The Origins and Early Development of Australasian Auditory Neuroscience

Dexter R. F. Irvine

Bionics Institute, Melbourne, Victoria, Australia

and

School of Psychological Sciences, Sub-Faculty of Biomedical and Psychological Sciences,

Monash University, Victoria, Australia

Prof. Dexter R. F. Irvine
Bionics Institute
384-388 Albert Street
East Melbourne, Victoria, Australia, 3002
Phone: +61 3 93874123

Email: dirvine@bionicsinstitute.org

Acknowledgements: I am grateful to the reviewers for their helpful comment and to the following friends and colleagues in auditory neuroscience who provided information for this paper and/or commented on an earlier version of the manuscript: Lindsay Aitkin, Harvey Dillon, Brian Johnstone, Jim Pickles, Ramesh Rajan, Don Robertson, Rob Shepherd, and Peter Thorne.

Abstract

The impressive achievements of Australasian auditory neuroscience largely derive from the establishment of three major laboratories, at the University of Western Australia, Monash University, and the University of Melbourne, in the 1960s. The research foci of these laboratories, and the achievements of the scientists who established them, and of their colleagues and students, are described in this paper. The early development of auditory neuroscience occurred in a context provided by research activity in a number of other areas of hearing science, among them audiology, otolaryngology, psychoacoustics, and vestibular science. The development of these and some other strands of Australasian hearing science is briefly reviewed.

Keywords: auditory neuroscience; audiology; cochlear implant; otolaryngology; psychoacoustics

1. Introduction

Australia and New Zealand have an impressive history of achievement in auditory neuroscience. Much of this achievement derives from the establishment of three major auditory neuroscience laboratories in the 1960s: the Auditory Laboratory at the University of Western Australia (UWA) (established in 1962), the Monash University auditory research laboratories (established in 1966), and the laboratories of the Department of Otolaryngology in the University of Melbourne (established in 1969), which subsequently gave rise to the Bionic Ear Institute. The major purpose of this paper is to give a brief account of the achievements of the scientists who established those laboratories, and of the contributions they, and their colleagues and students, made to the development of auditory neuroscience in Australasia.

Strictly defined, auditory neuroscience is concerned with the auditory nervous system. However, the auditory transduction process in the cochlea involves a range of complex and exquisite biophysical processes, and these processes are themselves influenced by efferent (descending) neural projections from the brainstem to the cochlea. It would therefore be inappropriate to separate investigation of the auditory nervous system from that of the basic middle and inner ear processes that provide the input to it. Furthermore, auditory neuroscience has developed in parallel with, and has been influenced by, a number of other areas of hearing science (e.g., audiology, otolaryngology, psychoacoustics, vestibular science). Although the emphasis here will be on auditory neuroscience, it will be considered broadly and in the context of these other aspects of hearing science.

2. The Auditory Laboratory at the University of Western Australia

This laboratory was established by Brian Johnstone (Fig. 1) when he was appointed lecturer in the Department of Physiology at UWA in 1962. Johnstone's initial training was in physics, and he

completed his PhD in Pharmacology at the University of Melbourne on ionic balance in muscle. In the course of his post-doctoral training at the University of Chicago he developed an interest in cochlear biophysics [1], and this became the focus of his research when he returned to Australia. An outstanding early achievement of his laboratory was the use of the Mössbauer technique to make the first measurements of basilar membrane (BM) displacement since those made by the Nobel Prize winner Georg von Békésy in the 1940s.

