

An Interview with Horace Barlow¹

Horace Barlow FRS was born in 1921 in Chesham Bois, Buckinghamshire, England. After school at Winchester College he studied natural sciences at Cambridge University and then completed medical training at Harvard Medical School and University College Hospital, London. He returned to Cambridge to study for a PhD in neurophysiology and has been a highly influential researcher in the brain sciences ever since. After holding various positions at Cambridge University he became Professor of Physiological Optics and Physiology at the University of California, Berkeley. He later returned to Cambridge, where he was Royal Society Research Professor of Physiology, and where he is a fellow of Trinity College. He has made numerous important contributions to neuroscience and psychophysics, both experimental and theoretical, mainly in relation to understanding the visual system of humans and animals. His many awards include the Australia Prize and the Royal Medal of the Royal Society.

This is an edited transcript of an interview conducted on the 20th July 2006.

Phil Husbands: Would you start by saying a little about your family background, in particular any influences that may have led you towards a career in science.

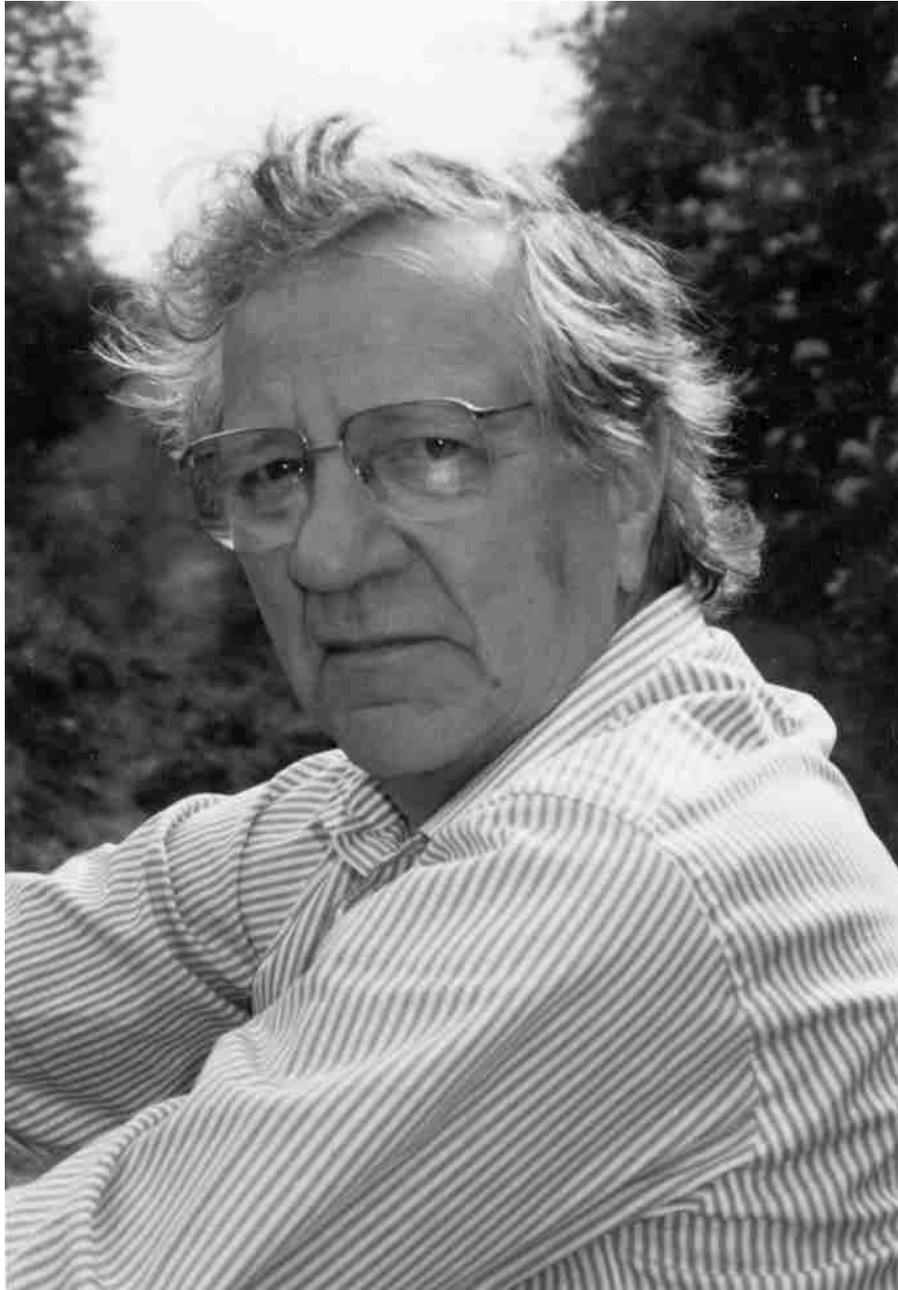
Horace Barlow: I come from a scientific family; my mother was Nora Darwin, Charles Darwin's granddaughter, and she was very scientifically inclined herself. In fact she worked with William Bateson on genetical problems in the early days of genetics at Cambridge and has one or two papers to her name in that field, although she never got a degree or anything. She was not only a good botanist, so to speak, but had a very scientific way of looking at things and kept asking herself and us children questions about why things were the way they were. So she undoubtedly had an influence in directing me towards science. She was instrumental in reviving Charles Darwin's reputation in the middle of the twentieth century, publishing an un-expurgated version of his autobiography and editing several collections of letters and notes^{1,2}.

Two of my elder brothers became doctors and they also had strong scientific interests. My father, Alan Barlow, was a senior civil servant and had read classics at Oxford. He was very keen on words and origins and that kind of thing but wasn't scientifically inclined. But his father, Thomas Barlow, was a very successful doctor in Victorian times, in fact he was physician to Queen Victoria's household and had a disease named after him. He was one of the people who was very keen on medicine becoming more scientific and had numerous medical publications, so there's some science on that side too.

