

# PN

Physiology  
News

Issue 102 / Spring 2016



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can be a sizeable problem



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## Physiology News

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edition of *Physiology News*

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# Limits of Perception: Advances in Bioimaging

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## Roger Thomas

Editor, *Physiology News*

This issue features articles on elite physiology in animals, to mark The Society's Theme for 2016 – 'Elite Performance' and the coinciding Topic Meeting in Nottingham on the Biomedical Basis of Elite Performance (in humans). Looking through the programme, I see no mention of non-human animals, though surely some of the experiments must have been done on rodents. *Physiology News* hopes to broaden the field with articles on horses, insects (twice) and bats. Also, we publish an article on nasal airflow, which apparently often switches from one nostril to the other.

A topic stimulating much argument in my host department recently has been our decision to stop giving our students hard copy handouts for each lecture. Typically, they were given 5 or 6 sides of A4 notes and illustrations, taken from the lecturers own notes and slides. The cost in paper and time was considerable, but the students did like this system. Many would simply highlight key phrases or headings during the lecture, and tended to lose their ability to take notes. Apart from saving money, one argument we deployed was that the ability to take notes is actually a valuable transferrable skill. Colleagues with children at other Universities said their children did not get handouts at all. Indeed when I was a student, we were lucky to get a printed timetable. Notes had to be written on paper, for later interpretation and amplification from textbooks. Now of course almost all students have tablets and/or laptop computers on which they might type notes if they have learned to touch-type. Some even make audio or video recordings, although supposedly only with special permission. We do still put some sort of brief handout on a

website and did leave files of last year's handouts on the same site. Thus, some students printed the latter and brought them to this year's lectures. One had the temerity to email me asking for an explanation of an experiment in last year's notes, which I had decided to leave out of this year's lecture!

I am still surprised how popular lectures seem to be in the sciences. I have come to believe that attending lectures is still seen as a key part of being student, and of course it's a good place to meet friends. Could it be a substitute for what used to be a religious ceremony? In the middle ages, students were in effect in monasteries, and had to attend chapel several times a day. Now they attend lectures instead, although there are many other ways to collect the material needed to pass exams.

I have been reading parts of the government white paper about Higher Education entitled "Fulfilling our potential: teaching excellence, social mobility and student choice." Apparently this was a manifesto commitment. The proposal is to reshape the higher education landscape to place students at its heart. (Do landscapes have a heart?) One way this will be done is a classic fudge – set up a new regulator that has a clear remit to champion value for money and the student interest in its decisions: the new "Office for Students". I am not making this up. Making the student at the heart of the HE system is a bit of a switch from placing research there. The authors of this paper do seem to appreciate that up until now very few universities assign teaching the same significance that they give research. Money has till now always been allocated by measuring research quality. They propose incentives to drive up teaching quality without damaging research. The incentives seem to be allowing Universities with a high rating in the Teaching Excellence Framework (TEF) to charge higher fees.

Details about how teaching will be judged are sparse. The four areas which will make up the quality rating seem to be: setting and maintaining academic standards, how learning opportunities are provided, how information about learning opportunities is provided and "enhancement of quality of students' learning opportunities". I don't understand what this means in practice. Lots of form-filling I suppose. More important than anything surely is deciding what to include in the curriculum, and how best to actually teach it.

Perhaps the main problem with the present system, which has employers complaining about graduates lacking useful skills, is that success as a student almost all depends on the ability to do well in written examinations. This surely is not a skill useful in a normal career. At least the Italian system of examining by viva does help prepare graduates for careers involving speaking in front of a critical audience. In the UK, vivas are rarely used since it is seen as important to minimise stress. I have long thought that employers should be involved in changing how students are assessed, since the assessment process drives so much of a student's learning efforts. I once introduced a paper involving critically reviewing a recent publication, but when I went on sabbatical the other examiners dropped it. To be fair, in some ways, University teaching does prepare students for one type of career – that of the University academic. But that is not going to increase the gross national product.

My photo above shows the facial effects of falling down a flight of wooden stairs in the dark. As well as many severe bruises my GI tract managed a complete shut-down for about 2 weeks. But no bones were broken, very luckily.



## AV Hill and the Death Ray

William Van der Kloot

It's good to know that a Blue Plaque now marks AV Hill's London home (*PN* 101, p16–17), but in addition to being celebrated as an eminent physiologist, he should be remembered as a great scientific statesman for his influential role in mobilizing scientists to solve critical problems in two World Wars.

In WWI, he was a serving infantry officer when asked to give up a leave day to advise the new Ministry of Munitions about devices for training anti-aircraft gunners. When he saw what they were trying to do he immediately showed them how to measure the heights of aircraft by using two mirrors about a mile apart. With the mirrors, they could also accurately measure where anti-aircraft shells with different fuse settings burst. Hill had broken new ground by fitting physiological data with equations. Now they should fit the shell data with the ballistic equations – a much more challenging task – which would enable them to provide the gunners with accurate range tables. To do this, he beat the bushes to gather a group of gifted, conscription-exempt youths and oldsters: they proudly called themselves Hill's Brigands. By war's end there were more than 50 of them. They also improved detectors to locate aircraft by sound. Hill earned a solid standing in the military.

In the early 1930's Hill was biological secretary of the Royal Society and the physicist William Henry Bragg was president. Bragg had struggled likewise to bring scientists into the war against the U-boats, they developed sonar just too late for use. Bragg and Hill saw the approaching war clouds and exploited their military credibility and contacts to set up the framework for the highly successful mobilization of British scientists in World War II, which among other notables brought Alan Hodgkin into the group developing microwave radar, which defeated the U-boats and night fighters.

Hill was invited to lunch at the Athenaeum on 14 October 1934 by AE Wimperis, director of research at the Air Ministry, who wanted to know whether a death ray was feasible. Hill recommended that the wireless section of the National Physical Laboratory be asked to calculate the power needed to bring a kg of water to the boil at various distances. The numbers showed that a death ray was not in the cards, but on the side, they estimated that it should be possible to detect the reflection of a wireless signal from an aircraft.

Hill pressed for the development of radar and – even more importantly – helped to plan how radar would be integrated into the air defence system.

In 1940, Hill was sent to Washington to coordinate military research with neutral American scientists. He was instructed to trade secrets, but how to swap without knowing what you will get in return? Back in London, he argued that they should tell the Americans everything, hoping that they would do likewise. Henry Tizard took to the US a suitcase containing every portable, secret device. This open-handed initiative established the bond of trust on which the brilliantly productive Allied scientific collaboration grew.

Van der Kloot W (2011) Mirrors and smoke: AV Hill, his Brigands, and the science of anti-aircraft gunnery in World War I. *Notes Rec R Soc* **65**(4), 393–410. Van der Kloot W (2014) Great Scientists wage the Great War: The first war of science, 1914–1918. *Fonthill Media*, p162–190 and 204–208. (E Starling's and WM Bayliss's contributions are on p49–73). Hill's skill as an amateur photographer is shown in *PN* 81 (Winter 2010) p17–21.

## Physiological aspects of reading (*PN*)

William Burke,  
University of Sydney, Australia

I enjoyed your article about the search for *PN* 1 in issue 100. I did respond to your earlier request, although not until June. In July I sent the first 6 issues of the precursors of *PN* to Hodgkin-Huxley House and their receipt was duly acknowledged. It's possible that they have not yet been brought to your attention.

Moving from *PN* 1 to the present day, may I make a suggestion about the design of the current publication? I have always enjoyed receiving *PN* but it can be greatly improved by avoiding mixtures of colour and text. Text is most readable when there is good contrast between the text and the background. The best contrast is when the text is black and the background is white. A bad contrast is when the text is white and the background is black or colour, especially pale colour. Pages 10 and 42 in the current issue (100) of *PN* are examples and are very hard to read. By all means use colour but keep it away from text.

*Editor's note: this has now been addressed*

## 3Don't

Jonathan Ashmore,  
University College London

I enjoyed both your editorial and the article on 3D printers, but alas the recommended printer company apparently stops trading in mid-January.

*Christof Schwiening (author) responds:*  
*'On the printer company closure I see that they have not gone bankrupt but are pulling out of 3D printers because the market is now very crowded with big manufacturers. The great thing about the Reprappro Company was that they made their machines entirely open source – so anyone could legally copy and make parts and software for them – which is already the case. Perhaps that ethical model inevitably meant that they were not going to survive China's ability to push out copies at lower prices. The open source model, and the fact that the owner was one of the main 'inventors' of 3D printing, led to my recommending them. It is a great shame since they were definitely one of the good guys in a rapidly developing market place.'*

## We were lucky in the 60s

Ron Whittam,  
Leicester

I don't do nostalgia, with one exception which is Physiology News. The reason is that all the news I get from Oxbridge Colleges and redbrick Universities is linked to donations. The good thing about the Phys Soc and the Roy Soc is unfettered giving without soliciting money.

I much enjoyed your items in the latest News. The pieces about 1965 meetings made me realise how lucky we were to enjoy the bonding of old and young and of members from different branches of physiology. When we sat through sessions we could appreciate advances across the board. It was perhaps a grave error to compartmentalise the subject. The reason for writing is to praise your publication of old minutes, I just want to ask if you might refer to the writer. In this case in 1965 it was Eric Denton. He was such a good secretary and wrote the Minutes on the train home after a meeting. I joined the Committee in 1967 and really valued the camaraderie of the dinners and meetings. Do you think young members today have any concept of the thrill of rubbing shoulders with the top people? Meetings were convivial, cohesive, full of confidence and vitality.

I hope you have a good run as Editor.

## Embracing change

Roland S G Jones,  
Department of Pharmacy and Pharmacology,  
University of Bath, UK

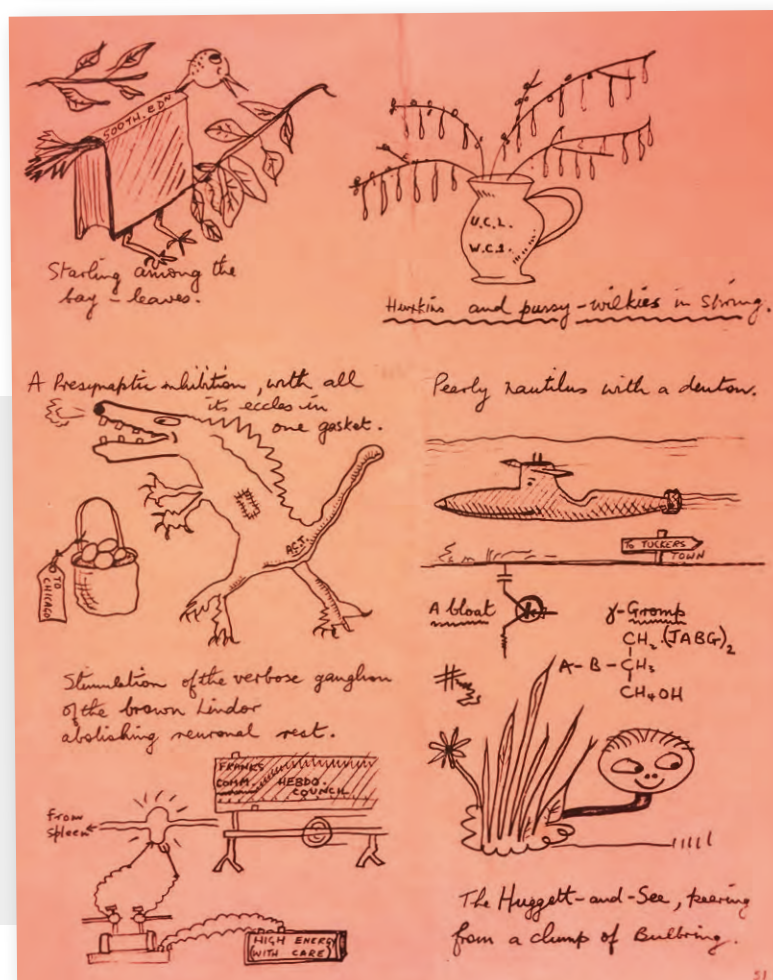
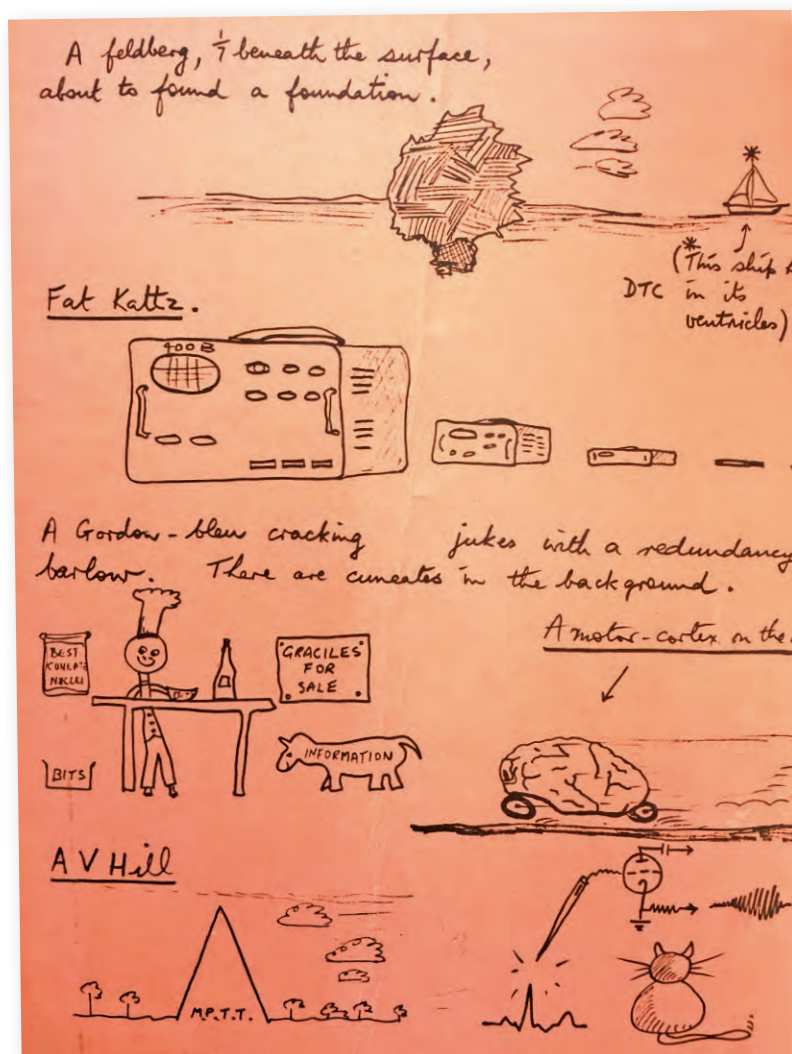
Having just read Roger Thomas' article on the early advantages and joys of using email (PN 101), I was reminded of my first encounter with it in the late 1980s. At the time, I was working as a Senior Research Fellow in the John Curtin School at ANU in Canberra. In 1988, John Lambert from the University of Aarhus joined me for 6 months sabbatical. John was also an early advocate of email use and was determined that we should use it to communicate when he returned to Denmark.

At that time, it did have the slight drawbacks of sometimes taking a day or two to arrive between sending and receiving (bouncing from node to node around the world), and, as Roger pointed out, required the active role of the recipient to check whether a message was there. This resulted in weekly, long-distance (very long!) phone calls from Aarhus to Canberra with John excited to know if his email messages had arrived or not, and what I thought of their content.

Question for the Editor or comment  
on a recent PN article?

Please send your correspondence  
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Doodles on the back of the menu  
for the AGM dinner in March 1966;  
from the archives held by the  
Wellcome Library.





## 2016 Honorary Members: call for proposals

We are now seeking nominations for Honorary Membership of The Society. Honorary Membership may be awarded to any eminent physiologist, and the privilege is not just limited to current Members of The Society.

If you know of any physiologists who can be considered 'persons of distinction in science who have contributed to the advancement of physiology or to the work of The Society', please send us their name and your statement of support. Your proposals will be considered by the Nominations Committee who will advise Council on formal nomination.

The new Honorary Members will be announced at the 2016 Annual General Meeting.

Honorary Members have the same rights and benefits as Members of The Society, but are not called upon to pay annual subscriptions. In addition, Honorary Members are also eligible to receive a print subscription to *The Journal of Physiology* free of charge as well as free attendance at Society meetings.

Please submit your proposals at <http://www.physoc.org/Hon-Membership2016> by 31 March 2016.

## Meet our interim CEO

In 2002, Casey Early was appointed as Director of Finance at The Society. He obtained an MSc in Financial Economics from Loughborough University and then qualified as a Chartered Accountant with haysmacintyre. As well as finance, his responsibilities cover human resources, governance and technology.

Casey says 'It is a privilege to support The Society at this level while the Trustees find a worthy successor to Philip Wright. It is a challenging but rewarding period of work experience and I have enjoyed the new interactions at the forefront of The Society's activities'.



Casey Early



Casey attending the Christmas Parliamentary Reception arranged by the Royal Society of Biology on behalf of the science and engineering community

## The Society celebrates its 140<sup>th</sup> birthday

In the early 19<sup>th</sup> century, experimental physiology was virtually non-existent in Britain, though it flourished in France and Germany. Medical students were largely taught by anatomists, surgeons and physicians. Things slowly started to change in 1836 with the appointment of William Sharpey, often described as 'the father of modern physiology in Britain' to the Chair of General Anatomy and Physiology at University College London.

The burgeoning of practical physiology involving work on living animals was paralleled by the emergence of those opposed to such experiments and in 1875, a Royal Commission of Enquiry into Vivisection was set up. The

Commission recommended that work on living vertebrates should be governed by an Act of Parliament that required experimenters to be licensed by the Home Secretary and special conditions being imposed for certain types of experiments. Physiologists recognised the need to have a say in any proposal: this need led to the formation of The Physiological Society.

At a meeting on 31 March 1876, 19 physiologists\* had gathered at the house of John Burdon-Sanderson at 49 Queen Anne Street, London. There, they proposed to form an association under the name of 'The Physiological Society' for 'promoting the

*advancement of physiology and facilitating the intercourse between physiologists'.*

Scientific meetings formed of communications, and demonstrations in conjunction with Society Dinners became more frequent, reflecting The Society's birth as a 'Dining Club'. The inaugural dinner was held at the Criterion Restaurant on 26 May 1876, the first ordinary meeting was held on 9 November 1876.

\*The 19 physiologists were: John Burdon Sanderson in the chair, William Sharpey, TH Huxley, Michael Foster, George H Lewes, Francis Galton, John Marshall, GM Humphry, F William Pavy, J Lauder Brunton, David Ferrier, PH Pye Smith, WH Gaskell, JG M'Kendrick, E Kline, Edward A Schäfer, Francis Darwin, George Romanes and Gerald Yeo.



## The Society continues its work on recognising teaching excellence

This is a key time for the work of The Physiological Society on improving the reward and recognition of teaching excellence in HE as the issue rises up the political agenda. It was pleasing to see mentions of teaching excellence in the Green Paper released by the Department for Business, Innovation and Skills concerning their planned changes to higher education. We hope the government has truly recognised that, in order to improve teaching, there has to be a clear-cut career path and sufficient incentive for the teachers as well as the institution.

A recent workshop held by The Society covered practice and policy concerning teaching excellence. We were pleased to welcome Nicolette Divecha, Assistant Director at BIS, who took us through the content of the Green Paper and explained the government's direction. She assured everyone that BIS really is listening to comments and will try to implement the Teaching Excellence Framework in the most effective way possible. The Green Paper consultation period has now closed and we are awaiting an announcement on plans going forward.

