



Denise Albe-Fessard • Julius Axelrod
Peter O. Bishop • Zachare H. Bullock
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The History of
David H. Hubel • Herbert H. Jasper
Neuroscience in
Sir Bernard Katz • Seymour S. Kety
Autobiography
Benjamin Libet • Louis Sokoloff
James M. Sprague • Curt von Euler
John Z. Young
Volume 1

Edited by Larry R. Squire

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The History of Neuroscience in Autobiography

VOLUME 1

Edited by Larry R. Squire

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Sir Bernard Katz

BORN:

Leipzig, Germany
March 26, 1911

EDUCATION:

University of Leipzig, M.D., 1934
University College of London, Ph.D. (Physiology, with
A.V. Hill, 1939)

APPOINTMENTS:

Sydney Hospital, Australia (1939)
University College of London (1946)
Professor of Biophysics Emeritus, University College of
London (1978)

HONORS AND AWARDS:

Fellow, Royal Society of London (1952)
Copley Medal, Royal Society (1967)
Fellow, Royal Society of Physicians (1968)
Foreign Associate, American Academy of Arts and
Sciences (1961)
Nobel Prize for Physiology or Medicine (1970)
Foreign Associate, National Academy of Sciences USA
(1976)
Ralph W. Gerard Prize, Society for Neuroscience (1990)

Sir Bernard Katz carried out fundamental studies of the neuromuscular junction. He established the quantal nature of neurotransmitter release, and described the mechanism of synaptic transmission.

Sir Bernard Katz

To tell you the truth, sir, we do it because it's amusing!

In October 1924 my great friend and teacher, A.V. Hill, made his first visit to America. He was known among his colleagues as one of the leading physiologists. Around that time, at the age of 37, he had received a Nobel Prize for his work on energy production in living muscle, which had led to invitations to visit the United States and lecture on this subject. The first evening after his arrival (one traveled by sea, and jet lag was unknown), he gave a public lecture to a scientific society in Philadelphia on "The Mechanism of the Muscle." At the end of his talk, a serious-looking elderly member of the audience got up and asked disapprovingly what practical use the speaker thought there was in his research. Professor Hill considered for a moment whether he should enumerate the many cases in which immense and obvious benefit to humankind had come from discoveries and experiments that were made purely to satisfy the intellectual curiosity of the investigator, but now I let him tell his own story:

To prove to an indignant questioner on the spur of the moment that the work I do was useful seemed a thankless task and I gave it up. I turned to him with a smile and finished, "To tell you the truth we don't do it because it is useful but because it's amusing." The answer was thought of and given in a moment: it came from deep down in my soul, and the results were as admirable from my point of view as unexpected.

My audience was clearly on my side. Prolonged and hearty applause greeted my confession. My questioner retired shaking his head over my wickedness and the newspapers next day, with obvious approval, came out with headlines "Scientist Does It Because It's Amusing!" And if that is not the best reason why a scientist should do his work, I want to know what is. Would it be any good to ask a mother what practical use her baby is? That, as I say, was the first evening I ever spent in the United States and from that moment I felt at home. I realized that all talk about science purely for its practical and wealth-producing results is as idle in this country as in England. Practical results will follow right enough. No real knowledge is sterile. The most

useless investigation may prove to have the most startling practical importance: Wireless telegraphy might not yet have come if Clerk Maxwell had been drawn away from his obviously “useless” equations to do something of more practical importance. Large branches of chemistry would have remained obscure had Willard Gibbs not spent his time at mathematical calculations which only about two men of his generation could understand. With this faith in the ultimate usefulness of all real knowledge a man may proceed to devote himself to a study of first causes without apology, and without hope of immediate return.

It was more than 10 years later that I came to London to join A.V. Hill’s laboratory to serve my apprenticeship with him. That time, 1935 to 1939, was the most inspiring period of my life. Hill’s personality had a profound influence on me; this influence is neatly summed up in the words that he addressed to his disapproving critic in Philadelphia. My own experience has taught me and has fully confirmed the truth of Hill’s provocative statement. We are, in fact, “professional amateurs,” lucky enough to maintain our amateur status throughout our professional scientific career. And if you think this is self-contradictory, I would remind you that a straight and simple definition of an “amateur” is someone who loves his work and finds great entertainment in what he is doing.

Nowadays such sentiments may be called arrogant, immoral, socially unacceptable, or elitist. I will not defend myself against such nonsense. I know that scientific research has become much more expensive during the last 50 years, and that scientists’ intentions have therefore become subject to more intense public scrutiny. It is true that the type of work that Hill and many of his contemporaries were doing in the 1920s and 1930s was done on a shoestring budget, costing practically nothing, and the public therefore was more tolerant of those eccentric researchers who did it just to amuse themselves. Today it would be more difficult to get away with a remark of such apparent flippancy. But I am convinced that Hill’s response still truthfully reflects the primary motivation of many of the most productive investigators in basic science. For those who have to decide whom to support in science, let them recognize that much of the best scientific work will continue to be done because of the thrill and excitement of ending up, after a hard struggle, with a successful experiment, with a discovery shedding new light on a problem—it will be done because it is interesting and amusing.

Growing up a “Stateless Alien”

I was born in March 1911 in the town of Leipzig in the middle of Germany. Although I was also brought up there, I never acquired German nationality. For the first six and a half years of my life, though quite unaware of

it, I was in fact a subject of the Russian Tsar. My father, who was born in Russia in the town of Mogilev on Dnjepr, had left the country in 1904 at the time of the Russo-Japanese War and the internal unrest it caused, and a little later settled in Leipzig. He had never bothered to apply for naturalization in Germany. Doing so was not a simple formality, and he most likely considered it a far too complicated and unnecessary procedure.

My father was engaged in the family business of the fur trade, of which Leipzig was an important international center. His business obligations and social contacts did not require him to travel outside the German borders, and even though we were officially regarded as "enemy aliens" during World War I (1914-1918), this did not seriously interfere with his activities. After the Russian Revolutions of 1917, our family members—like other Russian expatriates who did not opt for Soviet citizenship—lost their nationality and became stateless persons. This circumstance had few practical consequences unless we wanted to go on foreign travel, because the strict visa requirements made life quite difficult. I did not realize until I was a teenager that I was growing up as an "alien," and not as a German citizen. Although I resented this, I accepted it as a fact of life, which I thought I would be able to remedy in due course. I did not foresee that I was going to remain stateless and without a proper passport for the first 30 years of my life.

Although my alien status made it difficult for me to obtain the necessary documentation to travel and to emigrate to England, it made it much easier to tear up my few shallow roots that remained in Germany, the country of my birth, and to strike new roots in England in 1935.

I had a rebirth at the age of 24 when I arrived at the port in Harwich, England, one afternoon in February 1935. I had escaped from Hitler's Reich and my arrival in England was a terrifying experience. His Britannic Majesty's Officer of Immigration, though courteous and apparently quite sympathetic, questioned me for a long time. All the other passengers had gone through immigration while I still was being interviewed, and I feared that not only was I going to miss the train to London, but that I was going to be sent back to "Nibelheim" ("Nibelheim" is a grim scene in Wagner's "Rheingold," reminiscent of a concentration camp, with the dwarf-like Nibelung race being used as forced laborers, hammering away at the stone wall of a mountain cave. To me, Nibelheim is an apt description of Nazi Germany). But in the end the officer relented and, to my immense relief, allowed me to enter the United Kingdom. My difficulty was that I had no passport, but only a "Nansenpass," the green identification certificate that was issued to stateless persons by the League of Nations' Commissioner for Refugees.

The next day, I climbed a long staircase to the top floor of the physiological building of University College of London and presented myself to Professor Hill. He received me as a new member of his scientific family.

Having got away from dark and hostile surroundings, the contrast was a tremendous experience for me. I felt a little like David Copperfield when he arrived, bedraggled and penniless, at the home of his aunt and was put into a clean hot bath. This was a new life for me, and Hill's laboratory became a precious home. I was fortunate in many respects. I had no real scientific credentials to show; Hill took me on "as an experiment" on a simple hunch. Even as a physiologist, the day of my acceptance in his laboratory marked my transition from an embryonic to a postnatal stage.

Not until much later did I realize how much I owed my father for his decision not to seek German citizenship, or perhaps for his casual inactivity in this matter. This circumstance proved of inestimable advantage to me after the outbreak of World War II in 1939. This time, being a stateless person of Russian descent, I definitely was not regarded as an enemy alien by Australia or England, and I was able to become a British subject and an Australian citizen and soon after to enlist and to serve with the Australian forces.

Family Ties

I was very attached to my father—a good looking, humorous person who took life easy and was courteous and straight with his friends as well as his colleagues. He was, in fact, well liked by everybody who knew him. Yet like most nice people he lacked drive and was not a particularly successful business man. Any drive or initiative that I have inherited probably came from my mother's side.

I cannot trace my family back for more than two generations. They were all Jews of Eastern European, Ashkenazi origin. I have faint memories of my maternal grandmother who came from Warsaw and lived in a flat above my parents in Leipzig. I had two uncles whom I knew well, one on each side of the family, and I was on particularly good terms with my mother's younger brother whom I liked very much. He served as a noncommissioned officer in the German Army during World War I, later trained in the diamond trade, and moved to the business centers in Amsterdam and Antwerp. He traveled a great deal around the world, spoke several languages fluently, and possessed a strong sense of humor which appealed to me.

