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EDITORIAL

David H. Hubel MD FRS Nobel Laureate: A man of vision

David J. Paterson, Editor-in-Chief

Now what I call the images of things
Are scattered every way and cast abroad,
But we can see them only with our eyes;
And so, in every place we turn our gaze,
They meet it with their colour and their shape.
By them we judge of all things' distances
And separate existence in the world.

The poet Lucretius 'On the Nature of Things' attached special importance to explaining the nature of vision and the working of the eyes; here he is struggling to explain the connection between external reality and our sense perception of sight, anxious to make everything clear and certain. The problem he discusses, whether it was originally raised by him or by his master Epicurus, is one of the highest interest, and also of the highest difficulty. In fact it was quite insoluble, as long as men, however ingenious they might be, preferred to speculate about it in the abstract rather than to build up a body of knowledge by ingenious experiment and careful observation. One of the subjects which were obscure to our ancestors but have been illuminated by modern science is the nature of the brain. In that progress no one has made a greater contribution than David Hubel. When an object is seen by the eye, light is focused on 125,000,000 'receptors' which transmit an electrical signal to a great array of cells, positioned at various angles. The signal is passed on by a route of great complexity through the brain, which produces a visual image of the object. Our guest was the first to work all this out, to explain the working and function of the cerebral cortex, and to illuminate the nature of the brain and of vision itself.'

This was the citation to David Hubel when in 1994 he received an honorary Doctor of Science from the University of Oxford, having been a former Eastman Professor at this university.

David H. Hubel was the John Franklin Enders University Professor at Harvard Medical School. Having attended McGill University Medical School he qualified as an MD in 1951. His research pioneered the understanding of the cerebral cortex, and knowledge in the fields of colour vision, motion perception and stereoscopic vision.

In 1981 he won the Nobel Prize for Physiology or Medicine, shared with Torsten Wiesel and Roger Sperry. Professor Hubel was President of the Society for Neuroscience, and an Honorary Member of both The Physiological Society and the American Neurological Association. He was also a member of the American Academy of Arts and Sciences.

However, David Hubel was more than a brillant neurophysiologist. He was a man of great humanity, and this Journal is indebted to him. Physiology has lost one of its giants. *The Journal of Physiology* has lost one of its heroes. But more importantly, Carl, Eric and Paul have now lost their beloved father.

The photograph of David Hubel was taken by Brian Robertson in 2009.

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Republication of *The Journal of Physiology* (2009) 587, 2733–2741: An introduction to the work of David Hubel and Torsten Wiesel

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It is with enormous pleasure that I add my voice to that of others of my generation in celebrating the semicentenary of the 1959 publication of Hubel and Wiesel's first paper in *The Journal of Physiology* entitled: 'Receptive fields of single neurons in the cat's striate cortex' (Hubel & Wiesel, 1959).

This paper set the stage for the continuous flow of outstanding papers that emerged over the next twenty-odd years from the Hubel and Wiesel collaboration. Their work and that of Vernon Mountcastle opened up the modern study of the cerebral cortex. As a result of their extraordinary accomplishments, Hubel and Wiesel received the Gross Horwitz Prize together with Vernon Mountcastle in 1975, and the Nobel Prize in Physiology or Medicine in 1981 together with Roger Sperry.

It was on the occasion of the Gross Horwitz Prize, on whose committee I served, that I was invited to introduce Mountcastle, Hubel and Wiesel. My initial comments in that introduction were in fact directed toward an excellent scientist, a member of our Prize committee, who commented during our deliberations that Mountcastle, Hubel and Wiesel seemed to represent superb science, but their work had limited biological generality. To which I replied: 'You are right, it does not apply to the kidney or the spleen. It is much more restricted. It only helps to explain the workings of the mind.'

Hubel and Wiesel's names are enshrined together in the Pantheon of Creative Collaborations in Biological Sciences, much like Hodgkin and Huxley, Watson and Crick, and Brown and Goldstein. In each case, equal partners joined forces bringing unique skills to their collaboration to produce a new level of science and a new family of insights.

I first met Torsten and David in 1957, and we became friends in the period 1960–1965 when I overlapped with them at the Harvard Medical School. That friendship continues to this day, as does my admiration for the work, scientific and administrative, that they have accomplished since going their own directions in the early 1980s. In 1983 Torsten moved to New York, first as Professor and then in 1999 as President of Rockefeller University. I served on the Board of Trustees of the Rockefeller during much of Torsten's tenure and this provided me with the additional opportunity to toast his 80th birthday.

What follows in the ensuing set of papers in this issue is an outpouring of affection, respect, and gratitude for Torsten and David, for who they are, for what they have given us, and for setting the tone of our science for my generation in the United States.

