Bernard Katz

1911–2003

1911	Born, 26 March, Leipzig, Germany
1920	School – König Albert Gymnasium, Leipzig
1929	First preclinical work, University of Leipzig
1931	Preclinical exams
1931	Undergraduate work/physiological research with Martin Gildemeister
1933	Siegfried Garten prize
1934	MD degree, University of Leipzig
1935	Short period working at Leipzig Hospital, followed by arrival at UCL
1936	First publication with A.V. Hill in *Proceedings of the Royal Society*
1939/45	Australia, working with John Eccles and Stephen Kuffler
1941	Became a naturalised British citizen
1942/43	Pilot Officer Bernard Katz, Royal Australian Air Force
1945	Married Marguerite (Rita) Penly
1946	Returned to UCL as Assistant Director of Research, Biophysics Research Unit
1950	Appointed Reader in Physiology
1952	Professor of Biophysics and Head of Department, UCL
	Fellow of the Royal Society
1957/63	Editor, *The Journal of Physiology.* Chairman 1961 - 1963
1967	Copley Medal of the Royal Society
1968	Fellow, Royal Society of Physicians
1969	Knighted
	Foreign Associate, American Academy of Arts and Sciences
1970	Awarded Nobel Prize, jointly with Ulf von Euler and Julius Axelrod
1976	National Academy of Sciences (USA)
1978	Retired as Head of Biophysics Department, UCL
1982	Awarded Orden Pour le mérite für Wissenschaften und Künste
1990	Ralph W. Gerard Prize, Society for Neuroscience
	Honorary doctorate, University of Leipzig
1999	Rita Katz died
2000	Unveiling of BronzeTafel at the University of Leipzig
2003	Died, 20 April

In science, it is no bad thing to have heroes. True, there are some people who resent anyone cleverer than themselves, but personally I like them. I won't embarrass those of my heroes who are still alive by naming them (especially those who are younger than me), but I can safely say that Bernard Katz was one of them, along with his mentor A.V. Hill.

In the preamble to his inaugural lecture, given in 1952 when he became professor of Biophysics at UCL, Katz expressed his gratitude to A. V. Hill 'for all I have learnt, not only as a pupil of a great master of experimental research, but by having served my apprenticeship with a man who never, under any circumstances, allows the deceptive counsels of human vanity to enter into your argument –with a man whose one inflexible purpose has always been the pursuit and acknowledgement of truth'. It is very clear that BK learnt well from his own hero, because these words could serve as well to describe his own values as they described Hill's. That, as well as his science, was why he was an iconic figure for a whole generation of post-war physiologists and pharmacologists.

Bernard Katz was one of the last of the generation of distinguished physiologists who were refugees from the Third Reich and who contributed immeasurably to the scientific reputation of their adopted country. Like many others (Feldberg, Schild, Blaschko and Vogt, to name but four), BK's German accent never entirely disappeared. It seemed that through most of my scientific lifetime the most distinguished of my seniors mostly spoke with guttural accents (I remember my own boss, Heinz Schild, a kind and gentle man, announcing in a strong accent that he had been to a party and was the only English person there). It was a continuous, and salutary, reminder of the follies of the 20th century, and of the far harder time that these people had than we do now. Science may have become less gentlemanly, and funds may be short, but we do not fear for our lives.

Bernard Katz was born and brought up in Leipzig, so his native language was German, though he was never a German citizen. Bert Sakmann relates that when BK first spoke to him in German (after his arrival in Biophysics in 1970), BK 'warned me that his German had a strong Anglo-Saxon accent'. This was a pun on the fact that BK spoke German with a Saxon accent that 'was indeed strong, and in Germany the Sächsische Akzent of people from Leipzig or Dresden is the source of many jokes'. The time when I recall BK laughing the most was when a young German, Florian Dreyer, was working in my lab. We visited BK in November 1977, to discuss results with tubocurarine. In the Haldane room at UCL, BK said 'It's a real pity that nobody here can understand jokes in Saxon dialect', but Florian did and they started swapping Saxon jokes in German, accompanied by peals of laughter.

BK's father, Max, was a fur merchant who had left Russia in 1904, and met his wife, Eugenie Rabinowitz, who was of Polish origin, in Germany. Until he was six, Katz was a citizen of Tsarist Russia, but then, because of the Russian Revolution, became stateless, and remained so until he was 30 when he became a naturalised British citizen.

