

wrote. “Furthermore, alumni from 15 different colleges, including green energy entrepreneur Jeremy Leggett and journalist George Monbiot, have promised to hand back their Oxford University degrees if the University does not commit to divestment from fossil fuels.”

The UK newspaper *The Guardian* has recently launched a major campaign to lift climate change to the top of the agenda under the slogan “Keep it in the ground”. In a video message published by the paper, Naomi Klein has argued that the current plunge in oil prices provides opportunities to change course. “Low oil prices means that we can introduce a fair and meaningful carbon tax, something that is much harder to do when petrol is expensive. And if we don’t do it, well, low oil prices will just encourage more dirty consumption,” Klein said. “Now is the perfect time to unite behind demands to keep it in the ground,” she concluded. “Let’s turn this shock into the shift we need.”

As part of the campaign, the paper has called for the world’s two largest independent research funding organisations, the Wellcome Trust and the Bill and Melinda Gates Foundation, to divest from fossil fuel interests. Prominent scientists including Anne Glover, a former chief scientific adviser to the European Commission, and Robert May, the former chief scientist of the UK government, have backed the appeal. *The Guardian* reported in March that more than 200 organisations have now signed up to the global divestment movement.

The expectations are especially high for science organisations, as the argument for acting on climate change is based entirely on scientific results and has to be defended against a strong opposition from people with anti-science belief systems, such as Republicans in the USA. Much of the problem has ended up being a debate about whether or not the general population should trust scientists or not. In this situation, it would really help if scientists and their organisations were also seen to act according to their beliefs.

In this spirit, Corinne Le Quére and colleagues from the Tyndall Centre for Climate Change Research at the University of East Anglia, Norwich,

UK, have investigated the travel habits of scientists and asked if the traditionally high number of flights taken by active researchers could be reduced without damaging the progress of science.

In a preliminary working paper published in March (<http://tyndall.ac.uk/sites/default/files/twp161.pdf>), the researchers acknowledge the advantages of face-to-face meetings at international conferences, but argue that electronic alternatives can provide other equally important benefits, such as widening access. They find that there are “no clear obstacles to justify an exemption for the research community from the emission reduction targets applied elsewhere.” The authors conclude “that the research community needs a roadmap to reduce its emissions following government targets, which ironically are based on findings of the research community.”

#### Vanishing islands

While the island of El Hierro holds up a beacon of hope for a more sustainable future, other islands are already confronted with the reality of climate change and rising sea levels. Warmer waters in the tropics make storms more powerful, and the cyclone Pam, which devastated Vanuatu in March, is only the latest example of a type of natural disaster that is becoming commonplace.

Other islands in the south Pacific are likely to disappear below the waves even if the warming is stopped at 2°C. This is why the Alliance of Small Island States (AOSIS), also established in 1990, has been calling for a 1.5°C limit instead of the 2°C one. However, even the higher limit is increasingly seen as optimistic, as a warming of 4°C by the end of the century appears more likely (Curr. Biol. (2010) 20, R1052–R1053).

It would take a lot more divestment from fossil fuels, a lot more political will from all governments, and a major miracle at this year’s COP21 meeting at Paris to save the low-lying islands. Essentially, the whole world would have to follow the example of the good people of El Hierro.

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## Obituary

### Vernon B. Mountcastle (1918–2015)

Richard A. Andersen

Vernon Mountcastle, born in 1918 in Shelbyville, Kentucky, was one of the giants of modern systems neuroscience who will be remembered for his ground-breaking research centered on the topics of perception and cognition. His impact on the field of neuroscience has been profound, not only for the discoveries he has made but also for the key role he has played in the founding, promoting, and nurturing of the field through training and service. He has been referred to by some as the father of neuroscience, and long-time Hopkins professor Sol Snyder credits him with producing “the first functional map of the neocortex” (NY Times, Jan. 17, 2015, B. Carey).

Mountcastle is best known for his revolutionary discovery of the cortical column as the basic building block of the cerebral cortex. This was a finding he made early in his career with wide-ranging implications. However, he also pioneered two other major avenues of discovery in cortical neurophysiology: the elucidation of the neural codes of somatosensation; and the discovery of the workings of the posterior parietal cortex as a bridge from sensation to action. He has cited his work in the parietal lobe as his most satisfying contribution to the study of brain function. He published his discovery of the columnar organization in somatosensory cortex in 1957; this study was performed in cat, but he soon replicated the finding in non-human primates with the help of Tom Powell, a visiting anatomy professor from Oxford with training as a neurosurgeon.