¹ Preprint of P. Husbands (2008) An interview with Horace Barlow. In P. Husbands, O. Holland, M. Wheeler, (Eds), *The Mechanical Mind in History*, MIT Press, 409-430.

PH: You went to school at Winchester College. Were there any particular influences there?

HB: Yes. The teaching of science there was very good as you can tell from the fact that amongst my contemporaries were Freeman Dyson, the famous theoretical physicist, Christopher Longuet-Higgins, who made outstanding contributions to



theoretical chemistry and cognitive science, James Lighthill, who was an important applied mathematician, and many others who became distinguished scientists. One person who certainly had an influence on me was the biology teacher, whose name was Lucas. Because at that stage I wanted to go on and study medicine, biology was important but it did mean, because of the way the timetable was structured, that I was restricted to doing what was called four hour mathematics rather than seven hour mathematics, which I very much regret actually. There were some very good

mathematics teachers; I particularly remember Hugh Alexander who was British chess champion and who went on to work with Turing at Bletchley Park during the war.

PH: After Winchester you went to Cambridge to study natural sciences. Can you say a bit about your undergraduate days there?

HB: Well one of the big influences on me there was someone who later became a fellow member of the Ratio Club: the neurophysiologist William Rushton. He was quantitatively inclined and an inspiring teacher. He was my and Pat Merton's (another Ratio Club member) director of studies at Trinity. A fascinating character. He was a very good musician, playing the bassoon and viola. But he was also extremely knowledgeable about music and took a highly intellectual approach to it. He was also a marvellous person to talk to because he would always encourage any pupil who came up with a bright idea; I can see him now turning towards you and getting you to say more and help you to relate your ideas to him. At that time his work was on the electrical properties of nerves. He did some important work in that area and in a sense he was a precursor of Hodgkin and Huxley and I think they did both acknowledge him. So in a way he was a bridge between the old Adrian and the new Hodgkin and Huxley³. His work in this area was highly regarded but not very widely known. But later he went into vision and become one of the world's top ranking visual physiologists.

Another person I had supervisions from, and who made a big impression, was Wilhelm Feldberg who had worked on cholinergic transmission with Dale in the early days. The other thing that had a big influence on me when I was an undergraduate was the clubs. I was a member of the Natural Science Club which consisted of about twenty people, roughly half undergraduate and half graduate students with maybe one or two people of post-doc status. We met about four times a term and gave talks to each other on various subjects. That had a big effect on me and was a great means of teaching and learning without any staff being involved!

PH: During this time at Cambridge did you still have a clear career path in mind? Did you still intend to go into medicine?

HB: Yes. When I was at school I was rather inclined towards physics but being in the same school, and on occasions in the same class, as Freeman Dyson and James Lighthill, I realised there was a disparity in our mathematical abilities so I thought perhaps biology would be more appropriate for me! I did the Natural Sciences Tripos in anatomy, physiology, pharmacology, biochemistry etc. which was the normal thing for medical students at Cambridge, and then went on to do my clinical work. I was lucky enough to get a Rockefeller studentship to go and do that at Harvard. This was in the middle of the war and the Rockefeller Foundation realised that medical education in Britain was disrupted and furthermore they couldn't get the postdoctoral researchers they usually supported to do work in the States because they were all engaged in the war effort, so they spent the money on medical studentships instead. There were about twenty or thirty of us. Before I started at Harvard I worked for the summer of 1943 at the Medical Research Council's lab in London at Mount Vernon. I was working on problems of diving in relation to the war. In fact I stayed there for a year; I delayed the start of my clinical studies in America to continue this work. That

was my first proper laboratory science job. The lab was run by G.L. Brown and at first we were concerned with oxygen poisoning related to breathing oxygen under pressure, and then later on we worked on some problems with the essentially scuba-diving gear used for some operations. They used a self-contained system rather than the flow-through type so that far fewer bubbles were produced and the divers were less easily detected. But that kind of system has its own dangers and the equipment they were using was inadequate in some ways and we helped to sort that out.

PH: Did you come across Craik at all during that period?

HB: Yes, I did actually meet Craik when I was working at Mount Vernon. I was working for the navy but he was doing the equivalent work for the air force and they had mutual inspection visits so our paths crossed. I remember putting him on a bicycle ergometer to measure the oxygen consumption while using one of the self-contained diving sets we were working on. So it was only a rather brief meeting but of course I was very much aware of his work. His book, *The Nature of Explanation*⁴, had appeared by then and his work in vision was very interesting because he had a very different approach from what was prevalent in psychology at the time.

PH: Once you got to Harvard did you meet anyone who was a particular influence?

HB: Well there were a lot of very interesting people at Harvard Medical School at that time; this would have been 1944. One of them was Carroll Williams who was doing some very interesting molecular biology, as we'd now call it, on silk worms. He seemed a good deal older than the rest of us, but at the beginning of the war he had decided to take up medicine. Anyway, he was a fascinating chap who became a distinguished scientist and was later professor of biology at Harvard. I did a research project with two fellow medical students, Henry Kohn and Geoff Walsh, on vision. We investigated the effect of magnetic fields on the eye. This resulted in my second scientific paper⁵; I'd already published one with William Rushton⁶ from my undergraduate days, but it was my first work in vision. The three of us also published some work on dark adaptation and light effects on the electric threshold of the eye⁷.

PH: By that time was it clear you wanted to continue as a research neurophysiologist?

HB: Yes. What I planned to do, and actually did do, was to complete a full medical qualification on my return to the UK and then try my hand at a research position. In those days you could get a full medical qualification without having to do any house jobs, internships as they are called in North America, so when I got back I did a few more months additional clinical work at University College Hospital, London and was fully qualified. I then wanted to try research before I had to embark on many years of internships which was the way ahead in the medical profession. In 1947 I managed to get a Medical Research Council research studentship at Cambridge under E.D. Adrian, who later became Lord Adrian but was universally known simply as Adrian both before and after his elevation to the peerage.