Von Békésy had used stroboscopic illumination to measure displacement of Reissner's membrane in a number of species, mainly in cadavers. These seminal observations established the fundamental features of the traveling wave of displacement of the organ of Corti and the tonotopic organization of this mechanical displacement (i.e., the fact that the maximum amplitude of displacement occurred at different locations for different frequencies). Johnstone and Boyle [2] used the much more sensitive Mössbauer technique to make measurements of displacement of the high-frequency portion of the BM itself in living guinea pigs, at sound pressure levels that were in the physiological range and were much lower than those required by the stroboscopic technique used by von Békésy. The technique involves placing a small radioactive source on the BM and measuring the Doppler shift in the emitted radiation as the membrane moves. In addition to these important observations on BM mechanics, Johnstone and his colleagues carried out important work on many aspects of cochlear electrophysiology (see [3] for a review of this early work). The first investigations of the auditory nervous system in the UWA laboratories appear to have been the studies of the gross auditory nerve action potential and the responses of single auditory nerve fibres in lizards by an undergraduate ("Honours") student, Ray Johnstone (not related), under Brian's supervision [4,5].

Johnstone supervised a large number of graduate and honours students, many of whom went on to make outstanding contributions to auditory neuroscience. Among the early graduate students from

the laboratory to make such contributions were: Peter Sellick, Graeme Yates, Rob Patuzzi, Alan Cody, Eric LePage, Tony Gummer, and Ramesh Rajan. In addition to Ray Johnstone, a number of other Honours students supervised by Brian, notably Don Robertson and David McAlpine, completed doctorates elsewhere. Robertson completed his PhD at McGill University, supervised by Geoff Manley, who spent a year in the UWA laboratory as a QEII Fellow [6]. After post-doctoral studies in Belgium, where he studied the olivocochlear efferent system with John Desmedt, Robertson returned to the Auditory Laboratory in 1978, and worked there until his retirement in 2012. Manley has visited the laboratory many times over subsequent years to work collaboratively with Johnstone and his colleagues.

Any detailed account of the contributions of Johnstone's students is beyond the scope of this paper, but it is of interest to note the later work of Peter Sellick, which bears directly on a fundamental question that was raised by the earlier BM measurements and which dominated hearing science in the 1970s. Although Johnstone and Boyle's measurements of BM displacement were more refined than those of von Békésy, they nevertheless indicated that the frequency selectivity of the membrane was much poorer than that of individual auditory nerve fibres (i.e., the BM was much more broadly tuned). This puzzling discrepancy gave rise to the view that there must be some sort of "second filter" that acted to transform the broad mechanical tuning of the BM into the much sharper neural tuning (see [7] for review). As a post-doc at the University of Sussex, Sellick worked with Ian Russell and succeeded in making the first intracellular recordings of the sound evoked responses of cochlear hair cells (the mechano-electrical transducers) in living animals [8]. These recordings indicated that the hair cells were as sharply tuned as the auditory nerve fibres, and thus constrained the possible nature of any second filter. On returning to the University of WA, Sellick collaborated with Rob Patuzzi and Johnstone to make further measurements of BM displacement. They used an improved Mössbauer technique, but also, and critically, used the threshold of the pure-tone evoked compound auditory nerve action potential

(CAP) as a measure of the physiological state of the cochlea. In cases in which this threshold was not affected by opening the cochlea and placing the Mössbauer source, the BM proved to be as sharply tuned as auditory nerve fibres, indicating that no "second filter"' was required. In animals in which the CAP threshold declined, the BM became more broadly tuned, indicating that the earlier measurements showing broad mechanical tuning had been made in physiologically compromised cochleae. The paper in which these now classical results were presented [9] appears to be the most highly cited paper in Australasian auditory neuroscience

Johnstone retired in 1993, but the Auditory Laboratory remains active and over the decades since it was established has made major contributions to a number of areas of hearing science. In addition to cochlear mechanisms and biophysics, major research themes have concerned the response characteristics of auditory nerve fibres, the structure and function of auditory efferent systems, mechanisms of hearing loss, and the central mechanisms of tinnitus (for reviews see [10-13]).

3. The Auditory Neuroscience Laboratories at Monash University

The first of these laboratories was established by Bill Webster (Fig. 2) when he took up a position as Senior Lecturer in the (itself newly established) Department of Psychology at Monash University in 1966. Lindsay Aitkin (Fig. 2) was appointed to a position in the Department of Physiology, where he established a second laboratory, in 1970, after a very productive post-doctoral period at the University of Wisconsin in Madison. The group was strengthened in the early 70s by the appointment to a position in Psychology of Jim Saunders, who subsequently returned to the US to establish a laboratory at the University of Pennsylvania.