Mountcastle had received his MD from Hopkins in 1942, and had completed his surgical internship under famed Chief of Surgery, Alfred Blaylock. Mountcastle too had been preparing to enter a neurosurgery residency when World War II intervened. He joined the US Naval Amphibious Forces and served in a medical capacity for three years in Italy and France. Upon his return in 1946, the Hopkins neurosurgery program was

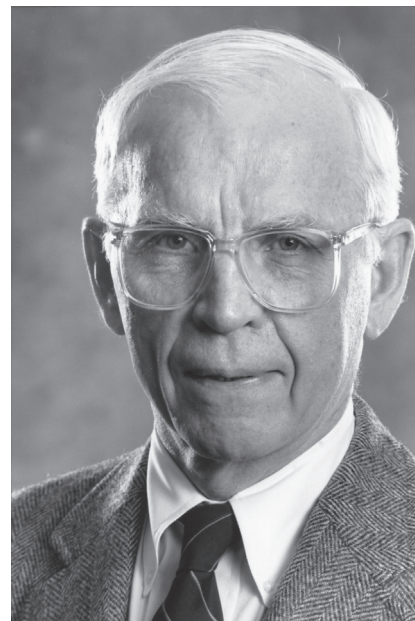
full so he took what was supposed to be a temporary rotation in a physiology laboratory. He reports that he became so fascinated with the neural recording work that he never left the lab to return to the surgical theater. Tom Powell returned to England and went on to become one of the most distinguished neuroanatomists of his generation.

At the time of Mountcastle's discovery of the cortical column, it was known that the cerebral cortex was important for many higher neural functions, including perception, reasoning, and language. In humans, this understanding came largely from neurological deficits. Neuroanatomy studies showed that the cortex, basically a large, folded sheet of tissue, had similar architecture throughout, with a laminar structure of six layers. However, lesions to different locations resulted in different impairments, and the finer anatomical features of cell packing densities and relative differences in cell types distinguished a large number (~50) of cortical areas. Moreover, these areas could also be distinguished through their different distributions of connections with, for example, other cortical areas and the thalamus. But the main physiological focus at the time was on the different cortical layers, which had different classes of connections; for example, the upper layers project to other cortical areas, the lower layers project to subcortical targets, and the middle layers receive heavy inputs from the thalamus and cortex. It was also appreciated that there was at least a coarse mapping of the periphery in sensory areas, for example, the body surface in primary somatosensory cortex, the retinas in visual cortex, and the cochleae in auditory cortex. The body representation had been coined the homunculus.

This historical context provides the background for the truly seminal study by Mountcastle, reported in a single author paper he published in the *Journal of Neurophysiology* in 1957, titled "Modality and topographic properties of single neurons of cat's somatic sensory cortex". In this work, Mountcastle mapped in detail the body representation and modalities within the primary somatosensory cortex of anesthetized cats, using the then new technique of single neuron extracellular recording. He made either vertical penetrations to the cortical surface, in which the electrodes traversed the

cortical layers or penetrations at a 45 degree angle to the surface. In the case of the vertical penetrations, he found that the cells throughout the layers of cortex were very similar in their receptive field location and modality. The receptive field is the region on the body that, when stimulated, produces activity in the somatosensory neurons. The modality refers to the subtype of somatosensory input. He studied two modalities of the skin: activity generated by displacing the hairs and activity generated by applying pressure to the skin. The third modality was activity evoked by applying stimulation to tissue deeper than the skin. He found a remarkable similarity in modality specificity along the vertical penetrations. In the oblique penetrations the location of the receptive fields shifted on the body, and the modalities changed. Mountcastle interpreted his results to mean that much of the intrinsic processing that occurs in cortex is along the vertical dimension, the cortical column. Previously, most of the focus had been on the processing within and across the layers and not along the dimension orthogonal to the layers. This hypothesis was put forth in a single succinct, three paragraph section of the discussion of his 1957 paper, and it has had an enormous impact to this day.

