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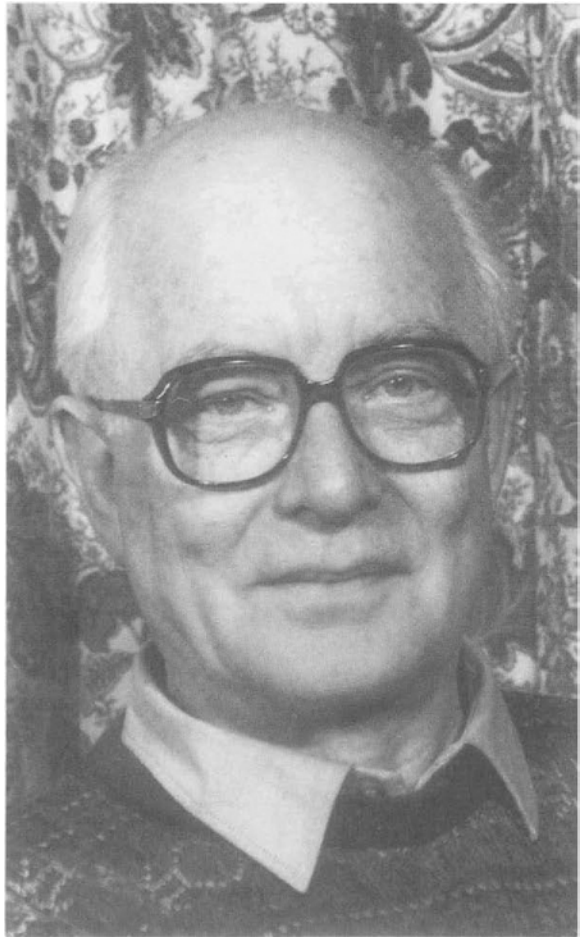

Brian B. Boycott

BORN:

Croydon, England
December 10, 1924

EDUCATION:

Birkbeck College, London, B.Sc. (1946)

APPOINTMENTS:

National Institute for Medical Research (1942)
University College London (1946)
Medical Research Council Biophysics Research Unit
King's College London (1970)
Emeritus Professor of Biology, University of London (1989)
Honorary Senior Research Fellow, Anatomy Guy's Hospital Medical School (1990)
Visiting Professor, Institute of Ophthalmology, University College London (1997)

HONORS AND AWARDS:

Scientific Medal, Zoological Society of London (1965)
Fellow of the Royal Society (1971)
Fellow of the European Molecular Biology Organization (1974)
Fellow of the American Association for the Advancement of Science (1987)
Honorary Doctorate of The Open University (1988)
Fellow of the King's College London (1990)
Proctor Medal (jointly with H. Wässle) of the Association for Research in Vision and Ophthalmology (1999)

Brian Boycott was first known for his work with J. Z. Young on the brains and behaviors of cephalopods. Since 1966 he is noted for defining the types of nerve cells and their synaptic contacts in mammalian retinae.

Brian B. Boycott

> Life without memory is no life at all.
> Our memory is our coherence, our reason, our feeling, even our action.
> In this autobiography where I often wander from the subject like a wayfarer in a picaresque novel seduced by the charm of the unexpected intrusion, the unforeseen story, certain false memories have undoubtedly remained despite my vigilance.
> —Extracts from Chapter 1 on memory by Luis Buñuel in his autobiography, My Last Breath (A Israel, Trans.). Jonathan Cape, London, 1984. For a while, sometime between 1917 and 1925, this great film director, then a biology student, prepared microscope slides for Ramõn y Cajal.

Preamble

Along with other Huguenot refugees Boycatts appeared in England when Louis XIV revoked the Edict of Nantes (1685). This action destroyed the limited legal privileges of French Protestants, established by Henry IV 87 years earlier, and increased dramatically their persecution by Catholics (Maurois, 1949). The Boycatts settled in East Anglia as weavers and dyers. Descendants became the rectors of Burgh-St-Peter, a village between Lowestoft and Norwich. The eponymous Boycott, Charles Cunningham Boycott (1832–1897), was a son of one of the rectors. He was born Boycatt but in 1841, for no known reason, the *a* was changed to *o* (Marlow, 1973; C. A. Boycott. 1997).

After a spell in the army, where he rose to the rank of captain, Boycott became a farmer and an agent for Lord Erne in County Mayo, Eire. Foreign landlords and their agents were then anathema to the Irish. Therefore, in 1877 C. S. Parnell and Michael Davitt founded the Irish Land League to coordinate the tactics of opposition to foreign domination and rack-renting. Increasingly, the league used an effective, and much feared, technique, whereby a family was blockaded socially and economically. This meant stopping any kind of contact and included cutting off supplies of food, water, labor, etc. By chance the long blockade of C. C. Boycott in his home, Lough Mask House, during 1880 became world

famous. A U.S. journalist, James Redpath, is thought to have been the first to describe these blockades as 'a boycott.' The term rapidly came into frequent usage and was soon adapted to many languages and other occasions. Personally, Boycott seems to have been a courageous but inoffensive fellow, greatly attached to Ireland and horse racing; a country gentleman no better or worse than his peers (Marlow, 1973; C. A. Boycott, 1997). The Irish Land Leagues' actions assured him a high count in the Citation Index.

Another historically notable Boycott (2) is Arthur Edwin Boycott (1877–1938), whose achievements deserve a longer historical article. (A number after a name refers to the volume of *Biographical Memoirs of Fellows of the Royal Society* in which a memoir and bibliography may be found. Most of the names are well-known to neurobiologists; this referencing may be useful to historians.) He was Professor of Pathology at University College London and for many years single-handedly edited the *Journal of Pathology*. He advocated pathology as an experimental subject that, he said, should include the study of animal pathologies. This could not have endeared him to the medical establishment of 75 years ago. His address in 1924, at the opening of the new Pathological Institute at McGill University Montreal (*Lancet*, November 15th, p. 997), is equally 'modern.' It discusses the relationships that should exist between business and universities and advocates the need to educate undergraduates, not just to produce people with qualifications. Academic problems seem not to have changed much since then.

Boycott's personal research was varied; much was on the physiology and pathology of blood. Of particular interest to neurobiologists is his work on decompression sickness (caisson disease, the bends). During the nineteenth century compressed air caissons were introduced for tunneling and bridge building. The death and injury rate among workers from this mysterious new disease was high. There was no basic understanding of the physiology of the 'disease' and thus no control of the decompression of the workers (Phillips, 1998). About 1870, some understanding began when P. Bert in France showed that during compression nitrogen dissolves in body tissues. Then upon decompression it rapidly comes out of solution and so forms bubbles. Their obstructions in the tissues and vascular system produce neurological and other symptoms. Boycott and Damant (1908) showed that the nervous system is especially vulnerable because the nitrogen of compressed air preferentially dissolves in fatty tissue. During this work Boycott produced some of the earliest measurements on the lengths of myelin between nodes of Ranvier. The practical importance of the work was that the authors introduced a new concept, that of staged decompression, to control the rate at which nitrogen left the tissues. They drew up tables relating decompression times with the depth and duration of a dive and so determined the safe times of ascent back to

one atmosphere (Boycott *et al.*, 1907). These have formed the basis for modern diving practice and all industrial health and safety regulations.

Boycott was also a significant naturalist. For many years he was the leading expert in England on British terrestrial and freshwater gastropods, not just their systematics but also their ecology (Boycott, 1934). He also initiated an original study into the genetics of dextral and sinistral torsion of the shells in a population of snails in a pond near Leeds (Boycott *et al.*, 1932).

I have briefly outlined the careers of C. C. and A. E. Boycott because I have so often been asked about them. The name is sufficiently uncommon to suppose a relationship somewhere, but I have never done the work to examine this. I do know that the three of us are not directly related and C. C. Boycott had no issue. Of my direct ancestry I know very little. My mother's father, a Lewis, was a veterinarian. He left his wife and three children in England and died in Australia. Nothing was said about him. His wife, my grandmother, died of cancer in her fifties, when I was about 5 years old. Her father, a Last, and his wife, my great grandparents, also died when I was young. I have fond though vague memories of the three.

Memories of Family Life and Medical Problems

I was an only and rather solitary child. My earliest memories, like those of most people, date from around the age of 4. A particularly vivid, pleasurable memory is standing in a field at the back of our garden and picking lots of black and yellow caterpillars off the leaves of a yellow-flowered weed (ragweed?). Another is of a morning digging trenches and tunnels in the soil by the hedge, aided by my terrier, Tim. I irrigated the system, my dog, and myself, with water. My mother scolded me vigorously for getting both of us very muddy. Tim, a loyal friend, diverted her anger by snapping at her ankles. Another clear memory, dated in reference works as approximately 3 months before my sixth birthday, is of seeing the airship R101 flying low past our house. We lived near the flight path from Croydon (the first London) airport. Then I was taken to see my Aunt's husband board an Imperial Airways passenger biplane for the flight to Cairo. There he was to inspect the R101's engines before it continued its flight to India. This never happened because the airship crashed in southern France. Within a few months of these events I went to school. I have no recollections of the day of this major event. From later days I remember the teacher and learning to write from a copybook of printed Italian cursive script. I could already read but had to learn to spell; proudly I was the only boy in the class who could manage 'caterpillar' during dictation of a spelling test. A year later I was awestruck when a master demonstrated that a coin would float on a liquid (mercury). I did not understand his explanation.

Now less good memories have to be recalled. Among the earliest is of Tim being killed under the solid rubber wheels of an omnibus that he had chased as it passed our home. Around this time I became aware of my father being frequently drunk, arriving home late, and often being abusive. Memories of these episodes need no further record. Their consequences determined much of my upbringing. My mother walked out on my father about 1932, taking me with her. Interestingly, I do not remember the drama of that moment of separation. There are many later recollections. Soon my father lost his job as manager of an insurance office. Ultimately, he gained work with a book publisher, but he provided no support for us. My parents never divorced. I met my father for an afternoon about three times a year during the school holidays. When he died in 1953 at age 63, he was living on his own in a small rented room. He had kept the birthday present thank-you's I had written; which is how the police found me. There were no other personal or family papers. Before his death, he drank moderately. I never knew him or his family. It was sad.

My mother was fortunate to get a job as a sales assistant at the firm where she had been apprenticed before her marriage. Unemployment was high and pay was low. At first we had no regular home. We stayed with sympathetic friends until mother could afford to rent a single room in the house of the mother of one of her colleagues. A new school had to be found for me. I well remember overhearing adults discussing this, not solely as an educational and financial problem but as a worry about what I would do for a job. This sort of concern for the adult future of an 8- or 9-year-old may now seem odd to a modern reader (at least in the Western world). However, the spectre of unemployment and the Great Depression was then always present. For many years I felt the oppression of a need to earn my living.