## Clarification of the Spending Review

Sajid Javid, the Secretary of State for Business, Innovation and Skills, recently gave evidence to the Science and Technology Select Committee on the fine details of last year's Comprehensive Spending Review and its implications for the science sector. He assured the Committee that nothing had been "tucked-in" to the science budget, so it does not have to stretch to cover more. The Global Challenges Fund has been incorporated into the science resource budget, providing around £1.5bn over five years. This money accounts for the increase of the resource budget with inflation; without it science would be enduring another flat-cash settlement. Mr Javid explained that this new money will fund research to benefit overseas development, and will count towards the government target of spending 0.7% of GDP on overseas development aid. Allocation of money from this fund will still respect the Haldane Principle of political independence in funding decisions, but must also meet official ODA criteria. The details of the application approval procedure have not yet been finalised.

Other aspects of the Spending Review which Mr Javid covered include innovation funding, where new innovation loans will release around £500m while grants (previously comprising all Innovate UK funding) will reach around £165m. This change was instituted following analysis of effective innovation support overseas, with France and Finland being specifically mentioned.

Changes to the structure of sectoral oversight were also discussed. The nature of Paul Nurse's mooted ministerial oversight committee for Research UK has not been determined, but Mr Javid described it as an 'interesting recommendation' and 'still to decide'. Similarly, changes to HEFCE were not yet worked out, but it was questioned whether there is currently enough focus on the 'consumers' of higher education.

## Research Excellence Framework review

Coming hot on the heels of the HE Green Paper, a review has been announced into the nature and outcomes of the Research Excellence Framework (REF). This is being led by Lord Stern, current President of the British Academy, who is supported by a high-level steering group. Representation from the life sciences comes from Professor Sir Leszek Borysiewicz: an immunologist and Vice-Chancellor of Cambridge University, and Professor Sir John Tooke: a medical scientist and Past President of the Academy of Medical Sciences. The review seeks to reduce the REF's administrative burden, bring in new incentives for excellence, and improve the efficiency of the funds distributed.

**Interested in these or any other policy related issues?**  
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*Bringing you snippets of the latest intriguing research*

### Stress could help activate brown fat

Stress can activate the body's natural fat-fighting defences. Researchers found that mild stress stimulates the activity and heat production by brown fat associated with raised cortisol. The variation in brown fat activity between individuals may be explained by differences in their response to psychological stress. This is important as brown fat has a unique capacity to rapidly generate heat and metabolise glucose.

DOI: 10.1113/EP085642

### Aerobic Exercise Can Make Your Brain Bigger

Sustained aerobic activity such as walking, jogging, biking, swimming etc. can increase neurogenesis in the hippocampus. Compared to sedentary animals, the rats exercised on a running wheel had 2-3 times more new hippocampal neurons at the end of the experiment.

DOI: 10.1113/JP271552

### Exercise eases hot flushes during menopause

Exercise that makes you hot, sweaty and fitter reduced the severity of hot flushes by minimising the symptoms that occur during a hot flush, such as the amount of sweating and elevations in skin, as well as blood flow in the brain. In contrast, the women who remained sedentary reported very little differences in hot flush severity.

DOI: 10.1113/JP271456

### Is man flu real?

Oestrogen, environmental oestrogen bisphenol A and selective oestrogen receptor modulator (SERM) compound raloxifene reduced the replication of the flu virus in women's nasal cells – but not men. The oestrogen triggers antiviral effects through oestrogen receptor beta.

DOI: 10.1152/ajplung.00398.2015

### Get up, stand up

Researchers report that even a 10-minute stroll can restore blood flow to legs affected by prolonged sitting. Researchers found that sitting was bad, reducing blood flow in two major leg arteries and the men's calves swelled by almost an inch, on average.

DOI: 10.1113/EP085238

# Public Engagement: Eat. Poo. Sleep.

## Sai Pathmanathan

Outreach officer,  
The Physiological Society

It's been a while since I've written for *Physiology News*... some of you might remember me...I used to work at The Society over a decade ago! I've since been working in science communication, and was thrilled to find that I was eligible for a Physoc Public Engagement Grant.

Last November, we kicked off the first of a set of events called, 'Eat. Poo. Sleep.' The project aims to get families thinking about how our bodies work, in particular the physiology of digestion, defecation and snoozing. Why DO we need to eat, poo and sleep? And what happens if we don't do any of them?

The disgusting bodily functions of humans and animals have been shown to be extremely engaging in outreach (e.g. 'Snot, Sick and Scabs'), children's media (e.g. *Operation Ouch*)

and health-edutainment programming (e.g. *Embarrassing Bodies*). This project idea came about following past outreach events where young children were interested in how their bodies work, and all the 'icky stuff' that goes on inside them.

The emotions elicited by 'gobbling', 'slurping', 'pooing' and 'snoring' can help audiences commit the science embedded within the humorous and disgusting aspects, to memory. Whilst we're not trying to produce formal learning events, the informal learning can, for example, help young people with curriculum science ('Living Things') as well as help adults learn about nutrition and what happens in our brains when we sleep.

And it's not only the 'ick factor' that acts as a hook. By involving storytellers and musicians, alongside practicing scientists, this offers the element of arts/science-integration that not only attracts those not usually interested in science, but allows those who are interested, to appreciate the arts as useful tools for creative communication.

This first event took place at a primary school in East London, and four main, drop-in style workshops were set up. Jonathan Forgham (my old primary school teacher, who now runs The Primary Works consultancy), ran an 'EAT' session on dissecting owl pellets. As humans, we might just vomit or excrete anything we can't digest, however, owls cough up a pellet. By carefully teasing these pellets apart, participants could find out what the owls had eaten: fur, bones and insect wings. Finding a mouse skull seemed to be quite amusing for some kids (though probably not for the mouse). One parent commented that it was the most engaged her son had ever been, and took away some owl pellets to dissect with her son later. This activity linked in well with the sleep activities, as owls are nocturnal hunters.

David Urry, from the Natural History Museum, brought along his 'entomophagy' exhibit i.e. edible bugs, with specially prepared cricket fritters, and mealworm cookies – for everyone to try. Being a vegetarian, I just couldn't, but most of the children and their parents had a try!

This activity linked well with the owl pellets... i.e. in the future, could our diets become more similar to that of other species? By 2050, we'll need to feed two billion more people. One of the options for solving the world's food shortage and ensuring that we have a sustainable source of nutrients is for us to start eating insects. There is 19–26 g of protein and 6 mg of iron per 100 g of beef. Which is about the same as 100 g of grasshoppers. David ended the event with his hilarious song, 'Stick It In Your Mouth', with everyone joining in with the catchy chorus.

The 'POO' activity involved talking participants through a digestion model (kindly delivered in person by Anisha and Angela from the Physoc office), followed by some messy hands-on activities with Amara Anyogu, a microbiologist from London Metropolitan University. Tights were used to simulate intestines, with pretend food (eventually turning into fake poo) in the form of loo rolls. Amara was also able to speak



Children dissecting owl pellets with Jonathan



about the trillions of microorganisms in our intestines that help in digestion, a lot of which ends up in our faeces.

Unfortunately, Nicola Davies (children's author and one of my favourite wildlife presenters when growing up) couldn't be with us for this particular event, but her book *Poo* was available for everyone to peruse. It was popular amongst the crowd (I did worry that I might not get it back), as it contains 'revolting, embarrassing and very important' information, such as the different types, colours and consistency of animal poo, and facts like how orang-utans have the smelliest poo, especially after eating durian fruit. Definitely worth a read.

I ran the 'SLEEP' section, and this was also a chance to do more Reaction Ruler experiments and test everyone's reaction times based on tiredness (rather than age). One group of children and adults started to get into complexities of the brain – a whole conversation on the Broca's area and language – which was fine for me, having a neuroscience background, but this is one of the reasons such events need more experts on hand. Anyone can communicate science, but only experts can answer specific questions. We also covered contagious yawning, brain cooling and the hormone of darkness, melatonin.

Previous family workshops have shown that parents appreciate the need for experts to help explain the basic science to them and their children, so that they may follow up with their children later. For example, a parent recently commented: 'I would like my kids to do more science-based activities because we are not a very 'scientific' household.' This resonates with the ASPIRES findings that 'science capital' is an important factor in what draws young people to science. In all family events, parents push their children to the front, but it's obvious that parents are the ones who want to know more, ask questions and have their doubts alleviated. Parents even said they fought over who could leave work early to take the kids to the 'Eat. Poo. Sleep.' event.



Amara discussing digestion and poo

These current 'Eat. Poo. Sleep.' activities are not brand new. They have been altered slightly to make them easier to replicate by parents and primary teachers, and we have provided activity sheets, which are available for Physoc Members too, to use during British Science Week and other national events.

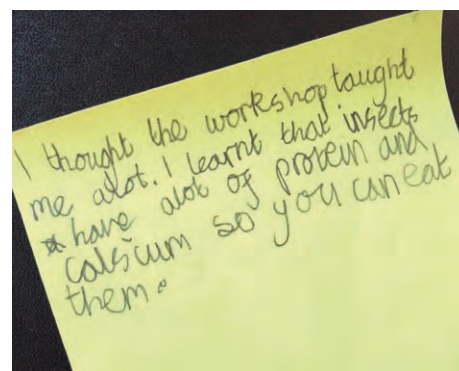
And there are more activities to come. 'Eat. Poo. Sleep.' is such an all-encompassing theme: we could discuss hunger hormones, obesity, sleep disorders...the list is endless. And the more Physoc Member expertise we can involve, the better. Funding is always nice, but support is even lovelier. Especially for lone freelancers like myself. The final set of resources generated will be presented in a free e-book.

Now, the hope is that more drop-in, family events will take place in 2016, as part of various festivals around the country. But with certain conditions. The festivals MUST NOT be science festivals and must reach new audiences, in order to be more equitable.

By taking activities to where the people are – to cheap or free events that they are likely to frequent (village fetes, county fairs) – they can get a free science experience too. Experiences like these need to be available to ALL. Many of the parents at our event were first generation immigrants, some not speaking much English at all. As an afterschool session, if children come, parents, grandparents, aunts, and uncles come too. It's a safe place, not intimidating and they know how to get to the venue and how to get back home with no issues. It's not easy for everyone to go to a science museum or discovery centre, especially if fees and travel are involved.

I would like to thank Jonathan, David and Amara, Physoc Member, Lizzie Hill for her expertise on the 'SLEEP' elements, and particularly the Physoc Public Engagement team, Chrissy Stokes, Angela Breslin and Anisha Tailor for all their help and advice.

To find out more (and how to get involved), contact me on [aloha@saipathmanathan.com](mailto:aloha@saipathmanathan.com) or drop Anisha Tailor a line in the Physoc office ([atailor@physoc.org](mailto:atailor@physoc.org)). And for more information about the grants: <http://www.physoc.org/public-engagement-grants>.



An example of the enthusiastic feedback from the children







**Question:** why are you so interested in how much exercise people get as they grow older? Is it because you would like people to stay as healthy when they are older, as much as they are when they were younger

Asked by boppy\_bat to Siana on 18 Nov 2015.



Keywords: elderly, exercise, healthy, older



Siana Jones

answered on 18 Nov 2015:



Hi Boppy,

You're absolutely right, I would like to see people stay healthy into older adulthood.

We are very good at keeping people alive but we should also aim to help people have good quality years of life in their old age. Measuring exercise capacity is a good way to test how healthy and capable someone is of living independently. If we can understand what behaviours in life result in older adults being healthy and independent then we will be able to advise best on how to achieve more quality years of life and reduce the number of people in hospital (which is expensive for the tax payers).

What do you think? good idea to stay healthy?

Siana tackles a question from a student about her motivations for research

'Teenagers ask questions that are most relevant to society and serve as a reminder of how far we are sometimes from answering the big questions'

issues, for example 'If you had cancer, at what age would it be easier to fight it' and 'If I was an old lady, would an illness affect me differently to an old man?'. 'My favourite question was 'Why do humans live longer than animals?'' says Peter, 'I learned that the simplest questions are the hardest'.

The researchers were also often faced with thought-provoking questions about the life of a researcher, such as 'Is there a downside to being a scientist?', and students weren't afraid to ask difficult questions on topical issues. For example, the scientists were asked for their opinions on care for elderly people with terminal illnesses, and whether being a female scientist affected their career experiences.

The feedback from students and teachers was really positive, showing how engaging directly with the researchers benefitted the student's understanding hugely. 'Initially when we talked about ageing our science students thought ageing was just about 'getting old', said one teacher, 'I think you have opened their eyes to the fact that it's much more than that!'

Siana and Peter would both recommend other Physiological Society members to give the online outreach experience a go.

'It's a brilliant way of getting experience communicating your ideas in a concise, clear and understandable way' says Siana, while Peter thinks that *I'm a Scientist* gave him a clearer sense of the bigger picture: 'Teenagers ask questions that are most relevant to society and serve as a reminder of how far we are sometimes from answering the big questions'.

Take a look all the big questions answered by Peter and Siana, including those mentioned here, at [ageingn15.imascientist.org.uk](http://ageingn15.imascientist.org.uk) and see more examples of great engagement in the Ageing Zone report available at [about.imascientist.org.uk/category/zone-reports](http://about.imascientist.org.uk/category/zone-reports). 'I wanted to show young people how fun being a scientist can be' says Siana, 'I hope we managed to inspire a few to take on the career!'



Want to be part of a future *I'm a Scientist* zone? The event runs in March, June, and November every year, and you can apply now at [imascientist.org.uk/scientist-apply](http://imascientist.org.uk/scientist-apply). It only takes 2 minutes and a one sentence description of your work. Contact [antony@gallomanor.com](mailto:antony@gallomanor.com) for more information.



## 2016 Forthcoming events

2–6 April

Experimental Biology 2016  
San Diego Convention Center,  
San Diego, United States  
[experimentalbiology.org/2016](http://experimentalbiology.org/2016)

7–9 April

Advances & Breakthroughs in  
Calcium Signalling  
The Hilton Hawaiian Village  
Resort, Hawaii, United States  
Minor Outlying Islands  
[calcium-signalling.weebly.com](http://calcium-signalling.weebly.com)

29–31 July

Physiology 2016  
Joint Meeting of the American  
Physiological Society and  
The Physiological Society  
Convention Centre Dublin, Ireland  
[www.physiology2016.org](http://www.physiology2016.org)

8–11 August

Limits of Perception:  
Advances in Bio-Imaging  
University of Warwick,  
Warwick, United Kingdom  
<http://www.physoc.org/bioimaging2016/>

### Meeting Notes

## Poster prize winner reports on recent H<sup>3</sup> symposium

7 December 2015,  
Hodgkin Huxley House,  
London, UK

*Samuel Bestall*

University of Nottingham, UK

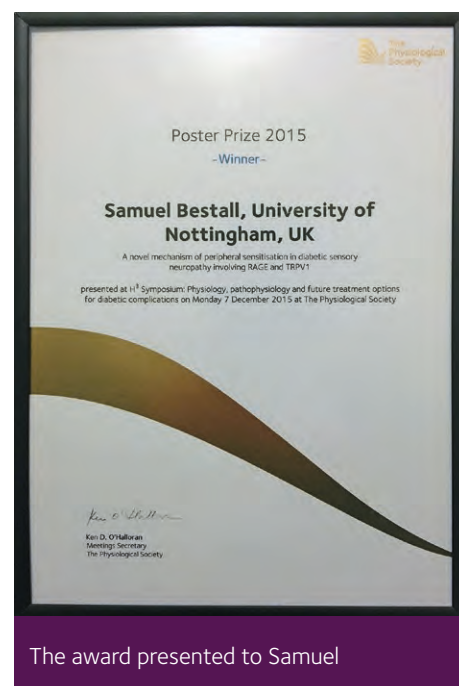
I am a final year PhD student at the University of Nottingham investigating mechanisms that cause diabetic neuropathic pain and the treatment of this with vascular endothelial growth factor, supervised by Dr Lucy Donaldson and Professor David Bates. As most of my time is spent at my lab bench or doing data analysis, I was thrilled to hear about the H<sup>3</sup> symposium specifically targeted at the pathophysiology and treatment of diabetic complications. This was an opportunity for me to get out of the lab and

discuss current research being performed by others, my own PhD work, and network with some of the field experts, so I submitted an abstract and it was accepted as a poster presentation.

The day itself had a vibrant atmosphere and included a series of thought provoking and informative talks focused on each major diabetic complication. Most notable for me was the diabetic neuropathy talk from Dr Nigel Calcutt (UC San Diego), which highlighted the complexity of the disease and considerations to take into account when using animal models of diabetes. I presented my poster titled 'A novel mechanism of peripheral sensitisation in diabetic sensory neuropathy involving RAGE and TRPV1, and the treatment with VEGF-A<sub>165b'</sub>, which went incredibly well and I received a lot of positive feedback. In addition to featuring heavily in my thesis, Nigel's rodent model of diabetic neuropathy formed the basis of my *in vivo* experimental work, so I used this opportunity to discuss the benefits and limitations of the model and receive feedback and critique on my data.

As I am shortly about to enter the writing stage of my PhD, this conference allowed me to think about my thesis and viva preparation, network, and consider my future

goals. I am extremely thankful to The Physiological Society for awarding me with the best poster presentation prize and to the event organizer, Lucy Donaldson. Overall, this was a terrific day and I urge researchers to attend future symposiums and hope the events are just as successful.





## Celebrating the 100 years of womens' membership of The Physiological Society

2 December 2015,  
Hodgkin Huxley House,  
London, UK

*Vijay Shankar Balakrishnan,*

City University, London, UK

The year 2015 must have been a triumphant year for women in science, if we look around us, but for women in physiology this is more special. On 2 December 2015, a group of female physiologists gathered at The Physiological Society, situated at Hodgkin Huxley House in London, to celebrate the 100 years of womens' membership of The Society.

The Society, which has been conducting a series of events throughout the year, commemorating the centenary of women membership, has marked an end to the series with this early winter event last year. Beyond celebration, the physiologists – mostly women and a few men – touched some of the sensitive yet important areas in the politics of doing science.

Soon after the warm welcoming and introduction to the day and the sessions by Professor Susan Wray from the University of Liverpool, the event began with a lecture delivered by Professor Tilli Tansey from Queen Mary, University of London. Tansey's lecture focussed on the hidden women of the early Physiological Society, with stories on not only female physiologists of those times, but those (house)wives of physiologists, who lit the subject to brightness. The lecture titled, 'Maud, Nettie, Ghetel and George' came to a climax when Tansey revealed who George was – she is none other than the writer, George Eliot. The session ended with Tansey being awarded the Paton Prize for her work and the lecture.

Chaired by Professor Susan Wray, the panel of scientists and gender equality advocates discussed whether there is a gender gap in research funding. While Dr Jackie Hunter, Chief Executive at the BBSRC, UK presented the data that the Research Council UK are collecting to determine the gender gap in the research funding in the UK, Professor Kim Barrett from the University of California, San Diego, USA shared her experience across the Atlantic.

Professor Uta Frith from the University College of London put forth not only the data from the Royal Society regarding the gender gap, but also her thoughtful questions on how the problem could be mitigated. The panel with Sarah Dickinson, Head of Equality Charters, Equality Challenge Unit, UK, discussed how initiatives such as Athena Swan SILVER awards help recognise the work of women scientists. The panel came to a consensus that there is not enough data to come to a concrete conclusion to show the magnitude of the gender gap, so more, particularly young female scientists should apply for grants to cement the gap.