In Leipzig, Katz was brought up in what he himself described as a 'completely "unorthodox" and liberal way', but nevertheless had his first experience of being an alien Jew in 1920 when, at the age of nine, he was refused entrance to the Schiller Real-Gymnasium (the head thought that it would be bad for their reputation to

Bernard Katz's school, the König Albert Gymnasium, Leipzig, in 1912 (left), and today

have the entrance exam topped by a foreigner –a Russian Jew), and consequently had a classical education at the König Albert Gymnasium.

There he chose to learn Latin and Greek rather than the more mathematical option (because, he said, it gave him more time to play chess in the cafés of Leipzig), though he acquired a good level of mathematics anyway. Despite his love of chess, and despite some unpleasant anti-Semitic experiences, he did well at school, and skipped a year. In his autobiographical essay he relates that one day, in the early 1920s, a fellow pupil had, in his absence 'called the boys together and informed them of a marvellous plan that his father had discussed with him at home. The plan was that the Jewish population of Leipzig should be invited to assemble in the underground fair hall, and after closing the doors should be killed off by filling the hall with poison gas' . . . 'This episode has never been erased from my mind, and it gives an indication of ideas that some people were harbouring in their heads for 20 years before they were able to put them into practice'. It is hard to appreciate what such an experience must have been like for a child of 11 or so.

Katz chose to study medicine, despite having no previous experience in the natural sciences, in part as a hedge against future financial problems. He started preclinical work at the University of Leipzig in 1929 (the classes started at 7 a.m.), where he was taught physics by no less than Peter Debye. He comments 'I suddenly realised the power and depth of scientific ideas and their continuous subjection to criticism and further trials by experiment. I felt almost revulsion against my previous preoccupation with what I now regarded as presumptuous philosophical speculations and with a genre of verbose literature that seemed to make a virtue of obscurities'. That reaction is

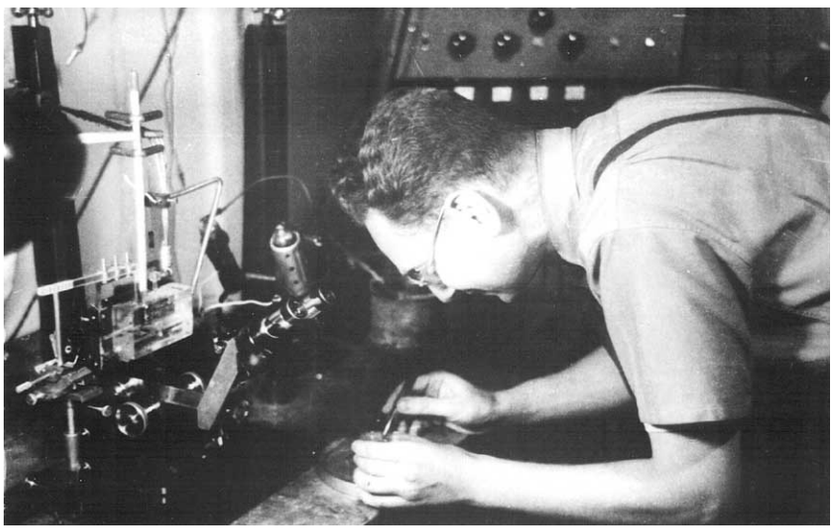
Martin Gildemeister (1876-1943)

A.V. Hill, c. 1935 (drawn by Edward Halliday in 1978, from a photograph)

certainly evident in BK's writing (and the same tendency can be seen in his disciple, Bert Sakmann, who, on being asked to speak to a distinguished philosophical society, told them that he actually preferred the motto of the Royal Society, *Nullius in Verba*, to philosophical speculation). His preclinical exams, taken in 1931, were entirely *viva voce*, the anatomy examination being conducted by Hans Held (of 'calyx of Held' fame), and the physiology exam by Martin Gildemeister.

After his preclinical exams, Katz combined his undergraduate work with part-time physiological research, under the supervision of Martin Gildemeister (1876-1943) who was interested in mathematical approaches to physiological phenomena. Working in the lab also had the advantage of keeping him away from the increasingly open anti-Semitic views of some of his fellow students. His work was on muscle stretch and impedance, and although he described the work as a 'prenatal effort', it resulted in two papers in *Pflügers Archiv*, which secured his MD degree and also led to his being awarded the Siegfried Garten prize. This was in 1933, the year Hitler came to power, and Gildemeister was forced to announce publicly that the prize could not be given to a 'non-Aryan' student, though he later gave Katz the prize money in private.

