill) R. Levick FRS,[10] Robert (Bob) W. Rodieck[11] (1937–2003) and Jonathan Stone[12] started their scientific careers in the Brain Research Unit.

In the late 1950s, Peter worked mainly with newly appointed senior lecturer William (Liam) Burke,[13] and BSc (Med) student Ross Davis, who later graduated in medicine. They first published a series of papers in which they presented evidence indicating that activation of single optic nerve can result in the discharge of a neurone in cat's LGNd.[14] Some years later, an autonomous research group working in Peter's Department in the John Curtin School of Medical Research at the Australian National University in Canberra elegantly demonstrated that most neurones in cat's LGNd receive their major excitatory input from only one or two retinal ganglion cells.[15] Second, and contrary to the apparent complete anatomical segregation of LGNd neurones innervated by the contralateral optic nerve fibres from those innervated by the ipsilateral optic nerve fibres,[16] the Bishop group found that some LGNd neurones could be activated (generate action potentials) by electrical stimulation of either optic nerve. Virtually all those cells were located in the interlaminar zones between the cellular laminae innervated by the contralateral eye and those innervated by the ipsilateral eye.[17] Consistent with those findings, a research group working in the UK[18] discovered that a small proportion of cat's LGNd neurones could be activated by visual stimuli presented via either eye. These findings were later confirmed in Bishop's laboratory.[19]

### *Optical Work*

In order to provide a quantitative framework for future quantitative studies of mammalian visual systems, Peter, working with George J. Vakkur (a refugee from the Soviet re-occupied Estonia and medical graduate of Sydney University) and Wlod Kozak, (University of Sydney Fellow, on leave from the Nencki Institute of the Polish Academy of Sciences in Warsaw) determined quantitative aspects of the visual optics of the eye of the domestic cat, an animal model used in virtually all of Peter's research.[20] This work culminated in the publication of a 'schematic eye' for the cat.[21] This work was inspired by the work of Alvar Gullstrand (1862–1930), a medically qualified Swedish mathematician and inventor who in 1911 was awarded a Nobel Prize in Physiology or Medicine for a very precise mathematical description of the dioptric system of the human eye and invention and design of several ophthalmological instruments. Indeed, Peter was often jokingly referred to as the

'Gullstrand of the Cat Eye'. The work of Peter and his colleagues on the schematic eye of the cat ignited great interest in the optics of small mammals as potential models for visual research and opened a new field of comparative neuro-ophthalmology. In the next couple of decades, schematic eyes for the rat,[22] rabbit[23] and mouse[24] were published. Later on, in the JCSMR, Peter maintained a keen interest in the continuing 'optical' work of one of the autonomous groups in his Department, headed by Austin (later Abbie) Hughes.

## *Early Quantitative Analysis of Receptive Field Properties of Single Neurones*

When in 1958, Peter Bishop visited Kuffler's laboratory, Hubel and Wiesel, the co-recipients of 1981 Nobel Prize in Physiology or Medicine for their discoveries concerning information processing in the visual system, were using the so-called multibeam ophthalmoscope designed several years earlier by Talbot and Kuffler to project small flashing spots of lights directly onto the cat's retina. Indeed, Steven Kuffler used the multibeam ophthalmoscope in his classical study of receptive field organization of mammalian retinal ganglion cells.[25] On his return to Sydney, Peter and his team built a multibeam ophthalmoscope and used it for studying temporal characteristics of responses of the retinal ganglion cells.[26] Meanwhile, Hubel and Wiesel realized that the multibeam ophthalmoscope imposes serious constraints on studying receptive field properties of cortical neurons and it might have been Wlod M. Kozak (1927–2010) who convinced Peter to follow their example and abandon the use of the instrument. From early 1960s, Peter and his group studied the visual system by analyzing responses of individual neurones to visual stimuli presented on the screen in front of the animal (usually a cat), and projected onto its retinae via optics in its own eyes.[27]