Introductory Comments on the Occasion of the Awarding of the Louisa Gross Horwitz Prize to Vernon Mountcastle, David Hubel and Torsten Wiesel (Columbia University, Fall 1978)

President McGill, Vice President Marks, colleagues of Columbia University, honoured guests. Even the most important contributions, such as the work by Vernon Mountcastle, David Hubel and Torsten Wiesel that we honour tonight, have in addition to their obvious strengths, certain clear weaknesses. I will discuss the strengths in a moment, but I think it important at the outset to consider its weaknesses. Many contributions in biology inform us about general principles – principles that are important for understanding all the cells of the body. The contribution of Mountcastle, Hubel and Wiesel is concerned with only one class of cells – the cells of the brain. Their findings are therefore somewhat parochial. They are only important for understanding the mind.

Despite that limitation, the contributions of Mountcastle, Hubel and Wiesel are nonetheless rich in meaning and have significance for many levels of thought. Their work will, I would suggest, be discussed by historians of science from three quite different vantage points. First, it will be discussed from a purely scientific point of view, as a central contribution to neurobiology; second, from a broader philosophical point of view, as an enhancement of our understanding of mental processes; and third, from a sociological point of view, as an example of the importance of scientific lineage and of small group interactions at large universities.

First and foremost, as a scientific contribution to neurobiology, the work of Mountcastle, Hubel and Wiesel stands as the most fundamental advance in our understanding of the organization of the brain since the work of Ramón Y Cajal at the turn of the century. By applying morphological techniques to the cerebral cortex – the highest and most elaborate part of the brain – Cajal revealed a hitherto unanticipated precision of the interconnections between populations of individual nerve cells. Using modern cell physiological techniques, Mountcastle, Hubel and Wiesel have revealed aspects of the functional significance for perception of these patterns of interconnections between nerve cells. They have shown us that the connections filter and transform sensory information on the way to and within the cortex, that the cortex is organized into functional compartments or modules, and that this organization can be altered by experience. By any scientific criteria, these contributions are of the highest rank.

But on a second level, the work of Mountcastle, Hubel and Wiesel takes on greater significance because it contributes to our understanding of mental processes, a contribution with profound physiological implications. We appreciate important science because it tells us something new and exciting about the world around us. What is at once so special and so parochial about the work that we honour tonight is that it tells us something new and exciting about the world within us, about ourselves.

Let me give you an example. We have the feeling that when we interact with each other – when I speak to you and you listen to me – that we are directly experiencing one another. Hubel, Wiesel and Mountcastle have made us realize that this is an illusion, a perceptual illusion. The brain does not simply take the raw data that it receives through the senses and reproduce it faithfully in the brain. Rather, each sensory system first analyses and decomposes, and then restructures the incoming raw sensory information according to its own built-in connections and rules.

These insights are not only remarkable; they are also timely. Hints that similar processes may be involved in the development of language and thought are now emerging from the studies of structural psychologists such as Chomsky and Piaget.

On still a third level, the work of Mountcastle, Hubel and Wiesel is interesting because it illustrates in a unique manner the role of social context upon discovery and how small groups in a university can shape social contexts so as to make them conducive to creativity.

Mountcastle, Hubel and Wiesel are exceptionally creative, bright and energetic. Each would have made an important mark on science no matter where he worked. But I think it fair to say that the special nature of their contribution was fostered by the particular collegial environment to which they belonged.

They, in turn, have now restructured their environment anew so as to foster creative activity in their younger colleagues. Thus, in a certain sense, their work illustrates the role of intellectual continuity and intellectual renewal in the achievement of excellence by segments of two American universities, the Department of Physiology at Johns Hopkins and the Department of Neurobiology at Harvard.

Academic life is now often challenged, beleaguered, and fragmented. It is therefore inspiring – and more important, it is instructive – to learn which aspects of academic life are most conducive for the establishment of a powerful intellectual environment that is resistant both to external and administrative pressures – an environment that is at once sensitive to historical perspective while at the same time it encourages the emergence of novel and important ideas.

I would like to consider these three implications of Mountcastle's contributions and those of Hubel and Wiesel – the scientific, the philosophical, and the sociological – by tracing the development of only one aspect of their contribution: the discovery of one of the central ideas in the functioning of the brain – the fact that the cerebral cortex is organized into computational modules consisting of vertical columns of nerve cells. That particular strand of research had its origins at Johns Hopkins Medical School in the mid-1930s.

Now, as you know, we experience the outside world through our five senses: touch-pressure (and the related skin or somatic sensation), sight, hearing, taste, and smell. Each sensation is first analysed by appropriate receptors and coded in lower relay stages. Most sensations are then elaborated in the cerebral cortex. Modern research on the role of the cerebral cortex in somatic sensation began in the Department of Physiology at Johns Hopkins Medical School in about 1936, with the work of Philip Bard and Clinton Woolsey.

Philip Bard was 34 years old and an Assistant Professor in Walter B. Cannon's Department of Physiology at the Harvard Medical School when he was called to chair the Department of Physiology at Hopkins. Not only was he extraordinarily young at the time of this appointment but he had published only three original papers. He was the sort of person whose future one would worry about nowadays. Dean Tapley assures me that he would never pass our Appointments and Promotions Committee. In fact, Dean Tapley was surprised that he slipped by even at Hopkins.