At some risk, Katz decided to complete his medical degree (1934) in Leipzig. During 1934 he had read A.V. Hill's Thomas Huxley lecture (given in Birmingham on 16 November, 1933), and had realised that the work he had been doing had some slight relation to work being done in Hill's lab at UCL. He had also read the correspondence between A.V. Hill and Johannes Stark, who had been an eminent physicist, but by this time was no more than a Nazi scientific Gauleiter. When Stark tried to defend the Nazi regime against Hill's criticism of their dismissal of Jewish scientists, Hill ended the correspondence by noting that gifts of money had been received in response to his appeal for assistance to help colleagues who had been driven out of Germany, but he was uncertain whether these donations were the result of his own eloquence, or rather should be attributed to Professor Stark's arguments, and he felt sure that some thanks were due to Professor Stark on this account. Katz quotes Hill as saying 'Laughter is the best detergent of nonsense' and goes on to say that these things 'gave me the first glimpse of A.V. Hill's personality, and I found it so attractive that I made every effort to go and work with him as soon as I could'. After working briefly in a Leipzig Hospital, at the beginning of February 1935, Bernard Katz packed his bags, took a third class train ticket to Holland, and then the Flushing-Harwich ferry. He was 23 and had only what he carried, a temporary British visa, his League of Nations stateless-persons pass, a letter of recommendation from



Working on squid axon, with Hodgkin, Plymouth Marine Lab, 1948 (Photo by Silvio Weidmann)

Martin Gildemeister and £4 in his pocket.

The next day, Katz climbed the stairs at University College London and met A.V. Hill for the first time. Hill was a remarkable man, not only a great scientist (he had received the Nobel prize, with Otto Meyerhof, in 1922), but also a statesman who took a large role in helping refugees in the pre-war period (see Katz's Biographical Memoir of Hill, 1978). It is very clear that Hill lived up to Katz's highest expectations. In his autobiographical essay Katz says 'It was an outstanding piece of good luck to have been taken on as an apprentice to A.V. Hill; it was the decisive influence on my life and career . . . He was the person from whom I have learned more than anyone else, about science and about human conduct. . . A.V. Hill was the most naturally upright man I have ever known. . . To be associated with a man of his stature at a formative period of one's life is indeed a great gift of fortune'. He described these first years in Hill's lab, between 1935 and 1939, as 'the most inspiring period of my life'.

Katz set to work at UCL on both nerve and muscle. Within a year his first paper with Hill appeared in *Proceedings of the Royal Society* (Hill *et al.* 1936). The full text of this, and of his many other papers in Royal Society journals are available on the JSTOR web site, though sadly his major papers in *The Journal of Physiology* are not yet so easy to obtain. Max Bennett of Sydney University has written a nice summary of Katz's scientific work (http://www.ibro.org/secondary/worldnews/index.asp?m=v&n=1005).

Shortly after getting his PhD at UCL, and a month before the start of the Second World War, he left Britain for Australia, where he worked with John Eccles and Stephen Kuffler. The work of Katz, Kuffler and Eccles in Sydney in 1940 and 1941 was, as Bennett points out, 'the beginning of a new era in synaptic physiology after the one begun 50 years earlier by Langley and Sherrington'. Use of more sophisticated electrical techniques allowed them to show, using an analysis provided by A. V. Hill, that transmitter action is very brief, and that most of the decay of the endplate potential occurs in the absence of transmitter. This became one of the basic beliefs about fast synaptic transmission for decades to come; it is undoubtedly true at the neuromuscular junction and at many (probably not all) central synapses.

Katz remained in Australia from 1939 to 1945, and in 1941 became a naturalised British citizen, so obtaining his first real passport. Soon after, he enlisted with the Royal Australian Air Force, and served as a radar officer on Goodenough Island, New Guinea, in the Pacific war against Japan.[1] 'The commanding officer of 305 Radar Station from October 1942 to March 1943 was Pilot Officer Bernard Katz' (http://rspas.anu.edu.au/papers/sources.html). John Eccles comments, in a letter sent at the time of BK's retirement, that 'In his nine months on Goodenough Island, behind the Japanese lines his station was never off the air'.

Later he met Marguerite Penly, known as Rita, who, incidentally, was not Jewish. They were married straight after the war. A month after the wedding he got a telegram from A.V. Hill inviting him to return to UCL as Henry Head Fellow of the Royal Society and assistant director of research in biophysics.