Both Webster and Aitkin had completed their PhDs at Sydney University, under the supervision of Colin Dunlop of the Department of Physiology. Dunlop himself had not previously worked on the auditory system, but he had developed expertise in evoked potential recording in awake animals

[14]. Webster was interested in the neural correlates of auditory habituation and attention, and used these techniques to investigate such changes in evoked potentials in the cochlear nucleus, the brainstem nucleus to which the auditory nerve fibres project. The papers in which the results of these studies were reported [15, 16] appear to be the first auditory neuroscience (strictly interpreted) papers from an Australasian laboratory; remarkably, they were published in the high impact journals *Nature* and *Science*, respectively. Aitkin's first paper reporting on his doctoral work [17], an account of the click-evoked response patterns of single neurons in the medial geniculate body, the major auditory thalamic nucleus, was published the following year, and appears to be the first auditory single-unit study from an Australasian laboratory.

During the period when Webster and Aitkin were doing their doctoral work in the Department of Physiology, they were influenced by the members of an outstanding group of visual neuroscientists led by the then Head of Department, Peter Bishop. As discussed below, one member of that group, Jack Pettigrew, was later to also make substantial contributions to auditory neuroscience. It is also of interest that another member of the visual neuroscience group, Bob Rodieck, an American who worked at the Massachusetts Institute of Technology before coming to Australia, had published a report on quantitative methods for studying the spontaneous activity of single neurons, which was based on recordings made from the cochlear nucleus [18].

The first two graduate students from the Monash laboratories were Dexter Irvine and Gregory Bock. Bock made his career in the UK, but Irvine returned to a position at Monash after post-doctoral fellowships in the UWA laboratory and at the University of California, and became a member of the group. Later graduate students who went on to make significant contributions to auditory neuroscience were Roger Coles, Dennis Phillips, David Moore, Mal Semple, Mike Calford, Russell Martin, Lisa Wise, and Janine Clarey. The major contributions of the Monash group covered a large number of areas of auditory neuroscience, mainly – but not exclusively –

relating to central auditory pathways. Among these areas were: the functional organization and connectivity of central auditory structures, at all levels from the cochlear nucleus to the auditory cortex; auditory system development; audiogenic seizures; auditory spatial coding, and auditory system plasticity (see [19 – 22] for reviews). Webster and Aitkin retired from Monash in 1993 and 1996, respectively, and Irvine in 2007, but auditory neuroscience research continues in the Department of Physiology, in the laboratory of Ramesh Rajan, who completed his PhD degree with Johnstone at UWA.

4. The Melbourne University Department of Otolaryngology and Bionic Ear Institute Laboratories

The laboratories in the Department of Otolaryngology at the University of Melbourne were established by Graeme Clark (Fig. 3) when he was appointed to the Foundation Chair of that Department in 1969. Clark was a highly experienced clinical otolaryngologist when he undertook doctoral studies in auditory neuroscience in the Department of Physiology at the University of Sydney, under Colin Dunlop's supervision. His first auditory neuroscience publication [23] reported a study of field potentials in the medial nucleus of the superior olivary complex, the first site of binaural interaction in the auditory pathway.

The research of Clark's group at the University of Melbourne was strongly focused on the development of a cochlear implant for the treatment of profound deafness, and covered a wide range of areas (the development of electrodes, surgical techniques, and processing strategies) in parallel with behavioural and neurophysiological studies in animals of responses to cochlear electrical stimulation. After the first clinical implants in 1978 and 1979, major emphases were on psychophysical studies of the performance of the implantees and on the further development of processing and stimulating strategies. This wide-ranging research program ultimately led to the development with industry partners (Nucleus, later Cochlear Pty. Ltd.) of the first commercial