After a short break, Dr Barbara Cassadei from the University of Oxford, shared her inspiring work life, and how she managed to balance both work and personal life well, or when sometimes not. One of her take-home messages was 'choose your partners wisely,' with which another senior female physiologist, professor emeritus at the University College of London, Dr Lynn Bindmann also agreed. Professor Maria Fitzgerald from the University College of London shared her experience on how to manage work-life balance. Her take-home message was, 'be brave and bold' and 'work hard'.

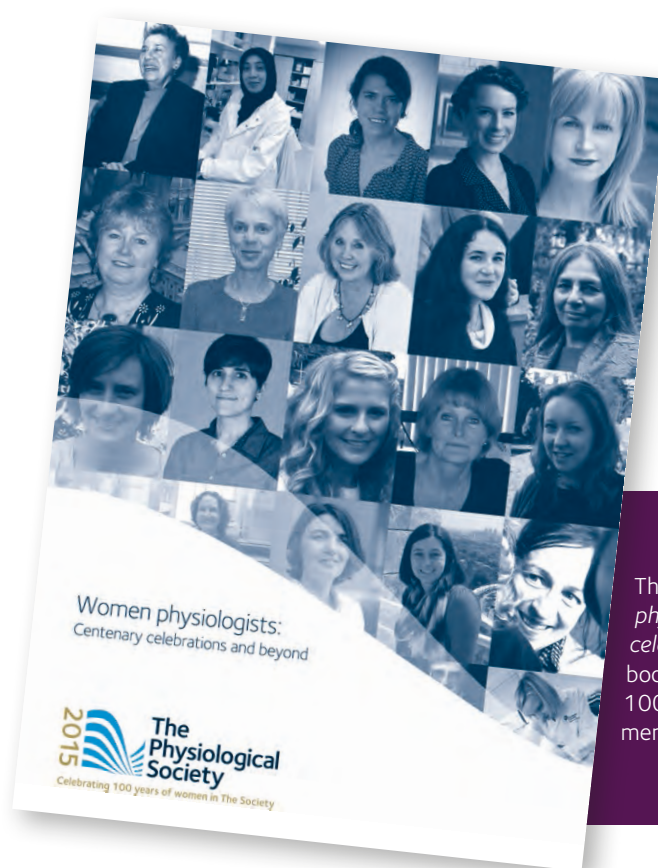
After a delightful work lunch the event continued with Professor Susan Greenfields talking about how important it is for early career researchers to engage with the public about their science. Her take-home message was that, the scientists should take it as a civil duty to talk to the public and the media, as the politicians get science only through the media.

Her inspirational talk captivated the audience also on public speaking and crafting a blockbuster CV.

A parade of young female researchers took to the stage explaining their interesting work in physiology. Each one of them was given only two minutes to talk about their work *sans* a digital presentation toolkit. All of their works were as inspiring as themselves, with notable examples such as Dr Pooneh Bagher, lecturer at Magdalen College, Oxford, who not only shared her science but also how she survived breast cancer and yet confidently continuing her good work as a scientist and a teacher.

After an in-depth and interesting lecture delivered by Dr Kim Barrett on her complicated and intriguing work on the intersection of physiology and gut microbiology, she was awarded the Bayliss-Stirling Prize. She was also announced to be the new editor-in-chief of The Society's *The Journal of Physiology*.

The event came to a climax when Richard Vaughan-Jones, President of The Society concluded the scientific events by reiterating and reinforcing the take-home messages from different sessions. The event officially ended when Dr Lynn Bindmann and Professor Tilli Tansey launched the resourceful and inspiring book titled *Women physiologists: Centenary celebrations and beyond*, which not only has the photos and profiles of female physiologists of different generations, but also their advice to the forthcoming generations, which were all as meaningful as the aim of this event.



The Society's *Women physiologists: Centenary celebrations and beyond* book, published to mark 100 years of women's memberships

## Report on The Physiological Society's education and teaching theme workshop: Promoting and sharing excellence in Higher Education teaching

15 January 2016,  
Hodgkin Huxley House,  
London, UK

*Nick Freestone*

Associate Professor of Physiology,  
Kingston University, UK

*"Good teachers possess certain virtues whose acquisition is a practical matter" (Winch, 2004)*

On 15 January, The Physiological Society hosted the latest in their series of workshops with an Educational and Teaching theme at Hodgkin Huxley House, London. This event was held in conjunction with The Royal Society of Biology (RSB) and the British Pharmacological Society (BPS), whose participation underlined the increasing importance of education in the activities of these societies. Colleagues from universities across the whole of the UK (England, Scotland, Wales and the Republic of Ireland) arrived eager to be involved in sessions spanning both educational best practice and policy. As the date of this workshop coincided with the deadline for responses to the government's Teaching Excellence Framework (TEF) Green Paper, delegates were particularly keen to hear from invited speakers who would be able to give a well-informed view of the government's motivations in promoting TEF.

As a prelude to these policy discussions the morning session, ably chaired by Blair Grubb and Dave Lewis (winner of the Physiological Society's Otto Hutter Teaching Prize in 2014), focussed on examples of best teaching practice, which was in keeping with the general theme of 'teaching excellence'. The first speaker was a very fine exemplar of this motif, Dr Manasi Nandi, winner of the British Pharmacological Society's Rang Prize for Excellence in Teaching, 2015. Manasi spoke eloquently about her commitment to understanding the learning needs of her students and how she reflected upon and changed her practice to enable all her students to reach their full potential.



Members participate in discussions during the workshop's 'Swapshop sessions'

After this masterclass on how to truly engage students with their learning a number of colleagues were involved in the 'Swapshop Sessions' – vignettes of 5 minutes duration and 5 minutes for discussion, giving everyone a flavour of the teaching innovations occurring in a number of settings across the UK. These talks covered topics as diverse as computer simulations, novel methods of assessing practical skills and student learning, improving feedback by using clickers or giving personalised feedback and use of Personal Development Plans, flipped lectures and online tutorials.

The lively discussions engendered by the morning's session were carried over into lunch where participants were able to view posters and talk to their colleagues in a more informal manner. After a very plentiful lunch, participants were suitably refreshed to continue with the afternoon's proceedings, which focussed on matters of education policy. These talks, expertly chaired by Mary Morrell, began with an overview of the HE work conducted by the Physiological Society, from Judy Harris, winner of the Otto Hutter Teaching Prize in 2015. Further perspectives on the current educational landscape were given by Ian McFadzean for the BPS and Jon Scott for the RSB (The HEA Bioscience Teacher of the Year in 2011). Bearing all these different perspectives in mind about what the learned societies were currently doing in terms of teaching practice it was an opportune time to hear about TEF from Nicolette Divecha, Assistant Director, Department for Business, Innovation and Skills (BIS) and Nick Hillman, Director of the

Higher Education Policy Institute (HEPI) an independent HE think tank.

Nicolette has probably faced more hostile questioning from audiences in her difficult role explaining and defending the TEF but probably not such well-informed and reflective engagement as she received from the polite, collegial and knowledgeable participants of this workshop. It is fair to conclude however that many members of the audience thought that various elements of the suggested TEF proposals had not been well thought through and need further elaboration and clarity.

Nicolette then passed the baton on to a panel made up of the afternoon speakers and Nick Hillman who, in particular, was eminently well placed to contextualise the proposed TEF changes having previously been a Special Adviser at BIS as well as working for David Willetts and now being Director of HEPI. With his widespread knowledge of the sector and insider view of government machinery, Nick was an inspired choice to round off the proceedings and provided some reassurance to the audience of the benign intent of the proposed TEF changes.

All in all this was a fascinating day, mixing exposure to pedagogic best practice in HE with unfettered access to senior policy makers. The Physiological Society should be commended for its commitment to the educational aspects of its mission and the support and help it provides its members in these changing times.



## From the Archives: minutes of meetings 50 years ago, written by the then Meetings Secretary, EJ Denton

Transcribed by Roger Thomas

### The Physiological Society Middlesex Hospital Meeting, 21–22 January 1966

At the invitation of the Treasurer, E. Neil, a meeting of the Society was held on the 21<sup>st</sup> /22<sup>nd</sup> January, 1966 in the Department of Physiology of the Middlesex Hospital Medical School.

With E. Neil, J.H. Green, C.A. Keele and F. Hobbiger successively in the Chair, 25 Communications were given with naturally a very strong bias towards work on the hairy cats and very hairy dogs beloved by cardiovascular physiologists. As might be expected in such difficult studies, criticism which was kindly but confident was met with an absolutely unyielding assurance of truth by the authors.

Immediately after dinner O.G. Edholm gave thanks and 'presentos' to E. Neil and Miss G. Fetherstonhaugh from those Members who had so much profited from their difficult, often discouraging, but completely successful work in arranging transport to and from the Tokyo Congress.

C. Heymans than made a very affectionate speech of thanks to the Chairman. He delicately touched on his complete dependence on Mrs. Nail and upon Miss Fetherstonhaugh, not so much for support but for restraint, and he spoke of the good old days when the Society generously elected 'Continentials' to the ranks of Ordinary Membership.

E. Neil in reply warmly welcomed Members and their Guests especially a Guest of the Society Dr. J.W. Duyff, who had single-handed undertaken the burden of almost all the arrangements for the Leyden Congress. It appears that unlike the Secretaries of this Society, who have the privilege of hearing every possible Communication, the Secretariat of a Congress arrange several hundreds of Communications of which they can hear not even one.

On Saturday afternoon 13 Demonstrations, mostly of the chancey 'wet' type which Members so much prefer, were shown.

The Meeting ended with tea leaving the Middlesex Hospital with the distinction of

having attracted and sustained the only full 2-day Meeting in January for at least 20 years.

Friday 21<sup>st</sup> January Tea 110, Dinner 138;  
Saturday 22<sup>nd</sup> January Lunch 128, Tea 149.

*Signed: John McMichael*

### The Physiological Society Joint Meeting at the Wolfson Institute, Postgraduate Medical School, 25–26 February 1966

On the 25<sup>th</sup>/26<sup>th</sup> February, 1966 the second Joint Meeting of the Physiological Society and the Medical Research Society was held at the Wolfson Institute, Postgraduate Medical School, London, under the shadow of the princely laboratories which J. McMichael and his colleagues had achieved by 'begging' since the first such Meeting.

With J. McMichael, C.L. Cope, Russell Fraser and H. Barcroft successively in the Chair, 22 Communications were heard and 3 were given after dinner.

At dinner, H. Barcroft, speaking as a Member of both Societies, warmly thanked J. McMichael who in reply disclosed that C.T. Dollery had done nearly all the hard work. After dinner the Secretary of the Medical Research Society explained that their minutes were so much shorter than those of this Society because clinicians worked so much harder than physiologists. This may well be true but it is the kind of argument which could lead to a 'reductio ad absurdum'.

Since only the Chairman, 2 Secretaries and 3 Foreign Visitors attended the Explanation of Demonstrations the Saturday morning was entirely given to 41 Demonstrations of great variety and interest.

The Meeting ended with tea and plans for a third Joint Meeting in 1969.

Friday, 25<sup>th</sup> February: Tea 210, Dinner 158;  
Saturday, 26<sup>th</sup> February. Lunch 142, Tea 142.

*Signed: Andrew Huxley*

### The Physiological Society University College London Meeting, 25–26 March, 1966

The Annual General Meeting of the Society was held in the Department of Physiology of University College London on the afternoon of Saturday, 26<sup>th</sup> March, 1966. At the invitation of A.F. Huxley, this was preceded by a scientific meeting, beginning at 2 p.m. on Friday, 25<sup>th</sup> March, under the Chairmanships of A.F. Huxley and J.A.B. Gray, 26 Communications were presented in the Physiology and Anatomy Lecture Theatres and there were 12 particularly interesting Demonstrations.

At 5.30 p.m., with C. Lovatt Evans in the Chair, I. de Burgh Daly gave the second Bayliss–Starling Lecture to an audience which not only crowded the Physiology Lecture Theatre but also the Pharmacology Lecture Theatre to which his lecture was relayed. He traced the interlacing pattern of the lives and work of Bayliss and Starling and painted a striking picture of two men whose characters, complementary in everything else, shared a sustained and infectious enthusiasm for physiology. After dinner G.L. Brown returned to this theme and spoke of the spirit of physiology at University College which was undoubtedly a legacy of Bayliss and Starling. A.F. Huxley in reply welcomed the Society's Guests, Mr. and Mrs. G. Bayliss, Mrs. Patterson, Mr. T. Patterson and Dr. and Mrs. H.J. Hufschmidt, and finally A.V. Hill presented T. de Burgh Daly with a silver dish as a memento of this occasion and of Members appreciation of his lecture.

The Society had now had the privilege of hearing, in one evening, from all of Starling's successors in the Jodrell Chair, A.V. Hill, C. Lovatt Evans, G.L. Brown and A.F. Huxley; yet as A.F. Huxley, in an affectionate tribute to Grace Eggleton for her innumerable kindnesses to Members and for her unselfish service to the Society and the College, had reminded us, these four represented only a part of all that had made and sustained the splendid traditions of Physiology at University College London.

Friday, 25<sup>th</sup> March Tea 450 Dinner 229;  
Saturday 26<sup>th</sup> March Lunch 170 Tea 210.

*Signed: J.P. Bouckaert*





## How visually driven tiny predatory flies achieve elite performance – my adventure from PhD student to PI

Understanding elite neural performance can be a sizable problem



*Paloma Gonzalez-Bellido*

Department of Physiology,  
Development and Neuroscience,  
University of Cambridge, UK

When we think about survival of the fittest, we imagine the power displays of lions, sharks and crocodiles, the pompous feather shows of peacocks and birds of paradise, the rugged agility of mountain goats or the speed of a cheetah. Such abilities raise a simple yet difficult to answer question that burns at the core of every physiologist: what adaptations allow a given animal to achieve the observed performance?

Technological development and ingenuity in the last 50 years has allowed scientists to understand how some animals survive extreme temperatures, salty environments, and even severe restrictions of water, oxygen and energy. We have also started to unravel which compounds and neural circuits play a role in the outcome of specific but complex behavioural interactions, such as the neuromodulators and circuits implicated in the fight or flight response. However, when it comes to understanding elite neural performance we face a sizable problem: framework and interpretation. Recent advances in technology and genetic modification developed for classic model animals now allow us to visualize neural activity simultaneously across many neurons in a brain with evermore increasing precision. But such tools do not help us interpret the data correctly. When recording from a neuron in a given model system, how can we tell if the information transfer value is at the limit of possible performance or a cheap but functional shortcut?

### A comparative approach might be useful

I first faced a similar question early during my PhD. With to the outlook of having a long scientific career, I decided that the best strategy was to study a topic that I am utterly passionate about (visual systems) and learn challenging and current techniques in a model animal (*in vivo* fruit fly intracellular recordings). Alas, after 1 year of experiments, it was clear that the genetic tools available were causing spurious side effects on the cells of interest and I abandoned such approach. As one of my PhD goals, I had successfully measured the spatial resolution of the photoreceptors in the wildtype fruit fly eye, but on its own, the data seemed meaningless. Although the dogma in the field stated that a small compound eye cannot achieve good resolution due to the size of the lenses (think diffraction limit), the resolution value that I recorded was twice as bad as predicted by the available model. My result was difficult to explain. Given the impasse, I decided that a comparative approach would be fruitful. After all, no one else had carried out such recordings in other small fly species, how could we know how good or bad that resolution was or even if my recordings made sense? I needed a framework, at least one further point for comparison!

‘Collecting them was not the challenge, keeping them alive was!’

.....



*Figure 1.* Close up: female Killer fly eating prey caught on the wing. Image credit: Sam Fabian

### Killer flies are fascinating and exhibit elite skills

I thought that a tiny predatory fly (extreme pressure for visual performance in the same body size as a fruit fly) would help me understand the true limit of visual resolution in a small dipteran. On the face of it, it seemed like a farfetched idea, but one thing that I had learnt during my undergraduate years in Australia is that if something is at all possible, there is an animal out there doing it. I took to the internet and found that killer flies met the conditions. Luckily, one of the groups that had worked with killer flies for biocontrol purposes was based near my hometown in Spain; and I was also supposed to fly home for my sister's wedding. The adventure had started! Before the wedding, my collaborator and husband Trevor Wardill and I escaped, drove for 3 hours to meet the contacts, see the field site and collect the flies. We were amazed when we witnessed for the first time the killer fly behaviour. They hunted so fast that it was difficult to see them fly, so efficiently that there was little prey around. So they just sat there, waiting for the next potential dinner to fly by, unfazed by our presence.

Collecting them was not the challenge, keeping them alive was! Their predatory habit meaning they had to be kept in separate vials. Thus, the top level of my parents' house quickly filled with flies, food, vials, pooters (devices to catch small insects), etc. After the wedding, and still on good terms with my family, we took the flies to the laboratory.

First, I recorded from their photoreceptors. The results blew us away. These flies had a spatial resolution three times better than that of fruit flies. Since the size of killer flies lenses were the same as those of the fruit fly, diffraction could not be the limiting factor, at least not for fruit flies. But that was not all. We also found that their photoreceptors were three times faster. The tighter, much narrower, beautiful recordings from the killer fly eye evidenced that higher resolution was possible in such small animals, and that we could record it. Such finding also gave me a breath of relief from the possibility that my original fruit fly results were caused by damage inflicted to the optics during the dissection.

### Unusually small photoreceptors triple visual acuity

There is extensive literature in the field, stating that the two other factors that could affect the spatial resolution at the level of the retina are the focal length of the lens and the size of the light detector, but after measuring the focal length, I found that it was similar between both species. Thus, I took to transmission electron microscopy. There, it was clear: the rhabdomeres – highly folded membranes in the photoreceptors that hold the light sensitive rhodopsin molecule and act as light guides – were three times smaller in killer flies than in fruit flies. This difference fully explained the physiological result. Moreover, the photoreceptors were absolutely packed with mitochondria, a hint to the energy supply requirements of the fast but ATP-hungry killer fly photoreceptors.