My father came from a large family. Grandfather David Katz was, judging from his photograph, a tall patriarchal man, which I thought fit his name. The surname Katz is common among Jews of Russian origin. The name has nothing to do with the German word for cat (*Katze*), but is an abbreviated form of the Hebrew words *Cohen Tsedek*, signifying a particular section of priests who claim to be descended from Aaron (the brother of Moses) and who have special religious duties and privileges. I, however, was brought up in a completely "unorthodox" and liberal way. My paternal grandfather, David Katz, married twice and had 15 children. He

was a well-to-do and respected fur merchant in the town of Mogilev. He barely survived the Russian Revolutions and died in his 90s in 1919. I have little knowledge of, and no contact with, the Russian branch of my family. I had many other relatives, among them several grandchildren of David Katz who had left Russia and gone to Leipzig, London, Milan, and New York, and were mostly engaged in the fur trade. The London branch was very generous and helpful when I arrived in England in 1935.

Dissension among Jewish Society in Germany

Before Adolf Hitler rose to power, there was a fairly sharp class distinction in the Jewish society in Germany, between the indigenous "German Jews," or more precisely those who regarded themselves as established German citizens of Jewish faith, and the "Ostjuden," the more recent immigrants from Russia and Poland who tended to be looked on as somewhat of an embarrassment by their brethren and as not fully assimilated to German culture. This distinction sometimes created social friction and mutual resentment between the two classes, which struck me as quite ludicrous. There were, however, antagonisms and recriminations of a more serious, political kind.

German Jews in their central organization (Central-Verein Deutscher Staatsbürger Jüdischen Glaubens) were preoccupied with defending their citizen rights against anti-Semitic propaganda. They felt threatened not only by racial attacks and vituperations from right-wing anti-Jewish groups, but also by the spread of Zionism which was prevalent among the the Ostjuden. The latter were critical and even contemptuous of the assimilatory tendencies of the "establishment." There were in fact no sharp boundaries between the two groups. Indeed, the founding father of modern political Zionism, Theodor Herzl, himself came from a culturally assimilated Viennese background. As later events proved, it was the Zionist doctrine that helped Jews maintain their morale and self-respect in an intensely hostile environment, not just during World War II, but beginning in 1933.

Realizing the irrational nature of racial hatred and particularly of anti-Semitism, it always seemed to me extraordinary that some of the native German Jews should have deluded themselves into believing that the root of all their exposure to hostility was the immigration of undesirable and ill-adapted co-religionists from Eastern Europe, the Ostjuden. This kind of self-indulging fantasy dies hard. After all that the Jews experienced in our lifetime, I was stunned when one of my colleagues—who comes from an established German-Jewish family and now resides in California—recently reasserted this belief to me in the strongest terms, and assured me of its historical accuracy and of his conviction that it is the Ostjuden who should be blamed for the misfortune that had befallen

German Jewry. He is a distinguished scientist and his statements made me ponder the peculiar sequestration of the human mind and its limited capacity for critical self-assessment.

School and University

The inter-war years in Germany can be roughly divided into three phases. The first, 1918 to 1924, was a period of revolution, continuing unrest, financial disaster, hyperinflation, and bitterness. The second phase, 1924 to 1929, was one of peaceful stabilization and gradual economic as well as political recovery. The third phase began with a second financial debacle, the Wall Street crash at the end of 1929, which had enormous international repercussions leading to years of mass unemployment, renewed unrest, and extreme political polarization until the takeover of Germany by Hitler and his Nazi thugs. The first two of these periods coincided with my school years and the third covered my life as a medical student at the University of Leipzig.

The immediate aftereffects of World War I and of the treaty obligations imposed at Versailles resulted in Germany's failure to pay the required war reparations, the occupation of the industrial district of the Ruhr by the French army, and a policy of passive resistance by the German government and people against French policy that could only be financed by hyperinflation (vast printing of increasingly worthless paper money), which led to the impoverishment of the middle class and left a legacy of bitterness and resentment. All these events were punctuated by abortive uprisings by German ultra-right wing groups that were countered by general strike and suppressed by the army.

This phase of revolution and attempted counterrevolution came to a sudden end when the newly appointed president of the Reichsbank, Dr. Hjalmar Schacht, managed to stabilize the currency in 1924 and instill new confidence in the nation's ability to survive and pay its way. During the next five years life became more quiet and peaceful, both in Germany and on the international political scene. The economy seemed to flourish, the extremist parties lost popular support, and even the anti-Semitic agitation fueled by Hitler and his followers seemed to subside and become latent for a while.

All this changed again after the worldwide financial disaster in 1929. A new wave of political extremism rose and led to violence in the streets. Until the spring of 1932, the German government, led by an able and courageous prime minister, Dr. Heinrich Brüning, managed to resist the onslaught of the rising Nazi party. But suddenly, by an amazing act of betrayal, Brüning was summarily dismissed by the Reichspräsident, the old Field Marshal von Hindenburg, who had owed his recent re-election to Brüning's personal efforts. From that moment, the takeover by Hitler seemed inevitable. At that time, in the summer of 1932, I began to make plans to emigrate after completing my medical course.

School Days, First Traumatic Shocks

I have only rather faint recollections of primary school, 1917 to 1921. I remember, at age eight or nine, challenging a teacher who had made a vicious and insulting remark about Russian Jews. He probably had not realized there was somebody in the audience who was likely to take offense, and he may have felt rather abashed to be taken to task. But my attack in the presence of witnesses clearly was an impermissible breach of discipline, and I paid for it by having my life made quite miserable during the rest of the term.

The first time the disadvantages of being a foreigner were brought home to me was at age nine. I still remember the occasion quite vividly. I sat for the entrance exam for a fashionable secondary school, the Schiller Real-Gymnasium, a sort of modern grammar school with a good scholastic reputation, situated in an affluent suburb of Leipzig. The written examination took place in the morning, and I thought it had gone rather well. In the afternoon, all the boys assembled with their parents in the big hall and the names of the successful candidates were called out in order of merit. I waited, and waited, to hear my name. Gradually my heart sank. Could I possibly have failed? But how? The others all left and I looked at my father, wondering what could have happened. Eventually he received a letter from the headmaster informing him that I had passed the examination with good marks, but unfortunately, because of the heavy pressure of applications, they could not take a foreigner.

At the time that did not seem too bad, it was only later that I began to wonder why they had let me take the exam in the first place. I was not altogether surprised when an acquaintance who seemed to know what was going on at that school told me that my examination marks had actually been a little too good for the headmaster, who considered it detrimental to the reputation of his school to have the new intake of pupils topped by a Russian Jew.

The headmaster's decision not to accept me turned out to be a blessing in disguise. On the basis of his letter and of my examination record, I was accepted without further tests by the König Albert Gymnasium, a classical "humanistic" school that specialized in Latin and Greek. The school was regarded as old-fashioned and so presumably had a smaller intake of pupils. I never regretted attending. The school was an easy walking distance from my home—which was not unimportant because we started early, even during the dark and cold winter mornings. But more important, I became fond of the school and still remember some of my teachers with gratitude and affection.

In retrospect I enjoyed the classical curriculum. Now I often wish I had the time and ability to read the works of the great Greek and Latin writers and poets in their original language. I also feel that I should have

made an effort to pick up more of the advanced mathematical teaching that was offered at the school, even at the expense of some of the classics.

I remain greatly indebted to some of the language masters, in particular to Hans Leisegang and Hans Lamer. Lamer was the headmaster, a devoted classics scholar with an international reputation, who instilled in me a real appreciation of the great Greek and Roman poets and gave me a feeling for my classical cultural heritage. Leisegang had an even greater influence on me. It was he who made me treat words and phrases with respect and to use the language as a precision tool. I might describe him as an ultraconservative reactionary—a representative of a German military officers' caste—but he was also a great teacher and scholar, and a man of strong principles. The standard of the school, old-fashioned as it was, can be gauged from the fact that several of its masters received calls to university chairs. Leisegang himself, who was a part-time lecturer in philosophy at the University of Leipzig, went from the school to the chair of philosophy at University of Jena, in 1931. He later was imprisoned for having made derogatory remarks about Hitler (as I recall, he publicly objected to the “corporal” taking up a prominent position at the funeral of Field Marshal Hindenburg). It was Leisegang who gave me a thorough grounding in the development of German literature and philosophy, from the idealistic and romantic schools to dialectic materialism and psychoanalysis, and he did this in a way that struck me as balanced and almost objective.

The normal high school curriculum took nine years. I did well in the academic subjects and, about halfway through the König Albert, was encouraged to skip one year so that I spent just eight years (1921–1929) there. My school reports were very good except in gym and singing, in which my performance was deplorable and from which I tried to extricate myself. This deficiency may have had something to do with the fact that I was growing up without any brothers or sisters. I was never a loner, but I kept away from congregational activities of any kind. I had good friends, but usually only one at a time. My out-of-school activities consisted mainly of reading and walking. I liked swimming, preferably at the seaside, when there was opportunity for it. I joined a football club, but did not make much headway with the game. I enjoyed the theater and became an opera fan, being particularly keen on Wagner's dramas. After several years I became put off by his medieval romantics, and thereafter I felt more attracted by the beauty and dramatic power of Verdi's genius.