Soon after coming to Hopkins, Bard teamed up with two even younger colleagues, Clinton Woolsey and Wade Marshall. Using gross electrophysiological recording techniques developed by Marshall and a strategy developed by Woolsey, these three young men discovered that the body surface of monkeys was systematically represented on the surface of the brain.

This was soon confirmed in humans by the Canadian neurosurgeon Wilder Penfield and established the fact that not only monkeys but each of us has within our brain a naked representation of our own body, the closest thing to our true self-image.

This remarkable discovery that animals and man have a representation of their body on the surface of their brain raised a number of conceptual problems. Somatic sensation is not unitary but a composite of several distinct sensations called submodalities. We can, for example, readily distinguish the pressure on deep tissue from the light touch on the skin. However, it appeared that the maps for these deep and superficial submodalities were completely congruent. Clearly with the relatively gross techniques used by Marshall, Woolsey and Bard – techniques that averaged the responses from thousands of nerve cells – some critical dimension in the map was overlooked.

After making this major contribution, Bard withdrew from the study of somatic sensation, leaving it to Woolsey and the younger members of his department who came along later.

The particular question of submodality perception was picked up in 1948 by Vernon Mountcastle, Bard's most gifted student. Born in Virginia and educated at Johns Hopkins Medical School, Vernon Mountcastle was dissuaded from a career in Neurosurgery by Bard, who enticed him into Physiology.

I have always considered Mountcastle's decision a great gain for Physiology, but having recently become familiar with the economics of neurosurgery, I am only now beginning to appreciate what a loss this decision has meant for Vernon Mountcastle. Over the years Mountcastle not only took over Bard's fascination with skin sensation but also other aspects of Bard's mantle. In 1946 when Bard retired Mountcastle assumed the directorship of the Department of Physiology. He also took on the editorship of Bard's distinguished *Textbook of Physiology*.

Mountcastle realized early on that by using the cellular techniques that became available in the late 1940s he might be able to detect new dimensions in the map of the somatic sensory system that eluded the gross recording techniques used by Bard and his colleagues. This task required a number of major technical innovations including new microelectrodes and precise quantifiable natural stimuli – innovations to which Mountcastle contributed importantly.

With these tools in hand – tools that formed the basis of modern cortical physiology – Mountcastle addressed the question of submodality specificity. He found that at the cellular level, there is within all areas of the somatic sensory system a segregation of submodalities that was not resolved with gross recordings.

First, he found that single nerve cells respond specifically either to superficial touch stimuli or to deep pressure stimuli, almost never to both.

Second, he found that cells responding to one submodality were located together and were segregated from cells responding to other submodalities. The most fascinating example of segregation is found in the cortex. In a classical paper published in 1957, Mountcastle described his remarkable discovery that submodalities were distributed in the cortex as vertical columns running from the surface of the brain to the white matter below it. Each column is submodality-specific. All the cells in a column receive information from a particular point on the skin and from a particular class of receptors, either superficial or deep. Thus, each region of the skin projects to a particular area of the cortex, and the separate receptor classes are distributed in adjacent columns. The distribution of neurons in columns is therefore the mechanism whereby the depth of the cortex is used to handle different functions for the same small region of the bodily map. Each column is an integrating unit, or logical module, comprising thousands of neurons that form the initial stage in the cortex for elaborating sensory experience into consciousness.

In order to follow the history of the discovery of columnar organization, I will now describe the numerous other contributions that have subsequently come from Vernon Mountcastle. These include the analysis of the flow of information from skin to the cerebral cortex, a correlation between cellular responses and perception, and recently a study of the mechanisms underlying attention and the control of purposeful movements.

In the 40 years that have passed since Bard, Woolsey and Marshall first mapped the representation of the body surface onto the brain, the Department of Physiology at Johns Hopkins, first under Bard and subsequently under Mountcastle, has been preeminent for research training in skin senses. As a result of Mountcastle's recent work, this preeminence has now been extended to the study of attention and behaviour.

Indeed as a result of the leadership of Bard, Woolsey and Mountcastle, Hopkins was for many years so outstanding in the study of sensation that it also dominated research in hearing and in vision.

For example, while he was still at Hopkins, Wade Marshall, who had already contributed importantly to the early study of skin sensation, teamed up with Samuel Talbot to demonstrate that the cortex also contains detailed maps of the retina. About 10 years later, in 1948, a young man, Stephen Kuffler – whom I am delighted to see here tonight – was recruited to the Wilmer Eye Institute at Hopkins. Upon arriving, Kuffler turned his attention from synaptic transmission to cellular studies of the retina, an area to which he immediately made fundamental contributions.

In 1955 Kuffler was joined by Torsten Wiesel, a young postdoctoral fellow from Sweden. Wiesel had experience in child psychiatry and a particular interest in vision. Three years later, David Hubel joined Torsten Wiesel in Kuffler's laboratory. Born in Canada, Hubel took his residency in Neurology at Hopkins where he met Vernon Mountcastle.

He then spent two years at Walter Reed working on vision when Mountcastle recruited him back to his laboratory at Hopkins. However, when Hubel arrived Mountcastle's laboratory was in the process of being renovated. Hubel therefore accepted a temporary invitation to work in Kuffler's lab. He turned out to be a guest who stayed for more than dinner.