multi-channel cochlear implant (see [24] for a fascinating account of this process). In 1984 Clark established the Bionic Ear Institute, and research was subsequently distributed between the Institute's laboratories and those of the Department. In subsequent years the research has focused on a wide range of prosthesis-related issues: the development of improved processing and stimulation strategies; animal studies of the effects of deafness and cochlear electrical stimulation on the structure and function of the central auditory pathways; the responses of auditory nerve fibres and central structures to such stimulation, and the effects of brain plasticity on those responses; various forms of drug therapy to preserve surviving auditory nerve fibres and to protect hearing (for reviews see [25-29]). The remarkable success of cochlear implants in infants with congenital profound hearing loss and in adults with some residual hearing (i.e., severe rather than profound hearing loss) has also prompted research on the assessment of infant responses to cochlear electrical stimulation and on electro-acoustic hearing.

Among the early graduate students trained by Clark who continued to make substantial contributions to the development of improved cochlear implants and to hearing science in general were Rob Shepherd, Joe Tong, Hugh McDermott, Richard Dowell, Peter Busby, and Stephen O'Leary. Many of these researchers have continued to work in the Bionic Ear Institute, the Department of Otolaryngology, or in affiliated organizations. In 2011 the Bionic Ear Institute, under its new Director, Rob Shepherd, renamed itself the Bionics Institute, reflecting a growing research emphasis on other aspects of medical bionics, notably bionic vision and deep brain stimulation, in addition to its continuing work on hearing

5. Auditory Neuroscience at the University of Auckland

There appears to have been no research on the auditory nervous system in New Zealand in the 1960s and 1970s, but John Irwin had an active auditory psychophysics research program with an emphasis on intensity processing (e.g., [30, 31]). In 1978 John Montgomery moved to the University of Auckland and developed a major research program in marine biology, which has

included studies of the vestibular and lateral line (hair cell system for the detection of movement and vibration) systems in fish (e.g., [32, 33]). Over a similar period, Martin Wild in the Department of Anatomy has carried out a sustained program of research on avian neuroanatomy, one component of which has comprised studies of the auditory system in song birds (e.g., [34]). Auditory processing in song birds is of great interest because of the many parallels between bird song and human speech, in respect to acquisition during critical periods, sensory-motor interactions, and perception (e.g., [35, 36])

Two early graduate students from the University of Auckland who have gone on to make major contributions to auditory neuroscience are Peter Thorne (who was mentored by Brian Johnstone during his doctoral studies) and Gary Housley (who now heads a major auditory neuroscience research group at the University of NSW). The major foci of research in the Department of Physiology in Auckland are mechanisms of auditory synapse formation and transmission, and of noise-induced cochlear injury (for reviews see [37, 38]).

6. The Broader Context of Australasian Hearing Science

Although the laboratories and research groups described in the preceding sections were the major contributors to the early development of auditory neuroscience in Australasia, a number of other institutions and individuals have contributed to the field itself or to the broader hearing science context in which the field developed. These diverse strands of influence are discussed briefly in the following sections

6.1. Early anatomical studies

Alfred Walter Campbell (1868 – 1937) is regarded as Australia's first neurologist. He was born in NSW, studied medicine at the University of Edinburgh, and had a distinguished research and clinical career in Europe before returning to clinical practice in Australia. In his 1905 monograph [39], which founded cerebral cytoarchitectonics, he made a remarkably prescient distinction

between what we would now call “core” and “belt” areas of the auditory cortex. The Australasian Neuroscience Society’s “A. W. Campbell Award”, which is awarded for the best contribution by a member of the Society in their first five postdoctoral years, is named in his honour.

6.2. Comparative Studies of the Auditory System

Early comparative studies of the auditory system were carried out by the group led by Murray Littlejohn in the Department of Zoology at Melbourne University, which was focused on auditory communication in frogs. Their first reported electrophysiological study (of evoked potential audiograms in nine frog species) [40] was carried out by a graduate student, Jasper Loftus-Hills, in collaboration with Brian Johnstone, who trained him in evoked potential recording techniques. Similar recordings were also made in insects (e.g., [41]). Over more recent years, a range of comparative studies, many of them in unique Australian animals, (e.g., [42-45]), have been carried out in the major laboratories described above. A number of investigators have taken advantage of the ready access to pouch young in marsupials, which makes them ideal subjects in which to examine auditory system development (e.g., [46, 47] (see [48] for review). As noted in section 5, research at the University of Auckland has investigated the auditory and vestibular systems in fish and birds.

