Evolution of the brain and sensory systems of the kiwi.

Jeremy R Corfield

A thesis submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy,
The University of Auckland, 2009.

Abstract

Kiwi (*Apteryx spp.*) have evolved under unique evolutionary pressures and uniquely occupy a nocturnal, ground-dwelling niche. They share few traits with other birds: they have small eyes, an elongated bill, and several features more characteristic of mammals. Early anatomical studies described a number of unique features in the kiwi brain, but their relevance to the behaviour and ecology of the species was not clearly established. This study aims to describe the structure of the primary cranial sensory systems of kiwi and comment on the evolutionary pressures that may have shaped their current form.

The external morphology and relatively large size of the brain of kiwi, in particular those of the telencephalon, contrast with those of other Palaeognaths. The relative size of the cerebral hemispheres is rivalled only by a handful of parrots and songbirds. This enlargement results from a differential enlargement of the nidopallium, mesopallium and, to a lesser extent, of the basal ganglia. In other birds these regions are associated with the integration of information, cognition and learning. Kiwi brain centres processing visual information were small, although the retina structure showed an adaptation to dim light. The olfactory and trigeminal systems associated with the bill were hypertrophied. The auditory system shows specialisations associated with an overrepresentation of high frequency coding areas that originates in the cochlea and is preserved throughout the auditory brainstem. In absolute terms, the upper frequency response limit, based on hair cell morphology, is estimated to be about 5 kHz, the lower limit to be about 500 Hz, with a slightly higher frequency range predicted from the morphology of central auditory

structures. The organisation of both nucleus angularis (NA) and nucleus laminaris (NL) in kiwi suggest that the central auditory system has retained the ancestral organisation except for the morphological features associated with the overrepresentation of high frequencies.

Overall, the brain and sensory structures of kiwi have evolved neural adaptations that accompany the very different behavioural strategies associated with the unique niche the birds occupy. A large telencephalic size and shift away from vision towards an increased reliance on olfactory, tactile and auditory cues constitute a collection of features that make kiwi unique among birds. These findings provide a unique glimpse of the evolutionary history that has led to this unusual design, in particular, and challenge many of our current views about the evolution of brains and encephalisation, in general.

Acknowledgements

I would first like to sincerely thank my supervisory team.

Dr Stuart Parsons, whose enthusiasm and passion for biology and supervision during my Masters degree inspired me to undertake a PhD. Thanks also for your continued support over the last 4 years and for hanging in there as I chopped and changed my original thesis proposal.

Dr M. Fabiana Kubke, for energetically introducing me to the world of neuroscience, and for showing me that brains are cool. Your in-depth knowledge and understanding of neuroethology has truly taught me a lot, and equipped me with the skills to continue a career in neuroethology.

Professor J. Martin Wild, who has been a source of unlimited wisdom during my PhD, and has taught me a lot about the fine art of writing.

Thanks to everyone from the lab and neuroethology group: Priscilla Logerot. Jean Sebastien Finger, Silke Fuchs, Nils Krützfeldt, Kate Lomas, Lin-Chien Huang, Thorin Jonsson, and Shane Windsor for your ideas and friendship.

I was very lucky to work with some amazing people during my PhD, thanks for your help.

Dr Christine Köppl, whom I worked with to examine the cochlea and auditory nerve in kiwi.

Drs Monica Acosta and Hugo Rios, who examined the retina in kiwi with me.

Professor Graham Martin, whom I collaborated with to examine the kiwi visual system.

Dr Heather Eisthen, who gave me some helpful insights into the olfactory system of kiwi.

A general thanks goes to Mark Hauber, Nick Duggan, Jacqui Ross, Peter Thorne, Greg Sands, the Kiwi Encounter team, Emma Bean, Suzanne Bassett, and Claire Travers, the Ponui kiwi team: Dr Isabel Castro, Susan Cunningham, Birgit Ziesemann, and Rose and Dave Chamberlin for their input and support during different phases of this project.

Thanks to everyone in the School of Biological Sciences and Department of Anatomy at the University of Auckland.

A big thanks goes to the following institutions for financial support:

SBSP PBRF fund, Marsden Fund (Royal Society of New Zealand), International Society of Neuroethology, Royal Society of New Zealand, Contestable SBS fund, PReSS graduate research fund, University of Auckland Graduate Research Fund, Centre for Advanced MRI, PGSA (FMHS). Heiligenberg Travel Awards, FMHS bursaries.

I am indebted to the New Zealand Department of Conservation for their support during this project, particularly C. Gardner, P. Graham D. Harding, D. Stuthridge, A. Walker, T. Shaw, P. Vankilnk, G. Townsend, L. Adams, K. Owen, J. Bishop, and B. Armstrong. Thanks also to the Tangata whenua of the Northland, Auckland, and West Coast Conservancies for allowing me undertake research on kiwi.