Confronted with two gifted young investigators each interested in vision, Kuffler set Wiesel and Hubel to work together in vision and went off on his own in a new direction. The largely accidental meeting of Wiesel and Hubel in Kuffler's laboratory in 1958 gave rise to what has been one of the most remarkable, sustained and productive collaborations in contemporary science. Although each has occasionally worked with another collaborator, almost all of their fundamental contributions have involved simply the two of them.

Soon after the beginning of their collaboration, Kuffler was invited to join the Department of Pharmacology at the Harvard Medical School to head a small laboratory of Neurophysiology. A true pater familias, Kuffler took with him the four young faculty people then working independently in his laboratory. Hubel and Wiesel, the two 'brain boys' as they were called, and Furshpan and Potter, the two 'membrane boys.' They were soon joined by a fifth colleague, an enzymologist, Ed Kravitz, whose function it presumably was to explain it all in the universal language of biochemistry.

Harvard responded to Kuffler's brilliant recruitment effort in a typical manner – it immediately demoted Hubel and Wiesel from the Assistant Professorships they held at Johns Hopkins to a non-professional rank. This was of course only to be expected from a university that had within recent years successfully denied tenure to two Nobel laureates, Georg Von Bekesey and Fritz Lipmann.

But Harvard found its match in Kuffler and his boys. Unlike Bard who devoted much time to administration in his later career, Kuffler was and still is the bench scientist's bench scientist. Nonetheless over a 10 year period, in his own quiet way, Kuffler turned the laboratory of Neurophysiology at Harvard, consisting of one professor and five postdoctoral fellows, into a Department of Neurobiology, the first in the country – 100 persons strong. A veritable intellectual dynasty, the department now occupies, as far as I can tell, about half of the available space at the Harvard Medical School. And you cannot open a door in all that space without some energetic, enthusiastic and aggressive young student coming out to criticize your every idea and replacing it with one of his own. Much of what we now consider modern neurobiology – the fusion of disparate scientific strands into one – was born out of Hopkins's gift to Harvard. You only have to visit the Harvard department to see why. As with Bard's department at Hopkins, so in Harvard's Department of Neurobiology, the world belongs to the young.

While still at Hopkins, Hubel and Wiesel began to apply cellular techniques to the visual cortex. Kuffler had earlier recorded from single cells in the retina and made the surprising discovery that the cells do not simply signal absolute levels of light; rather, they signal contrast between light and dark. The most effective stimulus for exciting these cells was not diffuse light but small spots of light. Hubel and Wiesel found a similar principle operating in the next relay stage, the lateral geniculate nucleus. However, at the level of the cortex, Hubel and Wiesel found that most cells no longer responded to small spots of light. To be effective, a stimulus had to be a line, a square, or a rectangle.

Thus Hubel and Wiesel found that these cortical cells did not simply and faithfully reproduce the input from the lateral geniculate nucleus but, by virtue of their connections, the cortical cells were able to abstract linear aspects of the stimulus. The stimulus requirements of the cortical cells are amazingly precise. In addition to requiring linearity, each cell is coded to respond to a specific axis of orientation; some cells respond best when the axis of the line stimulus is running vertically, others when the axis is horizontal, still other cells respond only to various oblique angles. Every small segment of the retina is represented in the cortex with every angle or orientation. It is attractive to think that these cells are the early building blocks in the perception of form and contour.

Hubel and Wiesel next found that cells with similar axes of orientation were grouped together into columns similar to those which Mountcastle had found in the somatosensory system. Now Hubel and Wiesel have profoundly original minds. To confirm someone else's work is anathema to them. They are most happy writing papers where all the references are only to their own work – a happiness they have somehow sustained with surprising regularity. Upon finding columns, they quickly proceeded to extend our insight into the nature of columnar organization. First, they predicted and found another completely independent system of columns in the cortex – the ocular dominance columns – a system concerned with information from the two eyes. These columns serve to elaborate binocular vision necessary for depth perception. Second, they utilized a variety of morphological techniques to visualize the columns in three-dimensional space. The early work of Mountcastle, and of Hubel and Wiesel described columnar organization strictly on the basis of electrical recordings from single cells. Routine histological examination had failed to reveal columnar organization. However, capitalizing on the current revolution in morphological techniques – a revolution that is based upon the use of marker substances that label cells according to one or another aspect of their functional activity – Hubel and Wiesel could independently label both the ocular dominance columns and their orientation columns. The results they have obtained with these methods are not only aesthetically breathtaking but have given us a completely new sense of the organization of the cortex – an insight made possible only by moving beyond the range of traditional anatomical approaches.

Thus, they have made us realize that we are just beginning to explore the structural organization of the brain and its possible alterations by disease. No wonder we have so little understanding of the biological basis of most forms of mental illness.