Their first study was a quantitative analysis of responses of single LGNd neurones to variously shaped figures made from white and black cardboard and moved by servomechanism across the perimeter mounted gray screen.[28] The action potentials (spikes) generated by the LGNd neurones were fed via the Schmitt trigger circuit into multi-channel analyser for the generation of peri-stimulus time histograms. Using the same system, Bob Rodieck, a Massachusetts Institute of Technology graduate in electrical engineering, and Jonathan Stone (PhD student) analysed the responses of retinal ganglion cells.[29] The combined results of these studies indicated that each individual neurone in cat's LGNd receives its principal excitatory input from a small number of retinal ganglion cells with spatially overlapping receptive fields.[30]

## *Early Studies of Disparity-Specificities of Cortical Neurones*

One of us (JDP), starting a BSc (Med) project in the mid-1960s, was faced with floor-to-wall banks of equipment, all using post-war thermionic valves, which had also been constructed by Peter in the Brain Research Unit at the University of Sydney. In those times, before the invention and widespread adoption of transistors, it took days for even fast learners to learn how to turn the equipment on, since the many filaments had to be turned on before the high tension switches, to avoid blowing up the thermionic valve components of the amplifiers, Schmidt triggers and oscilloscopes. Bishop's role in the discovery of 'stereo-specific' visual cortical neurones is covered in detail in review by Bishop and Pettigrew.[31] The work on the specificity of binocular neurones required a quantitative approach to overcome the problem of their stochastic firing patterns when a comparison was being made between the responses to visual stimulus presented monocularly and those to the same visual stimulus presented binocularly.

The significant technical advances that enabled discovery of stereo-specific cortical neurones in Bishop's laboratory included conversion of the multi-channel analyser (RIDL) for usage in the neurophysiological research including generation of peri-stimulus time histograms.[32] The other key instrument to the discovery of binocular disparity selectivity of single cortical neurones was a Risley bi-prism, originally developed for astronomical use but modified in the Bishop laboratory to allow change of alignment by small fractions of a degree, in contrast to the degrees of arc that are commonly used in astronomical and optometrical practice. The smaller prisms were re-mounted into the counter-rotating receptacles. The finest bi-prism had a power that could vary from 0 to 2 prism dioptres (or 0–1.14 deg).

## *Disparity-Selectivity of Binocular Neurones*

Hubel and Wiesel were the first to record and analyse the specific responses of visual cortical neurones to stimuli presented independently via each eye.[33] Because the eyes of the cat diverge under the influence of paralytic agents, the two receptive fields are usually separated on the tangent screen in front of the animal. Despite their separation, the receptive fields revealed by stimulation via right eye and those revealed by stimulation via left eye, usually have identical properties. However, the strength of the responses evoked by stimulation via each eye is usually not the same: the responses evoked by stimulation via one eye tend to be stronger than those evoked by stimuli presented via the other eye, a phenomenon known as 'eye dominance'. For example, if the optimal stimulus for the right eye's receptive field is an oblique dark bar moving upwards in a leftward direction, the same stimulus will be optimal for the left eye's receptive field, except that it may not generate the response of the same strength (the same number of action potentials). It is generally recognized that this interocular match of receptive field properties helps to solve the 'correspondence problem' of stereopsis where the ambiguities between the right and left eye images are eliminated by matching similar regions between them. This explanation has proved largely adequate, but matching between the properties of each eye's receptive field does not always occur,[34] and the same binocular neurones can also detect anti-symmetric stimulation of each eye.[35] The interocular similarity of receptive field properties of binocular neurones called for an examination of responses to a single visual stimulus presented binocularly. This was Bishop's motivation for the use of Risley bi-prisms, which have the potential to realign the receptive field revealed by stimulation via one eye so that it overlaps with receptive field revealed by stimulation via the other eye.

## *Binocular Interaction Specificity*

A remarkable phenomenon is observed when a single stimulus is used to excite a cortical neuron through both eyes, after the receptive fields of both eyes have been superimposed using the bi-prism. Since a strong burst of spikes can be elicited by an appropriate visual stimulus presented separately via each eye, one might expect a vigorous response when the stimulus is presented via both eyes. Instead, unless one carefully adjusts the setting on the bi-prism (with its tuning refined to minutes of arc) there may be no response to binocular stimulation at all! Plotting disparity-tuning curves was facilitated by the quantitative approach of the laboratory with its use of peristimulus time histograms to provide an average response at each prism setting. This phenomenon of disparity-selectivity was first seen by one of us (JDP) in Bishop's laboratory and is a testimony to Bishop's foresight in using a Risley bi-prism for this experiment. The role of a 'veto' signal that restricts effective stimulation to a very narrow range of possibilities is similar to that in other cases of sharply tuned neurons, for example, veto power underpinning direction and orientation selectivities of retinal ganglion cells in the rabbit.[36]