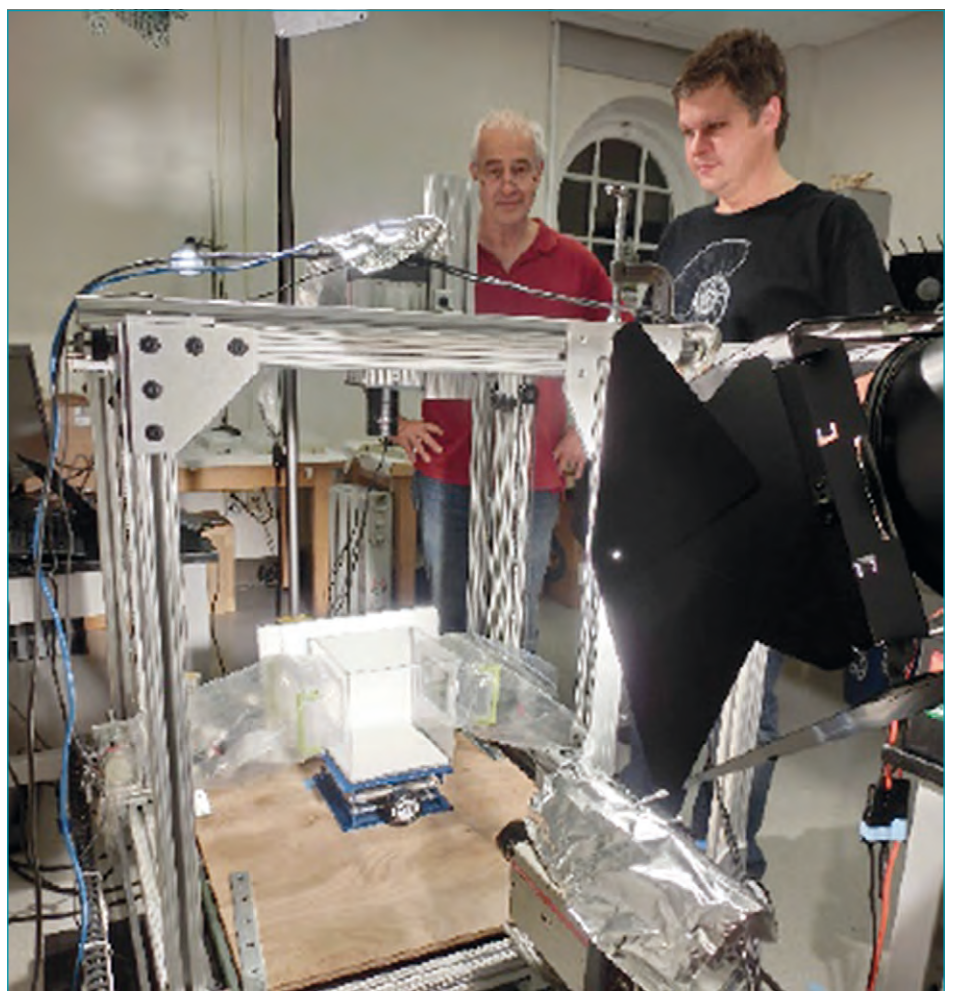


*Figure 2.* A lack of depth cues makes it difficult to discern close vs far objects, and thus their absolute size. Image credit: Sara E Jenkins

The PhD finished and the story published (Gonzalez-Bellido *et al.*, 2011), I later received the Neuroethology Capranica Prize for such work, which spurred me to continue investigating the elite performance of this average looking and tiny fly. Although killer flies have better spatial and temporal resolution than their prey, to be a successful hunter, they must possess further adaptations that allow them to overcome many other challenges, which seem unattainable with such small body size. For example, it is reasonable to assume that before attacking an animal, a predator would need to know the size of a potential prey and how far away it is. Humans and other predatory mammals do this through the stereopsis provided by the disparity between the two eyes. Here, the high resolution retina and the space between the two eyes is fundamental. Killer flies lack both. How do they know what to go for?

### Killer flies attack large beads that can not possibly be of suitable size

By this time we were postdocs in the USA, working on other projects, so we carried this work on our own time (finding the flies there required even more convoluted adventures). Together with our collaborator Rob Olberg, and armed with beads of different sizes and fishing line we headed to the hunting site during a sunny weekend. It was a crazy fun day. Most excitingly, as long as we moved the beads fast enough, killer flies would attack our large beads, which were up to 13 mm in diameter!



*Figure 3.* Rob Olberg and Trevor Wardill working on the first behavioural experiments in an indoor arena, controlling artificial beads with a robot. Such preliminary work was carried out in the laboratory of Rob Olberg (Union College).

‘Although killer flies have better spatial and temporal resolution than their prey, they must possess further adaptations that allow them to overcome the many other challenges’



**Figure 4.** Katie Knowles and Laura Barlow carrying out the latest killer fly behavioural work in the Cambridge Flysy Laboratory.

The behaviour was reminiscent of that described in a classic paper in the 70s. Collett and Land (1978) had shown that hover flies do not compute absolute size of their target, but that this is a suitable strategy because they only care about chasing conspecifics, the male ‘chaser’ can count with the female ‘target’ being a particular size and flying at a particular speed. Could killer flies be employing a similar strategy? Since killer flies do not have great resolution, they can only detect suitably small prey items when they are relatively close. Of course, detecting a prey only when it is close puts a premium on reaction time because its image crosses the retina very quickly. Indeed, by using two high-speed video cameras and reconstructing their flights, we found that the average distance at which killer flies initiate an attack is only 8 cm, and that they do not carry out any movement, body or head, before the attack is initiated.

Thus, all our data suggested that killer flies lack foveating movements and that these animals simply cope with the uncertainty of not knowing the exact size and location of their prey, using the probability of it being the correct target for deciding to launch the attack. To test this, a rigorous laboratory experiment was set up. By then we were newly established PIs in Cambridge, so the task was given to two brilliant undergraduate students in the laboratory, Laura Barlow and Katie Knowles. They tested a range of different bead sizes, presented at different speeds at different distances.

Their consistent and careful work yielded results that supported our preliminary observations. Killer flies make use of relative cues and lack absolute knowledge about the size or location of their potential prey. Independent of distance to the prey, we found that the ratio between the subtended speed and size of the prey predicted well the probability of attack, and that only after the flight had started, did the flies decide to turn around and return to their perch when then bead size was not suitable. We also found that although the probability of attack was 0.9 when the ratio was optimal, the slope decreased slowly, creating a ‘broad matched filter’, where the probability of attack is generally high, but highest when the ratio is optimal (Wardill *et al.* 2015).

We continue to work with killer flies, and we have expanded our study to other small flies too... after all, we still need the framework and the more comparative points we get the higher our chances that we would truly get to understand how such tiny visual systems can display elite performance, leading to a behaviour that first appears supernatural. We of course aim to transfer all the latest imaging techniques to such species, and look forward to a bright future, where classic neuroethology, model systems and technological advances are integrated, producing knowledge that amounts to more than the sum of the parts.

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## Why do we have two noses?

We have two eyes, two ears, two lungs and two kidneys but we always refer to THE NOSE in the singular and this singular terminology hides a wealth of unusual nasal physiology.



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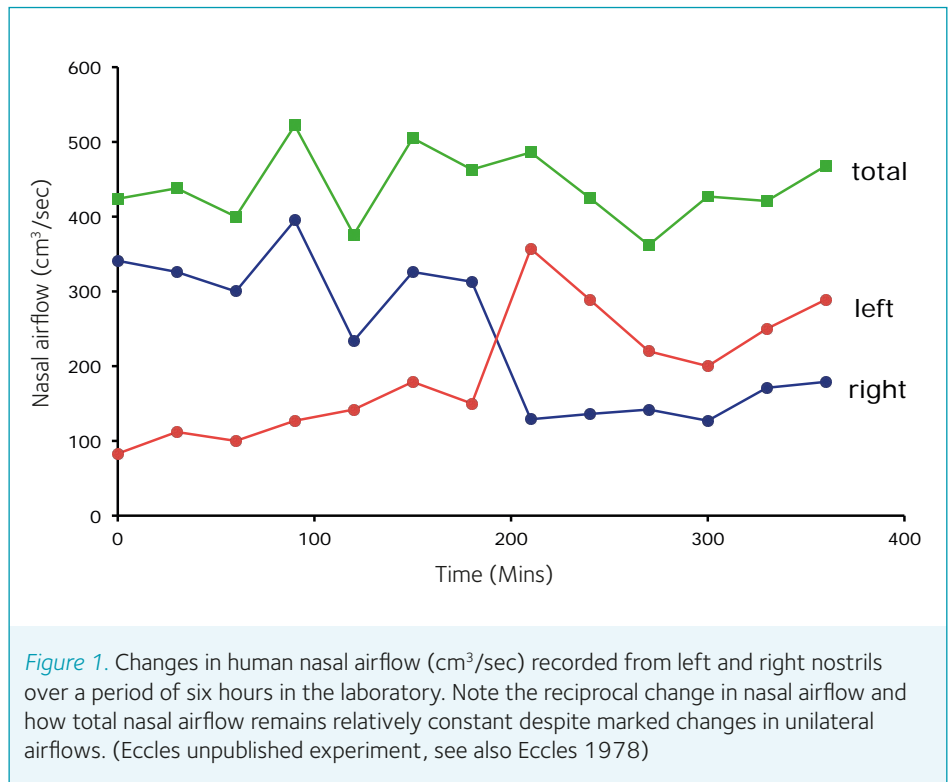
Try this simple experiment Place the ball of your thumb over one nostril and breathe in gently. Repeat the procedure with the other nostril. Notice anything? The first and obvious discovery is that you have two nasal passages and I would like to wager a bet that around 80% of you will find that you have asymmetrical nasal airflow with one side of the nose having a lower resistance to airflow than the other. Repeat this experiment in a couple of hours and many of you will make an even more unusual discovery, and that is that the dominant airflow has changed from one side of the nose to the other.

Experiments that record the nasal airflow from each nasal passage over a period of hours have described regular reciprocal changes in nasal airflow in man and this is often called a 'nasal cycle' like the one shown in Fig 1. If you take an infra-red photo of a moustachioed face on a cold day, it is possible to see that only one side is cooled by the nasal airflow (Fig 2).

Watch a cow or horse or sheep on a cold winter day and you can often see the same asymmetry of nasal airflow in the expired steamy nasal airflow. Studies on rats, cats, dogs, and pigs have clearly shown that nasal airflow is normally asymmetrical and that there is a reciprocal relationship of nasal airflow, which alternates over a period of hours. Elegant physiological and anatomical studies in the rat and rabbit clearly showed the asymmetrical nasal airflow, by looking at condensed nasal airflow patterns on a cold metal mirror in tranquilized rats and rabbits and then following up these experiments with post mortem examination of the nasal swell bodies (venous sinuses and cavernous spaces in the mucosa of the conchae and the septum) (Bojsen-Moller & Fahrenkrug, 1971).

When suffering from a common cold you may remember one side of your nose becoming so blocked that you could not breathe through it and the other remaining open so that you only breathed through one side of the nose. You probably did not feel up to doing much experimentation when suffering from this common cold but if you had been observant you would have noticed the dominant airflow to change sides with a periodicity of a couple of hours. In a study on subjects with common cold we demonstrated that during a cold one side of the nose becomes very blocked whilst the other side remains open (Eccles *et al.*, 1996). The unilateral blockage was explained by an increased filling of nasal veins due to inflammation, with this increase in blood flow superimposed on an asymmetrical sympathetic vasoconstrictor tone to the nasal veins.

‘But why do we have two noses? Is it because we are bilaterally symmetrical with two arms, two legs, two of most organs? Could one nostril be more beautiful and function better?’



Ever had one side of the nose block up when lying in bed? Lie on the left side and the left nasal passage blocks up, turn over and lie on the right side and the right nasal passage blocks up. Asymmetrical skin pressure triggers reflex changes in nasal airflow so our upper nasal passage always has the dominant airflow whilst the nasal passage at risk of occlusion from the ground or pillow blocks up. Human studies have demonstrated that lying down on one side stimulates slowly adapting pressure receptors on one side of the body to trigger a nasal reflex that opens one side of the nose and closes the other (Haight & Cole, 1986).

Applying a crutch to one armpit causes nasal airflow on that side to decrease and airflow on the other side to increase. This reflex was studied in healthy volunteers and showed that application of the crutch caused reciprocal changes in nasal airflow (Davies & Eccles, 1985). Our experiments have shown similar reciprocal effects on nasal airflow in a study on healthy volunteers by asking them to squeeze a plastic ball in the axilla (Preece & Eccles, 1993). In the dim and distant past Indian mystics used a small crutch (yoga danda) to alternate nasal airflow from one nasal passage to the other, and modern day yoga students of pranayama uses a yoga danda to control nasal airflow and alternate the dominance of nasal airflow from one side to the other at will.

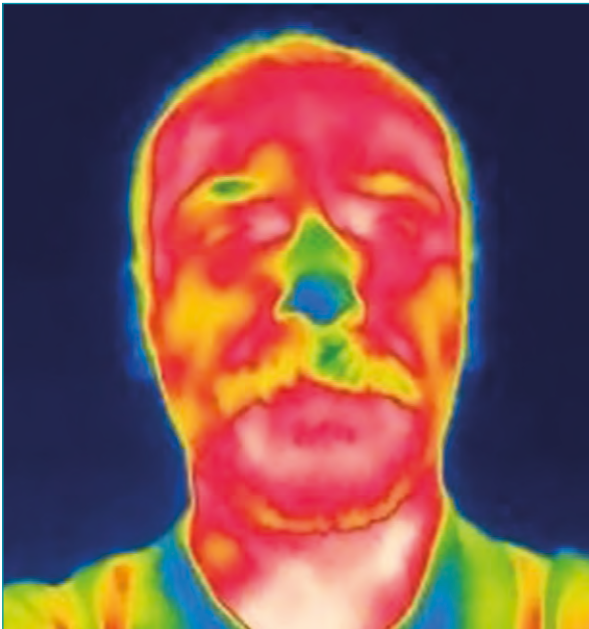
Cats provide some answers. Our studies on the anaesthetised cat have shown that nasal airflow is controlled from the hypothalamus via the sympathetic nerves that cause constriction of large veins lining the nose.

Electrical stimulation of alternate sides of the brainstem region in the cat demonstrated that there are control half centres in this brain region that regulate the sympathetic nerves to the nose and act as a flip-flop mechanism to control nasal airflow (Bamford & Eccles, 1982).

But why do we have two noses? Is it because we are bilaterally symmetrical with two arms, two legs, two of most organs? Could one nostril be more beautiful and function better? Surely a single large nostril placed in the centre of the face could function as effectively as is the case for the mouth where one opening serves us very well. It could take us a little while to appreciate the beauty of a single nostril as opposed to the beauty of our paired and smaller nostrils but I feel this would grow on us, especially us physiologists, as a single large nostril would have better aerodynamics and offer less resistance to airflow than our two smaller nostrils. The nose does present a considerable resistance to airflow – around two thirds of the resistance to airflow of the whole airway from nostril to alveoli. Most of the work of breathing is related to moving air through the nose and this is the price we pay for filtering and conditioning the air we breathe.

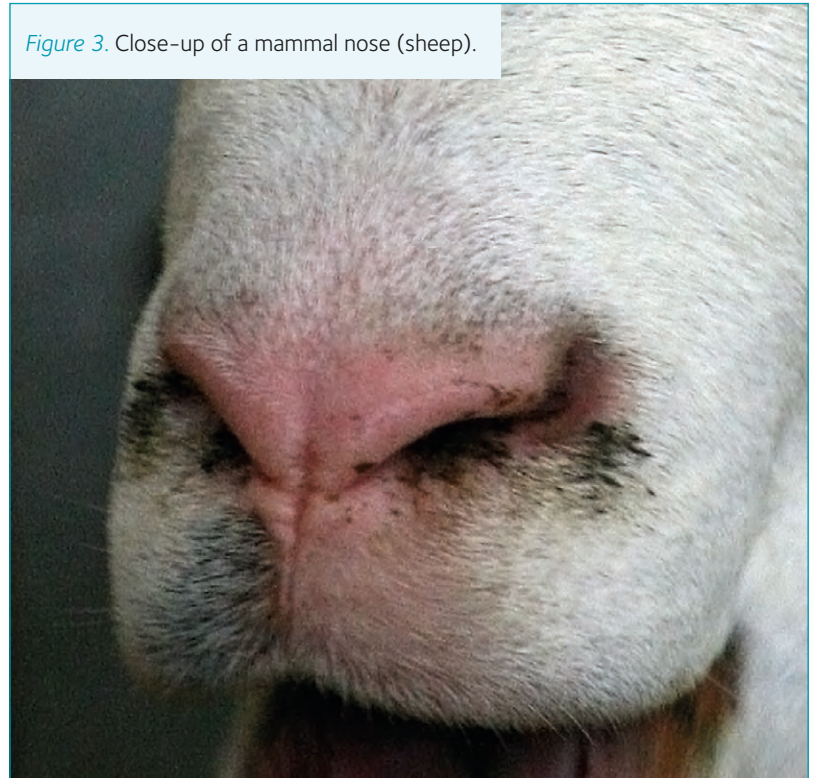
There's a twist to the nose, and the human nose is unique in two ways. Visit the zoo and get close up to the bars to get a very close look at the nose of any mammal (such as a sheep as illustrated in Fig 3). The nostrils come straight out of the face and the airflow is twisted as it passes through the nostril in a cork screw fashion. This twist aids filtration of particulate matter as dust is spun out of the airstream and deposited in the nose.





**Figure 2.** Infra-red selfie of a colleague on a cold day. Red is warm, blue cold. Only one side of his moustache is visibly cooled by the inhalant airflow.

**Figure 3.** Close-up of a mammal nose (sheep).



This is quite different from the human nose, which is unique in that the nostrils point downwards, unlike any other mammal, including our close relatives the chimpanzee and gorilla. Maybe the downward direction of the nostrils is an adaptation to our upright posture? However, we still have a bend rather than a twist to the nose to aid filtration as the airflow passes up through the nostril and then turns at a right angle to enter the nasal passages at the narrowest point of the nose and whole airway, the nasal valve. The change in direction of nasal airflow, and the decrease in velocity after the nasal valve, spin out any dust and acts as a very efficient filtration mechanism. Another unique feature of the human nose is the presence of small hairs or vibrissae, with more in men than women, as the development is sex hormone dependent. No other mammal has these vibrissae and they appear to have no function apart from acting as a barrier to flies and small insects that may creep into the nose and trigger sneezing.

But why do we have two noses? For an air conditioning unit that works 24/7, 365 days a year it makes sense to have two units in parallel and alternate the airflow from one side to the other over a period of hours. Two noses are therefore very useful as one can go through a rest and cleansing cycle whilst the other takes over the dirty and damaging work filtering and conditioning the 10–20,000 litres of air we breathe in every day.

Having two noses means that when we have a common cold caused by viral infection one side of the nose can become inflamed and blocked whilst the other manages all our airflow.

Inflammation is the natural response to infection as more blood flow is diverted to the infected area, but there is also another benefit of closing one nasal passage related to nasal temperature. The normal temperature of the nasal epithelium is around 33°C and common cold viruses have adapted to this temperature and replicate best at around 32°C. This is why all early attempts to culture common cold viruses failed as they were incubated at 37°C. The inflammation that blocks one nasal passage raises the nasal temperature to 37°C and this may help us to throw out the viruses as they do not replicate well at this higher temperature (Papadopoulos *et al.*, 1999).

Another benefit of having alternating congestion and decongestion of the large veins in the nose is that when the large veins on the blocked side of the nose contract, they squeeze out a plasma exudate containing antibodies that washes and cleans the nose and also helps to neutralise viruses and this is another benefit of the so called 'nasal cycle' (Eccles, 1996).

So, two noses are better than one! Having two noses may have some functional significance. Two noses allow for periods of asymmetrical airflow and therefore allow cycles of rest for the hard working air conditioners. Two noses also allow for periodic obstruction of one nasal passage without compromising ventilation and this may help in overcoming viral infection by raising the nasal temperature.

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# The horse – the athlete with the ultimate locomotor system

Horses are exceptional athletes but their anatomical and physiological adaptations which give them a competitive edge simultaneously put them at risk of injury.



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For the majority of us the word 'athlete' conjures mental images of the Olympics; Paula Radcliffe, Usain Bolt, Mo Farrah, Dame Kelly Holmes – human athletes. Nowadays, equestrian events might even spring to mind too, following the success of Team GB Riding at London 2012. However, horses in sport are nothing new. The very first official Olympic Games in 778 BC had four equestrian events. Furthermore, the very beginnings of veterinary education in the UK – the founding of the Royal Veterinary College in 1791 – is linked to the death of the unbeatable racehorse Eclipse (Fig. 1). His owner asked for a post-mortem examination to find out what made him so fast, resulting in the first post mortem assessment for performance.

A horse's specialised anatomy makes it suitable for a range of sports: gymnastic dressage divas, high jump show jumpers, agile polo ponies and of course the Ferraris of the horse world, the racehorses. However, you also find the more versatile all-rounders: triathlete eventers competing in dressage, show jumping and cross-country.

