like sea turtles are among those that have underlined the importance of seagrasses. But the fishing industry would also be well advised to engage with seagrass conservation.

Supporting fisheries

Seagrass meadows around the world provide nursery habitat for many species, including commercially important ones like the Alaska pollock (*Gadus chalcogrammus*). Due to their near-shore location and easy accessibility, they are also prime locations for artisanal, subsistence and recreational fishing.

Richard Unsworth at the University of Swansea, UK, and colleagues have conducted a worldwide study of the extent, importance and nature of fisheries exploitation of seagrass meadows (Conserv. Lett. (2019) *12*, e12566). They find that fisheries are targeting these ecosystems around the globe, mostly in an unregulated and undocumented way. These activities are important for the food security of many people in the developing world, but they also create the risk of a ‘tragedy of the commons’, in that people are endangering the very resources they depend on.

The authors conclude that there is a general disconnect between fisheries management policy and conservation efforts: “Fisheries modelling and management approaches tend not to consider the functional role of seagrass and other coastal habitats on recruitment to the spawning stock, for example, current UK marine protected area policy.” Thus, given that seagrasses are vulnerable to many disruptive factors and declining at an estimated rate of 7% globally, more joined-up thinking is needed to protect the role they are playing in global food security.

Unsworth is also the director of the conservation charity Project Seagrass, which aims to restore lost seagrass meadows by depositing sandbags spiced with seeds. A pilot project bringing out a million seeds in Dale Bay on the Welsh coast has recently seen its first green shoots sprouting. The project also engages in outreach work, visiting schools to raise awareness of the importance of seagrass for fisheries and the climate.

Blue carbon thinking

A broader umbrella under which seagrasses could gain some much-needed policy support is the concept of blue carbon, referring to the carbon that is captured and stored by coastal vegetated ecosystems, including seagrass meadows as well as tidal marshes and mangrove forests. All of these previously neglected coastal ecosystems can make quantifiable contributions to carbon sequestration and thus become part of climate policy.

Jeffrey Kelleway at the University of Wollongong, Australia, and colleagues have recently presented an assessment of blue carbon strategies that Australia could adopt nationwide (Glob. Env. Change (2020) *63*, 102083). Based on their previous finding that Australia hosts between 5% and 11% of the estimated global blue carbon stocks (Nat. Commun. (2019) *10*, 4313), the authors argue that their sustainable management could make a sizeable contribution to the country’s climate effort.

The authors analysed twelve separate types of policy action for their potential to abate greenhouse gases in a quantifiable way, in order to identify the five most promising. Among the five winners they find two that specifically address the conservation of existing seagrass meadows, with one focused on water quality and revegetation, and the other on the protection from physical disturbance.

Kelleway and others were also involved in a global assessment of the outlook for blue carbon, led by Peter Macreadie from Deakin University at Geelong, Australia (Nat. Commun. (2019) *10*, 3998). The authors discuss key questions and challenges that need to be addressed and call for a comprehensive research programme dedicated to blue carbon science to close the knowledge gaps still hindering its optimal use in climate mitigation.

Blue carbon strategies have the advantage of making a calculable contribution to the mitigation of climate change while offering additional benefits, including coastal protection and support for fisheries as well as vulnerable species. All the more reason to afford seagrasses the attention of global conservation efforts on the scale we already lavish on their animal counterparts, the whales and dolphins.

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Obituary

Horace Barlow (1921–2020)

David Burr[1] and Simon Laughlin[2]

Horace Barlow was one of the truly great neuroscientists of his time, in the Cambridge tradition of quantitative neurophysiology and psychophysics. His fundamental theoretical and empirical contributions to our understanding of brain function have inspired and influenced generations of neurophysiologists, psychologists and computational neuroscientists and are certain to endure for generations to come.

Horace Basil Barlow, FRS, was born in 1921 in Chesham Bois, Buckinghamshire, son of Sir Alan Barlow and Lady Nora Barlow (née Darwin). He was educated at Winchester College and studied medicine during the war years, first at Cambridge and then at Harvard Medical School, which awarded him an MD in 1946. He completed medical training at University College Hospital, London, before commencing research in neurophysiology with E.D. Adrian at the Cambridge Physiology Laboratory. After various positions at Cambridge University, he became Professor of Physiological Optics and Physiology at UC Berkeley. In 1974, he returned to Trinity College and the Cambridge Physiology Department to take the Royal Society Research Chair of Physiology, where he continued to make important contributions to neuroscience well after his formal retirement. Horace was elected a Fellow of the Royal Society in 1969 and won their Royal Medal in 1993. He was awarded the Australia Prize in the latter year and several others, including the Ferrier Medal in 1980 and the Ken Nakayama Prize from the Vision Sciences Society in 2016.