In the years following Mountcastle's discovery, columnar organization was found throughout cortex from recordings in sensory and motor areas and across species. Newer anatomical tracing techniques demonstrated periodic patterns of label consistent with interspersed cortical columns. In subsequent reviews in 1976 and 1990, Mountcastle summarized the evidence for columnar organization. In these reviews, he proposed that the cortical column is the basic functional unit of the cortex. Cortical columns varied in their size and shape depending on their location and also in the functions that they mapped; however, Mountcastle concluded that the cortical columns were in general less than 1 mm in diameter and each consisted of even smaller mini-columns. This organization included David Hubel and Torsten Wiesel's hypercolumns in visual cortex, composed of orientation columns and a pair of ocular dominance columns, and Mountcastle proposed that this general organization existed throughout cortex.



**Vernon Mountcastle.**

Photo credit: John Hopkins Medicine.

This idea that the cortical column is an essential building block is now a well-accepted idea, although what function it performs is still unclear and the topic of intense research.

Mountcastle also emphasized the distributed nature of cortical function, and suggested that local columnar organization is part of this distributed representation that includes columns in other areas of cortex. His insight came from anatomical findings by a number of investigators at the time that cortical areas are connected to large numbers of other cortical areas, often over large distances. This idea of distributed functional systems has been born out in subsequent human functional magnetic resonance imaging studies in which single tasks will activate widespread cortical circuits.

Over the next few years, Mountcastle extended his study of the somatosensory system and set himself the task of understanding the lines of sensory processing for different modalities that begin with specific receptors in the skin and deep tissue and continue through pathways into primary somatosensory cortex. These ground-breaking experiments, published in the 1960s and early 1970s, produced the framework for subsequent and current studies of the neural basis of perception. He and his colleagues during those years,

notably Gerhard Werner, William Talbot, Ian Darina-Smith, Hans Kornhuber, Hideo Sakata, Juhani Hyvarinen, Robert LaMotte, and Gian Carli, studied the perceptual capacities of humans and non-human primates for somatosensory stimuli and compared them to the sensitivity of somatosensory cortical neurons and primary afferents from the non-human primate hand. They found that the activity of single cortical neurons preserved information signaled by the peripheral nerves. Moreover, the activity of individual cortical neurons could account for the perceptual capacities of the modalities of pressure, flutter and vibration sensations.

Mountcastle was always interested in how perception can lead to action through cortical processing. To examine this sensorimotor transformation, he next followed the cortical pathway from somatosensory cortex into the posterior parietal cortex, a higher order area for cortical functioning. With help from Ed Evarts from NIH, who had begun recordings from behaving non-human primates, Mountcastle retooled his lab to perform these experiments for the first time in association cortex. Association cortex is a descriptor for cortical areas that are not directly linked to sensory inputs or to motor outputs. These areas were historically named association cortex for their presumed integrative functions beyond direct sensation or movement control. A study of these new areas required a new technique — recording electrical signals from single neurons in awake and behaving animals rather than anesthetized animals. The animals had to be trained in highly controlled tasks with an enormously larger number of variables to be accounted for. It took five years of dedication to transition the lab and to perfect the awake-behaving monkey paradigm, developing specialized equipment for eye tracking and visual stimulation, and writing computer code, a task Mountcastle thought best left to the programmers.

What Mountcastle found was truly amazing and has provided the foundation for the study of this interesting area of the brain. In his 1975 and 1977 papers on the posterior parietal cortex with James Lynch, Apostolos Georgopoulos, Hideo Sakata, Carlos Acuna, William Talbot and Thomas Yin, he described neural activities that were related to

complex actions and to higher order sensory phenomena. The action-related activity was neither directly motor nor directly sensory, but rather represented higher order intentions to make specific movements. Cells involved in oculomotor behaviors included those active when the eyes smoothly tracked a moving target, produced a ballistic eye movement (saccade), or fixated upon an object of interest. Other cells were related to reaching movements to locations in space and to hand manipulation of objects. The higher sensory properties included visual attention and the processing of more global motion fields that are typically evoked during locomotion through the environment.