My father had been a Mason. The Masons sponsored two charity schools, one for boys and the other for girls. My mother gained the support of a Mr. Hacker, a member of my father's lodge. He persuaded the authorities to consider me if I passed the entrance exam. This was exceptional because normally the father had to be dead for a child to be accepted at these schools. I was examined in a room at the top of the Masonic building in Covent Garden. I remember is being scared silly and being asked to spell colour. I did so correctly. At that time I think I was reading Zane Grey westerns from the public library. It was fortunate I had not learned his foreign spelling along with the cowboy heroics.

The junior and senior Masonic schools were modeled on leading British public (private) boarding schools. In the tradition of many Victorian charity schools, the boys were provided with clothing as well as tuition and schoolbooks and, during semesters, food. The school was my salvation and doubtless that of many others trapped by difficult circumstances. Approximately 15 years ago costs and other circumstances resulted in closure of the boy's school.

Currently, much publicity is given to the clandestine nature of Masonic organizations, especially in Italy; comment is frequently derogatory. My personal experience has been that I was the recipient of genuine disinterested charity. At no time while I was at the school, or at any time after I left, was I in any way approached or pressured to join or to favor Masonic activities. Their charity educated me; I am grateful. I am also indebted to them for the costs of a major medical emergency.

Before I was 6 years old, I had many of the childhood ailments of the time—measles, whooping cough, double lobar pneumonia, etc. I was regarded as a sickly child. I had been at the junior Masonic school for about a year when, in early 1935, I got acute bilateral mastoiditis. I was too ill to move to the hospital, so a surgeon came to drain the mastoid antra at the school infirmary. My memory of this remains vivid. Interestingly, it has always consisted of two separate parts. One is that of being carried in a nurse's arms to an operating table. (Nobody had explained what was happening to the 10-year-old.) I was terrified, and as I was etherized there was a suffocating sensation and I struggled violently. The other memory is detached and unemotional. It is as if I was an observer standing back and watching six masked and gowned figures holding me down and being rather proud of that person, me, putting up such a struggle.

There is a similar dualistic memory from my postoperative care. The same year I had mastoiditis, Gerhard Domagk published his experiments on the antibacterial action of Prontosil. This was, of course, not immediately generally available. Therefore, the drainage tubes for the pus in the mastoid bones had to be kept open. Every day or so this involved debridement of the granulation tissue that formed over the openings of the tubes. It was done with silver nitrate sticks; it is very painful. One memory is of the pain and the other is of watching myself holding onto the bed rails and screaming. Interestingly, this outside observer came to modify my behavior. In those days I read a lot of adventure stories. They were often concerned with building the British Empire (e.g., the author G. A. Henty), fighting various wars, and Wild West stories. The heroes were always heroic, capable of immense physical endurance; they never howled when hurt. The observer part of me determined I should not howl in the future. Indeed, I managed that and learned to think of the pain as less painful. In later years I have been able to do this with cuts and bruises. At the age of 10, I thought I was being brave. It was 30 years later that I gained some appreciation of the complexity of pain sensations and their control in stressful situations (Melzack and Wall, 1996). I have not read sufficiently in modern cognitive psychology to know how general this kind of dual memory experience may be. It was certainly very vivid when I was10 years old and is strongly remembered in this way 65 years later. I have had similar dual memories of experiences since then, although not after about the age of 40.

The sum of illnesses and family disruption during my early years meant that I developed as a rather solitary, self-absorbed person. I related more to adults than my peers. Thus, I tended to be the outsider, the observer. Because of months of lost schooling (I had scarlet fever soon after mastoiditis), I was always at the bottom of the class and especially backward in French, English grammar, and mathematics. Catching up was not helped by the misfortune of teachers whose style was publicly to ridicule any pupil mispronouncing foreign words or needing (as I sometimes still do) to aid mental arithmetic by using fingers as counters.

Education, 1936–1942

From 1936 onwards my health improved. I moved to the senior school where there were good sports facilities, a good library, different teachers, and new courses. Suddenly I was not always at the bottom of the class in everything. With new subjects, such as history, English literature, biology, physics, and chemistry, I became level with, or above the average of, my peers. Biological topics suited my outsider's temperament and my curiosity about living things. I wanted to know how they worked and behaved. By about the age of 13 I was committed to be a biologist. This decision eased some of the pressure on me at home to choose a career. It meant I would need to stay at school until at least age 17. (In those days the minimum age to leave school in Britain was 14 or 15. It was not until the Education Act of 1944 that this was raised to 16.)

During my years at the senior school I spent much of my spare time reading any biology books I could find. The reading was unguided and often too difficult for me. I was especially interested in pond life and spent hours observing pond water with a microscope. At 15, I even gained a special and, for a boarding school, unique dispensation to leave the school grounds on summer Saturday evenings to go collecting in the surrounding countryside. I learned a lot. However, I got a mere pass in biology but distinctions in history and English. I failed French and maths and just managed to pass physics and chemistry. Thus, the headmaster judged that I should stay on to do history and English in the sixth form. I managed to evade this fate by arguing that I had failed languages, which I supposed historians had to know. I think I even argued that biologists did not need maths. (What an ignorant idiot!)

Like many youngsters of the time, I admired and emulated the all-round athletic achievements of the great Jesse Owens. I became competent in most field and track events, played most games, and one year even led a successful gymnastics team. It would be tedious to give a longer account of school life; it was conventional growing up. There were, however, some extracurricular experiences associated with the approach and outbreak of war that were important and formative.

By September 1939 I had only a simplist's idea of what the declaration of war with Germany was about. I knew Mussolini and the Italians had invaded Abyssinia in 1935 and this was bad, but I was unsure where that was and had no idea of the reasons for the invasion. Similarly, the Germans were taking over other countries and were about to invade Poland. Germans were bad, so we British, and our Empire, had to stop them as we had done 21 years earlier. Most of the adults I knew did not want the war but thought it inevitable. They were confident, nationalistic, and triumphalist. The British always won their wars even when, for example, they lost in America and elsewhere. I cannot recall how the school history books of the day conveyed that impression, but they did. Two sporting incidents in the spring of 1939, the behavior of my Art-master, and the sermon of a German preacher began the development of a difference in my attitude to those not British (i.e., foreigners). They also introduced the ideas that there might be moral and ethical problems involved in going to war and not all members of a nation are the same.

In spring 1939, our school hosted a German schoolboy hockey team from Jena and soon after one from north Germany. The latter started and ended the game with a Nazi salute. They were arrogant, domineering, and played with no regard for 'fair play.' We did not like them. The team from Jena did not salute; they played very well and beat us. One evening they and their masters put on a delightful, impromptu, very funny review. We liked them. They presented our school with a framed picture of their school. It was hung in the library by the catalogs. I am proud it remained there for the duration of the war. Its removal was never suggested.

A weightier lesson came from the behavior of the Art-master, who was also junior housemaster of my house. The outbreak of war revealed him as a pacifist and conscientious objector. This was not a popular position. The senior housemaster was a colonel in the reserves and most of the boys were by then nationalistic. I liked him and tried to understand his reasons; he introduced me to Bertrand Russell's writings. This was important education.

The preacher was Pastor Martin Niemoeller, a leading anti-Nazi. He preached to us in the school chapel one Sunday about Nazism, its meaning, and the meaning of war. He was a compelling speaker. I cannot recall what he said any more than I can recall discussions with the Art master. I suspect this is because what was said has become part of my makeup.

At the time of the British retreat and evacuation from Dunkirk, the Art-master suddenly changed his position, for reasons I never knew, and decided to join the army. He was rejected on medical grounds and became an officer in the school cadet corps. He was a sincere but hopeless officer. By then I was a company sergeant major. I often had to take over when he misordered the company's march and marched it into brick walls, wrong-footed the company when ordering 'change arms' on the march, or got

the timing wrong when demonstrating pulling pins out of and throwing (fortunately dummy) hand grenades.

Birkbeck College, 1942–1946

I left school in the summer of 1942. There was about a year before I was due for call up into the armed services. I had failed to get a scholarship to Cambridge. My record did not suggest I would be more successful elsewhere. My biology teachers, Joe Webb and his wife, who were always very supportive, suggested I apply to Birkbeck College. Birkbeck was founded as the London Mechanics Institute in 1823. Its purpose was to enable members of the artisan classes 'to improve themselves in the evenings' after a day's work. After some years it became incorporated into the University of London as Birkbeck College. Its courses were then certified to be of the same standard as those of other colleges of the university. I registered to read honors zoology with subsidiary botany in September 1942 and at the same time went job hunting. My disrupted early education still haunted me. After I had begun the course the college administration found my elementary maths to be below the matriculation standard of the university. Therefore, I had to repeat this for a third time; my grade in chemistry was also too low, so that had to be repeated. Fortunately, the head of zoology, Gordon Jackson, was sympathetic and persuaded the university to let me do the exams while continuing the degree course. I staggered through with no profit to anyone.

The main zoology teachers were Alistair Graham and Vera Fretter. They were outstandingly good, enthusiastic, and helpful to students with academic or other problems. Together with their colleagues they gave us a very thorough grounding in comparative anatomy and physiology, marine biology, and the general systematics of most animal groups. Time constraints meant insects had to be left out, except for their basic structure in two lectures!

Just before I joined Birkbeck, most of the zoology department had been badly firebombed. Our classes were held opposite the main college in the remains of a building adjacent to an old graveyard. (This yard still exists in Breams Buildings between Fetter Lane and Chancery Lane.) The building's basement had been roofed with corrugated iron sheeting. It was significantly noisy when it rained and ferociously hot, seemingly especially during examination time, in the summer. However, because of night-time air raids, teaching was changed from weekday evenings after work to daytime on Saturdays and Sundays. This meant that for much of our course we could use the University College London zoology labs. Their full-time students had been evacuated to the safety of Bangor in North Wales. Because of my backlog of qualification failures it took me 4 years to graduate. As a result of great teaching, I gained a first class honors zoology degree in the summer of 1946.

I suppose there are great disadvantages in earning a living and obtaining a degree by part-time study. There is less time for reading in-depth, socializing, sport, and general cultural activities. That being said, my future wife and I did manage on Saturday nights to go to the theater and saw many of the now legendary productions of the Old Vic company. Also, the work I did during the day had major educational advantages. I would have become a lesser scientist had I only gone to college.