The work on disparity detection and disparity selectivity was controversial for a decade or so because the existence of binocular disparity in the receptive fields of cortical neurones was largely denied by the future (1981) Nobel Laureates in Medicine or Physiology, Hubel and Wiesel. The first denial occurred in an unrelated publication on the corpus callosum where a figure showing the location of receptive fields plotted for each eye separately was used to support the denial.[37] In fact, the figure clearly shows the phenomenon of binocular disparity of receptive field positions. Another criticism was that the phenomena were only clearly evident in macaque monkey's cytoarchitectonic area 18,[38] but not in the primary visual cortex of the cat.[39] The issue was largely resolved by Poggio and Fischer in 1977,[40] who showed that the processing for binocular disparities in visual cortices of macaque monkeys is essentially similar to that reported by the Bishop/Barlow group in primary visual cortices of cats.[41]

## The Engineer of Visual Science: Canberra

In his new laboratories in the John Curtin School of Medical Research (JCSMR) in Canberra, Peter was able to attract a brilliant international team and continue his quantitative approach to study binocular processing in the cat visual system. Building and development of sophisticated mechanical instruments was supervised by head technical officer, Lionel Davis (designer of mechanical instruments for Jack C. Eccles, the previous head of Physiology in JCSMR and co-recipient of 1963 Nobel Prize in Physiology or Medicine) while Robert M. Tupper developed and maintained electronic equipment.

### *Laser Accuracy of Laboratory Construction*

An apocryphal engineering story about Peter that feels true concerns the series of adjacent laboratories he built on moving to the JCSMR in 1968. It was said that a laser beam shone through the nodal point of the right eye of a cat in laboratory A would also pass precisely through the nodal points of the right eyes of each of the other cats in laboratories B, C and D! This purported accuracy was all the more remarkable when one considers the underlying construction. The stainless-steel head-holder was designed by Peter so as not to obstruct the eyes or ears, and had been copied and sold in Japan for the use of neurophysiologists. New postdoctoral fellows were personally instructed by Peter in the way the head-holder was to be used. They were all cautioned: 'never use force'. In front was a massive pull-down mirror that serviced a plotting table. The mirror brought the plotting table into exact correspondence with the tangent screen on which the computer presented visual stimuli. Some neurones, especially many cortical neurones are so highly specific in their stimulus requirements that it can take the best part of an hour or even more to discover 'what makes them tick'. Being able to sit down to explore the possible stimuli was a boon that the removable mirror provided. Of course, it was essential that the geometry provided by the mirror was exactly aligned with the computer screen, a solution provided with alacrity by Peter in solid steel. The head holder was surrounded by a huge ball-race, more than a metre in diameter, on which was mounted the fundus camera, which could then be swung precisely and reproducibly into position when needed. This arrangement of the fundus camera allowed Heinz Wässle, a postdoctoral fellow from Germany who worked with the Levick and Cleland team and was, later on, one of the world-leading retinal anatomists. He performed a *tour-de-force* in which he identified individual $\alpha$ retinal ganglion cells in a retinal whole-mount, each of which he had previously identified physiologically as a Y-cells in the retina of a preparation in this head-holder. Finally, the whole assembly was brought to waist height by four pillars of steel that enormously complicated laboratory reorganization, if needed, but were a key part of the extraordinary precision that underlay the 'laser-through-the-eye' anecdote.

Another technical development was triggered by the need to study suppressive (inhibitory) regions in the receptive field of neurones with very little or no 'spontaneous' (background) spike-activity such as simple cells in the primary visual cortex. In order to obtain the high level of apparent background activity, an optimally oriented light bar oscillated to and fro in the centre of the excitatory receptive field of the dominant eye (conditioning stimulus), while the second optimally oriented bar (testing stimulus) was driven asynchronously through the receptive field of the non-dominant (or even silent) eye. Spikes were collected in phase with the testing stimulus while spikes generated by conditioning stimulus were collected randomly. Consequently, the bins of the multi-channel analyzer were filled relatively evenly, creating relatively uniform apparent background activity.