At age eight my mother tried to make me play the piano; but I soon abandoned it. Seven years later I started again with better tuition and understanding. Although I never became proficient, I enjoy playing and it has given me a welcome diversion from intellectual tasks. Another hobby, which I acquired at the age of 16, and to which I became temporarily addicted, was the game of chess.

During high school I experienced several traumas. They stand out vividly in my memory and they were reinforced and accumulated during my undergraduate years at the university and led to my progressive alienation from Germany. I was shocked at the assassination of Walter Rathenau, the Jewish foreign minister, by anti-Semitic youngsters in the summer of 1922. Rathenau was the first patriotic German Jew who had risen to high ministerial office, and it was unacceptable and intolerable to a large section of the German people.

In the same year, a very unpleasant boy by the name of Rocca joined my form at school. He came from a viciously anti-Semitic family, and I was puzzled and dismayed to find that he tried to make life difficult for me—spreading slanderous insinuations behind my back—though he had no great success and was unpopular among my schoolmates. I could not make out why he used me as a target for his venomous hatred. In retrospect, I suppose he resented the fact that he himself belonged to an ethnic and religious minority in a predominantly Protestant Saxon population, but this hardly explains it. At that time, a large underground exhibition hall had been built below the old market square in Leipzig. One day, after I had been absent from school for a religious festival, Yom Kippur, a friend told me that Rocca had, during my absence, called the boys together and informed them of a marvelous 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. The boy who informed me was aghast and horrified and thought he ought to warn me about that venomous young devil. This episode has never been erased from my mind, and it gives an indication of ideas some people were harboring in their heads for 20 years before they were able to put them into practice.

The effect of these incidents became stronger during the next 10 years, though it was not until the dismissal of Heinrich Brüning by Hindenburg in 1932 that I finally decided there was little future for decent people, and none at all for me, in the Germany of the time. At the age of 11, however, my reaction was different. What impressed me was not so much the threat of violence—the situation was too far from reality at the time. I could not visualize such events actually occurring. What did upset me was the fact that a person with whom I was compelled to be in almost daily contact, should be possessed by such unprovoked venomous hatred toward me. This I found bewildering and hurtful.

In 1926, at the age of 15, I jumped a class and found myself among a group of older boys. I shared a desk with another Jewish scholar, Heinz Wydra, with whom I formed a close association during my remaining school years and who had a considerable influence on me. He was a strong chess player and acquitted himself well in local tournaments and club matches. It

was he who taught me the game, and we managed to play games in school during unimportant or boring lessons. I have never advanced to more than average club-player strength, but I can say that I have derived great entertainment and excitement from the occasional good game, to the extent that I usually lose a night's sleep replaying the moves and their alternatives in my head. My addiction to chess was replaced, for nearly half a century, by a similarly obsessive addiction to physiological experiments. The excitement produced by the occasional successful experiment was similar to that of a good performance at chess. In both cases, the sudden flash of insight after a long struggle in the dark, the intuitive vision of a solution to a seemingly intractable problem, is exhilarating. The trouble with chess is that it becomes a time-consuming occupation and is not compatible with other similarly demanding work, such as scientific research or even, as I soon discovered, with an undergraduate medical university course.

During my last three school years, we had to choose between a continuation of the classical linguistic course, and a mathematically and scientifically oriented curriculum. I chose the former which gave me more free time, and in the afternoons I drifted off to one of the cafés in Leipzig that had been invaded by chess players. How these establishments could manage to exist, catering to chess enthusiasts who sat around for hours consuming one cup of coffee, I have never been able to figure out. I spent quite an undue amount of time in those places, time that could have been better occupied, had I chosen the more difficult option at school. It was not the lack of natural science training that I later came to regret. This deficiency was made up quite satisfactorily by excellent elementary science teaching in the preclinical university course. But the weakness of my grounding in mathematics was something for which I have never been able to compensate. As to the time misspent on chess, this came to an abrupt end when I started my medical course, and I did not seriously resume this hobby until 50 years later, after my retirement from academic office.

My friendship with Heinz Wydra had another and more important consequence in that he succeeded in converting me to active Zionism. He started by persuading me to read the works of Theodor Herzl and introducing me to a Zionist youth club and later to a student organization. Until the age of 16 my contacts with the Zionist organization had been slight. My father was a sympathizer and supported the movement without being actively engaged. My own involvement increased slowly at first, but it became sufficiently strong to give me a powerful moral backing during the rise of the Nazis, which enabled me to treat antisemitic insults with complete contempt. Wydra himself emigrated to Palestine after completing his legal studies, and after the war played an important part in the economic development of Israel.

During my last year at school, I had to make up my mind what line of work to pursue during my lifetime. In those days such a decision carried for most of us a heavy responsibility. We had to commit ourselves irre-

versibly for all practical purposes. The thought of going along by trial and error, switching from one course or from one profession to another, horrified me and would not have been financially possible for my parents. My father accepted that I was not going to follow in his footsteps and join the next generation of fur traders, and my performance at the Gymnasium pointed to some sort of academic profession. A successful pass of the *Abitur*, the high school leaving examination, entitled one to enter any German university in any faculty and any subject regardless of previous specialization, or rather lack of specialization at school. There was no *numerus clausus*, no entrance examination or special interview barrier, with the result that some university courses became heavily and detrimentally oversubscribed.

My high school teaching might have inclined me toward the study of philosophy. I had done no natural science at all and had no high regard for it. But I felt that sooner or later I might have the responsibility of supporting my parents. My father, of whom I was very fond, had been a good companion but not a very successful business man, and I did not feel confident about his financial security. So I had to think of something more practical than philosophy, and it came down to a choice between medicine and the law. I talked to a few people, went to some public lectures at the university, and in the end chose to become a medical doctor and started my course at the University of Leipzig in April 1929. One of the factors that influenced me was an impressive lecture given by Professor Victor von Weizsäcker¹ on the social impact of medicine, which showed me that there was—potentially at least—a great deal of intellectual satisfaction to be derived from the practice of medicine.

Life as a Medical Student, 1929–1934

As soon as I entered the preclinical course at Leipzig, I found my timetable almost fully occupied, starting at 7 a.m. with botany and going on until the late afternoon in the anatomy dissection room. Fortunately students enjoyed a considerable amount of academic freedom and could skip lectures that they found too boring or redundant. Nevertheless, it meant an end to the chess sessions in the cafés.

During my first year I had to make up for my total lack of knowledge in the natural sciences. The medical students joined the scientists in their elementary courses in botany, chemistry, physics, and zoology, in addition to the preclinical subjects of anatomy, physiology, and biochemistry. I found

¹Victor von Weizsäcker (1886–1957) was a distinguished clinical neurologist, and as a moral and social philosopher, he was widely known and respected for his freely expressed liberal views. He was the uncle of the former president of the Federal Republic of Germany. In 1935, after I joined A.V. Hill's laboratory, I discovered that Victor von Weizsäcker had earlier in his life done some important physiological research and had preceded me, by some 21 years, as a pupil and collaborator of A.V. Hill.

it an advantage not having taken science in high school. All the material I was presented with during my first year at the university was fresh and new, some of it taught by persons of the highest caliber, and there was a good deal that I found absolutely fascinating. I had the benefit of an outstanding physics teacher, the famous Peter Debye (who a few years later received a Nobel Prize in chemistry). He gave his lectures, accompanied by experimental demonstrations, every morning from 8 until 9. Debye was both a great scientist and a great showman who took visible pride in his lectures. He was a marvelous expositor of facts, ideas, and theories. Debye clearly enjoyed teaching as much as research, and he showed his delight in all the successful tricks that he demonstrated in class with a constant smile on his face.

I spent a large portion of my free time in the Institute for the History of Medicine. The institute was directed by Henry Sigerist who, in 1932, followed an invitation by W.H. Welch to found a similar institute in the United States, at Johns Hopkins University. Sigerist was assisted by Owsei Temkin, a great scholar who joined and in due course succeeded Sigerist at Johns Hopkins. I have retained the greatest admiration for Temkin and always think of him as my teacher as well as a good friend, even though in later years we have had only few occasions to communicate. The institute provided a meeting place for the more civilized among the medical students, with opportunities for seminars and discussions on wide-ranging subjects, in the medical as well as the historical and literary fields.

My introduction to the natural sciences had a tremendous effect on my general outlook on life and human activities. I suddenly realized 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 out of obscurities. I was influenced strongly by the superb collection of Helmholtz's public lectures. In these, Helmholtz—one of the greatest experimental scientists of all time—explained difficult subjects with exemplary clarity.

During my undergraduate days I succeeded gradually in extending my social contacts, and I formed some new friendships which survived beyond World War II up to the present day. During my first semester I encountered Rudolf Bachmann, a most congenial colleague with whom I established close and enduring rapport. He became an accomplished histologist and in the postwar years occupied the chair of anatomy at the University of Munich. After my emigration from Germany we lost direct contact for some 30 years, but we resumed our friendship in the late 1960s and I have been visiting him and his family frequently since then. We share an appreciation of the classics and of music, and we closely converge in our sense of humor and our detestation of pretentiousness and pomposity.