Many interesting and charismatic people impacted on the young Horace. The first — and arguably most important — was his mother, granddaughter of Charles Darwin. She held no formal degree but worked as a biologist and later, as Darwin’s biographer, founded scholarly research into his life and achievements. Her example, together with his abilities and preference for maths over the humanities, veered Horace towards science. His contemporaries at Winchester College,

Horace Barlow.

Christopher Longuet-Higgins, Freeman Dyson and James Lighthill, all of whom became prominent scientists, played an influential role. During his university years there was no shortage of creative minds: his supervisor, the eminent Lord Adrian, and his tutor William Rushton, as well as Pat Merton and Tommy Gold. These latter three were part of the *Ratio Club*, a London-based club of about 20 carefully selected young neurobiologists, neurologists, psychologists, engineers, mathematicians and physicists, who periodically met in Queen's Square to discuss cybernetics, information theory and brain function (see group photo). Cybernetics and information theory were central planks in Horace's conceptual framework throughout his lifetime.

Horace started his scientific career early, publishing three papers before he completed his MD: one (in *Nature*) with Rushton during his Cambridge undergraduate days and two with fellow students at Harvard. His next project, assigned to him by Adrian, was to investigate the proposal of Marshall and Talbot that small scanning eye-movements serve a fundamental role in vision. Horace devised a novel method for measuring eye position precisely (photographing a small spot of mercury placed on the cornea) and found that, between rapid gaze shifts, the eyes were essentially still. He concluded that the fixations rather than scanning eye-movements were fundamental to vision, dismissed Marshall and Talbot's idea and moved on. However, the importance of the dynamics of perception, including 'temporal interpolation' of moving stimuli, remained central to his thinking, emerging clearly in his Ferrier lecture in 1980.

Adrian's supervision style was quite liberal, in the Cambridge tradition, described by Horace as "incisive, but economical, guidance". Thus, Horace was free to pursue his own scientific curiosities, such as how neurons integrate information. He observed that Sherrington's classic preparations used artificial stimuli, electric shocks applied to spinal roots, whereas applying light to the retina allows for behaviourally relevant natural stimuli. He developed a preparation for recording spikes from single ganglion cells in frog retina — no mean feat at the time — to study the most basic element of integration, signal summation. Inspired by Rushton, Horace took a quantitative approach and, by measuring thresholds as a function of stimulus area, discovered that integration was not uniform over the receptive field but that there were clear inhibitory surrounds forming separate 'on' and 'off' regions. More surprisingly, one type of ganglion cell could be a feature detector whose spike discharge anticipates the future position of a fly.

This study initiated 30 years of ground-breaking collaborative work on retinal ganglion cells. Horace joined Stephen Kuffler, who had independently described the inhibitory surround in cat retina. Together with Fitzgerald, they discovered that ganglion cells adapt their receptive fields to cover the full range of light levels, switching from cones to rods at low light levels and losing the inhibitory surround. In 1963, Horace and Richard Hill discovered motion-sensitive cells in rabbit retina. Working with the most exacting of retinal physiologists, Bill Levick, Horace revealed further hidden complexities in retinal processing: a motion-sensitive ganglion cell is driven by an array of subunits. Then, in classic experiments, they established the first physiologically informed model of the underlying mechanism: the Barlow and Levick model of elementary motion detection.

In 1964, Horace accepted a professorship at the Berkeley School of Optometry, where he continued his neurophysiological experiments, investigating integration by neurons in primary visual cortex (V1). One particularly influential study was conducted with former student Colin Blakemore (in Berkeley on a Harkness Fellowship) and the enthusiastic and charismatic young Australian Jack Pettigrew. Following leads from Jack's undergraduate work in Sydney, they demonstrated that cells in cat primary visual cortex were selective to binocular disparity, the signals that support binocular depth perception. This was important and unexpected, as stereoscopic depth was thought to be a high-level perceptual property emerging late in processing. However, the results meshed well with Béla Julesz's demonstrations in the early 1960s of 'random-dot stereograms', showing that depth can emerge from point-by-point disparities in otherwise random patterns. The discovery reinforced Horace's conviction that single sensory neurons coded meaningful information.

His work on retinal and cortical neurons brought home to Horace the fundamental realisation that physiological experiments could answer questions of psychological interest. Much of the sensory apparatus for complex behavioural patterns (like detecting and catching flies) may lie in the retina rather than 'mysterious centres' too difficult to study by physiological means. Furthermore, the lateral inhibition mechanism that he discovered in frog retina had been postulated by Ernst Mach and others to account for perceptual phenomena, such as simultaneous contrast and Mach Bands. This line of thought culminated in 'A neural doctrine for perceptual psychology', published in the fledgling journal *Perception* in 1972. The provocative formulation of 'dogmas' stimulated much important debate, theorising and experimental work, and the central idea of that paper, that perception corresponds to the activity of specific cells, has been hugely influential to physiologists and psychologists alike. Indeed, Horace's doctrine is still relevant, as it goes far beyond 'lock and key' feature detectors. His doctrine incorporates the concepts of statistical inference, efficiency and redundancy that he formulated earlier in his career and suggests the far-reaching idea that he subsequently pursued: single neurons use synaptic plasticity to capture the redundancy that is knowledge.