## Quantitative Work on Binocular Neurones at the JCSMR

### *LGNd Lamination and Binocularity*

In earlier work in Sydney, Peter and his colleagues had advanced the idea of a 'projection line' encompassing adjacent laminae in the LGNd, such that nearby neurones activated by visual signals from opposite eyes would be activated by the stimuli located in same point in visual space, allowing for the divergent eye position in paralysis.[42] The concept of visual field projection columns in the LGNd was further explored and the columns were quantified by Ken Sanderson, a PhD student of Peter's.[43] The arrangement of visual field projection columns strongly suggested that the LGNd might be involved in mechanisms underpinning binocular vision. However, as mentioned earlier, careful searches indicated that only a small proportion of cat's LGNd neurones could be activated (generate action potentials) by visual stimuli presented to either eye.[44] Thus, the LGNd neurones appeared to be essentially monocular.

On the other hand, almost immediately after establishing the laboratory in the JCSMR, Peter showed that binocular interaction was the rule in the LGNd. Working with a couple of colleagues, Ken Sanderson and sensory neuroscientist Ian Darian-Smith (1927–2017),[45] Peter discovered that in the domestic cat, at least, the great majority of LGNd neurones in addition to the monocular excitatory receptive fields have, in most cases, weakly suppressive (inhibitory) fields in the non-dominant eye that occupied the same location in space as the conventional excitatory field in the other eye![46] Unlike in the case of their excitatory counterparts, the suppression was triggered irrespective of the polarity of contrast of stimulus used (brighter or darker than the background) but like their excitatory counterparts, the inhibitory receptive fields tend to be hardly selective for orientation.[47] Peter's strategic provision of 'averagers' underpinned the discovery. Still, the discovery appeared 'to be in the air' as the inhibitory receptive fields in the non-dominant eye of most neurones in cat's LGNd were almost immediately and independently 're-discovered' by Wolf Singer. Some years later, Singer and his colleagues provided good experimental evidence that, in the cat, the primary visual cortex (cytoarchitectonic areas 17 and 18) modifies (via feedback corticothalamic projections) the interocular interactions in the LGNd.[48] Varela and Singer, in their 1987 work, had hypothesized that 'corticothalamic feedback modifies thalamic transmission as a function of the congruency between ongoing cortical activation pattern and afferent retinal signals'. However, the general proposal that in the mammals with frontally positioned eyes, such as carnivores and primates, the LGNd is involved in mechanisms underpinning binocular vision remains controversial—in the LGNd of primates only small sub-populations of cells receive suppressive or excitory inputs from both eyes.[49]

Overall, during the late Sydney period, Canberra period and post-Canberra retirement period there were eighteen full-length research papers on the binocular properties of striate and LGNd neurones and about a dozen learned reviews on the same topic (see Bibliography in the Supplementary Material). In a couple of those studies, Peter and two postdoctoral fellows—Jerry Nelson from USA and Hiroshi Kato, a graduate of Yamagata University in Japan—examined the proposal that since the interocular orientation differences occur when viewing surfaces slanted in depth, the interocular differences in the preferred orientations of binocular cortical neurones might constitute the basis of a 'second neural mechanism for depth perception'.[50] This proposal was based upon the interocular orientation differences that occur when viewing surfaces are slanted in depth. However, it transpired that as far as the striate cortices of cats[51] and macaque monkeys[52] are concerned, binocular neurones showing interocular orientation disparities are very selective for interocular position disparities and poorly sensitive to interocular orientation disparities. Interestingly, virtually all presumably monocular cortical neurones, have suppressive and/or subliminal excitatory receptive fields in the silent eye and preferred orientations for silent receptive fields are the same as those for their non-silent counterparts.[53] Later on, working with post-doctoral fellows Richard Maske (from South Africa) and Shigeru Yamane (from Japan), Peter conducted further quantitative analysis of receptive field organizations for the two eyes[54] and examined the putative role of 'end-stopped' (see below) cells in binocular depth discrimination.[55]

### *Parallel Processing of Visual Information*

A remarkable feature of the John Curtin School phase of Peter's career was the significant growth of the doctrine of parallel processing of information in the mammalian visual system that challenged aspects of the serial-hierarchical processing model championed by Hubel and Wiesel. Indeed, many of the principal tenets of parallel model were based on the findings of two autonomous research groups headed respectively by Bill Levick/Brian Cleland and Jonathan Stone.