Finally, Wiesel and Hubel have used these studies of the normal columnar organization to investigate the effects of sensory deprivation on newborn animals. They found that a fairly subtle procedure such as closing the eyelids of a newborn monkey for just a few days leads to prolonged and sometimes irreversible blindness. Concomitantly, the closed eye loses its ability to control the firing of nerve cells in the cortex. By contrast, similar experiences in an adult animal produce no effect on vision. In a brilliant series of studies, Wiesel and Hubel found that visual deprivation in infant monkeys profoundly alters the organization of their ocular dominance columns. Normally the columns for each eye are equal in size. After deprivation, the columns that receive input for the deprived eye are much narrowed compared to those that receive input from the normal eye.

The scientific and philosophical implication of this work is truly enormous. Here is direct evidence that sensory deprivation in early life can alter the structure of the cortex. As Hubel pointed out in his Bowditch Lecture of 1967:

> Experimental psychologists and psychiatrists both emphasize the importance of early experience on subsequent behaviour patterns – could it be that deprivation of social contacts or the existence of other abnormal emotional situations early in life leads to a deterioration or distortion of connections in some yet unexplored parts of the brain.

The columns were first discovered by Mountcastle in the somatic sensory system and their functional properties and their alteration by experience were analysed by Hubel and Wiesel in the visual system. More recently, columns, stripes, sheets and other types of functional modules have been encountered in other areas of the cortex and in yet other regions of the brain. Here these modules are related to other forms of sensation as well as to motor control. It is clear that we are dealing here with one of the key principles in the organization of the cortex and the cornerstone for future work on the brain.

In closing, I would like to return to the question of social context. I have already drawn analogies between the social values and attitudes of Bard and Kuffler and the resulting flowering of scientific creativity in Mountcastle, Hubel and Wiesel, who in turn have now created environments where others can be independent and creative.

Moreover, much as Mountcastle, Wiesel and Hubel sit here tonight to receive the same honour that this University bestowed on Kuffler six years ago, I am confident that this University will in the future honour the intellectual descendants of Mountcastle, Hubel and Wiesel.

By drawing this analogy, I do not mean to imply that these five distinctive and unconventional people – Bard, Kuffler, Mountcastle, Hubel and Wiesel – are cut from one mould. But I do want to indicate that they share two rare qualities that are often overlooked in considering why gifted scientists often train other exceptional scientists. This is a question that has now been examined by a number of sociologists, most prominently by our colleagues at Columbia, Professors Merton and Zuckerman. They have pointed out that good scientists can teach their junior colleagues the importance of working on really significant problems; they also offer resources and visibility, and make available to their students important channels of communication. All of these qualities, however, are in line with the direct expression of a senior person's own ambition, of his own desire for growth.

What is evident in the three men whom we honour tonight and in their scientific patrons are two features that are much rarer, much more special.

One is the ability to rein in their own ambition and to encourage without reservation the creativity of their gifted young colleagues.

The second feature is the ability to build around them an exciting environment made up of gifted peers, an environment where important science is routinely done because the environment is consciously structured around one or more absolutely central ideas. The resultant internal cohesion has the additional consequence that it buffers the environment from disturbing vicissitudes of academic and scientific life.

Both of these features derive, I believe, from the ability of these rare scientists to combine a remarkable intuition of what is important in their field with an almost childlike enjoyment of the day-to-day experimental and intellectual activity of science. They enjoy day-to-day science as a satisfying end in itself, an ever-changing intellectual adventure – a repertory theatre of ideas.

It is for these reasons that the Columbia community takes such special pleasure in honouring Mountcastle, Hubel and Wiesel. For their contribution to the biology of the brain – the most remarkable and profound of our generation – represents at once scientific and personal qualities at their highest. In honouring them, we are drawing attention to the excitement in learning and the respect of colleagueship that drew so many of us to academic life. Their contribution gives us not only an insight into the brain and into ourselves but it also gives us specific examples of how the best in personal and academic values can be achieved and sustained over generations.

Torsten Wiesel: an ever-evolving, self-reinventing post-modern Faustian intellectual

(From An Introduction to Torsten Wiesel's 80th Birthday Celebration, Rockefeller University, June 3, 2004)

I have the pleasure to serve as the after-dinner toastmaster for Torsten's 80th birthday celebration. Let me introduce things with an overview of Torsten's life and work. I will divide my comments in three parts. First, I will describe Torsten's scientific accomplishments and his style of leadership. Second, I will try to develop a theory of Torsten Wiesel's life and work based on a fundamental typology that distinguishes between different classes of scholars and scientists. Finally, I am going to outline some limitations to Torsten's greatness.

I begin with a description of Torsten's life and times.

Torsten was born in 1924 in Uppsala, Sweden, the son of a prominent psychiatrist who served consecutively as superintendent of two large psychiatric hospitals. One of the perks of being superintendent was a residence on the property, so Torsten spent most of his early years on the grounds of a mental hospital surrounded by mental patients.

In retrospect, it was probably this extensive experience with the institutionalized mentally ill that allowed him to function so effectively as president of Rockefeller University in the aftermath of David Baltimore's resignation.

I am here reminded of the story told by Douglas Bond, the great American psychiatrist who rose to become Dean of the Medical School at Western Reserve. A friend once asked him: 'Doug, I don't understand how you could take on an administrative job and give up seeing patients, which you always so enjoy doing.' 'I haven't given up seeing patients,' insisted Bond. 'I still see patients. It's just that now, my patients have tenure!'