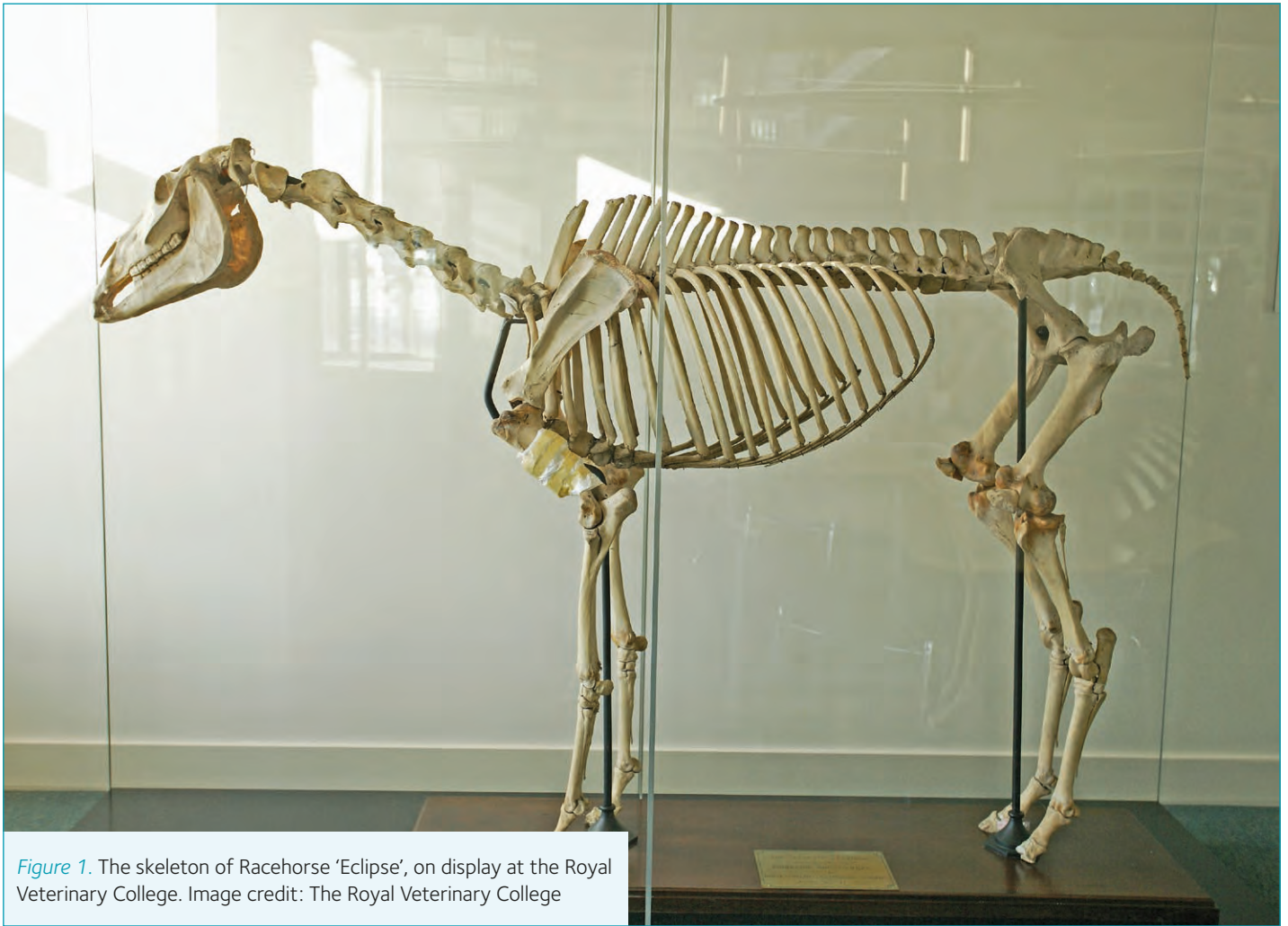
### Horses and humans are more similar than you'd think!

At first glance, you might think that equine athletes are far removed from their human counterparts and that it would be impossible to draw any comparisons. But you would be wrong. Prior to changing hands (and good horses go for vast sums of money), most horses undergo pre-purchase exams including thorough medical checks, radiographs and – more and more commonly – magnetic resonance imaging (MRI), much like football players. Top human athletes have a support team and so do horses: veterinarians, farriers, physiotherapists, trainers, saddle fitters,

nutritionists, grooms and biomechanists work together to ensure optimal performance and to safeguard equine welfare. Like in human sports medicine, veterinary sports medicine strives to be evidence-based and the body of scientific studies on exercise physiology, sports orthopaedics and equipment interventions has been increasing rapidly.

All athletes walk a fine line between being the best and risking an injury and equine athletes are no different. Like injuries to rugby players can reflect the position they play, equine injuries show associations with specific sports (Murray *et al.*, 2006). However, if things do go wrong, unlike humans, horses cannot tell us where it hurts. Ultimately, the same diagnostic techniques are used to investigate poor performance and injuries; however, the fact that horses cannot talk, are somewhat bigger than humans, and have a different anatomical and physiological make-up, means specific adaptations are required in diagnosis and treatment.





**Figure 1.** The skeleton of Racehorse 'Eclipse', on display at the Royal Veterinary College. Image credit: The Royal Veterinary College

As with most things in life, prevention is better than cure and there is extensive research into reducing injury risk in our equine athletes. This not only improves welfare but also optimises their performance as the athletes they truly are.

### Hybrid vehicles, pogo sticks and catapults

Horses owe their ability to perform in a number of different sporting activities to their highly specialised anatomy. Their cursorial nature means they are designed to cover vast distances at a slow pace, while grazing for nourishment: a prerequisite for survival on the sparse vegetation of the prairie type land the horse originated from. However, at the same time they have evolved as prey animals with the capacity to make a speedy escape if needed. The horse supports its locomotor requirements by having developed anatomical and physiological features that reduce the metabolic cost of locomotion. The horse has long and light limbs, which is achieved by reducing the number of lower limb bones to one weight-bearing column, and elongating the limb by essentially walking on their tiptoes.

Unlike human legs, that are pretty much straight from the tarsus (ankle) up, horse legs are angled with the metacarpophalangeal joint being the pivot point. This joint is in hyperextension during normal standing and goes into extreme hyperextension during movement (Fig. 2). While it may not seem very advantageous at first glance to have what is essentially an unstable joint, this configuration allows the horse to use its bodyweight to save energy during movement. Long and strong flexor tendons, with properties that make structural engineers jealous, run down the back of horse's legs and around the metacarpophalangeal joint. During movement, when the body weight compresses the leg, these tendons get stretched and store elastic energy. This energy is returned when the leg leaves the ground, tendons are known to be able to return up to 93% of energy. This mechanism pretty much resembles a pogo stick. At rest, tendons and ligaments contribute to the passive stay mechanism, which allows the horse to stand and sleep with minimal muscular effort.

The horse takes energy saving through tendinous elastic recoil even further. The biceps muscle has a specialised, internal tendon which stores elastic energy slowly,

whilst the hoof is in contact with the ground, before quickly releasing its elastic potential energy to rapidly accelerate the forelimb forwards into the swing phase (Wilson *et al.*, 2003). This process quite literally catapults the horse away from danger – or out of the starting gates.

Like hybrid cars, the horse uses metabolic energy (fuel) to feed its muscles to initiate locomotion. The movement of the horse and vehicle itself then drives energy storage mechanisms: elastic potential energy in the horse and the charging of batteries in a hybrid vehicle.

### A gambling problem

At the races it's not just the punters who might have a gambling problem. Horses training at the top of their sport are 'gambling' with their anatomy. All the adaptations that make them faster and more efficient also make them more vulnerable to injury. If you want to move your limb fast it needs to be light and you need gracile bones and tendons. Reducing the cross-sectional area of structures makes them more vulnerable to breakage.



‘Horses owe their ability to perform in a number of different sporting activities to their highly specialised anatomy’

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*Figure 2.* Horse legs are angled with the metacarpophalangeal joint being the pivot point. This joint is in hyperextension during normal standing and goes into extreme hyperextension during movement. Image credit: Claire Brown

We describe the horse as operating at a low safety factor. A safety factor is the load that can be applied to something before it breaks. Things like lifts and stairs operate at a safety factor of at least 10 times the maximal load they are expected to take. Horses, however, operate at full gallop to a safety factor as low as 1.5 times. This is reflected by the fact that approximately 50% of racehorses in training, at any one time, can be affected by injury to their superficial digital flexor tendon (SDFT).

### A pain in the leg

If you've ever been running and found that your shins hurt afterwards, then perhaps you can empathise with some horses! 'Bucked shins', as it is called in horses, is a very common and minor condition that affects racehorses, especially beginners. It is often the result of an inappropriate training regime leading to a shift from adaptive bone remodelling for repair to pathological bone remodelling on the front of the third metacarpal bones. Horses will have painful, hot and swollen metacarpal bones and you can easily feel this with your fingers and quickly make a diagnosis. Rest and modification of the training program is often all that is needed to resolve the problem.

Bucked shins is an example of a minor injury sustained due to repetitive exercise induced damage or cyclical overloading of the musculoskeletal system. Like humans, cyclical overloading of the musculoskeletal system is by far the most common cause of orthopaedic injuries in horses: the rate of exercise induced damage outstrips the body's capacity for repair.

Horses place their limbs under extreme loads. At full gallop, each limb is loaded with approximately 2.5x its bodyweight, that's 1250kg in an average sized 500kg racehorse. Considering the small cross-sectional area of a horse's limb, that is an enormous amount of pressure! What's more is that bones and tendons in horses have been estimated to have a 'working life' of as little as 10,000 cycles, before they wear out. A galloping horse will impose about 220 loading cycles per mile and it does not take advanced math skills to figure out that racehorses indeed 'skirt very close to the edge'. It is therefore no surprise that horses can suffer numerous injuries, which range from the common superficial digital flexor tendon injuries to the less common, more catastrophic injuries, such as stress fractures.

### Just tell me where it hurts

As with any athlete, injury is an inevitable part of the game and we owe it to these horses to provide prompt and thorough veterinary attention. Sometimes an injury will be obvious – a wound for example. Other times, it is not, and veterinarians do not have the luxury of being able to ask their patients where it hurts. They must be 'pain detectives'. Careful palpation of the horse's musculature, tendons and joints, as well as critical observation of the movement of the horse at walk and trot in straight lines and in circles on both soft and hard surfaces is the usual starting point. Some problems can only be observed under saddle when a specific movement or task is required of the horse, so observation of the horse during ridden exercise is therefore necessary too.

**Figure 3.** Horses are scanned with a specialised camera to detect issues. Image credit: The Royal Veterinary College



The first task is to decide which leg is the biggest problem. Since most orthopaedic problems are 'wear and tear' issues we often have to deal with multiple leg and multiple site problems. There is a limitation to human's ability to detect lameness in horses, so sensor-based movement symmetry analysis, as-well as force-plate and pressure mat-based systems can be used in referral centres to aid the veterinarian in this task.

Once we know which leg to start with, diagnostic analgesia is used to localise the area of pain. This involves the 'blocking' of specific nerves or synovial structures with injections of local anaesthetic solution. The first block is placed most distally on the limb (typically just above the heel bulbs) and the horse is observed exercising again. If the gait is not improved, another block is placed higher up the leg and so on until improvement is seen. Once an area is identified as the region where the pain is coming from, specific synovial structures within this area – joints, bursae or tendon sheaths – can then be 'blocked' with anaesthetic.

Sounds simple right? Not quite; the anaesthetic agents can unhelpfully diffuse to other locations, and in some horses, nerve anatomy varies from the norm, which can be misleading.

### Photoshoot

Diagnostic imaging is the mainstay of confirming orthopaedic disease in horses. The methods of imaging are the same as for humans: radiography, ultrasonography, magnetic resonance imaging (MRI), computed tomography (CT) and nuclear scintigraphy.

Radiography and ultrasound are the most commonly used imaging techniques in the veterinary world. They are relatively cheap and can be used in the standing horse in their own home. It is the norm for equine vets to make house calls and horses only get transported to see a veterinarian in more complex referral cases. Ultrasonography is, for example, commonly used to diagnose tendon and ligament injuries, which are especially common in the superficial digital flexor tendon. Osteoarthritis is the most common orthopaedic problem identified on radiographs, however the clinical significance of these findings is often questionable. This often makes interpretation of radiographs performed as part of a pre-purchase exam especially challenging.

Radiography and ultrasonography have their limitations. Some regions of the horse refuse to yield their pathologies willingly. The hoof for example contains many vital soft tissue structures that cannot be visualised radiographically and are not easily accessible with ultrasound as they are enclosed within the dense horn of the hoof capsule. In the forelimb, lameness can be localised within the foot in 80% of riding horses and MRI of this region is hence very common. In the past, horses tended to be anaesthetised and scanned using a human MRI scanner, however, nowadays it is more common today to use a system specifically developed for use in the standing horse. Horses carry a 1% risk of dying under general anaesthesia so veterinarians prefer to perform any procedure in conscious standing horses. Horses are flight animals and many standing procedures require careful sedation on top of expert handling.

### Size matters

While humans (and dogs) with back problems can benefit from MRI and/or CT evaluation, a normal sized adult horse cannot, they are simply too big to fit in an MRI or CT scanner. Areas like the back and pelvis can be radiographed and ultra-sounded, but the pure size of the horse often makes it difficult to get good quality images, and a technique called nuclear scintigraphy is often employed when bony lesions are suspected. Horses are given an intravenous injection of a radioactive nucleotide (e.g. technetium99) which seeks out bone tissue and accumulates in areas of increased bone metabolism such as a fracture site. The horse is then scanned with a specialised camera (Fig. 3) that detects the radioactive signal and creates an image of nucleotide distribution through the skeletal system. One such example of nuclear scintigraphy use is to diagnose pelvic stress fractures, which occur in horses racing over jumps. Many equine athletes that are presented for a performance issue suffer from multiple problems. It is therefore necessary to employ multiple imaging techniques, based on a thorough clinical investigation, to diagnose the problem(s) the horse has and to treat them accordingly.

### Straight from the horse's mouth – lessons from horses

The high numbers of racehorses suffering from injuries to their SDFT resulted in an intensive search for innovative treatment methods. Tendons heal, but their functional elastic properties are not fully restored as a result of scar tissue formation.

‘The big limitation of working with these speechless animals is that we have limited ways to detect sub-clinical problems’

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Researchers at the Royal Veterinary College addressed this problem by looking into the application of stem cell therapy in tendon lesions. Mesenchymal stem cells (MSC) are extracted from the sternum bone marrow, and are grown over three weeks before being injected into the SDFT lesion under ultrasound guidance. This technique has been successful in reducing the re-injury rate in horses with SDFT lesions (Godwin *et al.*, 2012). The use of stem cell therapy even features in the rags to riches film ‘Dark Horse: The incredible true story of Dream Alliance’. From this research, the use of stem cell therapy for the treatment of orthopaedic problems has advanced and translated into human medicine, e.g. in the treatment of rotator cuff and Achilles tendinopathies in human athletes.

### Silver and Gold

It is of great importance to investigate superior therapeutic techniques for injury management in equine athletes. However, this research is just the tip of the iceberg. Investigation of bespoke surfaces to ride upon, shoes, saddles and bridles for horses to wear, training, feeding and management techniques are just a few examples of current research areas. All focused on improving horse welfare, reducing injury and perfecting performance. In line with human athletes there is a constant strive to improve equine performance to make the often small difference between winning Olympic silver and winning gold!

### Technology Age

The big limitation of working with these speechless animals is that we have limited ways to detect sub-clinical problems. Experienced riders and trainers may detect subtleties in a horse’s performance, such as struggling to turn in one direction compared to the other, not moving as well, having poles down when jumping or not being as fast as they once were. However, small underlying concerns are often not addressed until they are causing much bigger problems in performance. The ability to intervene when an injury is very new, before it causes a significant loss of performance and pain, is essential in optimising welfare and performance. In the technology age, we are working towards improving early diagnoses in a variety of ways.

Biomechanical analysis and exercise physiology assessment of human athletes is common in detecting both underlying problems and driving training programmes. Performance in the horse has been assessed in gait labs for decades. However, recent advancements in sensor-based technologies allows assessment of the horse during sporting activities, and has led to a much more common use of objective parameters (Pfau *et al.*, 2014).

Racehorse trainers, for example, now routinely equip their horses with devices that record heart rate, stride length and frequency, and movement symmetry. Changes in these parameters alert trainers to potential problems and aid in the adjustment of training and racing strategies, shoeing and medication protocols. However, these techniques aren’t restricted to use in the horse, they can be applied to the rider to achieve a team perspective too.

### Conclusion

All in all horses are incredible athletes. They would be able to win medals in several human Olympic disciplines should we allow them to compete against humans or other animals and to top it off they would do it with a rider on top! This is in part due to their anatomy but also due to their cooperative and trainable nature. They deserve to have their welfare regarded as of paramount importance, which is only achievable through knowledgeable, multidisciplinary support teams and by furthering scientific research.

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## How nocturnal insects see in the dark

My journey studying the physiology of vision in nocturnal insects



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My childhood experiences growing up in a rainforest led me to a career in Biology, and in 1985, as a new PhD student at the Australian National University in Canberra, I became surrounded by people who were studying insects, particularly those whose behaviours so deeply fascinated me as a child. What's more, they were all doing research projects on the same topic – how insects see.

Ever since I was a child, growing up in an Australian rainforest, I have been fascinated by insects. Those in our garden – all manner of colourful butterflies, glistening beetles with endless jewel-like forms, and elusive slowly moving stick insects – captivated my imagination. Early on, it was their strange and wonderful colours and shapes that attracted me, but as I grew older, I began to see that they also had very interesting behaviours. Bees and flies could fly at breakneck speed without crashing, steering around trees to land. Large and venomous bull ants, the terror of every child's life in the Australian bush, wandered great distances to and from their nests to scout for food. Mud wasps collected mud at the banks of our creek, and flew off out of sight to build their nest in a distant tree, only to return a short time later to collect more. It seemed to me amazing that insects could do such complex things. It still amazes me!

Not surprisingly, my experiences as a boy led me into a career studying insects, and particularly their vision and navigational abilities. Once in Canberra, I found myself in the Department of Neurobiology at the Research School of Biological Sciences, a world famous centre for insect vision led by a colourful character, Professor George Adrian Horridge, who had been recruited to his post almost two decades earlier from the University of St Andrews in Scotland.

Horridge is famous for his authoritative 1965 two-volume 1800 page classic *Structure and Function in the Nervous System of Invertebrates*, which he co-authored with Theodore Bullock. My project was to work on the physiological optics of superposition compound eyes, one of the two broad types of compound eyes found in insects, the other being the apposition compound eye. Unlike this latter type, superposition eyes – due to their especially sensitive optical design – are typical of nocturnal insects like moths and beetles. Apposition eyes, in contrast, are much less sensitive to light and are typical of day-active insects like bees, butterflies, dragonflies and flies.

### Vision in the dung beetle

I was placed in the care of Dr Peter McIntyre, a mathematician who was developing optical ray-tracing models of superposition eyes using introduced South African dung beetles as a model system (Fig. 1A,B). These remarkable beetles were introduced into Australia about 20 years earlier by the Commonwealth Scientific and Industrial Research Organization (CSIRO) to rid Australia of the millions of wasted hectares of good pasture covered by cow manure every year.