National Institute for Medical Research, 1942–1946

Initially I could not find a job after I entered Birkbeck. I tried places such as the Rothampstead Agricultural Research labs, those of the Royal College of Surgeons, and several other institutions. Classmates at Birkbeck suggested I should try the National Institute for Medical Research (NIMR). This was located in its original building at Hampstead, the outbreak of war having delayed the move to its current site at Mill Hill. I got a job as an animal house attendant. This proved to be an important experience. I learned animal care the hard way and about people with no academic ambition or background—people who had sets of values and motivations different than I had experienced during my isolated middle-class upbringing. They were great characters and kind to my naivety.

I only worked in the animal house for a few months before I was moved to the physiology lab to be a general dogsbody and washer-up. Initially I had no idea that this was a lab of such worldwide fame and eminence. It was universally known as F4, i.e., the fourth room on the first floor of the research building. It was formerly H. H. Dale's (16) lab. He had retired the year before I joined NIMR, but his immense authority and analytical style permeated the place. The technicians were under the iron discipline of L. W. Collison, who had been Dale's assistant for many years. These were the days when apparatus had to be designed and made in-house for a particular experiment. Collison was famous for his ingenious inventions. Five years later I would have been helpless in Naples without the experience of improvisation I then acquired.

When I joined F4, G. L. Brown (20) had succeeded Dale as its director. He also became secretary of the Royal Naval Personnel Research Committee. In a short time he recruited H. B. Barlow, B. D. Burns, F. Dickens (33), C. B. B. Downman, J. A. B. Gray, F. C. MacIntosh (40), W. D. M. Paton (42), and A. Sand (5) to work on the physiological problems of personnel involved in naval warfare. There is no way in this article I can attempt a summary of the activities of the 4 years I had in F4. A few illustrative anecdotes of what a schoolboy in his first job experienced must be sufficient.

In addition to the distinguished faculty I have listed, there were often eminent visitors I had to show around, including C. H. Best (28), W. S.

Feldberg (43), J. B. S. Haldane (12), and A. Krogh (7). For a student it was exciting to discover that those names in textbooks were real people with varied personalities. Sometimes it could be overwhelming. Having heard I was a Birkbeck student, J. B. S. Haldane often chatted to me during his visits. Once, he suddenly stopped in the corridor and said 'I have just been reading Darwin's *Variation of Animals and Plants under Domestication*. You should. It's a much more interesting and important book than his *Origin*, you know.' I had not read the latter and had never heard of the former. Many years later, I think I can understand what he meant.

The first experiment I was given to perform was concerned with a search for drugs to ameliorate seasickness among troops making amphibious landings. Such drugs, now an accessory for queasy tourists, were then unrecognized. The experiment involved dogs standing on a swing that could be moved rhythmically backwards and forwards. It was rather like a child's playground swing but with a platform and rigid supports to the crossbar instead of a chain. The dog stood in a harness on the swing. However, children sit on swings and do not usually vomit. Place them on all fours on the swing and they and most adults will, like the dogs, get sick quite quickly. Things went routinely until one day a particular dog taught me that physiological and behavioral studies are not straightforward. The dog had had two experiences with the swing; one more test was needed to get his time to vomit baseline. He ran happily over from the animal house and into F4. Tail wagging, he trotted to the several desks in this large lab and got a welcoming pat on the head. Then his tail went down, his legs shortened, and he slunk to the swing. He looked at me woefully and vomited beside the swing. Job done, he cheered up; tail wagging, he ran around the lab again and raced to the animal house to get his first feed in 12 hours. My bosses hastily redesigned their experiments. Clearly, single trials on populations of dogs would be necessary.

The question was how could we get a lot of dogs? Somebody had the clever idea of advertising for local dog owners to volunteer their dogs for some harmless, although unspecified (i.e., secret), war work. Their reward was to be some free (unrationed) food for the dogs. This worked for a while; it was socially fascinating collecting dogs from the often wealthy owners in the Hampstead area. Then a problem occurred because the local antivivisectionists decided to picket the institute in defense of the dogs. Their demonstration fizzled out because for some reason the work was moved to Canada and the war effort in F4 became concentrated on problems of diving physiology, particularly the effects of oxygen at high pressure and carbon dioxide narcosis.

Despite my inexperience, I must have been more useful than just as a washer-up because when I received my armed services call-up papers G. L. Brown had a reservation order slapped on me. That meant I had no choice but to stay where I was until further notice.

The practical procedures for avoiding decompression sickness and much of its basic physiology had been established 40 years earlier (Boycott *et al.*, 1907; Phillips, 1998). The special demands of free diving for wartime operations raised new physiological problems. For example, divers needed to be freely mobile so they could enter enemy harbors and canals to place petards on vessels, harbor gates, etc. The underwater detonation of mines on invasion beaches and obtaining geological samples of beaches to determine if they could carry the weight of amphibious landing vehicles were among many other operations requiring divers. A diver in a conventional compressed air suit vents gas bubbles to the surface. These are observable by guards. Clearly, a suit using compressed oxygen, and with a rebreathing system to absorb carbon dioxide, could be operationally safer as well as less bulky. In theory, a dive could be longer because of the absence of nitrogen dissolving under pressure into the fat of the diver. (It was known empirically from the nineteenth century that fat laborers were more prone to caisson disease than were their slimmer colleagues.)

In practice, there were difficulties. About 70 years earlier P. Bert had shown that breathing pure oxygen at above 2 atmospheres pressure is toxic. It causes, often abruptly, violent epileptic seizures and loss of consciousness. Thus, the lab did much work with possible protectives in the form of antiepileptic drugs. Then F. Dickens, using a Warburg apparatus modified to work at high pressure, showed that hyperbaric oxygen irreversibly blocks some key oxidative enzymes. This was a good reason why protective agents were unlikely to work. The problem of how to safely breathe oxygen at high pressure remains unsolved to this day.

The lab was more successful in understanding 'shallow water blackout' to be an acute CO_2 narcosis. This helped to improve the design of diving suits and the procedures for scrubbing accumulated CO_2 from the atmosphere of crashed submarines. Thus, I was given the job of analyzing the amount of CO_2 in the canisters of rebreathing equipment. The procedure for estimating CO_2 in solids was slow and tedious. Then one day, since I could use large samples of the CO_2 absorbent, I realized I could release the CO_2 rapidly in a large flask and measure its volume through a water gasometer. It was my first piece of original research. Hank MacIntosh taught me how to search the literature and to write a paper. The result was to be submitted for publication but the authorities stamped it as 'secret.' It was circulated to various labs doing secret work and several petty officers were sent to me to learn the method. Therefore, in 1944 my first paper was unpublished!

When I graduated from Birkbeck College in the summer of 1946, I had in mind several equally attractive possibilities for my future. The experiences in F4 pushed me to want to be a physiologist. I could not do that because at that time there were no physiology courses for nonmedical students. I could not afford medical school, nor could I stay in F4; at that

time technicians could not cross over to become academic staff. I was also keen to be a marine biologist. I applied for a fisheries job at Lowestoft; I did not even get an interview. Instead, astonishingly, I got an assistant lectureship in zoology at University College London. The National Manpower Board allowed me to leave my reserved occupation at NIMR without a period in the armed forces because I 'would be teaching ex-servicemen and women.' This was a surprising reason for deferment of a new graduate, not yet 22 years of age and younger than most of the students he had to teach.

University College London, 1946–1947

The main task of an assistant lecturer in zoology approximately 50 years ago was to teach the practical part of the course. Thus, during the vertebrate year D. M. S. Watson (20) gave the lectures for the whole of the year-long comparative vertebrate anatomy course. He was superb, even though he restricted himself largely to skeletons and left only two lectures for birds and mammals. In 10 or 15 minutes of those two lectures he explained birds to be basically warm-blooded, feathered, ornithiscian dinosaurs. For the rest he advised the students to read whatever they found interesting about birds. His recommendation for mammals was to read Scott's *Mammals of North America*. He then spent the remaining time on the development of the chondrocranium and the segmentation of the vertebrate head. It was left to my colleague Pauline Whitby and myself to cover everything else during the practicals.

In retrospect, I do not know how we managed all this, including reorganizing the museum from its war-time diaspora. However, the students in our two classes were terrific. Many were ex-service; some were just old enough to have been my parents. A few had done significant, published research and had taught themselves the local fauna and flora while on duty in various parts of the world. They were very willing to be coopted to teach with us where they had special knowledge. Maybe this cooperative teaching approach I learned contributed to the fact that during the student riots of the 1960s my classes were always fully attended.

At the same time I registered to do a Ph.D. Regulations stated that as a member of staff I did not need a supervisor and only had to pay a registration fee. I cannot remember why I proposed a study of the control of sex change and sex reversal in mollusks. Then John Z. Young of giant nerve fiber fame advertised for a research assistant, supported by the Nuffield Foundation, to work in the University College London (UCL) Anatomy Department and the Stazione Zoologica in Naples, Italy, on the comparative study of memory mechanisms. The appointment was to begin in April 1947. My teaching for the year would be nearly finished by then. Without hesitation, Watson gave me permission to apply. Both of us suspected I

would not get the job because much better qualified people than myself were applying; against the odds I was appointed.

Anatomy UCL and Stazione Zoologica, Naples, 1947–1952

For a zoologist considering applying for Young's research assistantship, the romance and prestige of the Naples laboratory was as attractive as his very high and dynamic reputation (Boycott, 1998). Anton Dohrn, using his private fortune, had founded the laboratory in 1872. Further funding was complex and ingenious. It involved obtaining German and Italian government grants as well as local grants from the city, inventing a system of international subscriptions from universities, and building a public aquarium for tourists (Heuss, 1991). Dohrn's overriding motive for the foundation was his conception of biological research as the free international cooperation of individual scientists. He also wished to provide a research facility in which marine organisms could be studied live. The lab was enormously successful and internationally admired. It became a center at which most of the leading biologists of Europe and some from the United States worked at one time or another during their careers. Its success encouraged the foundation of labs at Woods Hole (USA), Plymouth (UK), and elsewhere.

Anton Dohrn's third son, Reinhard, succeeded him as director in 1909. He needed all his considerable diplomatic and administrative skills to keep this German-owned laboratory going through two European wars. During the second war, when the Allies landed at Salerno, Reinhard stepped aside and put G. Montalenti in charge. Heuss (1991) gives an account of how the lab survived the battle for Naples structurally intact. When this became known in England, G. P. Bidder (a long-time English benefactor) wrote to *The Times* (London) on the achievements of the lab and its role in international science. He gave reasons why the Allied Military Command should give it special care. Soon afterwards, the Council of The Royal Society of London voted Dohrn £1000 of immediate financial help. This was soon followed by donations from other countries. I remember this inspired us Birkbeck College Zoology undergraduates because there was still heavy fighting. Indeed, it was another 18 months before hostilities in Europe stopped.