Pinning Adrian down was never easy, so finding him to explore the possibility of a studentship took some doing. I knew he was in Cambridge, and often in the Physiological Laboratory, but whenever I called he was not in his office. After several visits his secretary rather reluctantly admitted that he was probably downstairs in his

lab, but when I asked if I could find him there her jaw dropped and she said 'Well, er...'. I got the message, but went down to look for him all the same. The entrance was guarded by his assistant, Leslie, who said 'He's in there with an animal and does not want any visitors'. This time I took the hint, but as I was leaving I met one of my former lecturers (Tunncliffe) and explained my problem. He told me I was not alone in finding it difficult to catch Adrian, but, he said, 'He usually goes to Trinity on his bicycle around lunch time, and if you stand in front of him he won't run you down'. So I lurked around the lab entrance for a few lunchtimes, and the tactic worked: as I stood triumphantly over the front wheel of his bike he said 'Come to my office at two o'clock'.

There he asked if I had any ideas I wanted to work on. My proposals, which were really hangovers from my undergraduate physiology days, included one on looking at the oscillations you sometimes get in nerve fibres. I thought that would be interesting to work on but Adrian brushed that aside rather quickly, along with my other ideas, but then said I might like to look at the paper by Marshall and Talbot⁸ on small eye movements to see if there was anything in their idea, and, by the way, he thought he could get me a research studentship from the MRC. The total duration of the interview was certainly no more than five minutes; Adrian believed in getting a lot done in his time outside the lab as well as inside it.

When I reported for work a few days later Adrian seemed surprised to see me, and even more surprised when I asked him what I should do, but said something like 'We've discussed that - Marshall and Talbot, don't you know'.

PH: You were already interested in vision before you started your PhD; can you pinpoint when that interest started?

HB: Well, while I was an undergraduate one of the talks I gave to the Natural Sciences Club was on colour vision. I read up on the subject for the talk and found it interesting and could understand what it was about. So that was an important point where I got interested, and then talking about it with William Rushton developed that further. Another piece of work that particularly interested me as an undergraduate was Hecht and Pirenne's research on the absolute threshold of vision⁹. Maurice Pirenne was at Cambridge working with William Rushton at the time so the three of us discussed this topic at length. I think I gave a talk about the statistical evidence for the visual system's sensitivity to single quanta of light that Hecht had obtained. I was interested in finding out more about the statistical aspect of this and William pointed me at R.A. Fisher's books which I read very keenly and learnt a great deal from. Of course the absolute threshold was a topic I was to return to a little later in my career¹⁰.

But I didn't have to make a decision on my research area until I'd done my clinical stuff and come back to Cambridge three years later. During that time I'd worked on visual problems with Geoff Walsh and Henry Kohn which furthered my interest. The reason I was interested in vision was because what we knew about the quantitative aspects of the integrative action of neurons and so on was derived from Sherrington's work on the spinal cord and most of that was done with electrical stimuli delivered to nerves, which of course doesn't produce patterns of excitation that are at all like anything which occurs naturally. With vision you are in the position to control quantitatively the properties of the stimulus. You can change its colour, size, shape,

duration and so on. And you can try and match it to natural stimuli. So I was interested in how the neurons in the retina would deal with these quantitative aspects of the stimuli. This was something you could do with vision and to some extent with hearing too, although just exactly what happens in the cochlea was not clear then and is still not quite clear now! When I started on my PhD, Rushton was moving into vision and we talked together a lot, which was very helpful.

PH: So after Adrian took you on, did you initially work on the eye movement problem as he suggested?

HB: Yes. The Marshall and Talbot paper suggested that the small oscillatory movements of the eyes were actually important in generating visual responses, playing a role in hyperacuity. So I spent six months or so working on eye movement and came to the conclusion that their suggestion was not a very good one and there was no good evidence that small eye movements played a role in hyperacuity, rather they might impair it through motion blur. But I developed a method for measuring small eye movements and was able to show that there is great variation in the fine oscillations from subject to subject but they didn't have any effect on the ability to resolve fine gratings, didn't seem to have any effect on acuity. But what struck me was that in the patterns of eye movements recorded there were fixational pauses where the movement of the eyes was remarkable small, the fixation was extremely stable – almost the opposite of what Marshall and Talbot suggested. So I dropped the eye movement research and switched to working on the frog's retina.

PH: Of course the frog retina work¹¹, where you gave the first account of lateral inhibition in the vertebrate retina, and suggested the idea of cells acting as specialised 'fly detectors', was the first piece of your research to become very well known and it is recognised as being very important in the history of neuroscience. It seems that even that early your work was strongly theoretically driven, there were theoretical notions behind the kinds of empirical work you were doing. Would you agree with that?

HB: Yes that's right. There were two theoretical inspirations behind that work. One was from the ethologists Lorenz and Tinbergen who suggested that at least the simpler reactions of birds, amphibians, reptiles and so on could be understood in terms of quite primitive discriminatory mechanisms occurring at early stages in the sensory pathways^{12,13}. So it occurred to me that the kind of sensitivity that the ganglion cells in the frog retina had might well be suitable for making frogs react to small moving objects. This was probably the basis for them snapping at flies and things like that – hence the idea of specialised fly detectors that I introduced in my 1953 paper¹¹.

PH: So you were looking for evidence for that from the start?

HB: Yes. But the problem was that beyond pointing out that the best stimulus for some of these retinal ganglion cells is a small moving object, I couldn't see any way of following that up further. The kind of things one might think of would be to ask whether this was any different in toads, for example, which look for slower moving objects such as worms and larvae rather than fast moving objects like flies. But it was going to be very hard work to build up a comparative case like that, so I rather shied off it.