In 1945, at age 21, Torsten entered the Karolinska Institute to begin medical training. At the Karolinska he particularly enjoyed the lectures on the brain by Ulf von Euler, the discoverer of noradrenaline, and by Carl Gustaf Bernhard, who worked on epilepsy. Bernhard went on to become Torsten's great mentor and friend.

During his last year of medical training, Torsten worked first in adult and later in child psychiatry. But by the end of that year he decided that the available treatments did not satisfy him. So he turned to the biology of the brain and in 1954 joined Bernhard's department of neurophysiology at the Karolinska Institute as an instructor.

One year later, in June of 1955, Bernhard asked him whether he might want to go to the United States to work on the retina as a postdoctoral fellow with Steven Kuffler at the Wilmer Eye Institute at Johns Hopkins. That was a major turning point in Torsten's ever-evolving career. Steve Kuffler, as you all know, proved to be an enormous influence on Torsten.

In 1957, Torsten and Steve attended a Symposium on Vision at the NIH that I also attended. At that symposium, David Hubel gave a talk on simultaneous recovery of the activity of the response of two cells from the visual cortex – area 17 – in intact freely moving cats. Hubel noticed that when he moved his hand in one direction – to the left – in front of the awake animal's eye, one of the two cells in the striate cortex would fire vigorously whereas the other was inhibited, but if he moved his hand in the opposite direction, the cells that had fired in the hand movement to the left were inhibited whereas the cell that was previously inhibited now fired vigorously. This directional selectivity of the response was the first complex property to be noted in the mammalian visual system. From that talk by David, it was clear to both Torsten and Steve that the striate cortex was likely to be much more interesting than the retina. So the question was how to get David to the Wilmer Eye Institute.

This was no simple task. David had just accepted an appointment in the Physiology Department at Hopkins from Vernon Mountcastle. But as fortune would have it, when David arrived at Hopkins in 1958, the laboratories in Physiology that were designed for him were not yet ready. So where was David to go? In stepped Steven Kuffler to the rescue. He invited David to the Wilmer Eye Institute and suggested that David collaborate with Torsten.

Together Torsten and David decided to record from anaesthetized cats rather than from awake animals and to do a systematic study of the receptive field properties of cortical neurons. The rest is well known to all of us. There followed the Wiesel-Hubel era – 20 uninterrupted years of extraordinary science. David and Torsten did more than open up the study of the primary visual cortex, they laid the basis for what was to follow in all sensory systems. They delineated the properties and the hierarchical organization of simple and complex cells, they discovered a columnar organization for both orientation and ocular dominance, and culminated their work in the remarkable finding of plasticity in the ocular dominance columns during a critical period of development. These cellular physiological contributions were made all the more compelling by beautiful and insightful anatomical verification. Together this body of work stands as one of the great biological achievements of the twentieth century. But it was not simply their work but also the style that was so great: a combination of insight, creativity, beauty and modesty.

I give but two examples of their modesty. Torsten and David asked me to read their 1965 paper on 'Binocular Interactions in Striate Cortex of Kittens Reared with Artificial Squint' before submitting it to the *Journal of*

Neurophysiology. I found it to be very important, and suggested, among other things, that since the findings were so critical, perhaps they should base it on more than one animal, one cat. They agreed and did a second cat. Second, I suggested that having 10 of the 12 references in the bibliography to their own work seemed a bit inappropriate. They also agreed and removed the two references to other people's work!

During the classic period of the Hubel–Wiesel collaboration, Torsten was seen by most people as a scientist who combined creativity with extremely high scientific standards. But none of us, including David, who knew him best, saw in Torsten great leadership potential. Most of us saw Torsten as modest, slightly shy, and not disposed to giving David Hubel-like bravura lectures.

However, in 1973, all that changed. That year Steve Kuffler decided to step down as the chair of the Harvard Department of Neurobiology. At first thought, one might reflexively turn to David to replace Steve. But by 1973, it was clear that this was not to be.

It so happens that a few years earlier, David had established the record for the shortest tenure as a departmental chair in the history of Harvard University, a history going back to 1636! In 1967 David had accepted the chairmanship of the Physiology Department. He began his term by ignoring the complaints of the most senior professor in the department that the pencil sharpeners in the physiology office never functioned properly and that they should install a new one. In response to this one complaint, David stopped returning telephone calls from other members of the physiology department, missed faculty meetings, and made no move to transfer his laboratory to physiology. Nevertheless, between his experiments with Torsten, his astronomy, his lessons in Japanese and on the flute, David did manage to free up the time to lobby for and obtain tenure in Physiology for two of his best friends. Having accomplished this one task in his first six months on the job, David decided that he had done enough for Physiology at Harvard. He therefore resigned the chairmanship and returned to the neurobiology department which he had actually never left. Thus, when looking for a leader who might actually spend time on the job, David's name did not immediately spring to mind.