All this, of course, was recent news when I arrived in Naples in April 1947. I had had high expectations of the place. I was in no way disillusioned. Reinhard Dohrn and his wife, Tania, were personally very kind to me. Over the years they, together with the resident children Peter and Antonietta and Dohrn's assistant Helena Hartmann, incorporated me (although I did not recognize this until the reflections of later years) into a family atmosphere that I had not experienced in my earlier years. Reinhard Dohrn was all that the memorial books have said of him (Götze,

1964; Valenzi, 1983), although I would judge him to have been a significantly more complex and deeply emotional person than the contributors to those volumes understood from his public persona. He was a man of wide culture. His shock, indeed horror, at the poverty of my cultural background was profound. He did much to correct this, as did most of his staff, who also became good friends (G. Montalenti, A. Monroy, E. Boeri, and G. Bacci). I slowly changed from a parochial English boy to much of what I am today. Then there were the graduate students, the fishermen, and the laboratory technicians. The latter were so like those I had worked with at NIMR and the former were hardly different from graduate students in England, except they were bi- and trilingual. How had we all come to be fighting each other?

The Neapolitans are a unique people and, as anyone from the North will tell you, not truly Italian. They and Naples were as unique as Burckhardt (1945) described them from medieval times. They did not like invaders or foreigners of any kind, as Burckhardt pointed out. Up the hill at the back of the lab, there were poor areas; these were not as bad as the center of the city but still very poor. At the entries to the warrens of narrow streets and tall buildings there were notices. The first, put up by Germans, instructed, in German, troops not to enter the alleyways at less than the strength of a platoon in charge of a sergeant. The second was the same notice in English, put up by the 'liberators.' These narrow streets were good places to ambush the unwary of any side. An example is brilliantly shown in a cameo of a U.S. soldier in Rosselini's film *Paesa*. However, Neopolitans readily accepted individuals they came to know and like. Thus, I became acquainted with a German deserter and his family living in a single room and, not far away, his Scottish equivalent.

One summer evening, Jean Hanson (21) and I walked up these hot and humid streets toward the Vomero. We talked and Jean's sandals slapped noisily on the ancient basalt pavement. A loud communal shushing noise came from around the corner. We quietened and crept round the corner to find a group seated in the street outside a one-room apartment. The center of their attention was a battered prewar wireless hissing and popping on a table. It was tuned to catch the beginning of the first postwar production of a Verdi opera to be broadcast from La Scala. We were invited to sit with them. I cannot forget this. Nor, on another occasion, coming upon two small children who were begging passersby for money to bury their dead mother. She was lying on the street with the grandmother by her head. My learning curve during those early years in Naples was very steep. I could fill this whole article with such vivid reminiscences, all influential to my development as a person. Indeed, I perhaps should list Naples and the Stazione under education rather than research.

John Young spent 2 weeks introducing me to the lab, discussing possible experiments, and infusing me with his enthusiasm. He returned to

London, leaving me with very general guidelines and a free hand. As I (1998) and Guillery (1998) have outlined, at the time this was a common way to handle Ph.D. students and research assistants. If they sunk, they disappeared; if they swam, they were treated as research equals. Young was always extremely helpful with resources and advice. Indeed, in a short time we became very busy with projects. If I sorted out a bit of work for my now neurobiological Ph.D. thesis Young always agreed, but insisted we should write this or that paper first. Therefore, I never had time to obtain a Ph.D. It is, in fact, a much tougher and appropriate discipline to write a piece of work suitable for submission to a journal than to produce a dilatory thesis. Therefore, I have never felt this to be a loss.

In March 1947, I chatted excitedly to my former boss in F4, F. C. MacIntosh, about going to Naples. As we parted he wished me the luck to discover experimental preparations equal to the ambitions of Young's program. It was nearly two decades before I thoroughly understood the wisdom of that remark. What exactly did I achieve scientifically in the years I worked with cephalopods? What was so perceptive about MacIntosh's remark?

The work on the anatomy of cephalopod brains went well. We further defined the different lobes of the brain and, using degeneration techniques, worked out their connectivity. We had a first draft of a book by 1952. However, Young decided to work on it for another 20 years (Young, 1971); my prelude to the book describes my role in it. Summaries of my experiments on memory mechanisms are to be found in Young's books of lectures (Boycott, 1998) and in a book by Martin Wells (1978). Thus, for this autobiography it is more appropriate to give a retrospective judgment of the importance of selected parts of my work than to summarize what has been already reviewed. Therefore, I will give a brief discussion of my two most important cephalopod papers.

As I have explained elsewhere (Boycott, 1998), part of Young's program was to contrast the structural organization of the motor control systems of cephalopod brains with that of their memory systems, a time-honored comparative anatomical approach in a search for the basic features of an organ system. For this we used electrical stimulation and surgical ablation of the brains (Boycott and Young, 1950). Most of the early work stimulating octopus and cuttlefish brains followed soon after publication of the results of Fritsch and Hitzig (1870) and Hughlings Jackson (1878, collected 1932) for mammals and humans. The responses obtained were limited because only Faradic stimulation was available. Fifty years later we were able to use a recently designed square-wave stimulator built by one of my former colleagues in F4. Thus, we evoked many more responses than had previously been observed and were soon able to classify the lobes of the brain of octopus and cuttlefish functionally. They could readily be ordered into a hierarchical scheme of the kind produced by Hughlings

Jackson (1932) for mammals: silent, or association areas, and higher, intermediate, and lower motor centers. This was encouraging, but we were interested in the neural control of behavior. By then I had heard of Erich von Holst's work and knew of N. Tinbergen's (1951), now famous, scheme for the hierarchical organization of patterns of behavior. There was also the stimulus of C. A. G. Wiersma's concept of 'command' neurons in the crayfish nervous system. He had shown that as few as four axons were responsible for the tail-flip escape response (Edwards *et al.*, 1999). By analogy with the giant fiber escape responses of decapod cephalopods, I hoped to define many command units of behavior and to see how these might relate to the scheme proposed by Tinbergen.

My initial experiments had been done with hand-held electrodes using restrained, lightly anesthetized, animals. For these more ambitious and interesting experiments, electrodes implanted in freely moving animals were required, as they were, for example, for the experiments on the mammalian hypothalamus (Hess, 1948). I spent much time trying to implant electrodes that would remain stable in a freely moving animal into octopus brains. The last attempt was with Don Maynard in 1963. We had enough success to confirm, using unanesthetized free-moving animals, that many of my results on anesthetized octopus were valid. There were indications that we could evoke discrete patterns of behavior, but we were finally defeated by electrode instability problems. Thus, I have only published the initial results on the cuttlefish brain (Boycott, 1961). The results for octopus brain are incorporated into Young's (1971) book. These were never formally written up because Don Maynard died suddenly while skiing in the Rocky Mountains after attending a meeting in Denver. He had the only copy of my manuscript. It was lost (no copying machines in those days). I never reconstructed the manuscript from my notes, which are now in the Smithsonian in Washington, DC as part of the J. Z. Young archive. There did not seem much point in publishing another paper demonstrating, yet again, a functional hierarchy of motor organization in a cephalopod brain. This work was a useful bit of physiological anatomy. It disappoints because it could not achieve the more interesting ambitions of the experiments.

After several false starts (Boycott, 1954) I found a simple procedure for training octopus. This was to produce a visual discrimination between crabs alone and crabs presented with a small white square from which, if they attacked it, they received a weak electric shock. The trials were at intervals of 2 hours throughout the day. This procedure (Boycott and Young, 1955a) became the basis for most succeeding learning studies (Boal, 1996). In our paper we showed that electrically inexcitable areas of the brain, association areas, were necessary for the memory of that discrimination. Thus, an octopus with the vertical and/or superior frontal lobes removed could not remember that an attack on a crab presented with

a white plate resulted in a nociceptive stimulus. It always attacked as if the stimulus was a crab presented alone. The duration of each trial was 2 minutes. During that time a normal octopus might attack four or five times in the first trial in which it experienced the crab + plate + shock. In succeeding trials attacks were always less at each trial, and within a few trials the animal learned not to attack at all. Animals without the vertical lobe system differed. They would attack at the beginning of a 2-minute trial but then stayed at home and stared at the crab and figure. Thus, in these animals some inhibitory mechanism operated while the stimulus remained in the visual field. Two hours after removal of the crab and figure they always attacked when it was reinserted into their tank.

Because 2-hour intervals between trials were standard training procedure, I wondered what would happen with these operated octopus if I increased the frequency of trials by decreasing the intertrial interval. The result was that animals without a vertical lobe system could learn the discrimination. However, the intertrial intervals had to be shorter than 30 minutes; this proved to be the maximum retention period of which they were capable. For normal octopus retention periods were upwards of a week (we never studied this systematically). The same results were obtained for a learned discrimination between crabs and sardines (Boycott and Young, 1955b). This led to the proposal that the neural mechanisms to establish a memory of these discriminations in the octopus brain had two components. The first component was a transitory or short-term mechanism that could persist actively for about 30 minutes. The second component was some mechanism which took longer to establish but then persisted longer and required the activity of the transitory mechanism in order to become consolidated. I was not aware that a distinction between short- and long-term mechanisms in consolidated memory formation had already been made qualitatively from human studies by H. Ebbinghaus and William James. The dichotomy is now widely accepted and is fundamental to most models of memory systems (Squire and Kandel, 1999).

Our papers (Boycott and Young, 1955a,b) received significant attention because, coincidentally, a group at the Montreal Neurological Clinic found that patients with bilateral temporal lobe lesions could retain preoperatively established memories but could not establish new ones. Their short-term memory mechanisms had been unexpectedly damaged during surgery for epilepsy so that consolidation of memories could not occur. [See Milner (1998) for an account of these patients and the later discovery that in patient HM certain nondeclarative memories could be established.] It was Eliot Stellar (1957) who first appreciated the similarity between our observations on octopus and those on these patients. In his discussion he expressed the expectation that this (the first) experimental demonstration in an animal of short- and long-term memory mechanisms would facilitate

electrophysiological approaches to studying at least part of the mechanism enabling nerve cells to store information. This, of course, had already become a major aim of my work. I tried many times between 1948 and 1965 to get stable recordings (Boycott *et al.*, 1965). I have related the reasons for the failure elsewhere (Boycott, 1988, 1998). Perhaps because of Stellar's review, Boycott and Young (1955a) was selected as a reading in *Contributions to Modern Psychology* (Duhany *et al.*, 1959). Because I had to return to a teaching appointment I could not follow up this work behaviorally. However, the main reason I did not follow up this work was that it began to seem not worthwhile to do so without being able to do any electrophysiology. Hank MacIntosh had been very perceptive in March 1947 when he wished me good luck with techniques. Had I succeeded with recording from octopus brains my research career might have been very different and octopus might have been competing with *Aplysia* in neurological interest. Our demonstration of short- and long-term memory in octopus is a good example of how an important piece of work, well-known and influential at the time, can disappear from the literature because it could not be developed further.