Peter had 'two–track' involvement in developing the model of parallel processing of visual information. On the one hand, during the regular weekday lunches in his office in the JCSMR, Peter was not only a witness, but very often a moderator of vigorous, and strongly personalized debates concerning the functional properties, number and naming of distinct information channels in the retino-geniculo-cortical pathways. Occasionally, when participants gave evasive answers to the questions posed, Peter prodded them with a very Australian colloquialism: 'come off the grass'. On the other hand, a serious challenge to the putative serial-hierarchical cascade of simple-to-complex-to-hypercomplex cortical cells of Hubel and Wiesel came from his own laboratory,[56] where it was found that the key feature of the hypercomplex cells, the presence in their receptive field of the suppressive region along the line of optimal orientation is not restricted to cells with 'complex-like' receptive field properties. The results were published in a series of papers from the Bishop group in the early 1970s (see Supplementary Material). Thus, in the striate cortex of the cat, there are two varieties of the end-stopped cells: one variety was complex-like, while the other variety, constituting the majority of end-stopped cells, was simple-like.[57] The existence of simple-like variety of end-stopped cells is inconsistent with hierarchical or serial information processing cascade (LGNd –simple cells-complex cells-hypercomplex or end-stopped cells) proposed by Hubel and Wiesel.

### *Quantitative Analysis of Receptive Field Properties of Striate Cortical Neurones*

The years 1968–75 saw a very fruitful collaboration with Geoff H. Henry (1929–2010) that resulted in nineteen joint publications (Supplementary Material). Other collaborators in parts of this period were Jack S. Coombs (1917–1993; designer of electronic stimulating and recording equipment for Jack C. Eccles) and two postdoctoral fellows, Bogdan Dreher (from Poland) and Anthony (Tony) W. Goodwin from South Africa who had completed his PhD degree in the USA. Several significant advances were made by this group. These included:

1. the discovery of purely inhibitory and/or sub-liminal excitatory regions in the receptive fields of simple cells in cat striate cortex;[58]
2. the discovery that in case of some simple cells, stimulating the discharge centre with short bars oriented at 90° to the optimal orientation results in reduction rather than an increase in spike activity (spatially overlapping orientation specific excitatory and inhibitory receptive fields);[59]
3. an early challenge to Hubel and Wiesel's (1962) popular model of mechanism underlying the orientation selectivity of simple cells in the primary visual cortex. According to this model the orientation selectivity of simple cells is based on the excitatory

convergence of a group of LGNd neurones with their partially overlapping excitatory receptive fields distributed along the axis of optimal orientation of the simple cell and thus underpinning typically elongated discharge field of the simple cell. However, Henry and his colleagues[60] demonstrated that the sharp orientation selectivity of simple cells is dependent on the extension of the stimulus to the silent suppressive 'side bands' beyond the excitatory (discharge) fields;[61] and
4. sophisticated quantitative analysis of mechanisms underlying the direction selectivity of simple cells in striate cortex.[62]

After 1975, Jonathan Stone left for Sydney while Geoff Henry led a separate research group. Peter, until his formal retirement in 1982, worked with several postdoctoral fellows—Hiroshi Kato, Guy Orban from Belgium, Shigeru Yamane, Richard Maske, R. Marcello Camarda from Italy and Esther Peterhans from Switzerland. They concentrated on several issues that attracted Peter's attention over the years. Apart from quantitative analysis of receptive field organizations for the two eyes, these included: quantitative analysis of properties of the end-zone of both simple-like and complex-like hypercomplex cells,[63] quantitative analysis of spatial relation between receptive fields revealed by stationary flashing stimuli and those revealed by moving stimuli.[64] In addition, working with Janus J. Kulikowski (visitor from England, originally from Poland), Peter made an early attempt on the linear analysis of responses of simple cells.[65] Furthermore, Kulikowski and Bishop, joined later by ANU mathematician Stjepan Marcelja, formulated a theory of spatial position and spatial frequency relations in the receptive fields of simple cells.[66]