6.3. The National Acoustic Laboratories

The National Acoustic Laboratories (NAL) grew from the Commonwealth Acoustic Laboratories, which were established in the late 1940s to perform a mixture of research, clinical services, and technical development in the area of hearing loss in humans. A fascinating aspect of the early history of NAL is that John Carew Eccles, the Nobel Prize winning Australasian neurophysiologist, played a pivotal role in the establishment, in 1943, of The Acoustic Testing Laboratory from which the later organizations evolved [49]. Under its first formal Research Director, Dennis Byrne, and his colleague Harvey Dillon, who is now Director of the

Laboratories, NAL have carried out research on a wide range of acoustic, psychoacoustic and electrophysiological topics relating to hearing disorders and the fitting of hearing aids. These include audiological and speech discrimination testing, the assessment and remediation of auditory processing disorders, and the use of electrophysiological methods for the assessment of hearing loss in infants (see www.NAL.gov.au for current and recent research, and [49] for a review of its earlier history). NAL is now located in the Australian Hearing Hub at Macquarie University, which recently appointed David McAlpine, who completed his Honours degree with Brian Johnstone, as its inaugural Professor of Speech, Hearing and the Brain.

6.4. Otolaryngology in Australasia

In his fascinating account of the early history of otolaryngology in Australia, Bulteau [50] reports that there was a separate "Eye, Ear, Nose and Throat" section at the Second Intercolonial Medical Congress of Australasia, which was held in Melbourne in 1889, and Australasian otolaryngologists have held scientific meetings since that time. The work of the University of Melbourne's Department of Otolaryngology under Graeme Clark's leadership has been described above. In 1983 William Gibson was appointed to the second Chair of Otolaryngology in Australia, in the University of Sydney, and he and his colleagues have made impressive research contributions to many aspects of hearing science. In recent years, both clinical and basic hearing science research has been supported by the Garnett Passe and Rodney Williams Memorial Foundation, which was established in 1986. As indicated by his last paper [51], Passe's clinical research interests were in topics which remain highly relevant today, viz., Meniere's disease, tinnitus, and nerve deafness.

6.5. Audiology in Australasia

The first post-graduate training course for audiology in Australia was established by Graeme Clark and Field Rickards at the University of Melbourne in 1973, and the investigation of

audiological procedures for cochlear implants was an important component of the commercial development of the device (e.g., [52]). The growing recognition of hearing impairment as a major health problem has led to the establishment of audiology training programs at a number of universities in both Australia and New Zealand, where the first program was established at the University of Auckland in 1990. Research in Departments of Audiology is focused on the causes, characteristics and treatment of different forms of hearing loss and balance problems, and on the improvement of auditory prostheses. As noted above, these are also major foci of research by audiologists and other hearing scientists at NAL.

6.6. Auditory Psychophysics

As noted in section 5, John Irwin led an active psychoacoustics research program at the University of Auckland from the mid-1960s. In 1972, Bill Noble established a psychoacoustics research laboratory at the University of New England; his major interests were in the perceptual and social consequences of hearing impairment (e.g., [53]), and he has collaborated extensively with colleagues at NAL.

Psychophysical studies of performance with prosthetic devices (cochlear implants and hearing aids) have also been a major component of research in the Departments of Otolaryngology and Audiology (sections 4, 6.4, and 6.5), the Bionic Ear Institute, and NAL (section 6.3). A major focus of more recent basic auditory psychophysics in Australia has been on the role of head-related transfer functions in sound localization and on virtual auditory space technology (e.g., [54]). This work was initiated by Simon Oldfield at Deakin University (e.g., [55]), and continued in an applied setting when he moved to the Defence Science and Technology Organization.