Zoology UCL, 1952–1970

During these years teaching took an increasing proportion of my time as courses changed and were modernized and student numbers increased. The first decade was also a period during which the direction of my research was uncertain.

Teaching

In 1951, P. B. Medawar (35) succeeded D. M. S. Watson as the Jodrell Professor of Zoology at UCL. He invited me to return to the department in 1952 to teach part of the main zoology course and share teaching comparative physiology with G. P. Wells (32). Wells was a hero of my young reading; he had coauthored *The Science of Life* with J. S. Huxley and his father H. G. Wells. This had been one of the best known popularizations of biology during the first half of the twentieth century.

The basic design of the zoology honors course at UCL in 1952 was approximately 50 years old. Wells' introduction of a comparative physiology course in the mid–1930s had been the only major innovation. After we had taught this course together for a few years, Wells believed that it needed to be replaced by a neurobiology and behavior course—neuroethology as it might now be called. The university agreed to our proposals. Thus, the first neurobiology course outside a London medical school was founded. I ran it jointly with D. Blest, who had done a doctorate with N. Tinbergen in ethology and was a former graduate of our physiology course. At first, the new course served all the colleges of the university. Later, each

college ran their own. Some of its graduates will be familiar to neurobiologists: R. Chapman, T. S. Collett, J. S. Lund, J. H. Scholes, S. Shaw, V. Sterling, and N. J. Strausfeld.

By the 1960s, it was thought that the old honors system, both in content and presentation, was too inflexible for the needs of modern students. Therefore, about the time Medawar became director of NIMR (1962), to be succeeded by M. Abercrombie (26), there was a major restructuring of courses in the university to bring in a modular system. The resultant scheme resembled that long established in North American universities. It is relatively easy to create specialist modular courses. However, to be educationally successful they must be accompanied by good mandatory basic general courses; without these students specialize much too soon. They have no context for their specialities. Thus, I came to be in charge of, and taught most of, a basic zoology course lasting three semesters. Ridiculously, it could not be a biology course because the botany department wanted, independently, to run its own basic cell biology and botany course. Essentially, my course was designed to provide cell and organism zoology for students majoring in psychology, chemistry, biochemistry, and anthropology. However, almost anyone of any background could turn up, of whom Alan Snyder (Canberra) is perhaps the best known. Initially, it took about 15 students a year. It proved popular so that toward the end of the 1960s it was averaging over 70 students a year and attracting them away from courses in other departments. This was gratifying, particularly because at that time students were openly critical of courses. With sit-ins, etc., they were attacking the perceived university establishment as remote and self-serving. We had no trouble and often quite a lot of fun debating the issues.

The change to modular courses soon brought a requirement for a basic neurobiology course that could be a preliminary to the more specialist courses springing up throughout the college. It fell to me to initiate this interdepartmental course. Myself, G. Dawson, B. Katz, and T. Shallice gave the lectures. It too became very popular, especially when B. Katz was lecturing. His lucidity and judgment of the level of the audience were remarkable. However, he always said that he could not examine them fairly because most of their backgrounds were not sufficiently biophysical and asked me to do his share. [This is somewhat different than Guillery's (1998) account of Katz teaching approximately 20 years earlier.]

Over time there came to be many difficulties with these two courses that had nothing to do with students and were mostly to do with funding mechanisms. The college allocated funds in proportion to the number of students taught and the number of courses a department gave. Departmental heads came to have a vested interest in not cooperating with each other to fund, or let their staff take part in, interdepartmental basic courses. (By then my basic zoology course also needed to become interdepartmental.)

A good basic general course has to provide an up-to-date synthesis of the subject. To do this is significantly more demanding than teaching a specialist course. For the average academic, a specialist course can be taught with minimum effort. It is a way of keeping up with his or her speciality. Giving the bulk of the lectures in two general courses I became increasingly under strain trying to synthesize the explosion of advances in biology during the 1960s. M. Abercrombie, the head of the department, was very supportive. However, in 1968 he became director of the Strangeways Laboratory in Cambridge. I shall omit here the long and often risible story of the search, beginning in 1967, for his successor. Eventually, in 1969 Lord Annan (the provost of the college) suggested I should succeed Abercrombie. (I think I was the search committee's 10th plus choice). I would have liked to accept, but I said no. The main reason I declined was that, at that time, UCL had practically no senior modern cell biologists as faculty, except for some nerve and muscle people in the medical school. I suggested Avrion Mitchison, a cellular immunologist. The committee accepted this and he brought Martin Raff with him. This decision began the growth of modern cell biology in UCL.

There was, however, to be a gap of nearly a year before Mitchison could move. I agreed to be acting head of the department, but on one condition. I explained to Annan the difficulties I was having organizing basic biology courses. He seemed to understand the problems. At my request he promised to set up a high-powered biology teaching committee, with me as a member, to plan and fund necessary basic courses. I explained that I would have to resign if there was no committee and no progress. Six months passed, nothing happened, and I accepted the long-standing persuasions of King's College London to join the MRC biophysics unit there. Annan expressed surprise and regret at my resignation. I can only suppose he did not believe what I had said and did not really care how basic undergraduate teaching was organized. It was a pity. I had been happy at UCL for nearly 25 years. I enjoyed combining teaching and research. Traditionally this was expected of university academics (Medawar, 1986); it was the way I had been brought up. That the tradition has become all but dead during my career is bad for researchers and students alike.

Research and Harvard University

I have given an account elsewhere of some of the research I did between 1952 and 1970 (Boycott, 1988). I did not finally give up cephalopod work until 1965 (Boycott, 1965a,b). Under Young's impetus the memory studies of octopus continued for many years, although they became more oriented toward cognitive approaches than the study of cellular mechanisms (Boycott, 1998).

On my return to the zoology department, I flirted with studying reinnervation of the optic tectum after optic nerve section in amphibia. I soon

found that what I planned was not as good as the experiments in M. Gaze's laboratory, so I stopped. The reasons for beginning work on the reptilian hippocampus with R. W. Guillery have already been related (Boycott, 1988). During this work, joined by E. G. Gray, we found temperature-dependent changes in the arrangement of neurofilaments in certain nerve terminals of the brains of lizards. They formed loops and rings in animals living at 19°C that decreased in density when the animals were moved to 32°C (Boycott *et al.*, 1961). This gave me an interest in neurofilaments that was to be important when I went to King's College London.

The end of the lizard work coincided with an invitation by John Welsh to teach, alongside D. M. Parry (Cambridge), half his invertebrate zoology course at Harvard in 1963. This was attractive because I had never been to the United States and because at Harvard Medical School C. Lyman had a colony of ground squirrels (*Spermophilus* sp.) that he was happy for me to use. Ground squirrels hibernate under lab conditions. Because of our lizard work, I was interested in examining the dendritic spines on the cerebral cortical cells of hibernating and awake mammals. At the end of the nineteenth century, several authors had claimed a decrease in the spines of cortical nerve cells when a hibernator's body temperature dropped to about 5°C. Similar changes were also claimed as a consequence of chloral hydrate or barbiturate anesthesia. Since it had recently been demonstrated by electron microscopy that dendritic spines were postsynaptic processes (Gray, 1959), the project was potentially of significant general physiological interest.

Neither the research nor the teaching planned at Harvard was especially onerous. From the time I entered Birkbeck as an undergraduate I had always been very busy. I had not had time to think about neurobiology as deeply as I should have done. At Harvard, away from all responsibilities, this was possible. Therefore, in a new and diverse environment I reassessed what I had been doing in neurobiology. With the research of the neurobiologists in the Boston area for comparison, I began to realize that I had not yet brought a research program into sharp focus. I began again to think of moving toward a more physiological problem and, back in the United Kingdom, discussed learning biophysical techniques with R. Miledi. However, this was not practicable; when carrying a heavy teaching load it is easier to fit in anatomical work. Therefore, for this and many other reasons I focussed on beginning to ask myself what neuroanatomical studies should aim to achieve, especially if they were to be more than descriptive.

When I left Harvard in June 1963 I had not observed any changes in the dendritic spines of cerebral cortical cells while comparing awake and hibernating ground squirrels. I had, however, found differences in the spines on the dendrites of Purkinje cells that made it worthwhile to return to Harvard in January 1964. It was then that I had a discussion with John

Dowling that was ultimately to alter the subject of my research for the rest of my career. I had first met John as one of the organizers of George Wald's Nat. Sci. 5 course. This course was particularly interesting for me. It had many innovations and improvements for the teaching of basic biology courses that were relevant for my course back home. When I returned to Harvard in 1964, John had been learning electron microscopy (EM) under the tutelage of Ian Gibbons. He had begun to look at synapses in the inner plexiform layer (IPL) of vertebrate retinae. It was apparent that there were many synapses to be observed ultrastructurally. However, beyond their description this did not reveal much about the synaptic organization of a retina. Over coffee one morning, we discussed my problems with measuring the dimensions of Purkinje cell spines and the problems of how to attach synapses observable by EM to the types of retinal nerve cells that could be seen by light microscopy (LM). We decided to attempt to combine LM and EM studies in both cerebellum and retina. Nowadays this sounds so commonplace that it is almost embarrassing to read that sentence. However, at that time, attempts such as that made by Gray and Guillery (1966) were rare. There were even EM enthusiasts broadcasting LM to be finished as a significant modern method.

Because I already had Golgi-stained ground squirrel cerebellum, John and I first related EM observable cerebellar synapses to the types of cells visible by Golgi methods. A qualitative correlation did not take long. This was never published because after discussion with S. L. Palay, we found that he was writing his, now well-known, monograph on the cerebellum. We never brought the temperature-dependent changes to a conclusion for many technical reasons which could be overcome today. Now dendritic spine changes can even be observed directly on hippocampal neurons after long-term potentiation (Engert and Bonhoeffer, 1999; Toni *et al.*, 1999). Indeed, particularly because long-term depression (Ito, 1998) and learning mechanisms have been demonstrated in the cerebellum (Squire and Kandel, 1999), it might now be worthwhile to examine the hibernating effects I described (Boycott, 1982).