‘Marcus told of how beetles rolled their large balls in almost perfectly straight lines, but was completely unable to explain how they managed this seemingly impossible task’

.....

Our local native species, evolved to deal with the dry fibrous pellets of Australian marsupials, were no match for the overwhelmingly large and moist discharges of our bovine imports. These dung beetles were a huge success, in fact one of Australia’s most successful biological control stories, quite unlike the notorious and catastrophic cane toad...

Under Peter’s expert guidance, I began to study dung beetle superposition eyes and to use electrophysiology to characterise the spatial and temporal acuity of their photoreceptors in an effort to find out how well this type of eye actually worked. Until then superposition eyes were thought to function as little more than sensitive low resolution imaging devices, sacrificing spatial resolution in order to maximise sensitivity at night. But the year before I started my PhD, Professor Mike Land from the University of Sussex (who was on sabbatical at Horridge’s department, but sadly left a few months before I arrived), used a home-built ophthalmoscope to measure the quality of images focused by the optics of superposition eyes in a day-active moth and a butterfly, two exceptional cases where superposition eyes have evolved for day use. He discovered that far from being blurry, these images were sharp and moreover diffraction limited (the best one could hope for in any optical system). My task was to find out whether this optical quality even extended to nocturnal superposition eyes, and whether the quality of the optical image was preserved in the neural image captured by the photoreceptor matrix.

### Better-than-expected vision by superposition eyes

The answer it turned out was yes – nocturnal superposition eyes create reasonably sharp images (not quite diffraction limited though), and this image quality is preserved in the retina (Warrant and McIntyre 1990). In other words, it made me realise that nocturnal insects probably saw the world quite well! But how well? With such tiny eyes and brains, exactly how much information could they realistically extract from a dim nocturnal scene? Could what I had found in the retina really be used to create those sophisticated behaviours I had seen in day-active insects as a boy? What started out as a project in physiological optics had suddenly grown to a much broader interest in nocturnal vision and visual behaviour.

With this new interest I moved to Lund in Sweden, to take up a postdoc with Dr Dan-Eric Nilsson, the other world-leading expert on the optics of compound eyes (the other being Mike Land – he and Dan have since written a beautiful and warmly recommended book describing the great variety of eyes found in nature, simply titled *Animal Eyes* (Oxford, 2012)).

While building up my new equipment (a brand new electrophysiology lab with a sophisticated optical stimulation system), I became increasingly curious about how well animals actually might see in very dim light.

### Vision in very dim light

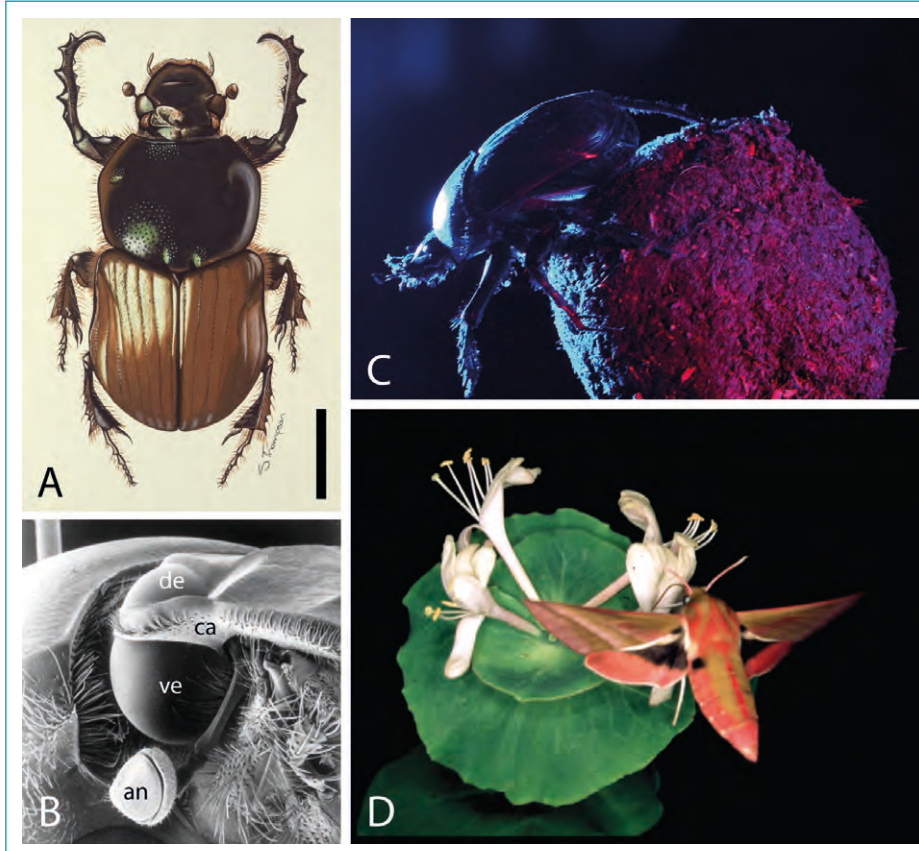
It occurred to me that nocturnal animals might be able to sum photons in space and time to increase sensitivity, akin to pooling pixels to create a larger and more sensitive pixel, or on a camera lengthening the exposure time. This would require neurons at some higher level in the visual system that sum the photoreceptor signals coming from small groups of neighbouring ommatidia (the optical building blocks of compound eyes, each consisting of a lens-pair and an underlying bundle of photoreceptors). Since each ommatidium is responsible for sampling a single pixel of the visual scene, this neural spatial summation would create a large ‘super ommatidium’ that samples a large ‘super pixel’. Similarly, some higher neuron, or circuit of neurons, might be responsible for lengthening the visual exposure time (which is equivalent to the visual integration time).

The downside of such a summation strategy is, however, that fewer larger pixels reduce spatial resolution, and a longer exposure time reduces temporal resolution. In other words, to improve sensitivity one would need to throw away the finer and faster details in a visual scene in order to see the coarser and slower ones a lot better. But this might be better than seeing nothing at all! With this realisation, I started to build a mathematical model to calculate the finest spatial detail that a nocturnal animal, with a given eye design, might see using such a summation strategy as light levels fell (Warrant, 1999).

The results were surprising – spatial and temporal summation should in theory allow nocturnal animals to see at light levels several orders of magnitude dimmer than would have been possible had summation not been used. But could nocturnal animals actually do this? The benefits of summation seemed obvious, and I became convinced that it must be a crucial component of nocturnal visual processing.

### Summation allows vision in very dim light with video too

I also realised that the same strategies could be used to improve video filmed in very dim light, and quite out of the blue, not long after I had published my model, I was contacted by the car manufacturer Toyota (who had realised the same thing). Toyota were very keen to develop an in-car camera system that could automatically monitor the road ahead at night – using only the existing natural light – and warn the driver of impending obstacles.



**Figure 1. Nocturnal insect champions with superposition eyes.**

**A.** The nocturnal dung beetle *Onitis aygulus*, one of the introduced South African dung beetles I studied during my PhD in Australia. Scale bar = 5 mm.

**B.** The superposition eyes of *Onitis aygulus* – there are two of them on each side of the head, one on dorsal side (de) and one on the ventral side (ve), divided by the canthus (ca). an = antenna.

**C.** The nocturnal ball rolling dung beetle *Scarabaeus satyrus*. Photo: Chris Collingridge.

**D.** The nocturnal elephant hawkmoth *Deilephila elpenor*. Photo: Michael Pfaff.

That led to a long collaboration in which we developed mathematical computer algorithms that could be used to dramatically improve the quality of video sequences captured in dim light (Warrant *et al.*, 2014), and as far as we know Toyota are now using this technology to develop camera systems for their cars. However, from our point of view the results of this exercise were telling – summation could improve the quality of dim video sequences dramatically, even restoring colour information! This convinced me further that summation could make a real difference for vision in dim light.

That chance call from Toyota was not the only out-of-the-blue event from that time that dramatically drove our research on nocturnal vision forward. A couple of years earlier I was invited by Professor Clarke Scholtz, South Africa's preeminent expert on beetles, to talk about the visual system of dung beetles at the first (and only) International Conference on Scarab Biology to be held in the beautiful Kruger National Park north of Johannesburg. One of the lectures – by Dr Marcus Byrne from the University of the Witwatersrand – dealt with the behaviour of ball-rolling dung beetles. These beetles fashion golf-ball sized balls of dung and then roll them away backwards for burial (prior to which a female deposits her egg at the ball's centre – the dung is used as food by the developing beetle). At one point in the lecture Marcus told of how beetles rolled their large balls in almost perfectly straight lines (presumably to most

efficiently escape the competitive fury of the dung heap), but was completely unable to explain how they managed this seemingly impossible task.

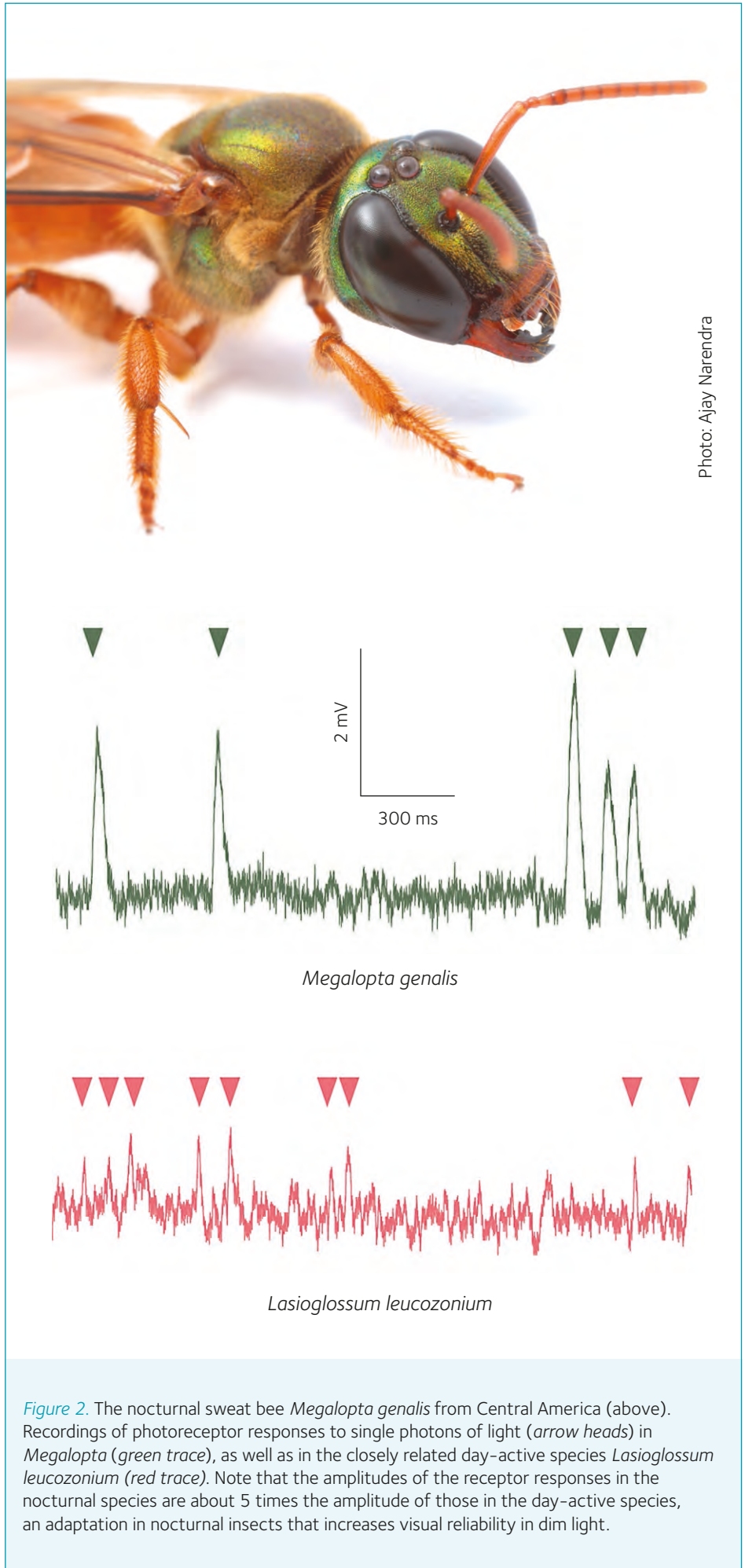
### How do insects navigate a straight line?

Sitting in the audience, I thought I might know the answer – many other insects are able to see the circularly symmetric pattern of celestial polarised light formed around the sun and to use it as a compass cue for orientation and navigation. Maybe dung beetles could too? Half a century earlier, Karl von Frisch, the great Austrian zoologist who had discovered the dance language of honeybees, also discovered that insects used celestial polarised light for orientation. Since that time, we now know that a wide variety of animals, particularly invertebrates, can see and use this celestial cue (mammals like ourselves, however, are not among them). A good chat with Marcus after his lecture was the start of a long and very fruitful collaboration that has continued to this day. As it transpired, not only do the day-active species roll in straight lines (and indeed rely on the solar polarisation pattern), but so too do the nocturnal species. These, it turned out, instead rely on the million times dimmer polarisation pattern formed around the moon as a compass cue. This remarkable navigational ability indicates that these dung beetles have exquisitely sensitive nocturnal vision.

After many trips to the wilds of South Africa with Marcus and Clarke – now in the company of my good friend Dr Marie Dacke from Lund, who these days runs this project – we discovered that not only do nocturnal beetles like *Scarabaeus satyrus* (Fig. 1C) have sufficiently sensitive superposition eyes to see and use the dim lunar celestial polarisation pattern to roll in straight lines (Dacke *et al.*, 2003), but even use the faint stripe of starry light formed by the Milky Way as a back-up when the moon and its polarisation pattern are absent from the sky (Dacke *et al.*, 2013)! To prove all this we resorted to methods, including designing and producing small cardboard hats we could tape to the head of the beetle and which blocked their view of the sky (but not of the terrestrial surround). Hatted beetles just rolled their balls around in circles. To show their dependence on the Milky Way on moonless nights, we moved the beetles into the Johannesburg Planetarium where we could turn the stars and the Milky Way on and off at will. We were surely the strangest visitors the planetarium had opened its doors to, but we were enthusiastically accommodated nonetheless. The IgNobel prize committee was also enamoured by our efforts and in 2014 they awarded us their first (and probably their last) IgNobel prize jointly in the fields of Astronomy and Biology! Since then we have discovered exquisitely sensitive neurons in the dung beetle central brain that are responsible for coding nocturnal compass information and for establishing the hierarchy of cues used in straight-line navigation (Jundi *et al.*, 2015).



‘In other words, it made me realise that nocturnal insects probably saw the world quite well!’



## Nocturnal bees in Panama

Not too long after the conference in Kruger National Park I received a phone call – again out of the blue – from Dr Bill Wcislo, a well-known bee ecologist from the Smithsonian Tropical Research Institute in Panama. He just wanted to inform me, in case I didn't know, that in Panama there were strictly nocturnal bees that foraged in the rainforest at night, and that maybe I would be interested in studying their vision. I was flabbergasted. I had never heard of strictly nocturnal bees, and of course I was interested! And we have been studying these amazing bees – sweat bees of the genus *Megalopta* (Fig. 2) – ever since. Together with my first postdoc Dr Almut Kelber (now a full professor in Lund), we discovered that these bees have remarkable nocturnal visual powers. Like their day-active relatives, *Megalopta* uses its eyes to learn visual landmarks around its nest (a small hollowed out stick in the rainforest undergrowth), as well as along the foraging route, and uses these landmarks to find its way home after a successful foraging trip (Warrant *et al.*, 2004). It does this at perishingly low light levels – we ourselves are almost totally blind, yet these bees are negotiating branches, tree trunks and bushes while flying through the forest understorey. What makes this all the more incredible is that they are doing it with apposition compound eyes – the compound eye design typical of insects active in bright light (including all other bees). By recording the responses of their photoreceptors to single photons (Fig. 2), we determined that at the light intensities *Megalopta* are active, each photoreceptor on average absorbs fewer than 10 photons per second. This is absurdly little light, in fact according to theory it should be at least 100 times too little for the bee to see its nest entrance! Yet it does, and we have since discovered that at these light levels it can fly and land on its nest with the same speed and precision as a day-active honeybee. How? Again visual summation likely provides the answer. We are currently investigating this possibility by studying their visual processing using two recently built state-of-the-art electrophysiology labs in Panama.

## The nocturnal elephant hawkmoth can see colours at night

After years of trying to find proof for the existence of summation in the neural circuitry of the visual system, we have finally found it in the optic lobes of the nocturnal elephant hawkmoth *Deilephila elpenor* (Fig. 1D). These beautiful moths have very sensitive superposition eyes, and are accomplished fliers; being able to suck nectar from flowers on the wing, while hovering to keep station.

Some years ago, Almut and I had discovered that these moths have trichromatic colour vision, and use it to locate flowers at night, the first nocturnal animal known to have colour vision (Kelber *et al.*, 2002). In more recent years, a talented PhD student in my group, Anna Stöckl, has managed to record from wide-field motion-sensitive cells in the lobula plate region of the moth's optic lobe, the brain region responsible for processing visual information. These visual cells – well known in other insects, particularly flies – are responsible for analysing the way the visual image of the world moves as an animal moves through it. An accurate analysis of this so-called 'optic flow' is essential for course control and obstacle avoidance, especially in a fast flying animal like a moth.

The responses of these neurons to moving patterns of black-and-white stripes (known as 'gratings'), at increasingly dimmer light levels, can be used to test for the presence of summation. By making the stripe width thinner and thinner, and by moving the grating faster and faster, one can measure the finest spatial and temporal details that the motion cells can resolve at each light level and then use the same stimulation regime to compare these to the finest details resolved by the retina (the visual input). Any coarsening or slowing of vision at the level of the motion-sensitive lobula plate cells relative to that in the retina would then indicate the presence of summation somewhere in the intermediate visual pathway. Using this method, Anna has found that substantial spatial and temporal summation occurs prior to the lobula plate. This summation increases as light levels fall, dramatically boosting visual reliability for coarser and slower details in the scene over four decades of nocturnal light intensity. Moreover, without summation the moths would become blind at light levels at least 100 times brighter than they actually do. These findings provide the long-sought proof of the benefits of summation for vision in dim light.

But even though we have now probably pinned down summation as the major player in extending the limits of vision in dim light, it doesn't detract from the fact that insects, and in particular nocturnal insects, are truly amazing. My boyhood fascination for them has not in any way diminished with the years. To the contrary, my fascination has only increased. To know that a small nocturnal bee, with tiny apposition eyes and a rice-grain-sized brain, can find its way to a lucrative source of flowers through the complicated tangle of a rainforest at night, and then find its way home again, is both humbling and awe-inspiring. For us to witness this spectacle requires a pair of night vision goggles and infrared illumination,

and even during the day we would become hopelessly lost in this jungle if we strayed even a few metres from the trail. How a bee manages to forage and home at night is still largely a mystery, and despite all our work we are still only a fraction of the way to understanding the physiological solutions that these and other remarkable nocturnal insects use in order to see, fly and navigate at night.

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## Aquatic and aerial animal athletes

Adaptations for muscle power and speed in tuna and hummingbirds



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Differences in skeletal muscle structure and function contribute to the diversity in animal locomotor capacity and at least partly explain remarkable feats of animal speed (like the flat-out hunting swims in tuna) and stamina (like fish and bird migrations). Integrative experimental approaches needed to study muscle physiology in specialised animal athletes are helping to refine our understanding of these mechanisms, including in relation to muscle function in humans. Ongoing analyses will also sharpen our predictions of how environmental changes might impact on migration patterns, hunting success, (re)distribution and survival of peak performers in the wild.