Torsten, on the other hand, had all along been concerned about young faculty members, about postdoctoral fellows and graduate students, and took on the chairmanship of neurobiology with vigour and imagination. This startled us all! A new Torsten was emerging. Torsten proved an outstanding chairman and a powerfully influential force as leader of the medical school. Behind that quiet façade there proved to be a man of steel!

During that period, David and Torsten began to move their separate ways scientifically. David began to collaborate with Marge Livingston on visual illusions and on the parallel processing of the visual image. Torsten started to collaborate with Charles Gilbert on how the cells of a cortical column are wired together. This quiet beginning led to the unanticipated discovery of the horizontal connections in the visual system – a major contribution to the functioning of the striate cortex that Charles now continues to carry forward.

In 1983 Torsten accepted an invitation from Rockefeller University to head a new laboratory there. Nine years later, in 1991, when David Baltimore resigned, Torsten as head of the faculty and now a mere $67^1/_2$ years of age, was asked by the Trustees to serve as president of Rockefeller University. Over the next six years he did an amazing job. He responded to the demoralized state of the faculty by energizing them with his optimistic view of the future. He brought to bear on this job his characteristic sense of decency, his humour, modesty, informality and intelligence. Over tea and cookies he met with the faculty individually and in groups and achieved consensus to recruit outstanding new scientists. I mention only Jim Hudspeth and Rod McKinnon in neurobiology to give you a sense of his taste and his accomplishments. He turned the fiscal problems of the university around and left in 1998 with the university rejuvenated and in superb shape. Since that time Torsten has continued to serve Rockefeller as director of the Shelby White and Leon Levy Center for Mind, Brain, and Behavior. In this capacity he has continued to exercise his taste and talent in recruitment, by convincing Cori Bargmann, who is here tonight, to move to Rockefeller as the new major star in neural science.

But, in a larger sense Torsten has turned from the provincialism of Rockefeller University and the City of New York to assume responsibility for science throughout the world. Torsten chairs the Latin American Fellows Program of the Pew Charitable Trust that supports training for post-doctoral students in the United States before their return home with requisite funding to set up their own labs.

He serves as chair of the Committee of Human Rights of the National Academy of Sciences which assists scholars who have been harassed for asserting their right to free speech.

Torsten is Chairman and President of IBRO – the International Brain Research Organization – and since 2000 has been the Secretary General of the Human Frontier Science Program. That program was moribund until Torsten revamped it by initiating exciting new international collaborations and by encouraging the training of post-doctoral fellows in outstanding laboratories throughout the world.

In addition to his scientific accomplishments, his leadership of institutions and international organizations, Torsten is a co-publisher with Jean Stein of the magazine *Grand Street*, and, as you will learn, he is an art collector par excellence with broad tastes and interests. Some of you may recall the one-person show at the Pace Gallery where

Torsten's personal collection was on view, a collection united not by adherence to a single school of art or period in art history but by the unity of vision of its collector.

How then, in the perspective of his 80 years and all that is still ahead of him, can we do justice to Torsten? How can we frame his contributions against the history of Western thought and in the context of Western academic leadership? How can we describe his style so that it can serve as a model for our students? Into what sort of leadership typology does Torsten naturally belong?

Clearly, Torsten is a European intellectual by nature and a northern European by temperament. One is tempted therefore to turn for guidance to the great northern European writers and thinkers – to Ibsen, Strindberg, Dinesen, Goethe, and Nietzsche. Of these, only Nietzsche and Goethe are helpful because only they have developed useful typologies for people of thought as well as people of action.

Nietzsche, whom I turn to first, divided thinkers and people of action into two types: Apollonian and Dionysian. The Apollonian leader is rational, intellectual, fair-minded, above the fray; the Dionysian is sensual, instinctive, volatile, creative. Torsten does not fit exclusively into one or the other of these two categories for he possesses parts of both. In many ways he is Apollonian. But anyone who has watched him enjoy a glass of wine or observed him on the dance floor knows he is also a sensualist to the core.

Goethe perhaps offers a more appropriate typology, one that distinguishes two broad subtypes: the self-satisfied and fully evolved intellectual and the never quite satisfied, ever-evolving intellectual. The satisfied scholar pauses when he reaches a plateau of accomplishment to enjoy his achievement and then proceeds further along the same path seeking more of the same knowledge or assuming a modest leadership role. Torsten clearly belongs to the other subtype. He is an ever-evolving, self-re-inventing intellectual who strives for more than knowledge, he strives for new ways of living not simply for himself but for the academic community and in the limit for the betterment of humankind.

In his search for new experiences in the service of humankind, Torsten is much like Goethe's reinvention of Marlowe's Faust, an intellectual who re-invents himself repeatedly. What Goethe's Faust most wants is knowledge beyond books; he seeks not simply sensual but intellectual adventure, and service on behalf of humankind. Simply to remind you, Faust bases his bet with Mephistopheles, which he wins, on the following premise:

If ever I lie down on a bed of ease, then let that be my final end: if you can flatter me with lies into a self-complacency; let that be the last day for me!