Katz returned to UCL in 1946, and

Pilot Officer Bernard Katz on the beach where a landing was made to reach Mwananoia (on north shore of Goodenough Island)

[1] Goodenough Island, Allied codename: MICROCOSM, formerly MORATA, one of the D'Entrecasteaux Islands, 20 miles (32 km) across Ward Hunt Strait from the eastern tip of New Guinea, in the Solomon Sea, southwestern Pacific. A part of Papua New Guinea, it lies northwest of Fergusson Island across Moresby Strait. The forested volcanic island, measuring 20 by 15 miles, rises to more than 8,000 feet (2,400 m) in its central mountain range. The island was visited in 1873 by Captain John Moresby, who named it after Commodore James Graham Goodenough. Occupied by Japanese troops for several months in 1942, the island was captured by Allied forces, who built Vivigani airstrip (open to commercial service since 1963).

his early work included the discovery of the phenomenon of inward ('anomalous') rectification. He also started a collaboration with Alan Hodgkin that led to the discovery that the overshoot of the action potential results from an influx of sodium ions.

In 1952 Katz succeeded A.V. Hill as Professor of Biophysics at UCL, where he headed a department of outstanding distinction until 1978. In the same year he was elected a Fellow of the Royal Society

The 1950s and 1960s were a golden era of important discoveries. With Paul Fatt it was established that acetylcholine, acting on receptors at the endplate, opens 'aqueous pores' in the muscle membrane. This was one of the roots of the modern idea of 'ion channels', though that term did not come into common use until later. During the 1950s, spontaneous miniature synaptic currents were observed (with Paul Fatt) and the essential facts about quantal transmitter release were established. For pharmacologists, his suggestion of a mechanism for partial agonism (del Castillo & Katz, 1957) was seminal. So was the first rigorous demonstration, by his PhD student Donald Jenkinson, that tubocurarine was a competitive antagonist, in a study that applied to the neuromuscular junction the methods devised by BK's fellow refugee at UCL, Heinz Schild.

BK's perceptiveness in distinguishing the important from the unimportant was legendary. He realised the small and unpromising spontaneous blips recorded at the endplate (miniature endplate potentials) were not just recording artefacts, but a phenomenon that eventually gave rise to the discovery of quantal transmitter release. A similar feat came 20 years later when he noticed that the increase in the noisiness of the recorded signal when acetylcholine was present was not as boring as it looked, but contained interesting information. His work on noise analysis with Ricardo Miledi in the early 1970s provided us with the first, albeit indirect, information about how single ion channels behave, and that allowed many of the remaining gaps in our knowledge of synaptic transmission to be filled in. Bert Sakmann arrived at UCL as this work was going on and relates how there was much discussion about whether recording from a single channel might one day be achieved. This of course, is something that Sakmann, with Erwin Neher, achieved not much later, in 1976, work that also got a Nobel Prize in 1991.

Portrait done in 1997, by Jenny Hersson-Ringskog (then an undergraduate student in Physiology-Pharmacology). The original hangs in the Starling room at UCL

The Bernard Katz building at UCL

The Orden Pour le mérite für Wissenschaften und Künste, awarded in 1982

At UCL all the important features of synaptic transmission were established, and subsequently many of these principles have been found to be true in the brain too. The influence of his work is inestimable, not only in physiology, but also in pharmacology, in which he laid down some of the most important fundamental principles. He was justly rewarded by, among many other honours, the Nobel Prize in 1970, jointly with Ulf von Euler (of Sweden) and Julius Axelrod (of the United States), 'for their discoveries concerning the humoral transmitters in the nerve terminals and the mechanism for their storage, release and inactivation'.

Katz's retirement in 1978 certainly did not mean the end of his influence. He continued to referee papers (with an astonishing speed – often within a day or two), and he took a direct and lively interest in new developments for many more years. In the 1980s I remember him coming, almost running down the stairs, asking to see David Ogden (at that time a post doc in my lab), because he'd seen an abstract that David had submitted for a Physiological Society meeting and wanted to discuss it. During that time, too, I spent two hard weeks working on the mathematics in a paper about sodium channel inactivation because BK had asked about some details, and somehow if BK asked, it was inconceivable to say that one was busy. I personally owe him a great debt because his penetrating questions about the meaning of a 1977 paper that he read, before it was submitted to *Proceedings of the Royal Society*, led to a whole new field of work for me.

At UCL, Katz is remembered by the beautiful portrait drawn by an undergraduate student, by the creation of the Bernard Katz Chair of Biophysics (at present held by

BronzeTafel at the University of Leipzig

Jonathan Ashmore), and by the naming of a building in his honour.