But the other theoretical area where my interests were developing, and which influenced the frog retina work, was the signal to noise problem. Tommy Gold was always an interesting person to talk to about that at Ratio Club meetings and other times when we met. I was interested in making quantitative measurements of, for example, the area threshold curves – measuring the sensitivity of the retinal ganglion cells as a function of the size of the stimulating spot (of light). That was what led to the discovery of lateral inhibition in the frog retina because I found that the sensitivity decreases as the spot gets bigger and spreads onto the inhibitory surround. That interest in the quantitative aspects was very much inspired by William Rushton who was always keenly interested in that aspect of things.

PH: What are your memories of Adrian as a supervisor?

HB: Well he would poke his head around the corner now and again to see how I was getting on and would occasionally point me to a useful reference or give me some advice. He could be quite a distant character. I wouldn't say he was exactly encouraging in his supervision! I remember his advice when I wanted to switch to working on the frog's retina. I was convinced there was something funny about Hartline's results¹⁴ on the size of the receptive fields for the retinal ganglion cells, because they were very large which would have given really rather poor visual performance, and if that was all the frog had it was very difficult to account for their actual performance. Well, Adrian wasn't having any of that and he said 'Oh, I wouldn't do that – Hartline is a very clever chap, you know. It would be a mistake to try and prove him wrong.' Well of course he was quite right on one level, but I was right too – there was more to be discovered. Anyway, I persisted and got his permission to go to London to buy the equipment I needed. At that time one could buy war surplus electronic equipment at absurd prices – it was sold by weight, and one could buy a photon-multiplier complete with all circuitry for a few shillings.

PH: Did you ever discuss with him later the fact that it turned out to be a very good change in direction?

HB: We never went back over the question of whether it was a wise move or not, but he certainly agreed that the results were very interesting, particularly the evidence for inhibition. But he was not at all theoretically based; his attitude was that we had the means of recording from nerve fibres and we should just see what happens. Of course he was absolutely brilliant at teasing out the first simple facts but then he never enquired further along any of theoretical lines that were opening up.

I remember when I had first got the apparatus for the frog retina experiments assembled and in sometimes-working-condition, Adrian made one of his unannounced visits to my lab, on this occasion with a visitor smoking a large cigar and speaking completely incomprehensible English.

A few minutes before I had dropped an electrode on to the floor; I had just remounted it and was lowering it on to a frog retina, without much hope of success, when they came in, so I turned on the light and started explaining what I was trying to do, and how. At this point the visitor was standing under the room light, and took a deep puff from his cigar. As he exhaled the smoke, its shadow fell across the preparation and it

gave a long and vigorous "off" discharge. Ragnar Granit, for that was who it turned out to be¹⁵, was astonished; so was I, and his English became at least partly intelligible as we discussed the technicalities of what makes a good electrode and so forth.

Adrian spent a lot of time in his laboratory where he definitely did not like visitors. I only recall making one very brief visit when Adrian was actually doing an experiment. Now, whenever he was in the Physiology Lab (the University department) Adrian was always moving, never at rest, always reacting. His body movements were like saccadic eye movements, jerking incessantly from one object of attention to another. Ordinarily these movements, while much more frequent than most people's, were quite well spaced out, and synchronised with other events occurring around him, so that he surprised one with an unexpected shift of attention only, say, once every thirty seconds or so. But in his own laboratory they seemed to occur every second, and each of one's own movements elicited a response. When I went there he was doing an experiment on a monkey that was infected with amoebic dysentery – the reason, he explained, why he was able to get hold of it. If I turned towards the table to ask a question he seemed to jump to intervene between me and the infected monkey, and my attention was so riveted by his heightened state of reactivity that I could take in nothing about his laboratory or the experiment he was conducting.

William Rushton also had a rather alarming experience on one of his rare visits to Adrian's lab. It was near the beginning of his postgraduate research under Adrian – about the mid 1920s. Most students in his position were, to put it mildly, awe-struck by the great man. So it was with some trepidation that Rushton ventured in one afternoon to borrow a galvanometer. There was no one in the lab so he set about searching. He eventually located one amidst all the clutter and went to pick it up. As his hand grasped the instrument, Adrian's voice suddenly boomed out of nowhere, 'Put that down, Rushton!' He was perched in a small dark cupboard at the back of the lab where he liked to shut himself in to think. He could see the whole lab through a crack in the door.

PH: During the early part of your PhD, before the Ratio Club started, did you have any interactions with people at Cambridge who were interested in cybernetics and machine intelligence?

HB: That mainly started with the Ratio Club, but before that I did interact with some psychologists who were developing interests in that direction. Hick, famous for Hick's law, and later a member of the Ratio Club, was one of them. Another character in psychology, C.G. Grindley, a physics-based psychologist, was a very interesting person. Unfortunately he was an alcoholic. I saw quite a lot of him because I'd often go for an after-work drink with Geoffrey Harris, who worked in the room next door to me. At six o'clock we'd go to The Bun Shop, a bar which was very close to the lab. Grindley was usually already there and I talked quite a lot to him about problems in psychology.

PH: Did you have an interest in the more psychological side of the brain sciences before that?

HB: I did. In fact in my final year as an undergraduate I had considered specialising in psychology rather than physiology – the way the natural sciences tripos is arranged at Cambridge involves studying many topics for Part I and then specialising for Part II. The professor of psychology at the time, Frederick Bartlett, ran a course of seminars – fire-side chats they were – in the long vacation term. We met once a week and discussed various problems in psychology. I was never very happy with the material we covered. The concepts and thinking seemed to me to be very strongly verbally-based whereas I think in a much more model-based and quantitative way. At any rate, at the end of that course I stayed behind and told Bartlett that I had to choose between psychology and physiology and asked for his advice. I explained to him some of the problems I had with psychology – that it seemed to me that in order to make progress in understanding the brain you had to get behind the words, you couldn't possibly explain it all in words. He agreed with that and said that the scientific advance that had done more for psychology than anything from within psychology over the past few decades had been Adrian's work in physiology, and no doubt there was going to be a lot more physiology-based work that would have a big influence in psychology. And that was what tipped the balance for me in favour of physiology.