Much like a modern Faust, Torsten's life has been a life of self-education and continued development in his search for ways to improve science first in his own laboratory, in his collaborations with David and Charles, then in the leadership of his department at Harvard, later as president of his university at Rockefeller, and now in his leadership of the scientific community throughout the world.

But on a path where risks are taken, there is always the risk of failure. So it will not surprise you to learn that Torsten's striving does not invariably succeed. Let me give you one example. Torsten and I independently fell in love with the paintings of an Israeli minimalist artist, Moshe Kupferman, who had escaped the Warsaw ghetto and emigrated to Israel where he spent the rest of his career in a kibbutz appropriately called The Fighters of the Ghetto.

In 1999 Torsten and I visited him in his modest studio at that kibbutz where he said to us with tears in his eyes, 'I dream – and I am getting too old to dream – that I can someday have a retrospective exhibition at a museum in New York.' Torsten and I turned to each other knowingly. We each thought that between the two of us and our friends we could certainly arrange that. We formed an influential committee and began at the top by first soliciting the Metropolitan Museum and then worked our way down. Everyone recognized Kupferman and thought him superb. But we were turned down time and time again. No one thought that his work would produce a blockbuster exhibit.

At last, in desperation we turned to the Jewish Museum. How could they refuse us! But they also had no difficulty in doing so. Kupferman is very good, they said. In fact, we have two of his paintings! But he lacks one characteristic. He is not Jewish enough. Not Jewish enough for the Jewish Museum! So you see – there are real limits even to Torsten's strivings.

Let me conclude these thoughts by asking: Where is this post-Faustian northern European intellectual heading in the future? Where is he leading us next? Clearly, the next step for Torsten is to combine his interest in art, science and leadership. So I propose we nominate Torsten to succeed Philip de Montebello, who, exhausted at age 60, is rumoured to be retiring soon from his directorship of the Metropolitan Museum. Having Torsten as head of the Metropolitan Museum will accomplish two purposes. First, it will give Torsten a new platform from which to combine his ideas about education and his love of art, with his interest in the biology of perception, and the nature of the aesthetic experience. In addition, it will give all of us another opportunity at a Kupferman retrospective exhibit.

Finally, although this is a celebration of Torsten, no celebration of Torsten is complete without a celebration of Jean Stein who during the last 25 years has heightened Torsten's and all our lives by sharing with us her deep insights into contemporary art, photography, and poetry. To continue the Goethean metaphor, Jean is the eternal feminine – Das ewig Weibliche – that inspires us all to perfection. Her taste, intelligence, and progressive vision has been a central component of all of our aspirations.

So let me raise a glass to Torsten on his birthday. Torsten, you are a friend and colleague of inestimable value. We who celebrate you today admire you fondly as a remarkable person, an extraordinary scientist, and a superb democratic leader with a sense of decency and style. And, since at age 80 you act, think and strive as a person half your age, we wish you and Jean another 80 years together, 80 more years of striving, reinventing, and pleasure. Torsten, Skoal!

Reference

Hubel DH & Wiesel TN (1959). Receptive fields of single neurones in the cat's striate cortex. *J Physiol* **148**, 574–591.

Republication of *The Journal of Physiology* (2009) 587, 2855: Expressions of gratitude to *The Journal of Physiology*, to our colleagues and students, and to the fates that placed us in such a great time to be scientists

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Torsten and I obviously feel it an immense honour to be celebrated in this way by *The Journal of Physiology*. It was there that we published our first papers, in many ways still our farourite ones. We found *J Physiol* a wonderful place to publish: among other things the figures were beautifully done, the reviews were always fair (i.e. laudatory). Our 1959 paper's submission was accepted by a letter, written we think by William Rushton, that began 'Congratulations upon a very fine paper. . .', and made no suggestions at all for changes. We were pleased because that paper had gone through 11 drafts and had even passed muster by Ed Furshpan, our fiercest critic. Above all, *The Journal* didn't follow the bizarre American style of ordering periods and closing quotation marks at ends of sentences. We hated to change journals, but felt forced to because at that time the strictly alphabetical order of authors' names in JP, though perhaps an advantage for me, was hard on Torsten. One could hardly expect Harvard deans or promotion committees to know the ways of the British. The problem came to a climax in the case of Ed Furshpan and Taro Furukawa, who had to change journals so Taro could get promoted in Japan.

We have always felt that any success we had over the years was a matter of sheer and consistent good luck, at every turn. We were roughly the same age, our abilities were complementary, and our scientific outlooks were similar. We started at a time when single cell recording from CNS was just taking off, and at first we had the field of visual cortex more or less to ourselves, aided by the myth that our kind of research was difficult and tedious. We did nothing to dispel that myth and so had little competition for over a decade. NIH support was generous and we never had to spend more than a few days every half-decade writing grant proposals. Animals were cheap, and there were fewer hoops to jump through – no long, detailed animal-use protocols to write or gloves or masks to wear during experiments. Above all we worked in a wonderful setting, with the huge benefit of the wisdom and gentle guidance of Steve Kuffler (our leader, and later the head of our department), and the company of postdoctoral fellows and graduate students who were so good that we could ignore them and let them get on with their work.