Thanks to P. Brennan (Yale University) for providing me with the tinamou brains, B. Gill and the Auckland Museum for providing access to the moa, kiwi and kakapo collections, R. Pennell at Northland Ostrich and Emu for the emu and ostrich brains, Brett Gartrell and Janelle Ward from the New Zealand Wildlife Health Centre, Massey University, for help obtaining the kiwi and godwit specimens.

I am grateful to the staff of the Centre for Advanced MRI, in particular B Cowen, S. Winsor, S. Park and B. Pontré; the staff at the Biomedical Imaging Research Unit: Hilary Holloway for sharing her skills in electron microscopy and Jacqui Ross for her advise on imaging; Adrian Turner at the school of Biological Sciences, UoA for help with critical point drier and gold splattering; the Research Centre for Surface and material Sciences, Faculty of Engineering, UoA, and the Electron Microscopy Unit at the University of Sydney for help with the Scanning Electron Microscope; the Greenlane Clinical Centre Imaging Facility for allowing me to image the skulls of the moa, kiwi and kakapo, gratis.

And finally a very special thanks to my partner Lorissa Wyllie and to my family. Their love, support and understanding throughout have been the foundation on which everything else was built.

Table of Contents

List of Figures

List of Tables

Abbreviations

A	arcopallium
APH	area parahippocampalis
Bas	nucleus basorostralis pallii
BF	best frequency
BP	basilar papilla
CA	commissura anterior
Cb	cerebellum
DCN	dorsal column nucleus
DIP	nucleus dorsointermedius posterior thalami
DLM	nucleus dorsolateralis anterior thalami, pars medialis
DMNX	nucleus motorius dorsalis nervi vagi
DMP	nucleus dorsomedialis posterior thalami
E	entopallium
EPL	external plexiform layer
FLM	fasciculus longitudinalis medialis
FPL	fasciculus prosencephali lateralis
GCL	ganglion cell layer
GCt	substantia grisea centralis
GgCL	granule cell layer
GL	glomerular layer
GLU	nucleus geniculatis lateralis
HA	hyperpallium apicale
Hp	hippocampus
IHA	intercalated hyperstriatum accessorium
Imc	nucleus isthmi, par magnocellularis
INL	inner nuclear layer
IO	nucleus olivaris inferior
Ipc	nucleus isthmi, par parvocellularis
IPL	inner plexiform layer
LHy	nucleus lateralis hypothalami
LLI	intermediate nuclei of the lateral lemniscus
LLV	ventral nucleus of the lateral lemniscus
M	mesopallium
mc	maxillary concha
MCL	mitral cell layer
Md	mesopallium dorsale
MesV	mesencephalic trigeminal nucleus
MLd	nucleus mesencephalicus lateralis, pars dorsalis
Mv	mesopallium ventrale
MVd	nucleus motorius nervi trigemini, pars dorsalis
MVI	nucleus ahducentes
MVv	nucleus motorius nervi trigemini, pars ventralis
N	nidopallium

NA	nucleus angularis
NAm	nucleus angularis mediale
nBOR	nucleus of the basal optic root
nIX	nucleus nervi glossopharyngeus et vagus
NL	nucleus laminaris
NM	nucleus magnocellularis
nTS	nucleus tractus solitarius
nTTD	nucleus et tractus descendens nervi trigemini
NV	nervus trigeminus
OB	olfactory bulb
OE	olfactory epithelium
OF	olfactory fila
OM	nucleus nervi oculomotorii
OMd	nucleus nervi oculomotorii, pars dorsalis
OMv	nucleus nervi oculomotorii, pars ventralis
ONL	outer nuclear layer
OPL	outer plexiform layer
OS	nucleus olivaris superior
Ov	nucleus ovoidalis
Ph	photoreceptors
PL	periventricular layer
PM	nucleus pontis medialis
PMH	nucleus medialis hypothalami, posterioris
PrV	nucleus sensorius principalis nervi trigemini
PrVd	nucleus sensorius principalis nervi trigemini, pars dorsalis
PrVv	nucleus sensorius principalis nervi trigemini, pars ventralis
PT	nucleus pretectalis
PVM	nucleus periventricularis magnocellularis
R	nucleus raphes
RAm	nucleus retroambigualis
RPE	retinal pigmented epithelium
RPgc	nucleus reticularis pontis caudalis, pars gigantocellularis
Rt	nucleus rotundus
Ru	nucleus ruber
SGC	stratum griseum centrale
SHC	short hair cell
SL	nucleus septalis lateralis
SLu	nucleus isthmi pars semilunaris
SPC	nucleus superficialis parvocellularis
SPL	nucleus spiriformis lateralis
SpM	nucleus spiriformis medialis
SRt	nucleus subrotundus
SSp	nucleus supraspinalis
St	striatum
T	nucleus triangularis

Ta nucleus tangentialis
TeO optic tectum
THC tall hair cell
TPc nucleus tegmenti pedunculopontinus pars compacta
TSM tractus septomesencephalicus
V ventricle
VeD nucleus vestibularis descendens
VeL nucleus vestibularis lateralis
VeM nucleus vestibularis medialis
XIIts nucleus nervi hypoglossi, pars trachosyringealis