Horace started thinking about signals, noise and perceptual judgements when as an undergraduate he presented a new paper to a discussion group. The landmark study of Hecht, Shlaer and Pirenne demonstrated that the absolute threshold of human vision is limited by noise: quantal fluctuations whose effects can be determined psychophysically by testing the predictions of statistical models. Horace also discussed the problem of signal and noise in the *Ratio Club* (it was one of their chosen topics), especially with his Cambridge colleague Tommy Gold (later Professor of Astronomy at Cornell University). After his experiments on frog retina, Horace revisited Hecht *et al.* with a penetrating statistical analysis of published data. He found that the number of quantal events required to reach threshold is elevated by the presence of background noise that he attributed to the thermal activation of visual pigment molecules. This novel conclusion was confirmed a quarter of a century later by recording from rods. His theoretical findings prompted Horace to consider that “thresholds are efficient statistical judgements of constant fallibility”, and he quickly confirmed this more general principle with new psychophysical experiments.

The young Horace Barlow (bottom right) in May 1952, together with members and guests of the *Ratio Club*, outside Peterhouse College, Cambridge: Back row (partly obscured): H. Shipton, J. Bates, W.E. Hick, J. Pringle, D. Sholl, J. Westcott and D. Mackay. Middle row: G. Brindley, T. McLardy. W.R. Ashby, T. Gold and A. Uttley. Front row: A. Turing, G. Sutton, W. Rushton, G. Dawson and H. Barlow.

Horace’s scientific approach, to try to understand the *principles* guiding brain function, was uncommon among physiologists. His 1961 paper on ‘Possible principles underlying the transmission of sensory messages’ (in *Sensory Communication*, W.D. Keidel, U.O. Keidel, M.E. Wigand and W.A. Rosenblith, eds) opens with, “a wing would be a most mystifying structure if one did not know that birds flew”. Horace argued that we need first to understand the goals of the system to avoid being buried in a mass of irrelevant neurophysiological and neuroanatomical details while missing crucial observations. He reasoned that, because neurons have limited representational capacity, they should economise on impulses by forming efficient representations. According to information theory, this can be achieved by eliminating redundancy using lateral inhibition and adaptation, and because both are observed in retina this must be a goal of early sensory processing. Two decades later, Barlow’s efficient coding hypothesis was validated. This prompted a new round of theory, measurements and experiments, which explained the function of mechanisms in the earlier stages of vision, olfaction and audition. Efficiency and ‘the economy of impulses’ continue to guide our understanding of neural codes at all levels.

Horace’s approach was intrinsically *interdisciplinary*, a popular buzzword in modern grant writing but less usual in his day. He looked for guiding principles of brain function without undue concern whether his supporting data came from psychophysics or physiology, humans or animals, vertebrates or invertebrates. He was always trying — and usually succeeding — to merge detailed observations into the big picture of brain function, following the example of his famous great-grandfather. He was very much a ‘hands-on’ scientist, in the Cambridge mould: he never led a large research group nor took on many graduate students. That was not his style. He led by example, and his example was highly influential. There are very few sensory neuroscientists who would claim not to have been influenced by Horace’s work, one way or the other.

Horace never stopped trying to understand the brain. During his own Festschrift in 1987 he gave the most interesting and original talk of the workshop. Following his major theme of how the brain maximises efficiency, he advanced a novel explanation for ‘adaptation’ (the fact that cells reduce firing rate after repeated excitation), suggesting that it is a complex phenomenon serving to ‘decorrelate’ sensory input, reducing inherent redundancy to take full advantage of the limited dynamic range of neurons. This changed the way many people thought about adaptation and again led to new lines of research.

The ideas of redundancy and correlated activity of sensory pathways also underlie his highly influential paper on ‘Unsupervised learning’ (Neural Comput. (1989) *1*, 295–311). This paper was one of the first to draw attention to the importance of unsupervised learning as opposed to supervised or reinforced learning. Unsupervised learning is about how a nervous system (or indeed artificial intelligence) recognises ‘statistical regularities’, or patterns in its inputs, and is of fundamental importance for understanding the cortex. Horace connected old ideas, such as Tolman’s ‘cognitive maps’ and Craik’s ‘working models’, with modern concepts of entropy, concluding that redundancy in sensory signals provides the knowledge incorporated in those maps. Such knowledge enables unexpected discrepancies to be immediately identified and dealt with. Horace's information theory-based approach underlies many modern approaches to unsupervised learning in neural networks and Bayesian learning.