Mountcastle studied these high level properties in his very quantitative style, carefully isolating and determining the selectivity of the various neuron types. He also examined the functional localization of these different cell properties, showing that they were aggregated along the electrode penetrations similar to the columnar organization he first reported in somatosensory cortex. More recent studies have shown that many of these properties are also hallmarks of subsequently discovered cortical fields. At the time of Mountcastle's study only two areas were recognized in the posterior parietal cortex, area 7 and area 5, defined on the basis of cytoarchitecture by the anatomist Korbinian Brodmann. It is now clear that both areas contain multiple subareas. Area 7 includes the lateral intraparietal area with saccade responses, the medial superior temporal area with neurons selective for tracking eye movements and global visual motion, and the anterior intraparietal area which is selective for grasping. Within area 5 is the parietal reach region which shows selectivity for targets for reach movements.

Teaching through research was one of Mountcastle's great strengths, and he helped populate the emerging field by training a large number of prominent neuroscientists among the 50 postdoctoral fellows and graduate students that passed through his laboratory. My own path was significantly influenced not only by him but also by his trainees. As an undergraduate at the University of California, Davis, I worked with Robert Scobey, who had been a student at Johns Hopkins with

Gian Poggio, a former postdoctoral fellow and later faculty colleague of Mountcastle. My PhD advisor at the University of California, San Francisco, Mike Merzenich, had been a graduate student with Mountcastle, and I had heard many stories indicating he was a tough task-master. In fact, Merzenich thought I could gain some much-needed discipline by training under Mountcastle, so in the spring of 1979 I drove with much trepidation from the West Coast to Baltimore. What I found upon my arrival was an amazing and devoted, if very exacting, teacher. Brad Motter, another postdoctoral fellow who had arrived before me, and I worked nearly every day with Vernon on recording experiments.

My work with Mountcastle centered on how eye position systematically influenced visual responses, which we called 'gain fields'. These gain fields have subsequently been found to be universal and implicated in a variety of neural computations including coordinate transformations. Although by this point he was the director of the Department of Physiology and busy with many other responsibilities, he nevertheless reserved most of his day for research. I was impressed by his tremendous focus on every detail of the experiment. There was no clutter in the lab; everything had its place, from electrical cables to surgical instruments. He dictated large segments of the experiments, down to the impedance changes of the electrode and the sound of dying neurons and had been in the habit of typing up his own dictation after each session until he discovered, to his delight, that I was also a good typist. Much of the transcription after that point fell to me, and I learned the importance of attention to all aspects of the recording protocol.

In the lab, Mountcastle kept us on our toes, and he was all business. Famously, each day he would ask, "So what have you discovered today?" This was not a rhetorical question, and I, like many students before me, learned quickly to show him an interesting neuron analyzed from the day before or to present a novel finding from a recent paper. I pitied a visiting friend of mine who once asked him for travel advice on an upcoming trip to China, when he quickly learned that Mountcastle "was not his travel agent".

Outside of work, Mountcastle and his wife Nancy were very gracious



hosts to the many students and visitors who passed through the lab, and his administrative assistant of many years, Mary Hilda Counselman, personally took care of generations of students as we arrived. In my case, she helped me move out of a hotel in an unsavory section of town to better accommodations and later lent her own furniture to me and my wife until ours finally arrived by moving van. It was a special treat and an honor when we post-docs and our wives were invited to join the Mountcastles at the Johns Hopkins University Faculty Club for lively dinners and conversation. Mountcastle was the epitome of both a serious scientist in his starched white lab coat and a distinguished Virginia gentleman outside the Medical Center.

Mountcastle was a pillar of the field of Neuroscience, but also a builder. He was the first president of the Society for Neuroscience. Its first meeting, in 1971, had about 1400 attendees; now the annual meeting attracts 30,000 neuroscientists. In 1960, he took over as editor of the *Journal of Neurophysiology*, a prestigious but flagging journal, and revitalized it into a rigorous flagship publication for neurophysiologists. He edited the major neuroscience medical textbook of the time, *Medical Neurophysiology*, for its 13<sup>th</sup> and 14<sup>th</sup> editions and wrote several of the chapters. The scientific rigor of this text made it required reading not only for medical students but also for graduate students and experts in the field.