6.7. Jack Pettigrew and the Vision, Touch and Hearing Research Centre

As mentioned previously, Jack Pettigrew was a member of Peter Bishop's visual neuroscience group at the University of Sydney when Webster, Aitkin and Clark were undertaking doctoral

studies there. In addition to his remarkable contributions to visual neuroscience, Pettigrew contributed substantially to auditory neuroscience. While a faculty member at Caltech, he collaborated with Eric Knudsen and Mark Konishi in the study [56] that initiated their outstanding program of research on auditory spatial coding in the barn owl midbrain. When he returned to Australia as Director of the National Vision Research Institute at the University of Melbourne, Pettigrew collaborated with Aitkin and a group of the Monash graduate students on an important series of studies of auditory spatial coding in the cat (e.g., [57,58]). Subsequently, he established and served as Director of the Vision, Touch and Hearing Research Centre (VTHRC) at the University of Queensland, and in 1989 recruited Jim Pickles as leader of the hearing group. Pickles, who moved to Brisbane from the University of Birmingham, had previously described the "tip links" between the stereocilia of mammalian hair cells [59], which are now know to apply the stimulus force to open the mechanotransducer channels [60]. VTHRC was absorbed into the Queensland Brain Institute in 2007.

6.8. Vestibular Neuroscience

The intimate connection between auditory and vestibular receptor structures and transduction mechanisms merits a brief consideration of the development of vestibular neuroscience in Australasia. The major figure in this field has been Ian Curthoys, who completed doctoral studies in auditory psychophysics at Monash University [61]. Curthoys began his work on the vestibular system as a post-doctoral fellow at UCLA [62], and subsequently established an extraordinarily productive experimental laboratory at the University of Sydney and clinical collaboration with Michael Halmagyi. Some of his contributions to vestibular neuroscience have concerned the responses of vestibular primary afferents to acoustic stimuli, and the use of clinical tests of vestibular function employing air-conducted and bone-conducted sounds (e.g., [63]). Among the early graduate students from Curthoys's laboratory, Paul Smith and Cynthia Darlington of the University of Otago have continued to contribute to vestibular neuroscience. Another productive

Australian vestibular neuroscience research group is headed by Alan Brichta, at the University of Newcastle. As noted in section 6.5, research on balance problems is also carried out in a number of Departments of Audiology.

7. Concluding Comments

In this brief review of the origins and early development of auditory neuroscience in Australasia Brian Johnstone emerges as a pivotal figure. He established the first of the major laboratories whose output established Australia's place in the field, and that laboratory has been productive throughout the subsequent 50 or so years. Furthermore, Johnstone served as a mentor and collaborator to many other members of the Australasian auditory neuroscience community.

The scope of this account is such that it has not been possible to refer to the work of many individual researchers and research groups who have contributed to the field in more recent times. A recent article by Peter Thorne on audiological research in Australia and New Zealand [64] provides a brief summary of current research activity, but there remain many substantial contributions in the intervening years that have not been described either here or in that paper.

Prompted by the retirement of the seminal figures who established the three major Australian laboratories discussed in this paper, and in an attempt to maintain the momentum established over the preceding years, the Australasian Auditory Neuroscience Workshop (http://aanw.bionicsinstitute.org/aanw2015.html) was established and held its first meeting in 2004. Its major aim is to provide a forum in which younger members of the auditory neuroscience community can present their work and receive constructive feedback and mentoring. It meets annually, with attendances of the order of 40-50 researchers, usually as a satellite of the annual conference of the Australasian Neuroscience Society.

Conflict of Interest : The author declares that he has no conflict of interest

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Figure caption

Fig. 1 Brian Johnstone, the founder of the University of Western Australia laboratory

Fig. 2 Bill Webster (left) and Lindsay Aitkin, the founders of the Monash University laboratories

Fig. 2 Graeme Clark, the founder of the University of Melbourne laboratory and of the Bionic Ear Institute