PH: Did you interact with Hodgkin and Huxley during the period when you were doing your PhD?

HB: Oh yes. I remember many tea-time conversations with them. I remember Alan Hodgkin explaining to me about the noise limit when recording through an electrode and how the resistance isn't actually in the electrode itself but in the sphere of saline surrounding the tip. I remember after I'd written up my work on eye movement, Andrew Huxley read it through and pointed out various things about the statistical treatment that could be improved. I had a lot of useful conversations with them.

PH: It was during your PhD studies that you became involved in the Ratio Club¹⁶. How did that happen?

HB: It was through Pat Merton. Pat worked with John Bates, who organised the club, at the National Hospital in Queen's Square. As I mentioned earlier, Pat and I had known each other since undergraduate days and he suggested me to Bates.

PH: How important was the club in the development of your ideas?

HB: Oh very. It gave me an opportunity to hear and talk to people who were leading experts in this area. Probably most important to my work were Tommy Gold and Philip Woodward. Tommy was a wonderful person. He started life as an engineer and then switched to physics. He had a very distinguished career and was extraordinarily versatile. He is well known as one of the founders of the steady state theory of the universe, for the construction and operation of the Arecibo dish and for many contributions to astrophysics, but he did much more than that and at the time of the Ratio Club he was working on hearing in the zoology department at Cambridge. He argued that there was a positive feedback mechanism involved in hearing. It was many years before he was proved right. He was very useful to talk to about signal to noise problems and statistical matters. He wasn't a particularly statistical sort of person himself but he knew it all, as an engineer essentially, and he was very keenly

interested in applying engineering ideas in biology. Anyway, he was always tremendously good value and always has an original point of view. Never listened to anyone else!

Philip Woodward was a marvellous person to interact with. He had a very deep understanding of information theory and could communicate it very clearly; he gave extremely good talks and his book on information theory applied to radar¹⁷ was very helpful. I learned a lot from him.

There were two other members who were particularly influential as far as I was concerned. One was Donald Mackay, who was a wonderful speaker; his talks were always brilliant expositions of ideas which often subsequently proved to be important. The other was Albert Uttley, who was at TRE, Malvern and then NPL. He had some very interesting ideas. Pat Merton was very keen on him because he had developed one of those servo feedback devices for controlling gun turrets and so on during the war. But there was always something difficult to understand about his ideas and he wasn't a very clear expositor of them! This meant he could be given short shrift by some of the more precise members of the club. But I think that some of the ideas he had were very good. He had an idea about unitary representation which I think is the same basic concept as sparse representation, sparse coding¹⁸, but was ahead of it. I think it was an important idea, but he didn't really get it across to us successfully.

The meetings were always very enjoyable and stimulating and I learned a great deal.

PH: Are there any particular meetings that stick in your mind?

HB: I remember the very first meeting where Warren McCulloch spoke. I think it's fair to say that he deeply failed to impress us. For many of us this was our first exposure to him. As we saw more of him that view tended to change as we got to appreciate his style. Donald Mackay and others went on to form close friendships with him; Donald went to visit him often and they collaborated on various pieces of research.

My memories are probably more of people and ideas rather than specific meetings. I remember Alan Turing talking about how patterns could be generated from reaction diffusion systems and how this might play a part in morphogenesis. One particular phrase of his really stuck in my mind as somehow summing him up. He was talking at one meeting about the brain and about looking at pictures of groups of hundreds of neurons and how they seem to be partially randomly determined; he said 'I don't know how to put this but they are not very accurately determined; they are more like a tree than a horse.' That was very much the way he thought. Very expressive but not very precisely formulated ideas. Of course he was more than capable of formulating them precisely when it came to the crunch, but in getting the initial idea across he didn't try to.

PH: Do you remember if there was any debate in the Ratio Club about whether brains should be viewed as digital or analogue or mixed digital-analogue devices?

HB: Yes there was a lot of discussion of that. I think the general consensus was that if it was digital it wasn't digital in the way that computers are. I think there was a general agreement that the fact that conduction down nerve fibres was by impulses rather than by graded potentials was because digital coding is more error resistant. Having an all or nothing impulse is in fact the same as one aspect of using digital, as apposed to analogue, systems – the all or nothing response means that you can eliminate one kind of noise. But that is more or less where the similarity ends, basically because of the very great asymmetry between the presence and absence of an impulse in a nervous system compared with digital coding as used in engineering where there is symmetry between the 1 and 0 – they both have the same information capacity and in many cases they are used that way. So I think we understood that the way impulses were used in nervous systems was very different from in digital electronic systems. William Rushton wrote a paper on some of these issues at about that time¹⁹. This was before the idea of sparse coding and its implications, although as I mentioned earlier I think Albert Uttley was actually onto that idea even though he couldn't get it across to us.

PH: In the late forties, when the Ratio Club started, what was the typical view of cybernetics within neurophysiology, or neuroscience as it was becoming?

HB: Well I think for some of us information theory seemed to be a great new thing – here was something else to follow in the brain other than just impulses and electric currents and chemical metabolism. Here was a definable quantity that was obviously important in the kinds of things the brain did. So there was a great deal of enthusiasm for that cybernetic approach among a group of us who made up a fairly small section of the neurophysiological community. But a lot of people regarded it as airy fairy theoretical nonsense. Neurophysiology was very untheoretical at that time; most of the important advances were made by people who took a very empirical approach, like Adrian for example. William Rushton wrote a kind of scientific autobiography in his later years²⁰ in which he says essentially that throughout his early years he was much too strongly theoretical and was trying to browbeat nature into behaving as he wanted it to rather than eliciting how it actually was.

PH: What is your view on that question, and has it changed since those early days?