I made some good friends when I joined student camps on the Baltic coast in the summers of 1931 and 1932. These camps had been organized by members of the German youth movement and were attended by about 50 undergraduates (males and females), as well as a few university dons. I still remember the occasion when I had gone with a small group to a nearby railway station to pick up the famous physicist, Professor Friedrich Hund, and escort him to our holiday campus. There was general applause and hilarity when we introduced ourselves, bowing to each other in the formal German manner and solemnly announcing: “Katz”—“Hund”!²

The vacation camps were interesting. There were plenty of seminars and discussions among students of all faculties who argued about social and political problems and about the philosophical foundations of science and the humanities. These events were interspersed with music, swimming, sailing, and even a sea journey to the Hanseatic city of Danzig. One outcome of those holiday activities was that I fell hopelessly in love with an attractive German girl. When I finally brought the matter to a head, she wisely, and not unexpectedly, turned me down. My ensuing state of depression did not last long, because it soon was superseded by the advent of Hitler’s regime and I was forced to think hard and make a new decision about my future.

What helped me was that I had joined a Zionist students’ association which brought me into contact with the local leaders of the Zionist movement. For about a year I was employed on a part-time basis to run public appeals and manage the Jewish National Fund. The purpose of this organization was the acquisition of land for new settlers in Palestine. This job was, in fact, only one of the various part-time jobs that I held as a medical undergraduate.

During my first year at the university I found employment as an assistant to two medical practitioners who ran a joint practice in one of the suburbs of Leipzig. These practitioners specialized in a combination of subjects: ear-nose-and-throat as well as eye diseases. My colleagues were amazed to hear that, as a green preclinical student I was allowed, and even able, to learn the diagnostic techniques of otoscopy, laryngoscopy, and ophthalmoscopy, that I was dispensing routine treatment and even performing minor operations (some of the patients actually preferred me), and that I was earning useful pocket money on the side. During my later clinical years my timetable did not allow me to continue this “surgery practice.” Instead, I formed an association with a scientific journalist and publisher who asked me to supply him with suitable popular articles on medical and scientific subjects for distribution to the lay press. This arrangement enabled me, at the cost of late-night work, to earn not only pocket money, but also to maintain financial independence at home, during a time of considerable political upheaval.

²In German, it sounds as though the two natural enemies (cat and dog) are meeting for a hostile encounter.

I took my preclinical exams in six subjects (anatomy, botany, chemistry, physics, zoology, and physiology/biochemistry) in the summer of 1931. The examination system consisted exclusively of "vivas." The students were expected to form up in groups of four and present themselves to the examiner. Somehow it seemed the right thing for four Jewish students to get together and make up one such group. I do not think it ever occurred to me to approach non-Jewish colleagues for this purpose; this would have been far too embarrassing and was simply "not on." In 1931 there was no difficulty in making up a Jewish foursome. But for our clinical examination in 1934, we only managed to get three of us together, and this was not quite the correct thing. I remember the reaction of our revered professor of anatomy, Hans Held (a famous neurohistologist and, as leader of the neural continuity theory, a lifelong antagonist of the even more famous Nobel Prize winner, Ramón y Cajal). Held sadly shook his head when he found there were only three candidates presenting themselves for the examination in topographical (clinical) anatomy. He evidently could not work out the reason and asked us where the fourth member of the group was. There was a moment of embarrassed silence. I only just restrained myself from replying that, while we were numerically incomplete, we made up for it by being 100 percent non-Aryan!

The "viva voce" type of exam had its pluses and minuses, its efficiency depending very much on the idiosyncrasies and general intelligence of the examiner. During our preclinical tests, the assistant examiner in physics allowed one of my colleagues to bluff him with fictitious quotations from the literature. I did rather well in zoology, being able to recite the Latin names of various exotic animals, but when Professor Johannes Meisenheimer asked me what the common German name for "echidna" was, I could not tell him. He kindly overlooked it.

Two other incidents from my preclinical exams stand out in my memory. Professor Held tested us by confronting us with a hessian-covered formalin-soaked bundle of stuff, lifting one small bit of tissue with a forceps through a gap in the hessian cover and asking: "Was ist das?" When he had heard the answer, he would say every now and then: "Meinen Sie?" ("Do you think so?"), the meaning of which was somewhat difficult to interpret. Professor Martin Gildemeister in physiology had a very different technique. In our session, he took a wooden ruler, drew it sharply across the back of his hand and asked us: "What happens?" This question did not permit one to push a preset mental button and deliver an answer to a well rehearsed question from a book. It was rather disconcerting, but it gave us the opportunity to discuss why the skin would turn first white then red, the mechanism of the hyperemic response, the possible involvement of local chemical agents or of a nervous reflex, etc. Each of us answered brief questions in turn and, by the end of the conversation, Gildemeister had assessed the four of us and allotted marks which, on that occasion, varied between top grade and failure.

One of the highlights in the physiology course was the annual demonstration of an experiment that had been performed in the 1860s by Carl Ludwig (the most distinguished head of the school) and his Russian assistant, E. Cyon. The experiment showed the existence and the function of a sensory nerve—the depressor nerve of the heart—the impulses of which originate in the region of the heart, travel to the central nervous system, and elicit a reflex discharge of centrifugal impulses slowing and depressing the heartbeat. Ludwig was one of the great founders of the study of physiology, and many of his pupils established famous schools all over the world.

Ludwig's assistant, E. Cyon, was a very strange character whose peculiar career has been described in a fascinating article by George F. Kennan in *The American Scholar* (autumn 1986). Having previously read some anecdotes about Cyon—he had the reputation of being an accomplished swordsman and an occasional duelist—and knowing that he often was quoted in the scientific literature as “von Cyon,” I imagined that he was a somewhat eccentric aristocratic Russian who amused himself by taking up physiological research. From Kennan's article I learned that he was, like myself, of Russian–Jewish descent, had studied medicine, and had become a physiologist. Cyon later was appointed to a prestigious chair of physiology at the Medical/Surgical Academy in St. Petersburg, but after falling out with most of the students as well as the staff, he had to leave. He emigrated to France where he dropped out of physiology and became a political agent, continuing to make few friends and numerous enemies. He clearly was an able scientist and had been acclaimed as an inspiring teacher by the young I.P. Pavlov. But Cyon was a difficult and resentful character, and probably his own worst enemy. I was fascinated and rather shocked by Cyon's story. It struck me that to some extent we had a similar background and we even walked the same floors, and perhaps worked in the same rooms, in the old Physiological Institute in the Liebigstrasse in Leipzig. Fortunately, our paths diverged completely after we left Leipzig, and any possible resemblance ended there!

I was attracted to neurophysiology at an early stage, from about 1930 onward. In those days, the establishment of the laws of electric excitation of nerve, and their precise mathematical formulation were regarded as a great thing. In retrospect it seems a somewhat naive approach, reminiscent a little of the attitude of Sinclair Lewis' *Dr. Martin Arrowsmith*, a novel that was fashionable at the time and describes a rather naive young scientist who takes special pride in mathematical formulations. The exact fitting of strength–duration curves to electric stimuli of various shapes and intensities was considered a wonderful achievement, even though it was only a formal exercise which shed little light on the physical mechanism of excitation. Nevertheless, I felt it was fascinating that one could make accurate and repeatable measurements of electric excitability on living tissues and express the results by a simple mathematical equation.

To do the experiments all one needed were some calibrated boxes of simple electrical gear, resistances, condensers, etc., and an isolated nerve—muscle preparation of a frog.

Now there's the rub. In our elementary physiology class, the first thing we were taught was to overcome our repugnance to the killing of frogs. Much of our basic knowledge of the normal function of living tissues and their cells has come from experiments on the isolated organs of cold-blooded animals, which survive for long periods when kept at room temperature and in a simple salt solution. I have no doubt that this kind of experiment will be indispensable for solving many remaining important problems. Whether this justifies the killing of animals is an entirely different matter and depends on one's personal religious belief and on what is regarded as acceptable by the society in which one lives. I have killed a very large number of frogs in my lifetime to use their nerves and muscles for my experiments and to find out how they work. I have never been able to overcome my utter dislike for the act of killing, although it was done as humanely as I was taught to do. I do not know whether one can produce any valid moral justification for such action. But I do not think that it is any more reprehensible to kill an animal for the advancement of natural knowledge than to do so for the consumption of food.

Immediately after my preclinical exam I went to see Professor Gildemeister and asked for an opportunity to do some experimental research in the Physiological Institute which might also form the basis of my medical doctor's thesis. Passing the final medical examination (*Staatsexamen*) at a German university was a separate thing: it did not entitle a person to call oneself Doctor of Medicine. For this, one had to submit a printed thesis and undergo a separate viva, though the standards required for the Dr.Med. degree were generally quite low and the degree could be attained without experimental work—for instance by the description of a few clinical observations. Again, while the prescribed timetable of my clinical curriculum was almost fully occupied, there were periods when I could absent myself from the formal lectures and clinical demonstrations, and in any case I was used to working late hours. What is more, I felt increasingly revolted by the behavior of the majority of my fellow students who no longer bothered to conceal their Nazi sympathies and anti-Semitic vulgarities. So, I welcomed, and made use of, every opportunity I could find of withdrawing into the solitary atmosphere of my laboratory.