Bernard Katz's work has been recognised in his birthplace in many ways, despite his never having been a German citizen. He was awarded the 'Orden Pour le mérite für Wissenschaften und Künste' (similar to the British Order of Merit) in 1982. This prestigious award was originally a military honour, but its military function ended in 1918, and the civilian version, founded by Frederick IV of Prussia in 1842 with the advice of Alexander von Humboldt, was reinstated in 1922. The charter of the award says 'The number of knights of this peace class is confined to 30 Germans; there may also be 30 foreign knights' (http://www.orden-pourlemerite.de/).

In 1990 Katz was given an honorary doctorate by his *alma mater*, the University of Leipzig, and in 2000 a bronze tablet was unveiled in the University grounds, by the Oberbürgermeister of Leipzig, the Dean of the Faculty of Medicine and the chairman of the Albertiner Bund ('old boys') of the König Albert Gymnasium. The existence of this memorial, and the wording on the plaque, was dependent on the efforts of, among others, Frederick Rose (now in Toronto), one of the few surviving 'Albertiner'. The inscription states (in translation) 'In honour of Sir Bernard Katz', followed by a brief CV which includes the words '1935 Emigration to England, because of repression on the grounds of his Jewish origin'.

BK did not himself supervise many PhD students (Paul Fatt, John Nicholls, William Burke, Bob Martin, Donald Jenkinson and Stuart Bevan), all of whom went on to do eminent work. But his department became a Mecca for postdoctoral students from all over the world. His influence on the training of a large number of the world's greatest scientists was huge.

BK's seriousness could sometimes make him appear forbidding, and there are many stories about experiences, sometimes quite traumatic, of presenting to him the first draft of a paper. Equally there are many stories of his jokes and light-hearted asides that punctured the pomposity of boring committee meetings. His lack of pomposity is nicely illustrated by an occasion in 1974 when a young PhD student was giving his first demonstration at a Physiological Society meeting. The demonstration involved voltage-clamp of muscle fibres, and his supervisor had properly suggested that when a visitor came in to see the demonstration, he should be asked if he was familiar with the methods before launching into an explanation. A middle aged man came in and 'I went through the motions and asked him if he was familiar with the method, to which he replied "..a little...". I then explained my demonstration, to which he listened patiently'. It was only later that the student discovered that his visitor had been BK, who had spared the student's blushes by not revealing his identity. It was the universal experience of his colleagues that he was a person with enormous enthusiasm, always willing to discuss with the most junior of them the details of their work and to offer advice. There can be few in the field of synaptic transmission and ion channels who have not benefited from his wisdom.

Although Katz spoke little English when he first arrived at UCL, his writing style was exemplary, and he was able and willing to correct the execrable style adopted by some native speakers of English. His prose was simple, straightforward and unpretentious, yet very precise, something that he attributed to his teachers at the König Albert Gymnasium. He would not use a long word when a short one would do, When it was proposed at the 1954 Mill Hill meeting of the Physiological Society that the terms 'sympathetic' and 'parasympathetic' should be replaced by 'orthosympathetic' and 'parasympathetic', his reaction to this quite unnecessary lengthening was to suggest 'sympathetic' and 'unsympathetic '(Bynum, 1976). His writing was totally free of the hyperbole that litters so many papers now, and also free of 'guest authors'. Those scientific bureaucrats who wish to force everyone to work in enormous groups should note that his papers rarely have more than two authors.

Bernard Katz had an uncanny knack for picking the important part of a problem, and to leave the rest of us dotting 'i's and crossing 't's. Every new entrant into the field should read his work from beginning to end.

David Colquhoun
Department of Pharmacology
University College London

Acknowledgements

The historical facts in this article are largely culled from Bernard Katz's autobiographical essay, published in 1998. I have also had generous help from his sons, Jonathan and David, and many of his colleagues and coworkers.

References

The History of Neuroscience in Autobiography, Larry R. Squire (Editor), 607pp, Academic Press 1998 (ISBN: 0126603014).

Katz, B. (1978) Archibald Vivian Hill 1886 – 1977. *Biographical Memoirs of Fellows of the Royal Society*, **24**, 71-149.

Bynum, W. F. (1976) A short history of the Physiological Society (1926 – 1976). *Journal of Physiology*, **263**, 23 – 72.

Secret Action of 305. The Story of RAAF Radar Station No. 305 in the War with Japan. Norm Smith & Frank Coghlan (1989). An occasional series (No. 1) published under 'Heritage Series' by the Royal Australian Air Force Museum (ISBN 1 86252 594 3), with foreword by B. Katz