HB: Well I have two views which are to some extent in conflict. One is that the purely empirical approach still has a very important role in neuroscience. A lot of advances will still occur because of the development of new techniques that enable you to have access to something else in the brain that had hitherto been hidden from view. The technique will be used to find out what goes on and people will be guided in what they do by the discoveries they make – just as has happened since Adrian and before. William Rushton described it as thinking with your fingers. I think this is just a fact of life in neuroscience because we understand so little theoretically about how the brain works. It is not like a well developed science where theory explains 95% of what you are confronted with so you have to use that theory, in contrast theory in neuroscience explains 5% or less so you have to make use of other approaches and tools. The other view is that neuroscience is so badly fragmented that it is really not one community but half a dozen different ones who hardly understand what each other are saying. So there must be some kind of unification through a shared approach

to trying to find a common coherent understanding of what the brain is doing. At this stage this might not be very theoretically elaborate, but it is crucial.

PH: I believe that sometime in the mid fifties Oliver Selfridge and Marvin Minsky, and maybe others, were trying to organise an international conference on AI – it would have been the first such event – and they were interested in holding it at Cambridge University. I understand that you were involved in trying to make that happen. Is that right?

HB: Yes indeed. Oliver Selfridge and I went to see Maurice Wilkes, head of the Computer Laboratory, to try and get his support as we would need a senior person in the University involved. He took an extremely negative view of it. He dismissed us with a comment like ‘Oh, an international conference – that’s just a way of getting unpublishable papers published without being refereed.’ Of course such considerations couldn’t have been further from our minds, but that was that, because he was the obvious person in the University whose support we needed. Of course the other anti-AI person at Cambridge was James Lighthill who some years later wrote a rather damning report on the area for the UK science research council.

PH: One concept whose development in neuroscience you have been involved in is that of feature detectors. The idea of object detectors originated in your 1953 paper where you postulate fly detector neurons in the frog retina¹¹. The idea of feature detectors, where features refer to more primitive constituent properties of objects – edge detectors, convexity detectors and so on – built on this, coming later. The idea is certainly present in Lettvin et al.’s 1959 paper²¹. Were you thinking in terms of feature detectors before that? What’s your take on where the idea came from?

HB: I think it originated more in computer science, in early work in machine intelligence. Early work on pattern recognition, particularly on systems for automatically recognising handwritten or printed letters and text, used the idea of features. Oliver Selfridge was working on it in the States and Grimsdale and Kilburn in Britain. Oliver Selfridge influenced Jerry Lettvin on this I think. The computer work is certainly where I first became aware of the idea and then thought it was very likely that feature detectors were used in biological vision. I was certainly influenced by the fact that this early work in pattern recognition showed that the problem was much harder than had been thought; the nature of the difficulties was very illuminating.

PH: Let’s talk a bit about information theory in neuroscience. You wrote some influential papers on the idea of redundancy reduction²⁵ in the nervous system. I think your first paper on that was at the Mechanization of Thought Processes symposium in 1958²². Could you say a bit about how the ideas developed? I suppose you had been thinking about it for some time before that.

HB: Yes I had. Actually the first time I talked about that was at one of a series of meetings on ‘problems in animal behaviour’ organised by Thorpe and Zangwill. My talk was in 1955 although it wasn’t published until 1961 when a book based on the meetings appeared²³.

I also talked about it at a great meeting on ‘Sensory Communication’ in 1959 at MIT, held at Endicott House²⁴. I remember it being a very interesting meeting, over several days, and also one of the first international meetings I went to, so I particularly enjoyed it. They had a very good swimming pool and a very good bar! It was also notable as the first time I got to speak to certain people for any length of time. For instance, this was where I first met Jerry Lettvin – one of the amazing personalities from that era – and got to visit his lab. I also renewed my acquaintance with Warren McCulloch and got to know him better. Later the proceedings from the meeting were translated into Russian for a Soviet edition. My contribution was the only one that was expunged; for some reason it was thought to be too subversive!

PH: Had you discussed it at the Ratio Club?

HB: I don’t recall giving a talk on it at the Ratio Club but I do remember trying to discuss it with Donald Mackay. He was extremely good at expressing his own ideas but he wasn’t always terribly eager to learn about other people’s. I got nowhere at all with him except for him to say something like he’d already thought about it years ago and that kind of thing. But earlier talks and discussion at the club would have influenced the development of the idea.

I was very enthusiastic about how information was now something we could measure but when you are actually confronted with doing an experiment on a physiological preparation the prevalent techniques were all based on classical statistical measures rather than Shannon information, as was most of signal detection theory. So there was a problem in using it practically. I think this is part of the reason the idea rather fizzled out in neuroscience to be reintroduced again in the 1980s by people like Simon Laughlin. Another reason may have been that important empirical advances were coming from people like Hubel and Wiesel who, like Adrian, were anti-theoretical. Of course now information theory and other statistical ideas are quite strong in some areas of neuroscience.

PH: Sometime later you moved towards the idea of redundancy exploitation²⁶. Can you say a bit about how you changed your mind?

HB: Well initially I thought the idea of redundancy reduction was a perfectly plausible supposition because there were so many cells in the brain and, for instance, in the cortex it appeared most are very rarely active. It was only really when people started recording from awake behaving monkeys, and particularly when they started recording from MT (middle temporal cortex), which has much higher maintained discharge rates than elsewhere, it became pretty difficult to hang on to the notion that the mean firing rate in the brain is so low that the information capacity dictated by that supported the idea of redundancy reduction. I probably hung on to the idea, which is a kind of extreme version of sparse coding, for too long.

PH: Of course your famous 1972 neuron doctrine paper²⁷ relates to these issues. In that paper you propose the influential idea of sparse, or economical, coding in which ‘the sensory system is organized to achieve as complete a representation of the sensory stimulus as possible with the minimum number of active neurons.’ In all you

laid down five speculative dogmas. How do you think that paper has stood the test of time?

HB: Oh, reasonably well. There were some new ideas that needed to be discussed and thought about and I don't think I was too wide of the mark with most of the ideas.

PH: One of the things you pointed out was the complexity of single neurons and the potential complexity of the processing they are capable of. Since then considerably more complexity has been revealed with the discovery of mechanisms such as volume signalling, and now intra-cellular processes are starting to be probed.