With Gildemeister's permission I was able to spend much time in the physiology department, learning some relatively advanced experimental techniques and doing some rather juvenile and inconsequential research on muscle permeability, under the direction of J.D. Achelis. Achelis was an intelligent person and an able experimenter, and I retained a high respect for his character despite his unfortunate later involvement with the Hitler regime. I regarded Achelis as an honest, upright person, but he belonged to a group of people who considered the rise of Hitler indispensable for the

rebuilding of a strong Germany and who in the end joined the Nazi party, ready to overlook its violence and vulgarity, or perhaps fancying that their personal participation might have a civilizing effect. I knew that Achelis' interests and activities were spread over a wide field, covering not just physiology, but the history of medicine, philosophy of science, and politics.

With surprise and shock I learned, in the spring of 1933, that Achelis had suddenly vanished from the institute and re-emerged as a high official in the Prussian Ministry of Education in Berlin, charged with responsibilities for the appointment and dismissal of university personnel. I believe, and this was also Gildemeister's opinion, that Achelis had romantic ideas and deluded himself into believing he would have enough authority to exert a moderating influence in the Nazi governmental machine. His service did not last very long. After 18 months when he had become disillusioned, he dropped back into academic life, taking the chair of physiology at Heidelberg University, but his short period as a Nazi administrator did him immense harm.

Gildemeister commented to me that although Achelis had tried to soften the blows, he was held responsible for the dismissal of many Jewish academics, and all he had achieved was an international reputation of a man with "blood on his hands." The most damaging case in which Achelis was involved was the dismissal of Otto Kraye, a young pharmacologist who was one of the few university dons who showed great courage in sticking to their moral principles. Kraye had been offered promotion to a university chair, from which the previous holder, Philipp Ellinger, a Jew, had just been removed. Kraye found it incompatible with his principles to accept such an appointment, and he did not simply refuse the offer, but wrote an eloquent letter explaining his reasons: He considered the dismissal of Jewish scientists to be an injustice, and his ethical beliefs as a scientist and a teacher did not permit him to remain silent. The result was Kraye's own immediate dismissal. This was not an instance of an internationally famous personage who could easily find a good job elsewhere, it took him some time to emigrate. Eventually, after a period as a professor at the American University in Beirut, he was able to build up a distinguished school of pharmacology at Harvard University. I learned about Kraye and his encounter with the Nazis from A.V. Hill, who never forgave Achelis for his role in that affair.

However, with all Achelis' faults and mistakes, I retained a personal regard for this man; he had been my teacher, and I was obliged to him for that. What is more, after he moved to the Berlin ministry in 1933, he did not immediately break off relations with me. When he realized that I was ready to throw up my medical course and emigrate to Palestine, he suggested that I visit him in Berlin and discuss my plans for the future. This action must have involved for him some risk, and I gave him high marks for it. After the war, he paid the price for his activity as a Nazi official and was himself removed from his university chair. He found satisfactory employment in the pharmaceutical

industry, but this hardly made up for dishonorable discharge from academic life. Many years later, his successor at Heidelberg University, Professor Hans Schaefer, visited me in London and we talked about Achelis. I told Schaefer that I regarded Achelis as an honest man who had been unwise and made serious mistakes, and had compromised himself by his association with the Nazi regime, but that I never considered him capable of a villainous act. I was glad to hear from Schaefer later on that he had reported our conversation to the senate of Heidelberg University and, as a result, Achelis had been formally rehabilitated, meaning that he had his formal academic title reinstated. This must have given him some pleasure during the last years of his life.

My part-time research at the Physiological Institute at Leipzig led to the publication of a couple of papers in *Pflüger's Archiv*, and I used these papers for my M.D. thesis in November 1934. What is more, I had entered the work in manuscript form in 1933 for a university competition and won the Siegfried Garten Prize of the medical faculty. Siegfried Garten had been the predecessor of Martin Gildemeister in the chair of physiology. After Garten's death his family had made a bequest to fund this prize which was open to medical students who were engaged in physiological research. For a non-Aryan to obtain a faculty prize in Nazi Germany was a somewhat less than straightforward matter. Fortunately, the custom required one to submit one's prize essay under a pseudonym. So Bernhard Katz became, for a time, Johannes Müller (the father of 19th century German physiology and teacher of Helmholtz). The judgment and, in fact, the management of the prize fund was left entirely to the discretion of the professor of physiology, Martin Gildemeister. There were only two candidates and Gildemeister knew, of course, who they were. It would have been much safer for him not to let the prize go to me. Nevertheless, he decided to award it to Müller, alias Katz. When Gildemeister "discovered" that the winner was a non-Aryan, he announced publicly that, under these circumstances, the prize money could of course not be handed out—and a little later gave it to me under the counter. I thoroughly appreciated this, as it happened to me at a time of domestic and financial difficulties.

The Garten Prize and the papers in *Pflüger's Archiv* may seem like a considerable achievement for a medical student, but I cannot say that I am proud of my first publications. In fact, I regard my work published during my Leipzig period as a prenatal effort, and my status as a physiologist, before my arrival in London, as purely embryonic. Nevertheless, my work in Leipzig had some slender but interesting connections with what was going on in Hill's laboratory at that time. The only reprint request I remember receiving in 1934 came from Ulf von Euler who happened to be working with A.V. Hill on a related subject. I reminded von Euler of this in 1970 (when we had just heard that we were to share a Nobel Prize in physiology for very different work), but he had quite forgotten the earlier episode. What I had found in 1933 was a curious reaction of frog muscle to stretching, a response that proceeded slowly and could be followed by measuring the elec-

tric impedance of the tissue. A year before, a stimulating effect of stretching on the muscle's metabolism, quite similar in time course, had been discovered by T.P. Feng, a young Chinese physiologist who was doing postgraduate work in Hill's laboratory, and with whom I was privileged to form a close friendship many years later when at long last we were able to meet.

When the Nazis took over early in 1933, I still had some 20 months to go before completing my medical course, and it was not at all clear whether I would be able to do so. For me the only practical alternative was to join the exodus to Palestine and try to make myself useful on a kibbutz. I thought very carefully about it, had long discussions with my friends in the Zionist movement, and made a day trip to Berlin where I consulted first my former teacher, J.D. Achelis, and then Enzo Sereni, an Italian Jew who played a prominent part in the Zionist labor movement and, at that time, was in charge of migration.³ Achelis advised me not to break off my clinical studies, but to complete the course if at all possible and then decide where I wanted to go. Sereni urged the opposite, namely to emigrate to Eretz Israel ("the land of Israel") immediately, suggesting that anything else was a waste of time. All this was not very reassuring, but I felt more confidence in the advice given by my ex-teacher who at least knew something about me. I returned from Berlin somewhat deflated, the only moral boost being that I was able to use my student's day return ticket to fly back to Leipzig without extra charge, my first experience of air travel.

For the next year, I just carried on. Toward the end of 1933, when I received the Garten Prize, my friends in the Zionist organization were so impressed that they themselves dissuaded me from any lingering thought of discontinuing my clinical course and encouraged me to complete it, with the idea of my ultimately going to Jerusalem and joining the Hebrew University.

Preparing for Emigration, 1934–1935

In 1934 it was still possible to obtain the British magazine *Nature* and read it in unexpurgated form in the university library. I found in it an article by A.V. Hill which had a great influence on my future. The article was a condensed version of his Thomas Huxley Memorial Lecture given at Birmingham on November 16, 1933. I knew of Hill's reputation as one of the great physiologists of the time, and I had heard of the warm friendship he had extended to his German colleagues at the end of World War I. I was all the more impressed by Hill's forthright condemnation of the treatment of his colleagues during the Nazi regime, and I much enjoyed the ensuing correspondence in *Nature* between the scientific Nazi boss, Professor Johannes Stark, and A.V. Hill. Stark was a well known physicist

³Sereni had a tragic end. During the later part of the war he was parachuted into Nazi-occupied Italy and fell into the hands of the S.S. who tortured and killed him.

and had received a Nobel Prize in 1919. After that he had ceased to be active scientifically, but became a strong supporter of the Nazi party, and in 1933 emerged as head of the Physikalisch-Technische Reichsanstalt in Berlin. This institution had been headed by people of the caliber of Helmholtz and Nernst, and in 1933 its director Friedrich Paschen, who was an old friend of A.V. Hill and a person of liberal views, was dismissed to make way for Stark who became a kind of scientific Gauleiter in the Third Reich.

When A.V. Hill denounced the Hitler regime and its persecution of Jewish and dissident scientists, Stark promptly took him to task and stated, in letters to *Nature*, that there was no factual basis for Hill's critical remarks, the German government had been obliged to protect itself against the influence of disloyal persons and was only taking lawful actions as any respectable government would do in similar circumstances. A.V. Hill terminated the correspondence with a brief note saying that gifts of money had been received in response to his appeal for assistance to help colleagues who had been driven out of Germany. He added that 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 some thanks were due to Professor Stark on this account. It was characteristic of A.V. to dismiss and poke fun at even the most vicious absurdities with an elegant and humorous touch. "Laughter," he said, "is the best detergent for nonsense." Hill's Thomas Huxley Lecture and the correspondence in *Nature* 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.

I discussed my plan with my superiors in the Zionist organization, and they were very helpful and arranged for me to meet Dr. Chaim Weizmann, the well-known Zionist leader, and put my case to him. I also approached Professor Gildemeister who agreed to write a letter of recommendation to A.V. Hill. And I wrote to my relatives in London who promised to help me in getting my British visa, and who did much more than that when I arrived in England. Without their support, I would not have been able even to cross the English Channel.