He was director of the Department of Physiology from 1964 to 1980, having taken over as director from his mentor, Philip Bard. Vernon built the department into one of the premiere neuroscience centers of its time. Hopkins and NIH were the places to go for training in behaving, non-human primate studies. During my time at Hopkins, Apostolos Georgopoulos had just been appointed to the faculty, and his postdoctoral fellows were John Kalaska and Roberto Caminiti. These neuroscientists are all now leaders in the field of motor control, Apostolos at the University of Minnesota, John at the University of Montreal, and Roberto at the University of Rome. Gian Poggio was also a faculty member at that time and was renowned for his work on primary visual cortex and its role in stereopsis. Ken Johnson, a leader in somatosensory research, arrived as a new faculty

member just before I left in 1981. Brad Motter stayed on at Hopkins to work with Poggio. As the neurosciences expanded at the medical school, Vernon later became a key figure in establishing a free-standing institute dedicated to neuroscience, the Zanvyl Krieger Mind/Brain Institute, which was created in 1994 at the Hopkins Homewood campus.

In the years subsequent to my time at Hopkins Vernon went on to study the attention and motion properties of neurons in the posterior parietal cortex with Michael Steinmetz, Brad Motter and Charles Duffy. He also revisited the topic of frequency discrimination in the somatosensory cortex, examining the temporal code for vibrating stimuli with Ranolfo Romo and Michael Steinmetz. Inevitably, when any of Mountcastle's students find themselves together, the "Vernon stories" flow. We who were lucky enough to have had him for a teacher can cite hundreds of examples of his rigor, intensity, and critical thinking. He prized hard work, preparation, commitment, and integrity and talked each day with us about scientific topics and personalities who shaped the field.

Mountcastle received a great deal of recognition for his lifetime of achievements. These include the Albert Lasker Award, the 'American Nobel' in 1983, the National Medal of Science from President Ronald Reagan in 1986, and the National Academy of Sciences Award in the Neurosciences in 1998. He became a University Professor at Hopkins, a rare honor bestowed on very few professors. In his later years, still filled with intellectual intensity, he wrote two books, "*Perceptual Neuroscience: the Cerebral Cortex*", published in 1995, and "*The Sensory Hand. Neural Mechanisms in Somatic Sensation*", published in 2005. These two books again demonstrate his prowess as a scholar of science. Besides Nancy, Vernon is survived by a son and a daughter, six grandchildren and two great-grandchildren.

Thus Neuroscience has lost one of its great pioneers and teachers at the age of 96. I last saw Vernon when I gave one of the annual Mountcastle Lectures in 2009 in Baltimore. He asked me "what have you been doing lately?" I was ready for the question.

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## Q & A

### Ron Laskey

*Ron Laskey was the Charles Darwin Professor of Animal Embryology in the University of Cambridge from 1983 to 2011, and Honorary Director of the MRC Cancer Cell Unit from its start in 2001 until 2010. His research interests have centred on the control of DNA replication and the transport of proteins or RNA between cytoplasm and nucleus. Some of the DNA replication proteins he studied are in clinical trials of screening tests for several common cancers. His most highly cited work has been on the detection of radioisotopes by fluorography or intensifying screens. He is a former President of the Biochemical Society and of the British Society for Cell Biology and former Vice-President of the Academy of Medical Sciences. On a lighter note he has written and recorded albums of Songs for Cynical Scientists and More Songs for Cynical Scientists, now combined as Selected Songs for Cynical Scientists.*

**What drew you to biology and cell biology in particular?** I was attracted to biology at 15 by two influences, curiosity about what the subject entailed and repulsion from other subjects that over-zealous teachers pressed me to take. I rebelled against this pressure and within a week of starting biology I was completely captured, thanks largely to two inspiring teachers. At university I benefited again from inspirational teachers, of whom the most influential was John Gurdon. I enjoyed his lectures so much that one morning when I overslept I decided to run to his lecture on an empty stomach. At 40 minutes I ran out of blood sugar and was carried out of the lecture feet first.

Perhaps this unfortunate event helped John to remember me when I applied to become a graduate student. For my PhD we extended John's classic nuclear transplant experiments to adult donor cells including keratinizing skin, and then continued to work together, or in close proximity, for the following 35 years. In addition to John Gurdon's influence I also benefited enormously as a postdoc in Lionel Crawford's lab at the former ICRF. Lionel had a low-key leadership style, but one that generated at least six