As mentioned earlier, there were several autonomous visual laboratories in Peter's department. The organization of the department was not rigid and researchers were free to participate in different projects run in different laboratories. For example, postdoctoral fellows Klaus-Peter Hoffmann, from the laboratory of Otto Creutzfeldt (1927–92) Germany (and later a very accomplished visual neurobiologist himself) and S. Murray Sherman, from the laboratory of Jim Sprague (1916–2002) in USA (later on a prominent researcher of the dorsal thalamus) pursued several projects in Peter's laboratory and later on joined Jonathan Stone in studying parallel channels in the retino-geniculo-cortical pathways and effects of monocular deprivation in early postnatal period on parallel information channels in the LGNd. During daily lunch-time discussions in his office, Peter kept abreast of all research in his department. Despite several administrative duties and trips overseas to participate in specialized visual neuroscience meetings, he actively participated in most experiments conducted in his laboratory. Indeed, unless he actively participated in data collection he refused to be a co-author of any experimental paper based on the data collected in his laboratory even when the findings were inspired by Peter's work.[67] Furthermore, once convinced about the quality of the data collected, Peter strongly supported publications even if the results challenged some of his own strongly held ideas.[68]

## Festschrift on Lord Howe Island

A celebration was held on Lord Howe Island to mark Peter's retirement in 1983. Virtually all his students and collaborators attended. The meeting was also attended by several distinguished sensory neuroscientists influenced by Peter's work and/or collaboration with Peter's students/collaborators. The tiny church hall was used for presentations. The compact, but varied, island topography ensured that participating colleagues, friends and family all got to interact frequently on the walking and bicycle tracks, beaches and coral reefs of this beautiful island, amply justifying the choice of the venue (Fig. 1). A few years later (1986), twenty-seven papers presented at the *Festschrift* were published in the volume entitled *Visual Neuroscience*.[69]

## Australia Prize

In 1993, Peter Bishop received Australia's highest science honour—The Australia Prize. The Prize was awarded jointly with Vernon B. Mountcastle (1918–2015) of Johns Hopkins University in Baltimore and Horace B. Barlow (b. 1921) of the University of Cambridge. All three made related contributions to sensory neurophysiology. Many would argue that the work of all three was very close in importance and relevance to the Nobel Prize-winning work of Torsten Wiesel and the late David Hubel. Indeed, the insights of Vernon Mountcastle concerning the columnar nature of neocortical topographic and functional architecture played a big role in the later demonstration and analysis of columnar organization in visual cortex. Similarly, many would argue that the contributions of Bishop and Barlow to our understanding of the binocular neural mechanisms underlying stereopsis (3-D visual perception) should bring them into the Nobel Prize-recipients rank.[70] The demonstrable incredibly high precision of stereopsis puts it into the group of phenomena called *hyperacuity*, the concept formulated by another Fellow of the Royal Society, the Australian Gerald Westheimer,[71] a pre-World War 2 refugee from Nazi Germany.

## Final Years: Work on Vertical Disparities and Binocular Neurones

In his latter days, Peter grappled with another of the controversial aspects of binocular vision, addressing the question: do the interocular vertical disparities play a role in stereoscopic vision? The late Bob Rodieck who in the mid-1960s was working in Peter's department at Sydney, was unrelentingly critical about the putative role in depth perception of interocular disparities among binocular visual cortical neurones. His argument was as follows: mammalian eyes are separated from each other horizontally rather than vertically, the interocular disparities in the receptive field position are reflection of the 'sloppiness' in the system and the fact that frequencies and the range of interocular vertical and horizontal disparities among cortical neurons are very similar, does not imply that vertical disparities play a role in depth perception. Many researchers were swayed by Rodieck's argument.