Decades of comparative animal biology have revealed remarkable diversity in animal activity metabolism. There are examples of swimmers, flyers and runners that are legitimate elite athletes, although it is clear that, compared with human athletics, it is chiefly the processes of evolution and survivorship that shape athleticism in wild animals, rather than routine training and motivational accolades. Comparative researchers are drawn to measurements of animal speed, power, stamina and metabolism, partly with the aim of advancing our understanding of the physiological limits and environmental constraints for wild animals living in diverse, and changing, habitats. A key aim is also to seek the basic features of striated muscle design that underlie speed and endurance adaptations across species, including humans.

Animal performance is popular to review. Recent excellent reviews by Sharp (Sharp 2012) and Williams *et al* (Williams *et al.*, 2015) comprehensively summarise the diversity of particularly mammalian and avian athleticism, including useful speed and endurance statistics and comparisons with human performance limits. Our understanding of behaviours which might normally be overlooked as athleticism, such as mechanisms of dive-time endurance and extreme cardiac function in marine mammals, are useful for highlighting the physiological limits of organ-level function and possibly for predicting the circumstances when physiological demands might exceed performance capacity in humans (Williams *et al.*, 2015). Similarly, recent work shows us that skeletal muscle adaptations for speed and endurance in elite swimmers (tunas) and flyers (hummingbirds) can inform us about the limits and extremes of muscle plasticity and locomotory performance.



## Tuna Swimming Muscles: adapted for power

Arguably, the swimming musculature of fast swimming fishes, including tunas, billfishes and lamnid sharks (e.g. great whites and makos) is the ultimate in top performance design. The tunas, for example, display both fast sustainable cruising swims and super-fast anaerobic (hunting) bursts. While the capacity for performing both aerobic and anaerobic work is not unique amongst animal athletes, it is rare to find a generalised top-performance phenotype. The two extremes of human anaerobic and aerobic training tend to develop either the muscly high-power sprinter or the lean long-distance endurance racer. In contrast, tuna swimming musculature is adapted for high aerobic, and higher still anaerobic, power output. The flexible performance capacity of tunas, together with the anatomical separation of fibre types into distinct red (aerobic cruising fibres) and white (glycolytic, burst fibres) muscle masses, makes tuna an ideal model for investigating the fibre-type dependent features of peak power and speed.

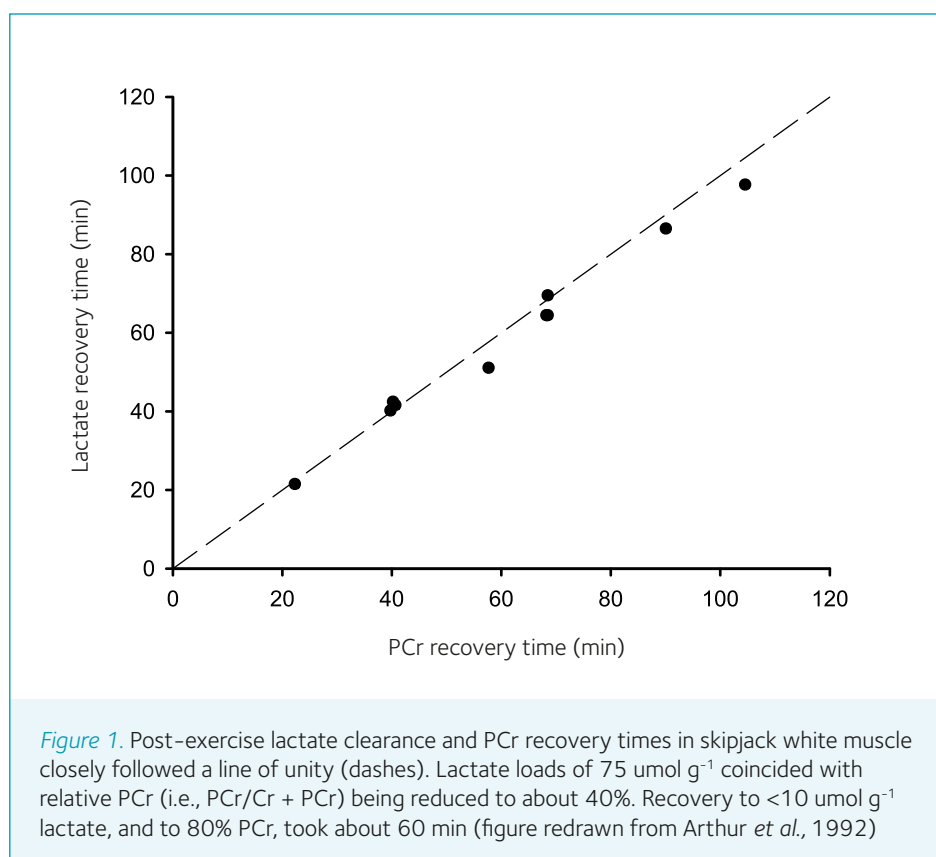
Many factors contribute to sustainable aerobic performance. Tunas are streamlined Thunniform swimmers, using high frequency oscillations of the hydrofoil shaped tail, rather than rhythmic body undulations of the trunk musculature, for high speed cruising. The red muscle is an aerobic power-house; (i) there is a lot of it compared to other fishes, and oxygen delivery, fibre capillarity and mitochondrial function are all relatively high for fishes, (ii) the anterior and medial position of red muscle within the trunk, rather than in the peripheral mid-line area, confers a biomechanical advantage for high power caudal oscillations, and (iii) red muscle temperature is typically 10°C above ambient sea temperature, so pathways of energy demand and supply operate at the upper end of their temperature dependencies (Mathieu-Costello *et al.*, 1995; Moyes and West 1995; Shadwick and Syme 2008). It seems that optimal red muscle contractions, tested in vitro, are likely to support cruising at or near peak aerobic power (Shadwick and Syme 2008). This may constrain tunas to a relatively narrow, high-performance-only, lifestyle (discussed later). Anatomical measures of tuna red muscle aerobic capacity (eg., fibre cross-sectional area, fibre capillary length, volume density of mitochondria) are not all outstanding compared to those of athletic and non-athletic mammals and birds (Mathieu-Costello *et al.*, 1995), suggesting that red muscle endothermy and the biomechanical advantage of its medial-positioning are the main aspects of tuna aerobic cruising performance.

Fewer factors contribute to the maximal burst power in tuna. Maximal bursts of 20 body-lengths  $s^{-1}$  are supported by anaerobic contractions of a large white muscle mass and are dependent on the breakdown of intramuscular glycogen, phospho-creatine (PCr), and adenosine triphosphate (ATP). Glycogen content of skipjack tuna white muscle is about 150  $\mu\text{mol g}^{-1}$  (Arthur *et al.*, 1992), and glycolytic enzyme activities are some of the highest measured in vertebrates (Moyes and West 1995). Different durations of maximal swimming result in variable levels of lactate accumulation, but the molar stoichiometry of glycogen-used:lactate-formed is nearly 1:2. Remarkably, lactate accumulation of >100  $\mu\text{mol g}^{-1}$  occurs in skipjack white muscle (Arthur *et al.*, 1992), and this is still only one-third depletion of the total glycogen store. The stoichiometry between glycogen breakdown and lactate build-up highlights that maximal power is not dependent on either circulatory oxygen or glucose. Human sprinters and power athletes are similarly poised for anaerobic power output, but with lower glycolytic capacity than tuna. Interestingly, the intramuscular handling of metabolites in tuna persists during exercise recovery.

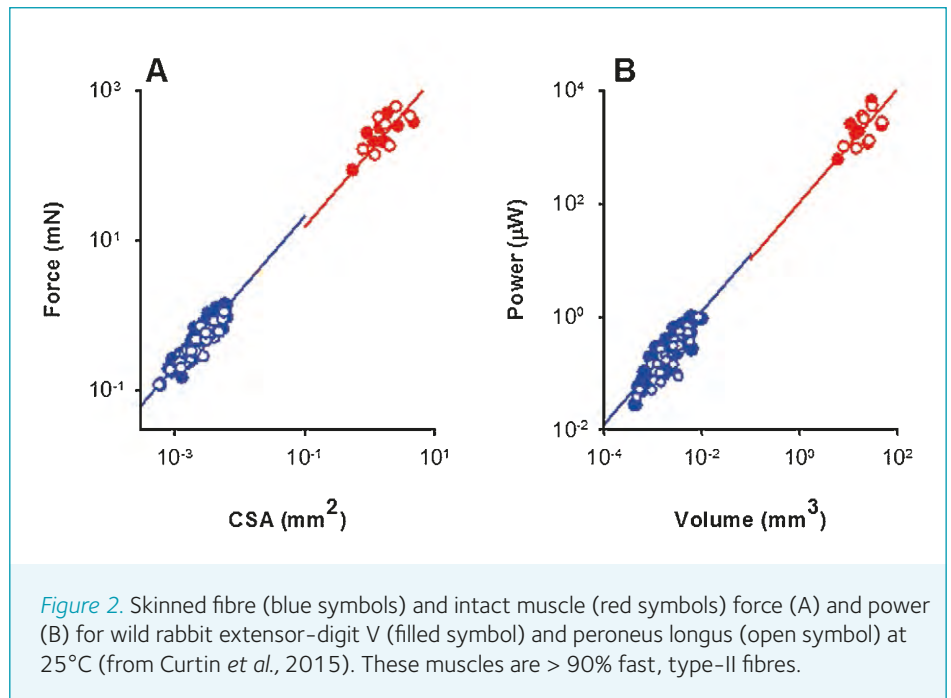
Figure 1 depicts recovery times for lactate and PCr in post-exercise tuna white muscle. Intramuscular pH regulation, together with high creatine kinase activity, is the likely

mechanistic link between muscle lactate removal and PCr replenishment; proton removal accompanies lactate disappearance in recovery and, in turn, pulls the creatine-kinase equilibrium in the direction of phosphate exchange from ATP to Cr. Muscle lactate clearance via the circulation and by oxidation, as occurs after maximal exercise in mammals, seems insignificant in tuna (Arthur *et al.* 1992, Moyes and West 1995). Nevertheless, lactate, PCr and glycogen all recovery rapidly in tuna, despite relatively low temperatures, and even after accumulation of large lactate loads. Lactate disappearance and glycogen restoration in recovery show an approximately 2:1 stoichiometry, mirroring the metabolic state seen during anaerobic contractions (Arthur *et al.* 1992), and suggesting activity of chiefly an intramuscular pathway of lactate-to-glycogen conversion during recovery.

Tuna white muscle is an extreme phenotype, but there are useful benchmarks for improving human performance; including, the large muscle mass and high glycolytic capacity needed for burst power, the marked intramuscular management of fuels and metabolites, and rapid post-exercise recovery. Different factors control the fate of lactate and speed of recovery in tunas and trained humans, but both recover fast – humans so they can train often to get better and tunas so they can hunt often.



‘The full power of the reductionist approach is realized only when it is reincorporated into the integrationist one’



### Hummingbird flight muscle: adapted for aerobic fuel efficiency

Hovering/feeding flight in hummingbirds may be the near-limit of striated muscle shortening speed and fuel oxidation rate. Aerobic metabolic rates during hovering are some of the highest values measured among the vertebrates, and it is estimated that the fast-twitch oxidative flight muscle accounts entirely for the metabolic costs of hovering. The evolution of heightened functionality at multiple steps in the lung-to-mitochondria oxygen cascade (e.g., lung diffusion, cardiac output, muscle mitochondrial volumes) seems to underpin the efficiency of oxygen flux, and fuel (fat and carbohydrate) usage, during hovering flight (Suarez *et al.*, 2011). carbohydrate quickly becomes the preferred fuel for muscle activity during subsequent feedings. The transition between fuel types is interesting because it occurs without a change in work intensity – hovering flight is hovering flight. A fat-to-carbohydrate transition in exercising mammals usually accompanies a change from low to high aerobic metabolic rate. The hummingbird result shows that fat is actually suitable for peak aerobic muscle work, but if both fuels are available for flight then carbohydrate is preferred. Flexibility in fuel selection is important for hummingbirds, as they will undoubtedly use both fat and carbohydrate during migration. However, in the non-migratory state, the shift towards carbohydrate promotes (i) efficient exploitation of carbohydrate-rich nectar and (ii) efficient oxygen usage – the yield of ATP per atom of oxygen is higher when muscle is burning glucose than it is when burning fatty-acids (Suarez *et al.*, 2011).

The second remarkable aspect of hovering flight is that fuel (nectar) intake supports muscle energy supply (i.e., glucose oxidation) very soon after ingestion. Up to 95% of the metabolism of hovering flight is fuelled by recently ingested sugar. Suarez *et al.*, (2011) call the flow of sugar, from flower to muscle mitochondria, the ‘sugar oxidation cascade’. Good synchrony between glucose and oxygen delivery to muscle is important for matching energy demand (contractile ATP use) with energy supply (mitochondrial ATP synthesis) and for maintaining oxidative efficiency with a carbohydrate-based metabolism. The nectar bats seem to have also evolved the strategy for glucose uptake and oxidation (Suarez *et al.*, 2011). Similar supply-demand balance must also characterise steady-state cruising in tunas and endurance exercise in humans, but with greater dependence on ‘on-board’ fuel stores and perhaps less clear-cut patterns of carbohydrate oxidation.

It seems clear that exogenous glucose, via the sugar oxidation cascade, is the main ATP source for hovering flight. An advantage of the sugar oxidation cascade in hummingbirds is that any energetic burden of carrying on-board fuel masses is minimised. The day-to-day risk of this strategy, and even longer-term danger due to habitat change, is that the animal needs to locate fuelling-up sources quickly. The capacity to fuel costly hovering flight with on-board fat is one safety factor that the birds can exploit in the short term.

## Integrating muscle energy supply and demand with animal locomotion

Near the end of PW Hochachka's book *Muscles as Molecular and Metabolic Machines*, he writes that 'The full power of the reductionist approach is realized only when it is reincorporated into the integrationist one' (Hochachka 1994). A good example is how we integrate the mechanisms of muscle energy supply with muscle energy demand and, in turn, integration of muscle energetics with animal locomotion. Muscle energy balance (supply matching demand) is a key to maintaining flexible muscle performance for both migration and foraging/hunting success in the wild. Comparative or ecological physiologists would naturally extend the meaning of Hochachka's point to include the role for plasticity in activity capacity in the face of environmental change.

Tuna and hummingbirds possess remarkable features of muscle energy supply, including oxygen and fuel delivery rates, fuel oxidation capacities, and high glycolytic enzyme activities. Integration with energy demands (cross-bridge and activation/deactivation kinetics and costs) is critical, since it is these properties that dictate muscle force, speed and power, and in turn drive the upregulation of energy supply. Hummingbirds and tunas are ideal models for studying the integration of energy supply and demand because (i) fibre-types are either entirely homogenous (hummingbird fast-twitch oxidative flight muscle) or segregated into functionally distinct fibre masses (tuna red and white swimming muscles), and (ii) both tuna cruising and hummingbird hovering are near-peak aerobic activities, so it is relatively straightforward to integrate muscle power with specific patterns of real-world locomotion and with metabolic rates.

Cruising in tuna, during schooling and migration, is not only normal behaviour it is also essential life-support. Tuna match high aerobic demand with efficient oxygen supply from water; they do so by swimming continuously, with mouth wide open, in order to 'ram ventilate' the gills. While different tuna species have different preferred cruising speeds, it seems that optimal red muscle contractile demands are likely to support cruising at a very high level of aerobic power (Shadwick and Syme 2008). This level of muscle demand/supply integration is possible because *in vivo* tail beat frequency and amplitude can be compared with, or directly replayed onto, movement patterns in isolated muscle preparations. The finding that red muscle activity may keep tunas at or near peak power output *in vivo* is interesting because rhythmic activation of the red muscle itself must be a major component of the metabolic demand associated with ram ventilation.

Cruising at a high level of aerobic power seems in a sense to be a costly mode of locomotion. This is possibly offset partially by muscle operating *in vivo* in a zone of peak efficiency. Moreover, a major trade-off is that high speed coupled with a degree of red muscle thermoregulation expands the tunas' range of locomotion and hunting habitats. The impact of ocean temperature-change on the capacity for habitat expansion needs to be explored. Interestingly, similar red muscle anatomical design has evolved independently in fast swimming tunas and lamnid sharks, indicating that a high-power design, together with mechanisms to keep cruising muscle warm, is a superior phenotype amongst the top pelagic predators.

There are not many studies of hummingbird isolated muscle mechanics. A recent study found that demembrated (or 'skinned') single fibres generated low isometric forces per cross-sectional area (CSA), perhaps indicating that low stress favours high shortening speed in this special system (Riser *et al.*, 2013). This fits with the suspected rapid calcium kinetics which should keep twitch forces low and muscle cycling rate high, and with observations of high mitochondrial volume density relative to myofibril volume in hummingbird flight muscle (Mathieu-Costello *et al.*, 1995; Riser *et al.*, 2013).

It would be of further interest to measure directly the muscle shortening properties in order to characterise fibre force and velocity at peak power. Physiologically relevant length changes are expected to be quite short in hummingbird flight muscle because of the rapid cycling time and short fibre lengths. This could make measurements with skinned hummingbird fibres challenging, especially at high temperatures. One way forward is to make measurements of length changes during force-clamp after temperature-jump activation of the skinned fibre. The temperature-jump approach keeps skinned fibre activation time short, and allows for more repeatable activations at elevated temperatures. Recent work integrating skinned and intact (electrically excitable) muscle mechanics, in the same lab and using the same muscles from wild rabbit, shows that isometric forces and peak powers at 25°C are equal in the two kinds of preparation (Fig 2; Curtin *et al.*, 2015). Oxygen consumption during hovering flight seems to interrogate a peak energy supply/demand steady-state of primarily the flight muscle of hummingbirds (Suarez *et al.*, 2011). Since the demands are expected to be largely ATP usage for cross-bridge turnover and calcium handling, it would be valuable to integrate direct measurements of skinned and intact muscle power with the *in vivo* hovering flight physiology.

Together with the emerging ideas about a sugar oxidation cascade, this work could make the elite hummingbird one of the most completely integrated models of vertebrate muscle mechanics and energetics.

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# ‘Teach the Teachers’ – a workshop on Bioscience approaches in the Nigerian classroom

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Participants at the workshop

The importance of science in promoting international development cannot be overemphasised. However, in Africa, cultural and religious misconceptions about science strongly restrict the extent to which science is appreciated, partly contributing to hampering science development on the continent. In Nigeria for instance – Africa’s most populous nation – science literacy has been estimated as below 10%. In most schools, science teaching is too often based on outdated models that are long known to be ineffective. Additionally, science teachers rarely employ innovative teaching approaches, and, as a result, many students never develop a passion for science. These collectively contribute to low student enrolment in sciences and the generation of poorly qualified teachers and scientists, which additionally contributes to low science awareness and thus poor science policies.

To begin to tackle these problems; with support from The Physiological Society, we organised the first hands-on ‘Teach the Teachers’ workshop on bioscience approaches in the Nigerian classroom, targeting science teachers. This was aimed at reinvigorating their passion for science, thereby help in creating a sustainable system where students would continue to get excited by their teachers about science. To this end, at least two science teachers were invited from nine primary and secondary schools to participate in a one-day hands-on science workshop on running simple and enjoyable experiments for a low-cost setting that can be adopted to the classroom. To enable teachers fully to benefit from the workshop, the activities were run in three sessions, covering chemical interactions, cells and system physiology, and electrophysiology, which are all partly contained in their school curriculum.