The experiments with the cerebellum gave us experience in matching EM and LM observations. Initially the ground squirrel retina proved too difficult. It was not until John moved to the Wilmer Institute at John Hopkins Hospital in 1964 that we made serious progress. The turning point was a melanomatous but otherwise normal human eye that had to be removed from a patient by the director, E. Maumenee. This fixed very well. In the human retina many of the bipolar cell terminals in the IPL are large. Thus, while I was in England making Golgi preparations of a wide variety of vertebrate retinae, John was able to make the crucial observations that led to the hypothesis that in the IPL only bipolar cell terminals contain synaptic ribbons. Wherever we looked in the IPL this proved to be true. The ribbon synapses were the only sites of synaptic output of bipolar

cell terminals. At the ribbons we always found pairs of postsynaptic processes—dyads. In human retina these were often made up of a ganglion cell dendrite and an amacrine cell process. The amacrine cell process usually had a reciprocal synapse back onto the bipolar cell terminal. Following the amacrine processes, serial sections showed they could be pre- and postsynaptic to other amacrine cell processes and also presynaptic directly onto ganglion cell dendrites. Separately, and unknown to us, E. Raviola and his wife (Raviola and Raviola, 1967) were coming to the same conclusions regarding the rabbit retina. Also, Dowling (1968) soon showed from frog retina that this too has the same basic connectivity pattern. The observations have proved to be the general rule for the synapses of the IPL in all vertebrates.

Our observations by EM on the amacrine cells, showing one and the same process could be both pre- and postsynaptic, are a good example of how a technical improvement can very simply resolve an intractable problem. Because amacrine cells appeared to have no axon, they seemed to break the van Gehuchten, Cajal 'law of dynamic polarity of nerve cells.' Because of the absence of an axon, Cajal, up to his last paper (Cajal, 1933), was frustrated trying to interpret them. Also, Polyak's (1941) discussion shows vividly how the absence of knowledge of the input and output of amacrine cell processes confused their functional interpretation. Amacrine cells are true interneurons. About the same time Reese, Rall, Shepherd, and Brightman showed that the dendrites of the mitral cells of the main olfactory bulb are pre- and postsynaptic and, along with the granule and periglomerular cells, are analogous to the retinal amacrine cells. It is now thought that lateral inhibition through dendrodendritic reciprocal synapses with granule cells may sharpen the tuning specificity of individual mitral and tufted cells to odor molecules (Mori *et al.*, 1999). Unfortunately, this is not the place to attempt a discussion of the extent to which there may be basically similar interneuronal networks in retinae and olfactory bulbs. This could be interesting because in mammalian retinae there seem to be many more morphological types of interneurone, at least 26 in the rabbit (MacNeil and Masland, 1998), than in the main olfactory bulbs.

Cajal (1893) and Polyak (1941) provided an immense amount of LM detail on the vertebrate retina, largely derived from Golgi studies. Thus, John and I were often asked, when we started, why we bothered to make our own Golgi preparations. The fact is that, at that time, it was difficult to translate the small series of EM sections through the retina into the three-dimensional appearance of cells obtainable in thick Golgi sections. Looking at real Golgi material we could make abstractions and guesses, impossible to achieve from published work. I give here but one example. Early on we observed by EM, as did several other workers, the presence of membrane densities on cone pedicle bases and the triadic invaginations

into the cone pedicles. When we looked in Golgi at bipolar cell dendrites we could see that some had small processes on and others did not. At first we thought this was variation in staining. Eventually, we thought the differences to be more systematic. We resolved the problem by taking a Golgi-stained cell off the slide and sectioning it for EM study. In this way we unexpectedly found that there are two types of midget bipolar cell, one whose dendrites are the central elements of the cone triads (the invaginating midget bipolar) and the other that makes basal synapses on the cone pedicle base (the flat midget bipolar) (Kolb, 1970). They are now thought to be ON- and OFF- bipolar cells, respectively. Details of their connectivity and those of diffuse invaginating and flat cone bipolar cells are still being worked out, but now in terms of the types of glutamate receptors on the dendrites (Boycott and Wässle, 1999).

The EM study also fed back onto the understanding of the LM of the retina. We became committed to a lengthy reassessment of Polyak's description of the primate retina in terms of our LM and EM data. It was during the long process of drafting Boycott and Dowling (1969) that I first began to think more about attempting to define morphological types of cells on a more objective and quantitative basis and to wonder how better to relate morphological types to the physiological units that were beginning to be described. In 1964, M. Colonnier used the newly introduced histological fixative glutaraldelhyde for Golgi fixation. We hoped, as happened with the earlier introduction of formaldehyde by Kopsch, that we might find further types of retinal nerve cell. This indeed proved to be true and we were able to confirm the interplexiform cell as a component of mammalian retinae (Boycott *et al.*, 1975).

I also tried Colonnier's method on the insect brains that my colleague D. Blest was studying. Indeed, to save sectioning effort, I placed the first insect brains I tried adjacent to ground squirrel retinae in the same block. Until then it was, of course, Cajal's lab (Cajal and Sanchez, 1915) that had provided the best Golgi neuroanatomy of insect brains. Others had tried with little success. With glutaraldehyde in the fixative I got lucky immediately. It was exciting. For some days I thought I would be able to take on insect neuroanatomy alongside the vertebrate retina. Not being an equal of Cajal, I did not do so. The insect neuroanatomy was taken up by Blest's doctoral student N. Strausfeld and summarized in his monograph in 1976.

King's College London, MRC Biophysics Research Unit, 1970–1989

For the reasons already related, my actual move to King's College was abrupt. It had, however, been thought about for several years. The then director, J. T. Randall, was near retirement. His successor was to be M. H. F. Wilkins. He had attended our neurobiology and behavior course in 1965

and had asked my advice about moving the unit toward neurobiology when he took over. I had suggested several possible neurobiologists to join the unit, but Wilkins thought I was the most suitable. In this opinion, he was backed up by a friend from my first year in Naples, E. J. Hanson. She ran the muscle side of Randall's unit.

Although I did not want to leave UCL, and probably would not have done so had there not been an impasse over teaching reorganization, there were significant personal research reasons for me to consider a move to King's. Toward the end of the 1960s my research was all in retinal structure. I was then in the phase of drafting Boycott and Dowling (1969) and thinking about simplifying and ordering the diversity of cell types that had been described. I had also come to believe that the way to further understanding of the retinal neural net was through developmental and tissue culture studies. King's was attractive because of the presence of cell biologists from whom I could learn. Thus, my proposal to MRC for appointment to their unit gave emphasis to using the vertebrate retina for studying mechanisms of development of the different types of nerve cells and their connections. To that end, one of the first appointments I made was of J. H. Scholes to look into the development of nerve cells in the goldfish retina. This seemed to have advantages for experiments since the periphery of the retina continues to grow and differentiate throughout adult life. My 1970 proposal also argued that the growing tips of nerve cell processes were of fundamental interest because they must be involved directly in the mechanisms that determine whether or not a synapse is formed with this or that neural process. D. Bray was appointed to study nerve growth cones and the mechanisms of movement of molecules along axons. This is now a sophisticated and busy field of research (Hong *et al.*, 2000).

An important reason for joining King's was a hope that the physically minded molecular biologists there, who had worked on the structure of DNA, would be able to contribute to an understanding of how any nerve cell gains and maintains its shape in the adult brain. This seemed relevant to also asking why different nerve cells are morphologically different. I thought, when I wrote my proposal, that these problems might not be too difficult. I learned rather quickly, in a cell biological atmosphere, that they are far from easy to state in practical analytical terms. However, in one respect some significant progress was made. I appointed David Gilbert to study neurofibrillae (neurofilaments) using his preparation of the giant axon of the tubiculous polychaete, *Myxicola infundibulum*. The axon has essentially only one structural component, the neurofilament. It therefore provides an unparalleled opportunity for experimental study. The work went well for several years and included isolation of neurofilamentous protein, the beginning of X-ray diffraction studies, and the development of a model of how the filaments coil and supercoil. An abrupt end came when David died prematurely (Boycott, 1980).

Sometime before I went to King's, Maurice Wilkins, at my suggestion, turned his expertise to an X-ray diffraction study of rod outer segment membranes (Blaurock and Wilkins, 1972). This work had an interesting and unexpected fallout when two members of the department used X-ray diffraction to study the effects of general anesthetics on the properties of phospholipid membranes. Contrary to the almost universal belief of the time, Franks and Lieb (1975) showed that changes in the dimensions of the unit membranes of cells could not be the site of action of anesthetics.

When I joined King's, MRC administration split the biophysics research unit into a neurobiology and muscle group. Jean Hanson died suddenly in August 1973, so the units were reunited under Wilkins as a cell biophysics unit. This change of policy was precipitated by Jean's death but it was caused by a particularly dramatic downturn in government funding of universities and the MRC. The cutback represented approximately 25% of our funding. Together with the departure of Jean Hanson's second-in-command, Ed Taylor, the unit suddenly went through a period of stasis and uncertainty. Wilkins was due to retire as director in 1980, so for 5 years it was doubtful if it would even survive. Details of this period would be a tedious account of politicking, indecision, and general stress. It ended, surprisingly, in the fall of 1979 when MRC suddenly asked me if I would direct a cell biophysics unit jointly with D. A. Rees. He would retain his position with Unilever and work part-time at King's. Rees was known for his studies of carbohydrate structure and had recently been applying this expertise to fibroblast locomotion. I accepted, with the proviso that if we ever disagreed I would make the final decision. We never did. We appointed R. M. Simmons and J. Sleep to bolster the muscle group and G. Dunn to study fibroblast locomotion. I was also able, at last, to get studies on growth and differentiation in nerve cells going in the unit through the appointment of J. Brockes to study the neural control of mechanisms of regeneration of urodele limbs. Although Rees soon left to become director of NIMR and, later, executive secretary of MRC, the unit settled down to a productive period. It received very favorable reviews when I had to retire as director at the end of 1989. It is not relevant here to describe ensuing events, which were complex. The unit was supposed to be the basis for the foundation of an interdisciplinary research center together with UCL. However, colleges, like departments within them, prefer to compete for money unless they are forced to collaborate. Therefore, despite much noise little came of this initiative.