My interview with Chaim Weizmann stands out clearly in my mind, and I have also kept detailed minutes of our conversation. Weizmann had gone to spend a holiday at Karlsbad, a spa in Czechoslovakia, in July 1934. My friends in the Zionist office knew about his movements and were in touch with him through their London contacts. My friend, Dr. Fritz Loebenstein, who headed the local (Leipzig) branch of the Zionist organization said, "Why don't you just hop across the border and see what he can do for you?" and handed me an appropriate letter of introduction. This task was not quite so simple for a stateless person without proper travel documents. However, I managed to obtain a 24-hour tourist's permit from the guard at the Saxon border, went to Karlsbad where I booked myself in for one night, and then presented myself at Weizmann's hotel. We had a long talk at the end of which

he promised to try and get some financial support for me when I went to London (this resulted in a grant of £50 per annum for two years, that only lasted but actually sufficed for several months!). The final arrangement was that I should correspond with Weizmann's personal assistant, Dr. Josef Cohn, to fix the dates and details of my planned emigration. I found Chaim Weizmann a most impressive person. To me he is not only the outstanding political leader of the Zionist movement, later to become the first president of the Jewish state, but I regard him as one of the outstanding men of this century, and I feel privileged to have been able to meet him.

I felt elated when I left Karlsbad the next day, slipped back across the border without the guard noticing that I had overstayed my permit, and entered the coach going back to Leipzig. During the trip I settled down to pleasant meditations about my future, but was interrupted by a Sudeten German girl, who had joined the coach and seemed to regard me as one of her Nazi saviors, telling me how they were longing to be liberated by us. She was evidently puzzled by my coolness and total lack of response.

In the autumn of 1934 I took my clinical finals and in November obtained my M.D. Thereafter I worked for a few months as an unpaid intern in the Jewish Hospital in Leipzig, doing both medical and surgical rounds.⁴ I liked working with patients, and I think I should have enjoyed practicing as a physician, had I not been taken on by A.V. Hill and become addicted to experimental physiology. At the beginning of February 1935, I packed my bags and, equipped with travel tickets, a Nansen certificate with a temporary British visa, and the princely sum of £4, I took the train (wooden seats, third class) to Holland. There I transferred to the English Channel ferry at Flushing and arrived in Harwich, England, the next day.

University College of London, 1935–1939⁵

On the day after my arrival in London, I climbed the staircase in the physiology building of University College right up to the top floor, and there I found A.V. Hill, an impressive figure of a man, tall, good-looking,

⁴The Jewish Hospital in Leipzig had been founded and named after Chaim Eitingon, the head of a wealthy family of fur merchants who, like my father, had emigrated from Russia at the beginning of the century. Eitingon's family had succeeded in building a large business with important international connections and were known, well beyond the Jewish community, as benefactors to the town of Leipzig and its university. I knew them slightly through my father who had been on friendly terms with the Eitingon family from the early days. I was quite appalled to read of vicious attacks by some political writers on the family's good name, accusing them of undercover activities and complicity in the Stalin purges during the 1930s! Fortunately, a full discussion of the case has subsequently been published in the *New York Times Book Review* (16 June 1988), which reveals the baselessness and absurdity of those claims.

⁵Reprinted with permission from Bernard Katz's Bayliss-Starling Memorial Lecture published in *J. Physiol.* (1986), Vol. 370, pp. 1–12.

of youthful appearance with contrasting gray hair. He was talking to Donald Solandt about some experiment that was in progress. He took me into his tiny office where we started a bilingual conversation. I had very carefully rehearsed one sentence in English, namely, "Would he allow me to speak in German as this was easier for me?" To which A.V. replied, all right, but it was easier for him to speak in English, and so we continued bilingually for a while. At the end of our conversation, he said he would take me on "as an experiment," with which I felt very satisfied.

He then showed me around the laboratory and introduced me to the people. I met J.L. Parkinson, A.V.'s incomparable laboratory manager and general scientific assistant. Parkinson soon took me in hand, saw that I was provided with the necessary equipment, frogs, dissecting instruments, Ringer solution, etc.; instructed me in the English language; and generally saw to it that I was kept going and happy. "Parky" was very quick in improvising, putting simple bits of apparatus together and helping the research workers to get started and to overcome irksome difficulties. He also made it his job to protect A.V. Hill from unwanted cranks, uninvited journalists, and in general from visitors whom Parky regarded as undesirable characters. In those days, the anatomy front door on Gower Street was kept closed with a Yale lock at all times, and you needed a key to let yourself in from outside. If somebody whom Parkinson diagnosed as a crank came to see A.V., the hapless caller would be led through a labyrinth of corridors, then into a lift, and finally—after a devious passage through more corridors—would suddenly find himself being ushered through a large impressive door onto Gower Street with the door banging irreversibly shut behind him. One day, A.V. Hill saw Parkinson escorting Sir Charles Sherrington in the direction of the anatomy front door and had just time to stop them with the shout: "Hello Sherry, it looks like Parkinson is going to throw you out!"

After meeting Parky, A.V. took me into A.C. Downing's workshop. Downing was a skillful instrument maker who had built the highly sensitive moving-coil galvanometers and constructed all the thermopiles and most other delicate instruments that A.V. Hill had designed for his experiments on the heat production of nerve and muscle. To complete the introduction to A.V.'s small research laboratory I met Donald Solandt, from Toronto, who had come to join A.V. in his work on electric excitation theory, and Miss Barbara Garrard (later Mrs. Solandt), who was using tiny thermocouples for measuring the osmotic pressure of minute volumes of blood and tissue fluids. Finally, I met Mrs. Melville, who was half-time personal secretary to Hill, the other half looking after the editorial correspondence connected with the *Journal of Physiology*, and I shook hands with Arthur Treadwell, who was the junior laboratory assistant. This completed the outfit in biophysics, which for administrative purposes formed a subdivision of the department of physiology.

I saw all that during my first hour at University College. Before I left the laboratory, A.V. showed me some items on display which had been imported from Germany. Among them was a toy figure of Hitler, in brown-shirt uniform and swastika, with a movable saluting arm, mounted on a plasticine pedestal stuck against the wall. This was to make people like me "feel at home," though later I heard A.V. explain to an official type of visitor from Germany that he was really keeping the miniature statue in his laboratory as a sign of gratitude for the scientific workers Hitler had thrown out and sent him. In successive years the number of these symbols gradually increased, and some of them were distinctly vulgar and caused varying degrees of amusement and occasionally embarrassment to casual visitors.

So that was my first day's experience at University College of London. I left the laboratory feeling on top of the world. Having been accepted by A.V. Hill was a tremendous boost. His personality was extraordinary, it lifted my morale, and nothing would have deflected me from going to work with him despite an income of a £50 per year and despite the advice of other colleagues that I should get a medical diploma and then see where I wanted to go. I did in fact consider this, but I became so absorbed by the work in Hill's department that I could not face re-immersing myself in textbooks of pathology again.

It was an outstanding piece of good luck to have been taken on as an apprentice by A.V. Hill; it was the decisive influence on my life and career. I still harbor the hope that a first-class biographer will undertake the job of writing a full life of A.V. Hill. I have tried, in the *Biographical Memoirs of the Royal Society*, to describe how he managed to combine a life's devoted work in the laboratory with public service: defending science against what he termed "the enemies of knowledge;" helping refugees from Nazi Germany; directing anti-aircraft defense in World War I and initiating and organizing radar in the 1930s; working as a member of the British parliament and advising the government of India on postwar reconstruction during World War II; and many other instances of public service. He was the person from whom I have learned more than from anybody else, about science and about human conduct. A.V. Hill was the most naturally upright man I have known. Without ever being rude, he always said precisely what he meant, and you were never in any doubt exactly where you stood with him. In later years, I often found it helpful, when I was confronted with an awkward decision, to sit back and ask myself: "Now, what would A.V. have done in this situation?" To be associated with a man of his stature at a formative period of one's life is indeed a great gift of fortune.

I retain vivid memories of the spring and summer of 1935, especially of meeting and at times seeing in action, some famous physiologists whose achievements I had heard about as a student, but whom I had not dreamt of encountering in person. Shortly after my arrival at University College, I listened to a lecture on brain waves which E.D. Adrian gave to the students'

physiological society and I recall Henry Barcroft, who was a lecturer in our physiology department, eloquently introducing Adrian's talk. A.V. himself made a special point of introducing me to visiting colleagues. I was thrilled to shake hands with Joseph Barcroft, whom I had also admired, and getting to know William Rushton who, although already a well-established scientist, had to prepare himself—at Joseph Barcroft's behest—for medical finals across the road. In his spare time, Rushton came over to do the odd experiment with me. I was well aware of William Rushton's formidable onslaught and demolition of Professor Louis Lapicque's theory of neuromuscular isochronism, and I was amazed to learn that this accomplished neurophysiologist from Cambridge University had to work hard to remember things for his medical exam which I was in the happy process of forgetting.