The first session kicked off with experiments on how to create density columns and a rainbow reaction tube. After demonstrations, teachers were tasked with creating density columns and reaction tubes using varying

## Getting involved with practical experiments



‘Many teachers were thrilled with the experience and wished that the workshop be run more frequently’

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components (e.g. low and high salt and sugar concentrations for the columns). This greatly stimulated and made them engage in brainstorming sessions, especially on how manipulating components, like sodium carbonate concentration or vinegar, could produce an ideal rainbow reaction tube (pictured right).

Many science teachers lack basic microscopy skills, such as how to prepare microscope slides. Consequently, many students end up knowing little about the use of microscopic techniques in bioscience. Therefore, in the second session of the workshop, experiments on how to make slides for microscopy from cheek and blood cells were demonstrated. Participants were tasked with making their slides, with or without methylene blue. This enabled teachers to learn not only about the preparation procedure but how stains with affinity to different cellular compartments (e.g. the nucleus) can practically be used in the identification of cells. They were further shown various tissues (e.g. Testis) under the microscope using already prepared slides. This session stimulated many thought-provoking questions and discussion on cellular changes in diseases like Alzheimer's.

Backyard Brains Electromyography (EMG) Spikerboxes were used in the last session to introduce teachers to basic electrophysiology. Considering that the experiment was designed to focus on muscle electrical activity, teachers first received a basic lecture on brain-muscle relationship, followed by demonstrations on how to measure muscle activity. This session tremendously stimulated the science teachers, especially, the realisation that fatigue could lower muscle potentials. Participants divided into groups were allowed to measure the EMG of their

colleagues. Many teachers were thrilled with the experience and wished that the workshop be run more frequently. In the end, reagent leftovers and manuals for running other simple and fun experiments were donated to the teachers. They also received leaflets, pens and other freebies on neurosciences and molecular sciences.

To ascertain the impact of these activities, we administered questionnaires to the participants and also observed their enthusiasm during the hands-on activities. All the teachers confessed that the outreach introduced them to simple approaches of designing simple science experiments that they now intend to use in connecting theoretical teaching with practicals in their classroom. For instance, a teacher said, *‘learning how to measure EMG was the most important part of the workshop for me, I will introduce it to my students’*. The feedbacks from the events were overall overwhelmingly positive.

The events demonstrated to participants that science can be taught in a fun and simple way. We received many messages of appreciation from the participants and their schools, confirming that the activities were helpful. The event was covered and published by the local media. Thus, we are hopeful that its success would increase the awareness and perception of science by the public, increase students passion for science, motivate similar activities by local scientists and encourage the government to consider a regular curricular review to accommodate modern classroom science methods.



Rainbow reaction tube



## Obituary:

### Susan Noble 1940 – 2015



Susan Noble

*Dario DiFrancesco  
& Hilary F Brown*

Susan Noble who died on 4 October 2015 aged 75 had worked for many years in the Oxford cardiac group led by her husband, Denis.

Susan's parents were both schoolteachers (of mathematics) and she was the eldest of their three children. Although always keenly interested in the arts and the theatre, she specialised in science at school, and in 1959 was accepted at Somerville College, Oxford to read for a degree in Physiology. After two years of the course, however, she became ill and had to withdraw from Oxford. On recovery, she completed her undergraduate studies at University College London. Shortly after she graduated, Susan and Denis Noble were married and in 1965, when Denis was appointed to a University Lectureship in Physiology and Fellowship at Balliol College, they settled in Oxford. Their daughter, Penny, was born in 1967 and their adopted son, Julian, joined the family in 1972.

When Susan returned to Oxford, Jean Banister, who had been her tutor at Somerville and who provided her with lifelong support and friendship, found her funding for graduate work and provided space in a corner of her own lab. Here Susan worked with others

(Hilary Brown, Anne Clark and Wayne Giles) investigating the membrane currents in strips of frog atrial muscle voltage clamped using the double sucrose gap technique. Of particular interest was the induced pacemaking that resulted from applying steady depolarizing currents to atrial muscle. This type of pacemaking was shown to depend on the decay of outward potassium currents, though in multicellular preparations things are complicated by slow current changes caused by the accumulation of potassium ions in extracellular spaces.

In 1972, Susan was awarded her D.Phil. for a thesis entitled 'Membrane currents in frog atrial muscle'. She went on to study potassium ion accumulation in detail (Noble SJ (1976). *J Physiol* **258**, 579–613).

A classical paper with Wayne Giles (Giles W, Noble SJ (1976). *J Physiol* **261**, 103–123) demonstrated for the first time the inhibitory action of acetylcholine on the calcium current in atrial muscle. This was the first evidence that the negative inotropic cholinergic action on the heart is attributable to calcium current inhibition.



Susan gets involved in the discussion at a conference



Susan Noble at home



‘As a mathematical biologist, Susan, with her husband, Denis, published the first numerical reconstruction of sinoatrial node electrical activity incorporating the newly described  $I_f$  channel’

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When Dario DiFrancesco joined the group in Oxford in 1976, the investigations shifted to the very challenging technique of voltage clamp of the ‘small preparation’ of rabbit sinoatrial node impaled by two microelectrodes. A 1979 paper (Brown HF, DiFrancesco D, Noble SJ (1979). *Nature* **280**, 235–236) first described the ‘funny current’ in sinoatrial node, an inward current activated at diastolic potentials. This was a revolutionary concept at a time when all pacemaking was thought to arise from the decay of an outward (potassium) current.

The discovery of the ‘funny’ ( $I_f$ ) current was a milestone in the field of cardiac pacemaking. It was subsequently found in other cardiac tissues that show pacemaker activity (AV node and Purkinje tissue) and its key importance for the generation and control of cardiac rhythm has been fully recognized. Further studies of  $I_f$  using single cells and eventually membrane channels led several decades later to the development of the commercially available f-channel blocker ivabradine used clinically in angina and heart failure therapy.

As a mathematical biologist, Susan, with her husband, Denis, published the first numerical reconstruction of sinoatrial node electrical activity incorporating the newly described  $I_f$  channel which provided a theoretical validation of the new finding (Noble D, Noble SJ (1984). *Proc R Soc Lond B* **222**, 295–304). This was written in conjunction with another paper reconstructing by computer modelling the electrical activity of cardiac cells (DiFrancesco D, Noble D (1984). *Phil Trans R Soc B* **307**, 353–398) which was recently recognized by the Royal Society as among the most influential life sciences reports in 350 years.

Susan’s interest in mathematics – which perhaps came in part from her parents – led her to obtain a Maths degree with the Open University.

Susan had a kind and understanding nature and a talent for putting younger scientists who joined the group at their ease and helping them to integrate into the team. In the lab she was an extremely friendly and helpful colleague with quick wit, good conversation and a great sense of humour. Her cheerfulness was contagious. One of us (D.DiF.) recounted to her this scene he had witnessed soon after joining the lab: Bob Torrance—who was very large indeed—opened the swing doors into Jean Banister’s lab with such force that a big  $\text{CO}_2$  cylinder standing by the door fell down. When Susan heard the description of the huge crash, the shrieks from Jean and the baritone excuses from Bob Torrance she started to laugh so infectiously that both of them laughed till the tears ran down.

Susan was full of humanity and love of life but was constantly shadowed by ill-health. This she bravely fought with as much strength and determination as she could muster, supported in everything by her close family. But inevitably her involvement in lab-based activity declined over the years. Despite these limitations, she contributed to findings, which have been fundamental to understanding the mechanisms that generate and control cardiac pacemaking.

## Obituary:

### Roger C Woledge 1938 – 2015



Roger C Woledge

#### *Nancy Curtin*

Imperial College London &  
Royal Veterinary College, UK

#### *Di Newham*

#### *& Stuart Bruce*

King's College London, UK

Roger died suddenly in March following a riding accident. His favourite recreational activity was riding his horse in Epping Forest near his home. Despite being 76 years old and having officially retired from University College London (UCL) over a decade earlier, he continued to work virtually full time. His father, Brian, was Head of French at UCL but encouraged Roger and his sister to study science. Roger went to UCL as an undergraduate Physiology student, essentially due to a general interest in biology. He remained in the UCL Department of Physiology, becoming Professor of Experimental Physiology and subsequently Head of Department until he moved to UCL's Institute of Human Performance at Stanmore as its Director. After his 'retirement' at 65, which was the compulsory retirement age at the time, he continued his productive research career, particularly with colleagues at Imperial and King's Colleges, Queen Mary University of London and the Royal Veterinary College.

Throughout his career, his driving research interest was the physiology of skeletal muscle in which he had an exceptionally broad range of experience and expertise. His early work, under the supervision of A.V. Hill, involved measuring the heat produced during contraction in frog muscle and was followed by measurements on tortoise, mouse and fish muscle. Interestingly AV did not 'believe' in the PhD degree, but later Roger was encouraged to register for one by Doug Wilkie who supervised his studies. For many years, he spent part of the summer working at the Marine Biology Association laboratory in Plymouth which he particularly enjoyed. The interest in muscle energetics continued throughout his life and earned him an international reputation. Much of this work was carried out with his friend and collaborator Nancy Curtin, with whom he was still working at the time of his death at the Royal Veterinary College. Latterly his research interest broadened to encompass human muscle physiology, particularly the muscle changes associated with ageing and their relation to the clinical problem of falls.

In addition to his research achievements, Roger was an inspiring teacher who strove to make his subject, and Physiology in general, interesting and understandable. His enthusiasm, clear delivery and sense of fun made him as popular with students as he was with his peers and colleagues. While Director of the Institute of Human Performance at Stanmore he developed an MSc programme which had a huge impact on many clinicians by giving the research knowledge and skills to evaluate and modify their clinical practice. Despite his phenomenal intellect, his broad interest and personality made him a very approachable man who never made anyone feel they were asking a stupid question.

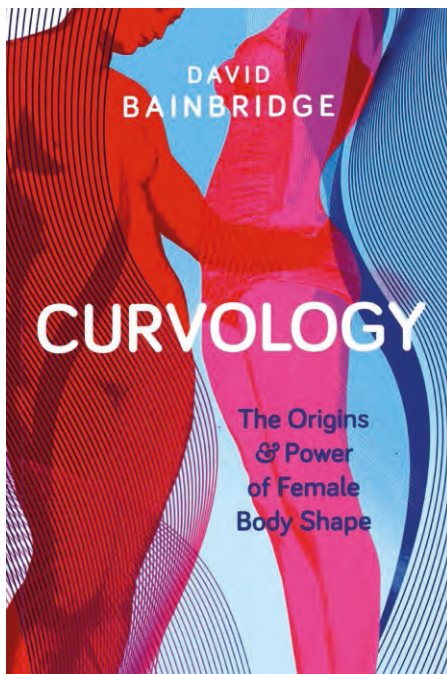
Roger was an exceptional person who combined his remarkable intellectual knowledge and ability with a great sense of humour. He had a real interest in whatever research people were working on and gave generously of his time and expertise to anyone who approached him. As a result of his generosity combined with his expertise in data analysis and statistics, he became mentor, colleague and friend to many. He is much missed.

## Book review:

# Curvology: The Origins & Power of Female Body Shape

*Roger Thomas*

Editor, *Physiology News*



Portobello Books, London 2015

ISBN: 978-1-84627-550-0

This book is written by a veterinary anatomist but is really about human anatomy. Never having studied the subject myself I found it a fascinating account of the reasons believed to explain the many anatomical differences between adult men and women. Physiological aspects are also covered. Such differences apparently mostly relate to the large size of the new-born infant, and the need to allow vaginal birth of the large head of a baby.

The title is unnecessarily provocative. All animals have anatomical curves. Nevertheless as the author describes, womanly body shapes have huge importance in attracting mates and nurturing infants, and their origin and importance are worth discussing.

Indeed the book has a great deal of cited research to back up its conclusions. Topics covered include the effect of female body shape on the male brain, and the role of the media in influencing woman's own view of the shape to which she should aspire. Apparently the media have little or no effect on men's views. Why do women dress to impress women, not men?

The book has very few illustrations, but has 11 pages of references and an 8 page index. I should declare an interest perhaps in that the author is a member of the department formed in Cambridge by the merger of Anatomy and Physiology, which occurred just after I retired. But I have never met him more than in passing.

My own interest in the female body shape led me to purchase the small statue shown on the right on Corfu, from a shop selling garden ornaments. I took the photograph.

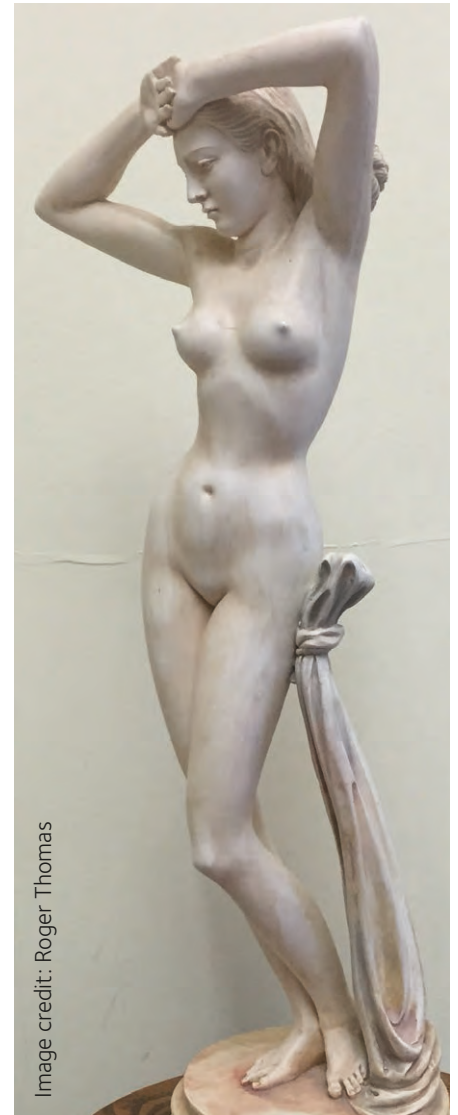


Image credit: Roger Thomas



# Experimental Physiology

## Reports on recent symposia

*Interested readers might like to consult the following:*

Report on a Symposium organised by Carsten Lundby – **Skeletal muscle adaptations to endurance training: is tissue hypoxia the main signal** – <http://bit.ly/1nilc2>  
Video introduction – <http://bit.ly/1JKstUB>

Report on a Symposium organised by Peter Wagner – **Oxygen transport adaptations to exercise in native highland populations** – <http://bit.ly/1PX9IN2>  
Video introduction – <http://bit.ly/1I5YhY8>

The 2015 GL Brown Lecture – **Extreme Threats – origins, consequences and amelioration in humans** by Mike Tipton – <http://bit.ly/1SOtPzx>

## New Editors

**Ming Lei** is an Associate Professor and Principal Investigator of Department of Pharmacology at University of Oxford and a Senior Investigator of BHF Centre of Research Excellence at Oxford. He obtained MB, BS and M Med at Tongji Medical University in



China and D.Phil. in Physiology at University of Oxford. After completing his postdoctoral fellowship at Universities of Leeds and Oxford, he was awarded the Wellcome Trust Research Career Development Fellowship and started his research group in 2001 at University of Oxford. In 2005, he moved to University of Manchester as a senior lecturer and became Reader in Cardiac Physiology later. His research seeks to understand cardiac ion channel function and its regulation under both physiological and pathophysiological conditions in a direction that will lead to a better understanding of hypertrophic and arrhythmic disorders, and the development of effective new therapeutic modalities.



**Dr. Jian Wang** is now working as a visiting Professor in the Department of Medicine at the Guangzhou Medical University. He has been working in the field of ion channels in pulmonary arterial smooth muscle for over 19 years. He started in 1996 as a post-doctoral fellow at the University of Maryland. In 2001, as a Research Associate, he became a faculty member in the Department of Medicine at Johns Hopkins and was promoted to Instructor on July 1, 2004. Since 2001, he has been studying transient receptor potential cation channels (TRPCs), store operated calcium entry (SOCE) and their roles in chronic hypoxia-induced pulmonary hypertension (CHPH). He was promoted to Assistant Professor on December 1, 2008. During the past 19 years, he has published over 70 research articles in peer-reviewed journals in this field. His training and experience, have prepared him well for this position.

# Experimental Physiology

## Biomedical Basis of Elite Performance

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Dinner at The Athenaeum Club to mark the end of David Paterson's term as Editor-in-Chief of *The Journal of Physiology*. (L-R) David Grundy, Ian Forsythe, Mike Spyer, Nick Boross-Toby, Jerome Dempsey, David Paterson, Kim Barrett, Simon Rallison, Sally Howells, Priya Mistry, Ann Watson, Yoshihiro Kubo and Julian Paton



# The Journal of Physiology

## Passing the baton: reflections of the retiring Editor of *J Physiol*

David J Paterson  
Editor-in-Chief, *The Journal of Physiology*

Since taking on the role of Editor-in-Chief for *The Journal of Physiology* in 2011, I believe that we have achieved a lot. This is a brief summary of the past five years' activities. A full Editorial appears in issue 6 of *The Journal*.

Submissions have continued to grow, as has the Impact Factor (5.037 in 2015) as well as other indicators of success. One critical indicator of impact is 'visibility'. To get cited you must get read, and to get read, you must get downloaded. *JP* articles have a higher-than-average download rate, which shows that our efforts to promote *The Journal* really are working.

Several factors have probably contributed to our enhanced visibility. During my time as Editor-in-Chief, we have sponsored 27 scientific meetings, published 15 special issues, and travelled 305,039 miles to engage our community directly. The trademark *JP* stand is now a regular feature at Experimental Biology, Society for Neuroscience and Biophysical Society annual meetings, on top of one-off appearances at other major scientific meetings and a host of smaller satellite meetings.

Jerry Dempsey's unique contribution to the visibility of *JP* via the Cross Talk debate series has been invaluable, and we have published over 25 debates so far.

Providing a defined home for neuroscience was an important part of my vision as Editor-in-Chief. It was increasingly apparent that this competitive area had to be better represented so we began to publish our neuroscience articles as consolidated issues (8 per annum) that evolved into *JPN*, as a way of reconnecting with our neuroscience community.

We have also engaged with the computational physiology and modelling community; reinforcing *JP*'s quantitative roots.

Several of our consulting editors and reviewing editors have shared their excitement for discovery in physiology by allowing us to film them talk about their research. We also filmed a conversation between Denis Noble and Mike Joyner, in which they discussed the integration of evolutionary biology with physiological science. All videos are available on The Physiological Society's YouTube channel *PhysocTV*.

It has been a real privilege to lead *The Journal of Physiology*. *JP* has always been a world-class journal, and to be world class, you need world-class editors to attract the best manuscripts. I think if you look down the list of current editors, you will see *JP* is in good shape in this department.

I am indebted to all our editors, not only for maintaining the high standard of *The Journal* but also for their support and advice; including Carol Huxley, my first Managing Editor, and her successor Sally Howells, both of whom have 'steered the ship' with 24/7 dedication. My sincere thanks also to our publisher Wiley-Blackwell and *The Journal* staff, who have been simply outstanding. And of course, my grateful thanks go to all our contributors without whom *The Journal* would not be the leading publication it is today.

It now just remains for me to wish Kim Barrett, as incoming Editor-in-Chief, and her new team every success in taking *The Journal of Physiology* forward. I hope she will enjoy the challenges and rewards as much as I have.

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