The late Francis Crick (co-winner of 1962 Nobel Prize in Physiology or Medicine for 'the discoveries concerning the molecular structure of nucleic acids and its significance for information transfer in living material') became interested in many unsolved problems in visual neuroscience, including the putative role of binocular vertical disparities in depth perception. Crick's brilliance and fame had brought him great donated resources, such as a credit card with a virtually infinite limit and no repayment schedule. He was able to invite known scholars of the problem of vertical disparity from afar, to 'hold court' with him at his beautiful office overlooking the Pacific Ocean at the Salk Institute.

One of us (JDP), having co-generated (with Peter Bishop and Tosaku Nikara) the provocative data showing abundant interocular

**Figure 1.** Peter Bishop with his family and colleagues at Lord Howe Island Meeting, September 1983. Peter Bishop is sixth from the right, in the second back row (all participants are identified in the photograph in the Supplementary Material).

vertical disparities among binocular neurones in the primary visual cortex, was very interested in these meetings. Many scientists were involved on both sides of the controversy, but only key aspects, and Crick's solution, are covered here.

Christopher Longuet-Higgins was a 'mathematical' friend of Crick, from Cambridge, who was able to counteract effectively the argument that vertical disparity could not play a role in binocular depth perception. Indeed, together with Mayhew he showed that vertical disparities can make an extra, useful, contribution to depth perception that horizontal disparities are quite unable to make.[72] Consider the following example: you stand close to a wall, with your body's transverse axis at right angle to the wall, so that your right eye is closest to wall, while your left eye is further away. The geometry is such that vertical disparities are generated between the larger targets on the right retina and the slightly smaller images of the corresponding targets on the left retina. A gradient of decreasing vertical disparities at greater distances would be generated by the wall. This would aid a three-dimensional reconstruction from the distribution of vertical disparities in the neuronal population. This gradient is not affected by vergence eye movements, which generate large horizontal disparities that must be cancelled out by any system that uses horizontal disparity to measure depth. Indeed, a system that is fine enough to use small vertical disparities for depth, just as visual cortical neurones can do, is superior to the horizontal disparity system because vergence eye movements do not mar it. Of course, horizontal disparities are not redundant, they have great value in other situations, such as determining the depth of local targets.

One of the most compelling demonstrations of the role of vertical disparity in depth perception was a display developed by Brian Rogers that enabled a subject to track three-dimensional images without realizing that pure vertical disparities were being introduced. As envisaged by Longuet-Higgins and demonstrated by Rogers and Bradshaw this was true only over a wide field of view.[73] The many experiments that have failed to show any connection between vertical disparities and depth perception all involved narrow field displays instead of the necessary wide field gradients of vertical disparity.

On the subject of interocular vertical disparities, Peter Bishop was clearly 'on the side of the angels' not only by creating the laboratory where they were first discovered, but also by reasoning and arguing insightfully that they play a key physiological role.[74]

## Epilogue

Peter Bishop was awarded the Australia Prize, the highest honour that the nation can bestow on its scientists. Peter was cited for his insights and experimental contribution to our understanding of the neural basis of stereopsis, the three-dimensional sense of extraordinary precision. Peter's highly quantitative approach to his science might have stemmed from his adolescent ambitions to become an engineer. There was apparently an early dialectic between engineering, as represented by his surveyor father's optical instruments, and preparation for medical school, his mother's choice for Peter. Although his eventual medical training led him down a path involving successive Chairs of Physiology at the University of Sydney and the Australian National University, his memorable legacy is the detailed quantitative study of the visual system using instruments that he designed and were unparalleled in their precision at the time. Those instruments played crucial roles in allowing him and his students and collaborators to make several important discoveries concerning some of the mechanisms underpinning functions of the mammalian visual system.

In June 2013, the Bosch Institute at the University of Sydney organized a commemorative symposium for Peter O. Bishop entitled: 'Visual Neuroscience: Modern Challenges and Australian Pioneers'. Many Australian and overseas-based presenters described their current work on 'Peter's themes'. In 2015, Bishop's family established The HL and PO Bishop Fellowship in Neuroscience. The Fellowship is administered by the Bosch Institute at the University of Sydney.

Overall, Peter's work had and continues to have a substantial impact. Indeed, according to Thomson Web of Science, by the end of 2016, his h-index was 46 and his papers have been cited almost 8000 times, including ~200 citations in the last three years.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Endnotes

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