Personal Research at King's College, London

Boycott and Dowling (1969) was published just before I went to King's. It was a paper that took a long time (from 1965) and many drafts (about 12) to complete. During that time we had shown by sectioning Golgi-stained

cells that primate cone bipolar cells had either flat or invaginating contacts with cone pedicles, and that the dendrites of horizontal cells contacted only cone pedicles (Kolb, 1970). I knew by then that there were triads in cat cone pedicles. It seemed important to determine if the cone bipolars of this retina also had flat and invaginating types and that rod bipolar dendrites invaginated only into rods. This turned out to be so (Boycott and Kolb, 1973a). Within the flat/invaginating dichotomy there were a variety of cone bipolar cell types. However, these could not be classified until later (Kolb *et al.*, 1981). By now I had good, but unpublished, Golgi material showing two types of horizontal cell in cat and rabbit retinae. This made the primate retina different since Polyak (1941) had only found one type. We confirmed his observations (Boycott and Kolb, 1973b). However, Golgi and methylene-blue staining were letting all of us down. Seven years later (Kolb *et al.*, 1980) a second type of monkey horizontal cell was found. We now know that two morphological types of horizontal cell are basic to all mammalian retinae (Peichl *et al.*, 1998), with the exception of murid retinae, which have only the B type (Peichl and Gonzalez-Soriano, 1994).

The horizontal cell paper coauthored with Kolb was important to my observing and thinking about the retina. I had always been aware that the exact morphology of a retinal nerve cell varied with its position relative to the fovea, central area, or visual streak (eccentricity). However, until I examined HI horizontal cells at different eccentricities in rhesus monkey, I had not realized how radically cell morphology could vary with eccentricity nor how important it was to examine the cells in retinal whole mounts rather than sections. The Golgi procedures I was using produced all sorts of obscuring precipitates on the surface of the retina. Therefore, only occasionally could a fragment of retina be made into successful whole mounts. This led me to use the Golgi–Cox procedure on cat retina. The resolution of cellular detail using this mercury salt-based method is not as good as that for other Golgi procedures, but when it works the cells are stained black on a clear transparent background without overlying crystal precipitates. It worked well for whole mounts of cat and rabbit retinae but for monkey's retinae it never stained anything. In none of these retinae did I stain even one bipolar cell with Golgi–Cox procedures. Golgi staining is indeed a strange and precarious procedure.

These were some of the immediate practical activities I undertook while drafting Boycott and Dowling (1969). The reason drafting took so long was that as much thought as new observations went into the paper. In this respect, I have a particular affection for Fig. 96 and its legend. While composing the figure I was making my first attempts to think about the relative numbers of the cellular components of retinae, their spatial relationship, and how to quantify the different types of cells. At that time (early 1970s) it seemed that the only methods that would give quantitative

results for a cell type were the neurofibrillar methods. They selectively stained the types of nerve cells that had bundles of neurofilaments (Gray and Guillery, 1966). However, staining of these cells in a retina was often patchy. I hoped that, properly handled, all of a population of cells could be stained in one retina. This first proved possible for A-type horizontal cells in the cat retina and later its alpha ganglion cells. It never worked for the A-type cells of the inferior retina in the rabbit (as we now know because the neurofilamentous protein of these cells is not in filamentous form; Löhrke *et al.*, 1995). Reduced silver procedures on monkey retina resulted in the staining of a few patches of alpha ganglion cells. At the time I viewed all these activities as the final phase in what I had been doing in retinal anatomy, a preliminary before turning to developmental studies. In fact, it turned out to be a new anatomical beginning and this was largely due to my meeting with Heinz Wässle. In 1971, I went to a symposium, organized by Otto Creutzfeldt in Scholss Neubeurn, as a satellite to the International Physiological Congress in Munich. Heinz approached me after my talk with some questions about cat retinal ganglion cells relevant to his Ph.D. thesis. From my Golgi–Cox preparations I already knew that much of what had been published was misleading but I had not analyzed the material. The upshot of our discussion was that Heinz came to London to work on the slides in early 1972.

We grouped cat ganglion cells morphologically into three types: alpha, beta, and gamma. The first two types were homogeneous groups and the latter mixed. We could not define the detail of the types of cells in the gamma grouping from the material we had. We could define the alpha and beta cells and show how their morphology and dimensions changed with retinal eccentricity. We suggested that the alpha cells were the Y cells of physiology and the smaller beta cells were the X cells. We expected other physiological types to be in the gamma cell category (Boycott and Wässle, 1974). This has now been worked out in more detail. The morphological types of ganglion cells in the gamma grouping are now defined by D. Berson's group as far as theta and correlated with the different physiological types of W cells (Isayama *et al.*, 2000).

After we had drafted our paper, Heinz left for a postdoctoral period with P. O. Bishop and W. R. Levick in Canberra. By the time Heinz returned to Europe I had sufficient A-type horizontal cell preparations for quantitative evaluation. We joined forces again. A crucial feature of our new work was Heinz's application of nearest-neighbor analysis to define the spatial relationship between cells (Wässle and Riemann, 1978). Using this we were able to show that A- and B-type horizontal cells form statistically regular mosaics and that the A and B mosaics are arrayed independently of each other. Thus, the regularity of a mosaic provided a measure confirming that the cells were a homogeneous morphological grouping. We could also measure the dendritic field area and the density of the cells and so

calculate a coverage factor for each type of cell (Boycott *et al.*, 1978; Wässle *et al.*, 1978a,b). All the different types of retinal cells we have examined since these three papers were published have been found to be organized in regular mosaics. This seems obvious now because without regular spacing the dendrites of each type of cell could not tile the retina economically. Indeed, dendrites of homologous cells interact during development so that they obtain the right degree of coverage (Wässle *et al.*, 1981). There are therefore no blind spots or irregularities in visual space for the function of a particular type of cell.

Leo Peichl, Heinz's Ph.D. student, had joined us in the horizontal cell work. Like Heinz, he began as a physicist who turned to biology. During his postdoctoral at King's we developed the 'on the slide' reduced silver staining of whole retinae so that alpha ganglion cells in cat retina could be consistently stained (Peichl and Wässle, 1981). Later, this enabled us to examine a variety of mammalian retinae and show that in most orders alpha ganglion cells comprise about 5% of the ganglion cell population (Peichl *et al.*, 1987a,b). We were also able, together with D. Vaney, to identify cholinergic amacrine cells as neurofibrillar staining in the rabbit retina (Vaney *et al.*, 1981) and to describe a population of long-range amacrines in that retina (Vaney *et al.*, 1988).

As time has gone by I have become involved in many collaborations with Heinz and Leo and their colleagues and students. These have been among the most pleasurable and profitable of my research career. It is difficult to believe that Heinz and I began work together approximately 30 years ago, and that during the past 10 years, since my official retirement in 1989, I have published approximately 16 papers together with Heinz or Leo. The data for these papers have largely been derived from injection of cells with fluorescent dyes and the use of immunostaining techniques. This autobiography is a good place to record that my colleagues have done most of the hard work. My contributions have essentially been to make a bridge with the past—to check out where possible on our old Golgi and other silver preparations that what is observable with modern techniques is in agreement with these older methods (Wässle *et al.*, 1994, 1995; Löhrke *et al.*, 1995).

One of our more significant papers during this period was a classification of monkey cone bipolar cells (Boycott and Wässle, 1991). This was based on differences in the level of stratification of their axon terminals in the IPL. Since then, in a series of six papers, Hopkins and I have been able, by EM study of Golgi-stained cells, to show that the details of the synapses with the cones are different for each bipolar cell type (Hopkins and Boycott, 1997). It is not at all clear why this should be so; perhaps it will prove to be something to do with types of glutamate receptors. Whatever the answer, for the moment it is agreeable to have a collateral confirmation of the bipolar cell typing that was based on other criteria.

Cajal (1893) believed, and I too expect, that the retinal cells of all mammals will be basically the same. This appears to be so when the number of types of bipolar cells in rat and monkey retinae are compared (Boycott and Wässle, 1999; Wässle, 1999) or when the large number of types of amacrine cells in rabbit retina are compared with those of other mammals (MacNeil *et al.*, 1999). Of course, that does not mean their connectivity is quantitatively the same, e.g., there is no midget (single cone) bipolar cell in a rat retina. Again, there are basically two types of horizontal cell in most mammalian retinae but the details of their connectivity can differ. An example is the A-type horizontal cell of horse retina which is directly connected anatomically only to short wave-sensitive cones, a unique and very puzzling connectivity pattern (Sandmann *et al.*, 1996).

I must stop this discussion; I vowed when I began that I would not end with a review of current interests and work. Indeed, we have published several reviews: Wässle and Boycott (1991), Peichl *et al.* (1998), Boycott and Wässle (1999), and Wässle (1999). It would be more enjoyable to discuss science than write more about me, but this is hardly appropriate to terminate an autobiography. How should I end? I suppose I should draw profound conclusions from my 60 years spent in research labs and compose wise messages for successors. Neurobiological information has expanded enormously since I began. The subject seems to have become more fragmented and specialized, certainly more molecular biological. With the multiplicity of transmitter receptors that are currently being discovered in the vertebrate retina, it sometimes seems as if there are more facts available than achievement of understanding of how the retina translates visual images into what the cerebral cortex 'sees,' etc. It is obvious that this should be the main interest; however, such commentary verges on platitude. It is an old man's game. I still find science too exciting and interesting to play it.

A fair summary of myself would be to say that I have not made contributions of any great originality in terms of methods or ideas. My general contribution has been as a sound and reliable observer, whose persistent need to understand living things has perhaps, incidentally, encouraged others. My personal research has been neurobiological, yet the reason I liked teaching was because I had cause to keep up with a wider range of biology than nervous systems. Perhaps this is why in my lab I never built up staff and students dedicated to my immediate research (a somewhat unusual policy judged by the standards of today's senior scientists). This was particularly true when I was staffing the King's unit. Here, it was topics that were as interesting and important as what I was doing personally that I wanted to sponsor.

From the start of my career in F4 I have been immensely fortunate to have had contact with top-class scientists as bosses, colleagues, and often

friends. I have interacted with many more well-known biologists and neurobiologists than I have mentioned here. While agonizing over the drafting of this autobiography, I came to realize how these contacts have raised my level of achievement beyond what could have been predicted from my poor academic beginnings. To all these people I am grateful that they, by example, have helped me achieve as much as I have in research.

Finally, I express some detailed 'thank-you's.' First, and most important, to my wife, Marjorie, who for more than 50 years has so loyally supported me and made sure I had a secure family base from which I could do what I wanted to do. She and our son, Antony, have been a wonderfully supportive and tolerant family. Marjorie, Heinz Wässle, and Leo Peichl made helpful comments on the first draft of this account. John Hopkins has been my research assistant since 1970. He has done all I could wish for, indeed sometimes more; I am most grateful. Finally, there are two recent acquaintances, Dr. Richard Jones and Mr. P. Taylor of the Guy's, King's, and St. Thomas's Hospital group. This article would not have been finished without the clinical alertness of the former and the surgical skills of the latter. I hope any readers of this account will feel they can thank you both; I do.