In the 30-odd years after his formal 'retirement', Horace continued to make highly original and creative contributions to the field. He published 56 articles during this period, many as the single author. His interests were very varied, including information redundancy, predictive coding, Bayesian inference, unsupervised learning, development and many others, but all were motivated by the common themes of information theory and neural efficiency. A recent example of his creative thinking was his talk at the symposium on 'Turing Enduring: Information Processing by Brains and Machines' (Rockefeller University, December 2012), published in the journal *Visual Neuroscience*. There, Horace challenged the traditional (and still prevalent) wisdom that orientation-tuned simple and complex cells in primary visual cortex act as 'edge-detectors'. Looking for more general guiding principles of brain function, he claimed that "the prime role of V1 is to search for regularity or redundancy in the input", leading to the hypothesis that simple cells perform cross-correlations between the retinal input and internal templates, while complex cells calculate auto-correlations in the retinal input. Characteristically, he did not leave this as a simple hypothesis but provided solid quantitative psychophysical data in favour of his theory.

Horace was renowned for his intelligence and quick-wittedness. Neuroscientists presented their research to the Cambridge 'Craik Club' with some trepidation. But this was unwarranted, for besides being smart Horace was kind, especially to young researchers. He quickly understood the message of the talk and gave many useful suggestions, absolutely on point, and never intended to humiliate. But his clever quips could also be fun. At a dinner that he gave for a bunch of graduate students, he invited his friend Francis Crick, who held forth on several topics throughout the evening. At one stage, Francis brought up his lineage, lamenting that he could trace it back only to Elizabethan times. With a disarming smile, Horace instantly retorted, "oh yes Francis, and which Elizabeth is that?"

Most of Horace's ideas have survived the test of time, stimulating and motivating generations of neuroscientists and leading to a cascade of advancements far too extensive to summarise here. But if we are to apply his cherished information theory, we know that there is more information in the rare and unexpected event: so did he get anything wrong? Probably not seriously. One idea that clearly evolved over time was his intuition about information redundancy in the image. Initially, he emphasised the role of reducing redundancy for efficient neural coding and economy of neuron numbers as well as impulses, but later he realised the importance of redundancy in identifying structure and statistical regularities in the environment, as sensory redundancy is the main source of knowledge. But this was not a mistake, merely a change of emphasis. If we go right back to the beginning, to his experiments that led him to dismiss the importance of eye drift, perhaps we might say that his assessment was premature, as recent work is showing how the small eye-movements serve an important functional role, conditioning the spatio-temporal frequency spectrum of the image. But while he did not exactly predict this, his intuitions about the importance of temporal dynamics and interpolations, prominent in his Ferrier lecture, were not too far off the mark.

The last scientific gathering with Horace was for his 95th birthday, in December 2016. This was a fun occasion for his scientific family, some 100-odd people whose professional lives had been touched by Horace and who had passed the legacy down to their students and students' students. The celebrations were followed by a workshop, which Horace concluded with a first-rate scientific talk, highlighting the role of information processing in the brain and urging us to consider the importance of information and entropy. His scientific curiosity never escaped him.

Horace leaves his wife Miranda, 7 children and 13 grandchildren. His extended scientific family will miss him dearly.

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Book review

Revealing the mysteries of insect metamorphosis

Lynn M. Riddiford

Insect Metamorphosis: From Natural History to Regulation of Development and Evolution
Xavier Belles
(Academic Press, London; 2020)
ISBN: 978-0-128-13020-9

Metamorphosis is a common form of development throughout animal evolution except in the higher vertebrates. Among the marine invertebrates, metamorphosis is a feature of most life histories, with a larval form that is often specialized for dispersal. In crustaceans, such as shrimp and lobsters, the larva metamorphoses to a juvenile (miniature immature adult) that molts several times to become a reproductive adult, which then continues to grow and molt throughout its life. The terrestrial insects evolved from the Crustacea and with the evolution of wings and flight have come to dominate the terrestrial environment in terms of both overall biomass and the number of species. This domination has been achieved through the evolution of insect metamorphosis, from that of the pestiferous firebrats and silverfish, which also continue to molt as adults (ametaboly), through the incomplete metamorphosis of dragonflies, cockroaches, and true bugs, which molt directly from the immature nymph to a terminal adult stage (hemimetaboly), to a three-module system of larva–pupa–adult (holometaboly), which allows exploitation of different habitats by larvae and adults. The advantages and impacts of this complete metamorphosis can be seen in the four major orders of the Holometabola: the beetles (Coleoptera) have become the most speciose of all animals; the bees, wasps, and ants (Hymenoptera) have evolved sociality and achieved the distinction of having the most biomass of any group of insects; the butterflies and moths (Lepidoptera) are not only beautiful to behold but also have major impacts on our agriculture and forests,