In May 1935 I got my first glimpse of Cambridge when I went up for a day to attend the meeting of the Physiological Society. To my great astonishment I witnessed what seemed almost a stand-up fight between J.C. Eccles and H.H. Dale, with the chairman E.D. Adrian acting as a most uncomfortable and reluctant referee. Eccles had presented a paper in which he disputed the role of acetylcholine as a transmitter in the sympathetic ganglion, on the grounds that eserine, a cholinesterase inhibitor, did not produce the predicted potentiating effect. I had some difficulty in following the argument as I was not fully acquainted with the terminology: The word transmitter conveyed to me something to do with radiocommunication, and as this did not make sense, the matter was a bit confusing. When Eccles had given his talk, he was counterattacked in succession by Brown, Feldberg, and Dale, all persons whom I saw on that occasion for the first time, but whose work was to have a very important influence on my own activities in later years. At that meeting, however, what impressed me most was Dale's rebuttal of Eccles' criticism. Eccles had used a somewhat unfortunate form of words, I think it was "*pace* Dale" (meaning "with due respect" or possibly the opposite), which Dale interpreted as peremptory and considered more appropriate for a Hyde Park oration than for a scientific argument at a meeting of the Physiological Society. It did not take me long to discover that this form of banter led to no resentment between the contenders, it was in fact a prelude to much fruitful discussion over the years and indeed to growing mutual admiration between Dale and Eccles.

In the summer of 1935, I went to the Marine Biological Laboratory at Plymouth, England, where I learned something about the crustacean nerve-muscle system from Carl Pantin. A.V. Hill had gone to attend the International Physiological Congress in Leningrad and Moscow. He returned to his cottage at Ivybridge, some 10 miles from the Plymouth laboratory, and I remember visiting him and his family at their pleasant little house, "Three Corners." It was during that Plymouth period, 50 years ago, that I first met another person from whom I was to learn a great deal about neurophysiology, a younger man by the name of Alan Hodgkin.

I have the most pleasant memories of my first summer in Plymouth, not on account of any scientific achievements, but because of the beautiful countryside, the magnificent view from the laboratory window on Plymouth Hoe, the welcome relaxation through swimming, cycling, and walking through Devonshire lanes and along the Cornish coast. I remember walking through Cawsand one day and arriving at a little public house in Whitsands Bay where I ordered a simple lunch in my recently acquired, imperfect English. I shall always recall with great pride the publican addressing me with the question: "Are you from the north of England?"

In 1935 to 1936 the experiments in Hill's laboratory centered around a theory of electric excitation and accommodation which he had developed and which was capable of coordinating a vast range of observations and putting them on an easily calculable basis. The fundamental assumptions were very simple: An electric current causes excitation if it displaces the membrane potential (in the depolarizing direction) by a critical amount (the threshold); this is opposed by two processes of different relaxation times: (a) the potential change itself tends to decay with a brief time constant, (b) the threshold rises slowly so that the effect of a steady potential change maintained by a constant current is gradually neutralized. Although these were oversimplified assumptions, they were sufficient to give an excellent quantitative description of a great variety of stimulation phenomena. These assumptions also fit most of the classical strength-duration curves obtained with constant-current pulses and condenser discharges, the characteristic relation between intensity and frequency of sinusoidal alternating currents (with an optimum frequency the value of which is determined by the two relaxation times), the reduced effect of slowly rising currents, etc. Hill's theory was not the only one of its kind, nor did it explain the physicochemical mechanism of excitation, but its great success in coordinating all kinds of stimulation data on very simple premises probably helped to put an end to half a century of similar, but less successful attempts.

Having myself been involved in the experimental tests, I can say that I found the work attractive and indeed fascinating for two quite different reasons. In the first place the work enabled one to make reproducible measurements of quite extraordinary accuracy with simple equipment. Secondly, although the verification of the theoretical equations was not by itself very fruitful, a number of discrepancies from the predictions of the simple theory gradually emerged which did have important consequences. Such discrepancies led to the recognition of the nonlinear characteristic of the nerve membrane, and of the occurrence of a regenerative voltage change even in the subthreshold range of membrane potentials (the local response), which in turn provided a clue to the mechanism whereby an impulse is initiated.

My association with Hill's work on excitation theory had a peculiar sequel. In 1938, A.V. was approached by Professor Asher of Bern, who was

then the editor of the *Ergebnisse der Physiologie*, with the request for a lengthy review article on this subject. Hill's interests had changed, he said he did not have enough time, and suggested me as a possible author; so the request was passed down to me. I felt honored, of course, produced a long manuscript, and sent it off in good time. The next thing was a letter from Professor Asher addressed to A.V. Hill informing him that the article could not be published without an Aryan co-author! Somebody suggested to A.V. Hill that perhaps Mr. Winston Churchill might be approached for this purpose (all this happened some time before the outbreak of war). I decided, however, to ask for the immediate return of the manuscript, and it was published in September 1939 as a monograph by Oxford University Press, whose generosity in taking on such a loss-making proposition I have never ceased to admire.

In some respects it could be said that Hill's efforts in 1935, devoted to establishing a descriptive formal theory of electric excitation, were a retrograde step. In previous years he had been much concerned with the mechanism of the nerve impulse, and his famous lecture in 1932 on "Chemical Wave Transmission in Nerve" was full of stimulating ideas and speculations about the physical chemistry of the nerve impulse, only to be deliberately set aside and ignored in his 1935 theory. It was, however, a not entirely unfashionable attitude at the time. It is sometimes difficult to realize that even the basic concept of the membrane potential being directly involved in the process of electric excitation was not accepted by some of the most eminent neurophysiologists in the 1930s. One only has to look at the monograph by Erlanger and Gasser to see that this is not an exaggerated statement. And although the idea had been circulating for several decades, it became firmly accepted only during the single cell/intracellular recording era which followed soon after.

After a year or two, A.V. Hill recovered from his temporary diversion into theoretical excitation laws and returned with great vigor to his first love, the energy exchanges and heat production in muscle. In 1938 he produced his classical paper on "The Heat of Shortening and the Dynamic Constants of Muscle," a remarkable single-handed effort made at a time when he was busy with organizing air defense, aiding refugee scholars, and attending to his job as secretary of the Royal Society. My own research activities went in a different direction. Although A.V.'s personal influence remained as powerful as ever, I was not greatly attracted by the myothermic work, the interpretation of which seemed too difficult to me. The events that influenced my own experimental plans came from several other directions: the single axon approach which I learned from Alan Hodgkin, the rather advanced electronic and oscillograph techniques introduced into our laboratory by Otto Schmitt, and the discovery by Dale and his colleagues of chemical transmission at the neuromuscular junction. Certainly, the work I was doing in 1938 to 1939, before I joined Eccles

in Australia, was in line with these tendencies and had little connection with Hill's personal research.

In March 1938, A.V. took me in his old open-air Humber car to Cambridge. We went to E.D. Adrian's house on Grange Road so that Hill and Adrian could examine me for a Ph.D. I remember Adrian stipulating at the beginning of the procedure that I was not to test their knowledge of the contents of my thesis, which contained a lot about electric excitation and the evidence for a local response to subthreshold stimuli. The examination was uneventful; what I remember best is the pleasant lunch with the Adrians that followed it. For me the importance of obtaining a Ph.D. was that it allowed me to apply for, and to obtain, a Beit Memorial Fellowship, which at that time was the preeminent junior research award in the biomedical sciences in the United Kingdom. I held the Beit Fellowship for less than one year and at the beginning of August 1939, one month before the start of World War II, departed for Australia, together with my parents whom I fortunately was able to extricate from Germany in March of that year.

I left A.V. Hill and University College with very great regret and much reluctance, but there was one compelling reason why I regarded Eccles' invitation to join him in his Sydney laboratory as an offer I could not refuse. The reason was not the better salary—the Beit paid £400 per year and that was perfectly adequate to keep the three of us—financial improvement alone would not have induced me to go. But I felt it would have been a poor show and would have looked very bad, if a person like myself who still had to regard himself as a guest in a foreign country, were to decline a call from a colleague far away in an isolated position. So, with a heavy heart I packed my few things, said goodbye to University College, and with my parents sailed from Southampton, England, on a Dutch liner. We were supposed to transfer to another boat in Colombo, Ceylon, and one day before we reached Colombo we heard that the German foreign minister, Herr von Ribbentrop, had gone to Moscow to sign a nonaggression pact with the Soviets. I knew the game was up and that war was imminent—indeed the ship that was to take us on from Colombo to Australia was commandeered and we got stuck in Colombo for a few unpleasant weeks.

I did not relish the idea of going on to Sydney and had the quite unrealistic idea of trying to obtain a passage back to England, thinking somewhat naively that I would be of more use during the war in England than in Australia. After a few weeks of haggling with local shipping agents and persuading some of the local authorities that it would be unwise to keep me in Colombo without a job and with the prospect of our becoming destitute and a burden to them, we eventually managed to continue our journey and arrived in Sydney in October. I remember that while we were marooned in Colombo, the University of Ceylon happened to advertise a vacant professorship in physiology. What deterred me from applying was the requirement, which was explicitly stated in the advertisement, that

the applicant had to be able to repair the broken string galvanometer in the department.

Australia, 1939–1945

When I arrived in Sydney, I was welcomed by Jack Eccles who himself had returned to Australia in 1937 and had built up a small research laboratory on the top floor of the Kanematsu Institute of Pathology at Sydney Hospital. It took me several months to settle down to experiments because the events in Europe, even during the so called “phony,” inactive period of the war, had absorbed my interests, and the neuromuscular junction seemed to be of second-rate importance at the time. I was greatly helped in the settling-down process by young Stephen Kuffler who had arrived on the scene the year before, having left Vienna as a newly hatched M.D., about as raw as I was when I first joined A.V. Hill at University College. Stephen and I took to each other. We liked making the same sort of jokes and had an uncanny capacity for generating identical puns almost simultaneously at the slightest provocation.