HB: Indeed, and I think that there is probably a great future in that direction – intra-neural processing may well turn out to be very important. It was work on *E. coli* that really opened my eyes to that possibility. Intra-cellular mechanisms successfully run their lives with all the important decisions being made by biochemical networks inside a single cell about the size of a bouton²⁸ in the cortex. If all that can go on in one bouton, one has to wonder if we're missing something about what a pyramidal cell can do. Maybe over the next decade or so we shall find out a bit more.

PH: Some people have remarked that the neuroscience establishment never really showed researchers like you and Jerry Lettvin the kind of appreciation you deserved, partly because they thought you were too theoretical.

HB: Well they would be dead right up to a point. But it shouldn't be either/or. In this context I'm reminded of something Rutherford was supposed to have said in the 1930s when Jews were under threat in Germany and scientists like Einstein were looking to get out. In many ways Cambridge was an obvious place for Einstein to go, but it is claimed Rutherford said something like 'Einstein's theories are all very well but I think we can manage without him'. So it wasn't just in neurophysiology that there was this prevailing anti-theoretical attitude.

PH: I'd like to finish with a few rather general questions. First, looking back at the development of neuroscience over the sixty or so years you have been involved in it, has it turned out very different from what you might have imagined going back to the start of your career?

HB: I think it is a pity that more attention is not paid to trying to find simple preparations that exemplify particular cognitive or brain tasks. I think we have much more chance of ironing out the basic principles by studying these simpler systems. For instance, there seems to be some progress in understanding the cerebellum partly because people have found electric fish and things like that where it is possible to do observations and experiments which actually reveal what the cerebellum is doing. This ties in with what I was saying earlier about the need for a coherent theoretical framework.

On more theoretical developments, I'm a bit critical of what has happened in some areas of computer modelling. I don't think many, if any, of the neural network models are good models in the sense that the Hodgkin Huxley model was – that dealt with quantities that could be defined and measured in a single cell. The neural network models tend to be considerably removed from anything you could measure at the cell

level. I think they have got to be pulled down to a more biophysical basis. I'm more interested in the Bayesian approaches because I think that there they are getting much closer to realistic models of what certain quantities (here probabilities rather than simple physical values) might actually represent. The emphasis on probabilistic inference in certain strands of modern modelling is very good; I think that has a future.

I remember that when I was starting out in my research career there was quite a bit of optimism about how quickly some form of machine intelligence would be developed. Those members of the Ratio Club more involved in that area were very hopeful. But a computer wouldn't beat a grand master at chess until the 1990s. None of us would have predicted that back then; we all thought it would be much sooner. I remember being more sceptical than many at how much progress would be made, but obviously not sceptical enough. But of course there have been tremendous advances in processing power and miniaturization of electronics and so on, much of which most of us wouldn't have foreseen, which has meant that the use of computer based technology has had a big impact on neuroscience. Initially this was more for data collection and analysis. But now, and even more in the future, the important thing is that you can test whether a theoretical idea, or a model mechanism, can actually perform in the way the real brain performs. That's a fantastic advance.

PH: Are you surprised at how much progress has or hasn't been made in neuroscience during your career?

HB: It's come a long way in one sense. When I was a graduate student, in neurophysiological circles the idea of being able to understand what was going on in the cortex was dismissed as being utterly impossible. It was just too complex. Of course we don't believe that now; we think we'll find out all about it next week. That's equally far from the truth, but the outlook is much more hopeful. I was one of the few people back then who thought we would understand these things physiologically, and I think we have made a lot of progress but there is still a hell of a way to go.

PH: Finally, you've made a lot of important contributions but is there any particular piece of your research that stands out for you?

HB: I'm always rather disappointed by the general response to the attempts that I've made to measure the actual statistical efficiency of both psychophysical performance and neural performance (see e.g. ^{29,30}), because it does seem to me that when you can say that the brain is using whatever percentage it may be of the statistical information that is available in the input, this has an importance for understanding the brain comparable with being able to say that a muscle uses whatever percentage it is of available chemical energy in generating mechanical movement. I think this is a big step forward in getting to grips with one aspect of what the brain actually does. Imagine how we would regard intelligence test if they were of this nature, if they were actual measures of mental efficiency at performing some task, which they obviously are not; they're ad hoc plastered up God knows what.

Notes and References

¹ Darwin, C. (1958). (Ed. N. Barlow) *The Autobiography of Charles Darwin, 1809-1882: With Original Omissions Restored*, London: Harcourt Brace and World, Collins. (Later reissued by Norton and still in print.)

² Barlow, Emma Nora (1963). *Darwin's Ornithological Notes*; *Bulletin of the British Museum (Natural History) Historical Series* **2**(7):200-278.

³ The great neurophysiologist Lord Adrian shared the 1932 Nobel Prize in Physiology or Medicine with Charles Sherrington for pioneering work on the electrical properties and functions of nerve cells. He was Professor of Physiology at the University of Cambridge 1937-1951, President of the Royal Society 1950-1955 and Master of Trinity College, Cambridge 1951-1965. In 1952 Alan Hodgkin and Andrew Huxley, researchers in the Physiology Laboratory at Cambridge, wrote a series of now classic papers presenting the results of a set of experiments in which they investigated the flow of (ionic) electric current through the surface membrane of a nerve fibre of a squid. The papers culminated in a mathematical description of the behaviour of the membrane based upon these experiments – the Hodgkin-Huxley model - which accounts for the conduction and excitation of the fibre. This model has been used as the basis for almost all other ionic current models since. For this work they were awarded the 1963 Nobel Prize in Physiology or Medicine. The reference for the summary paper containing the model is: A. L. Hodgkin and A. F. Huxley, A Quantitative Description of Membrane Current and its Application to Conduction and Excitation in Nerve, *J. Physiol*, 117, 500-544, 1952.

⁴ Craik, K.J.W. *The Nature of Explanation*, Cambridge University Press, 1943.

⁵ Barlow, H.B., Kohn, H.I. and Walsh, E.G. (1947). Visual sensations aroused by magnetic fields. *American Journal of Physiology* **148**:372-375.

⁶ Rushton, W.A.H. and Barlow, H.B. (1943). Single-fibre responses from an intact animal. *Nature* **152**:597.

⁷ Barlow, H.B., Kohn, H.I. and Walsh, E.G. (1947). The effect of dark adaptation and of light upon the electric threshold of the human eye. *American Journal of Physiology* **148**:376-381.

⁸ Marshall, W.H. and Talbot, S.A. (1942). Recent evidence for neural mechanisms in vision leading to a general theory of sensory acuity. *Biological Symposia – Visual Mechanisms*, **7**, 117-164.

⁹ Hecht, S., Schlaer, S., and Pirenne, M. (1941). Energy, quanta and vision. *Journal of General Physiology*, **25**:891--40.

¹⁰ Barlow, H.B. (1956). Retinal noise and absolute threshold. *Journal of the Optical Society of America* **46**:634-639.

¹¹ Barlow, H.B. (1953). Summation and inhibition in the frog's retina. *Journal of Physiology*, **119**:69-88.

In this classic paper Barlow demonstrated a particular organisation of inhibitory connections between retinal neurons (lateral connections between neighbouring cells) and was able to provide accurate measures of retinal cell receptive fields (previous estimates were shown to be wrong as they were based in incorrect assumptions about functional network structure and did not take account of the inhibitory affect of surrounding cells). This paper gives the first suggestion that the retina acts as a filter passing on useful information; this is developed into the idea of certain types of cells acting as specialised 'fly detectors' – an idea that was to become very influential.

¹² Lorenz, K. (1952) *King Solomon's Ring: New Light on Animal Ways*. London: Methuen.

¹³ Tinbergen, N. (1952). Derived Activities; Their Causation, Biological Significance, Origin, and Emancipation During Evolution. *Quarterly Review of Biology*, **27**(1):1-32.

¹⁴ Hartline, H.K. (1940) The receptive fields of optic nerve fibres. *American Journal of Physiology* **130**:690-699.

¹⁵ Ragnar Granit, the great Finnish neurobiologist, shared the 1967 Nobel Prize in Physiology or Medicine with Hartline and Wald for his work on vision. He also made many important contributions to the neurophysiology of motor systems.

¹⁶ The Ratio Club was a London-based dining club for the discussion of cybernetics and related issues; see the chapter in this volume by Husbands and Holland for further details.

¹⁷ Woodward, P.M.(1953) *Probability and Information Theory, with Applications to Radar*, Pergamon Press.

¹⁸ In this context sparse representation is the idea, later developed as "cardinal cells" in Barlow's 1972 paper on single neurons and perception (see note 27), that stimulus features are represented by a few neurons within a large neuronal network. Thus, the representation of the stimulus feature is sparse within the population of neurons. More generally, a sparse representation is one that uses a small numbers of descriptors from a large set. The idea was further developed recently by various groups including Field and Olshausen, who coined the term sparse representation (see e.g. Olshausen BA, and Field DJ. (1996). Emergence of Simple-Cell Receptive Field Properties by Learning a Sparse Code for Natural Images. *Nature*, **381**: 607-609).

¹⁹ W. Rushton (1951). Conduction of the nervous impulse. In *Modern Trends in Neurology*, 1-12, Butterworth.

²⁰ This refers to Rushton's 'Personal Record', a document The Royal Society asks its fellows to write.

²¹ Lettvin, J. Y., Maturana, H. R., McCulloch, W. S., & Pitts, W. H. (1959) What the frog's eye tells the frog's brain, *Proceedings of the I.R.E.* **47**: 1940--1959.

²² Barlow, H.B. (1959) Sensory mechanism, the reduction of redundancy, and intelligence. In A. Uttley (Ed.) *Mechanisation of Thought Processes : Proceedings of a Symposium held at the National Physical Laboratory on 24-27 November 1958*. Her Majesty's Stationery Office, London, 537—559.

²³ Barlow, H.B. (1961). The coding of sensory messages. In Thorpe and Zangwill (Eds), *Current Problems in Animal Behaviour*, 330-360, Cambridge University Press.

²⁴ Barlow, H.B. (1961) Possible principles underlying the transformations of sensory messages. In W. A. Rosenblith (Ed), *Sensory Communication*, MIT Press, 217-234. (See the interview with Jack Cowan in this volume for further discussion of this meeting).

²⁵ One way to compress a message, and thereby make its transmission more efficient, is to reduce the amount of redundancy in its coding. Barlow argued that the nervous system may be transforming 'sensory messages' through a succession of recoding operations which reduce redundancy and make the barrage of sensory information reaching it manageable.

²⁶ As more neurophysiological data became available, the notion of redundancy reduction became difficult to sustain. There are vastly more neurons concerned with vision in the human cortex than there are ganglion cells in the retinas, suggesting an expansion in redundancy rather than a reduction. Barlow now argues for the principle of redundancy exploitation in the nervous system. In relation to distributed neural 'representations', learning is more efficient with increased redundancy as this reduces 'overlap' between distributed patterns of activity. Learning exploits redundancy. For more details see: Gardner-Medwin, A.R. and Barlow, H.B. (2001), The limits of counting accuracy in distributed neural representations, *Neural Computation* **13(3)**:477-504.

²⁷ Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception* **1**:371–394.

²⁸ A synaptic bouton is a small protuberance at the pre-synaptic nerve terminal which buds from the tip of an axon.

²⁹ Barlow, H.B. and Reeves, B. (1979) The versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Research* **19**:783-793.

³⁰ Barlow, H. B. and Tripathy, S.P. (1997) Correspondence noise and signal pooling in the detection of coherent visual motion. *Journal of Neuroscience* **17**:7954-7966.