When I first met Stephen, he was still somewhat bewildered by the interpretation of and the involved terminology adorning the electrical traces from muscles and motor endplates which he and Eccles were recording. Each bump had a different name, and there were also special names such as detonator responses for things which one could not see. It took a few years before Stephen took off under his own steam and showed his great powers as an experimenter. Once he had started on his single nerve–muscle fiber preparation, Eccles and I felt he had clearly outrun us. But every now and then he used to joke about his pretended total ignorance and scientific limitations. I remember one of his prize remarks: “They say, if the threshold goes up, the excitability goes down. Isn’t it funny: It’s fifty-fifty, and I always seem to get it wrong!” thus betraying his apparent contempt for terminology and also for statistics. Another characteristic comment of his came after a lecture that I had given to the junior medicals at Sydney University. I noticed that the students had been reasonably quiet and had not talked too much during the lecture, which suggested that they may have been paying some attention. Nevertheless I was surprised to have seen quite a number of the female students busily getting on with their knitting during the lecture. Stephen commented: “That’s all right; it gives them something to think about, while they are talking.” Stephen told me that the real reason why Eccles had taken him on in the first place was that he was looking for a suitable tennis partner and he had tested him on his nice grass court. I am afraid my own proficiency as a tennis player was negligible, but I can tell you a little anecdote about my experience with Eccles’ grass court.

It took Eccles many years, until 1947 to 1948, before he accepted without reservation the idea of chemical transmission at the neuromuscular

junction. We had plenty of arguments about it in those days in Sydney. But I think I can claim to have converted him, temporarily at least, in 1939 shortly after I joined him. I vividly remember visiting him in his pleasant house with its fine tennis court and beautiful view of Sydney harbor. One day he asked me to cut the grass for him. I had never used a mowing machine before and I did not think it required much intellectual effort or preparation. He had an electric lawn mower operated from the 240 V mains. I rapidly cut down one lane and on the first turn about managed to cut through the mower's electric cable, and there I was, in a state of incomplete tetanus for several seconds, unable to release my hands from the machine, to the great horror of the onlookers. Jack Eccles was very nice and sympathetic about it; he never asked me to replace the machine or pay for the repairs, in fact he was so concerned that he threw the electric mower away and bought a petrol-driven machine instead. And I believe that was the precise moment when I converted Professor Eccles from electrical to chemical transmission. Of course, his reply is that even the petrol mower needs an electric spark, a detonator, to make it work!

I spent about two years working full time at the Kanematsu Institute in Sydney. When I got there, Eccles and Kuffler had been doing their experiments entirely on the whole cat, recording *in situ* from innervated zones of the soleus muscle. Having been trained as a "frogman" in A.V. Hill's laboratory, I did not much like this type of experiment, nor was I much good in setting it up. I ganged up with Stephen Kuffler, and I was pleased when we succeeded in getting hold of some nice Australian tree frogs, the sartorius muscles of which proved to be very suitable for the experiments we wanted to do, and this kept me busy and moderately happy for two years.

In 1941 I obtained my British naturalization papers in Sydney and shortly afterwards managed to enlist with the Royal Australian Air Force (RAAF), first as a rookie, then graduating as a radar officer. Otto Schmitt had taught me some fairly advanced tricks that one could play with thermionic valves, and that helped me a great deal during my period as a radar trainee. But my four years in the RAAF taught me a great many more useful things, about electronics as well as about human beings. I spent a good deal of time tramping around New Guinea together with an Australian radar mechanic, Norman Smith. He was an excellent companion, one of those men who can put his hands to everything, from farming to house building, from catching snakes in the bush to constructing electronic apparatus. He is, in fact, a schoolteacher now in retirement living in Murwillumbah, New South Wales, and I am proud to say that we still keep up a friendly correspondence. My service in the RAAF had a very important effect on my life: it greatly increased my self-confidence and I felt that no longer would I need consider myself a guest when I returned to England after the war.

My enlistment in the Australian forces greatly boosted my morale, and somehow I felt that now I had bought my ticket to return home to England when the war was over. But in no way did my enlistment diminish my feeling of gratitude and indebtedness to the friends in England who had offered me a home and a refuge in 1935, who had made it possible for me and my parents to escape from the indignities and humiliations of Hitler's Reich, and who had given me my education as a scientist.

During the last year of the war I was posted back to Sydney as a liaison officer at the Radiophysics Laboratory. This was quite an interesting place, housed within the University of Sydney and harboring a number of young physicists who later became Fellows of the Royal Society. I believe I may have been at the Radiophysics laboratory during a time when among the female typists in the office there was one young lady by the name of Joan Sutherland, who subsequently became one of the world's greatest operatic stars. During that year I found I had plenty of spare time on my hands, and I used it most diligently, partly to do some more experiments together with Stephen Kuffler on crustacean nerve-muscle junctions, and—more importantly—to pursue and eventually marry Miss Marguerite Penly, who, I am glad to report is still putting up with me even though she still is not fully acclimated to the English weather. A month before the wedding I received a telegram from London, which was in fact A.V. Hill's wedding present, inviting me to return to University College of London as Henry Head Fellow of the Royal Society and assistant director of research in biophysics. A.V.'s wedding present caused a great deal of consternation to some members of my wife's family, but fortunately did not prevent the marriage from taking place at the appointed date. My marriage to Marguerite Penly was undoubtedly my most important achievement during my period in Australia. I am convinced that my marriage greatly enhanced my reputation among friends and colleagues who were probably no less astonished than I was that a young lady of such outstanding charm and attraction should have accepted me as a husband.

Back in London, 1946—Onward

My wife and I had some difficulties in arranging our sea voyage from Sydney to Southampton. It was a time when ocean liners had not yet been taken out of war service and refurbished. The ships were used to send troops home from various parts of the globe, and once I had got myself demobilized from the RAAF, I found myself at the end of the queue—one of those odd civilians who was regarded not only as the lowest form of animal life but who had to pay a first-class fare and be thankful for not being thrown into the ship's hold. Actually, we had to spend our two months' sea passage in the style of returning convicts, being confined to separate dormitories, and pretty squalid ones at that. But I did not mind that very

much; I felt I was going home, and as it turned out that journey did conclude my wanderings over the globe.

When we arrived in London early in 1946, my wife and I were fortunate in being offered accommodation at the top of the Hill's very pleasant house in Highgate, and this tided us over for the first two postwar years. University College was still recovering from war damage and various kinds of civil-service occupation. I remember spending a week painting the walls in the biophysics laboratories and ending up with a rather vicious dose of painter's colic. With J.L. Parkinson's help, we soon managed to put Otto Schmitt's oscillograph and amplifiers back into working order. In addition, Parky conspired to collect a lot of Royal Air Force surplus radar gear, and we converted a nice CHL Mark V receiver and display unit into a large demonstration oscilloscope for the physiology lecture theater. Once we had got the equipment functioning, I quickly picked up the threads from previous work and did some more experiments on the local response. I then spent over a year trying to sort out the electrical membrane properties of muscle fibers, and I came across an odd phenomenon that still arouses some interest and goes under the name of anomalous or inward rectification.

In the summer of 1947 our first son was born. A little later I joined Alan Hodgkin in Plymouth where I participated in the work on the squid axon, and continued to do so during several successive summer vacations.

For a couple of years at the college I became interested in the local generator potentials elicited by stretch in the muscle spindle of the frog. After that, practically all my experimental work had to do with neuromuscular and synaptic transmission. When I became head of the newly created biophysics department in January 1952 I was lucky in having excellent friends to support me. I want to pay special tribute to an outstanding provost of University College, Ifor Evans, and to my colleagues in my neighboring departments, John Young, Andrew Huxley, Heinz Schild, and above all, Lindor Brown, with whom I developed a close personal rapport of the kind I used to enjoy with Stephen Kuffler. In the laboratory I was equally blessed in having admirable friends to collaborate with, Paul Fatt, José del Castillo, Stephen Thesleff, and, for some 25 years, Ricardo Miledi. We worked on miniature endplate potentials, on quantal release of transmitter substances, on the role of calcium in transmitter release, on the postsynaptic action of acetylcholine, on acetylcholine noise and the statistical derivation of the molecular transmitter action, and on various related problems that cropped up from time to time. Perhaps the most exciting discovery among these was the realization that nerve cells talk to each other by secreting droplets of transmitter, discrete packets containing thousands of active molecules at a time. Together with ultrastructural evidence, this discovery led to the theory of vesicular exocytosis which, after 40 years, retains a focal position in synaptic research.

I have had the good fortune not only of deriving much first-class entertainment and excitement from my work, but also of seeing some beautiful experiments come out of the laboratories of my younger friends and colleagues: the observations on vesicular exocytosis by John Heuser and Tom Reese and their co-workers; the direct demonstration of single ion channels in chemosensitive membranes by Erwin Neher and Bert Sakmann; and more recently, the experimental induction of neuroreceptors and ion channels in amphibian oocytes by Ricardo Miledi and his colleagues. Needless to say, it is most gratifying to see outstanding advances being made by the next generation of scientists and to witness the important part played in it by colleagues who at one time were actually members of our own group.

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