Selected Bibliography

Boycott BB. Learning in *Octopus vulgaris* and other cephalopods. *Publ Staz Zool Napoli* 1954;25:67–93.

Boycott BB. The functional organization of the brain of the cuttlefish, *Sepia officinalis. Proc R Soc London B* 1961:503–534.

Boycott BB. Learning in the octopus. *Sci Am* 1965a;212:42–50.

Boycott BB. A comparison of living *Sepioteuthis sepioidea* and *Doryteuthis plei* with other squids and with *Sepia officinalis. J Zool* 1965b;147:344–351.

Boycott BB. Some further comments concerning dendritic spines. *Trends Neurosci* 1982;5:328–329.

Boycott BB. Cephalopods, memory, neurofilaments, mammalian hibernation, the vertebrate retina: An autobiographical research note for John H. Welsh in his 85th year. *Comp Biochem Physiol* 1988;91C:25–29.

Boycott BB. John Zachary Young. *Biog Mems Fell R Soc London* 1998;44:485–509.

Boycott BB, Dowling JE. Organization of the primate retina: Light microscopy. *Phil Trans R Soc London B* 1969;255:109–176.

Boycott BB. David Scott Gilbert. *Nature* 1980;284:290.

Boycott BB, Kolb H. The connections between bipolar cells and photoreceptors in the retina of the domestic cat. *J Comp Neurol* 1973a;148:91–114.

Boycott BB, Kolb H. The horizontal cells of the rhesus monkey retina. *J Comp Neurol* 1973b;148:115–139.

Boycott BB, Wässle H. Morphological types of ganglion cells of the domestic cat's retina. *J Physiol London* 1974;240:397–419.

Boycott BB, Wässle H. Morphological classification of bipolar cells of the primate retina. *Eur J Neurosci* 1991;3:1069–1088.

Boycott BB, Wässle H. Parallel processing in the mammalian retina: The Proctor Lecture. *Invest Ophthal Vis Sci* 1999;40:1313–1327.

Boycott BB, Young JZ. The comparative study of learning. *Symp Soc Exp Biol* 1950;4:432–453.

Boycott BB, Young JZ. A memory system in *Octopus vulgaris* Lamarck. *Proc R Soc London B* 1955a;143:449–480.

Boycott BB, Young JZ. Memories controlling attacks on food objects by *Octopus vulgaris* Lamarck. *Publ Staz Zool Napoli* 1955b;27:232–249.

Boycott BB, Gray EG, Guillery RW. Synaptic structure and its alteration with environmental temperature: A study by light and electron microscopy of the central nervous system of lizards. *Proc R Soc London B* 1961;154:151–172.

Boycott BB, Lettvin JY, Maturana HR, Wall PD. Octopus optic responses. *Exp Neurol* 1965;12:247–256.

Boycott BB, Dowling JE, Fisher SK, Kolb H, and Laties A. The interplexiform cells of the mammalian retina and their comparison with catecholamine-containing retinal cells. *Proc R Soc London B* 1975;191:353–368.

Boycott BB, Peichl L, Wässle H. Morphological types of horizontal cell in the domestic cat retina. *Proc R Soc London B* 1978;203:229–245.

Boycott BB, Hopkins JM, Sperling HG. Cone connections of the horizontal cells of the rhesus monkey's retina. *Proc R Soc London B* 1987;229:345–379.

Dowling JE, Boycott BB. Organization of the primate retina: Electron microscopy. *Proc R Soc London B* 1966;166:80–111.

Hopkins JM, Boycott BB. The cone synapses of cone bipolar cells of primate retina. *J Neurocytol* 1997;26:313–325.

Löhrke S, Brandstätter JH, Boycott BB, Peichl L. Expression of neurofilament proteins by horizontal cells in the rabbit retina varies with retinal location. *J Neurocytol* 1995;24:283–300.

Peichl L, Buhl EH, Boycott BB. Alpha ganglion cells in the rabbit retina. *J Comp Neurol* 1987a;263:25–41.

Peichl L, Ott H, Boycott BB. Alpha ganglion cells in mammalian retinae. *Proc R Soc London B* 1987b;231:169–197.

Peichl L, Sandmann D, Boycott BB. Comparative anatomy and function of mammalian horizontal cells. In Chalupa L, Finlay B, eds. *Development and organization of the retina* (NATO ASI Series No. 299). New York: Plenum, 1998;147–172.

Sandmann D, Boycott BB, Peichl L. Blue cone selective horizontal cells in the retinae of horses and other *Equidae. J Neurosci* 1996;16(10):3381–3396.

Vaney DI, Peichl L, Boycott BB. Matching populations of amacrine cells in the inner nuclear and ganglion cell layers of the rabbit retina. *J Comp Neurol* 1981;199:373–391.

Vaney DI, Peichl L, Boycott BB. Neurofibrillar long-range amacrine cells in mammalian retinae. *Proc R Soc London B* 1988;235:203–219.

Wässle H, Boycott BB. Functional architecture of the mammalian retina. *Physiol Rev* 1991;71:447–450.

Wässle H, Boycott BB, Peichl L. Receptor contacts of horizontal cells in the domestic cat retina. *Proc R Soc London B* 1978a;203:245–267.

Wässle H, Peichl L, Boycott BB. Topography of horizontal cells in the domestic cat retina. *Proc R Soc London B* 1978b;203:269–291.

Wässle H, Peichl L, Boycott BB. Dendritic territories of cat retinal ganglion cells. *Nature* 1981;292:344–345.

Wässle H, Grünert U, Martin PR, Boycott BB. Immunocytological characterisation and spatial distribution of midget bipolar cells in the macaque monkey retina. *Vision Res* 1994;34:561–579.

Wässle H, Grünert U, Chun M-H, Boycott BB. The rod pathway of the macaque monkey retina: Identification of A11–amacrine cells with antibodies against calretinin. *J Comp Neurol* 1995;361:537–551.

Additional Publications

Blaurock AE, Wilkins MHF. Structure of retinal photoreceptor membranes. *Nature* 1972;236:313–314.

Boal JG. A review of simultaneous visual discrimination as a method of training octopuses. *Biol Rev* 1996;71:157–190.

Boycott AE. The habitat of land mollusca in Britain. *J Ecol* 1934;22:1–38.

Boycott AE, Damant GCC. Experiments on the influence of fatness on caisson's disease. *J Hygiene* 1908;8:445–456.

Boycott AE, Damant GCC, Haldane JS. Prevention of compressed air illness. *J Hygiene* 1907;7:343–425.

Boycott AE, Diver C, Garstang SL (Mrs A C Hardy), Turner FM. The inheritance of sinistrality in *Limnaea peregra* (Mollusca, Pulmonata). *Phil Trans R Soc London B* 1932;219:51–131.

Boycott CA. *Boycott: The life behind the word*. Ludlow Shropshire: Carbonel Press, 1997.

Burckhardt J. *The civilisation of the renaissance in Italy* (SGC Middlemore, Trans.). Oxford: Phaidon Press, 1945.

Cajal SR y. La rétine des vertébrés. *La Cellule* 1893;9:119–257.

Cajal SR y. Les problèmes histophysiologiques de la rétine. *XIB Concilium Ophthalmologicum Hisp*. 1933;2:11–19.

Cajal SR y, Sánchez DS. Contribucion al conociemiento de los centros nerviosos de los insectos. Parte 1: Retina y centros opticas. *Trab Lab Invest Biol Univ Madrid* 1915;13:1–168.

Colonnier M. The tangential organization of the visual cortex. *J Anat London* 1964;98:327–344.

Dowling JE. Synaptic organization of the frog retina: An electron microscopic analysis comparing the retinas of frogs and primates. *Proc R Soc London B* 1968;170:205–228.

Duhany DE, De Valois RL, Beardslee DC, Winterbottom MR (eds.). *Contributions to modern psychology*. Oxford: Oxford University Press, 1959.

Edwards DH, Heitler WJ, Krasne FB. Fifty years of a command neuron: The neurobiology of escape behaviour in the crayfish. *Trends Neurosci* 1999;22:153–160.

Engert F, Bonhoeffer T. Dendritic spine changes associated with the long term synaptic plasticity. *Nature* 1999;399:66–70.

Franks NP, Lieb WR. Where do general anaesthetics act? *Nature* 1975;274:339–342.

Fritsch G, Hitzig E. Ueber die elektrische erregbarkeit des grosshirns. *Arch Anat Physiol wiss Med* 1870;37:300–332.

Götze H. *Dem Andenken an Reinhard Dohrn*. Berlin, 1964:1–70.

Gray EG. Axo-somatic and axo-dendritic synapses of the cerebral cortex. *J Anat London* 1959;93:420–433.

Gray EG, Guillery RW. Synaptic morphology in the normal and degenerating nervous system. *Int Rev Cytol* 1966;19:111–182.

Guillery RW. Ray Guillery. In Squire LR, ed. *The history of neuroscience in autobiography*, 2nd ed. San Diego: Academic Press, 1998:132–167.

Hess WR. *Die functionelle organization des vegetativen nervensystems*. Basel: Benno Schwabe, 1948.

Heuss T. *Anton Dohrn: A life for science* (L Dieckmann, trans.). Berlin: Springer-Verlag, 1991. (Original work published 1940)

Hong K, Nishiyama M, Henley J, Tessier-Lavigne M, Poo M-m. Calcium signalling in the guidance of nerve growth by netrin–1. *Nature* 2000;403:93–98.

Hughlings Jackson, J. *Selected writings of John Hughlings Jackson 2* (J Taylor, ed.). London: Hodder & Stoughton, 1932.

Isayama T, Berson DM, Pu M. Theta ganglion cell type of cat retina. *J Comp Neurol* 2000;417:32–48.

Ito M. Maso Ito. In Squire LR, ed. *The history of neuroscience in autobiography*, 2nd ed. San Diego: Academic Press, 1998:168–191.

Kolb H. Organization of the outer plexiform layer of the primate retina: Electron microscopy of Golgi-impregnated cells. *Phil Trans R Soc London B* 1970;258:261–283.

Kolb H, Mariani A, Gallego A. A second type of horizontal cell in the monkey retina. *J Comp Neurol* 1980;189:31–44.

Kolb H, Nelson R, Mariani A. Amacrine cells, bipolar cells and ganglion cells of the cat retina: A Golgi study. *Vision Res* 1981;21:1081–1114.

MacNeil M, Masland RH. Extreme diversity among amacrine cells: Implications for function. *Neuron* 1998;20:971–982.

MacNeil MA, Heussy JK, Dacheux RF, Raviola E, Masland RH. The shapes and numbers of amacrine cells: Matching of photofilled with Golgi-stained cells in the rabbit retina and comparison with other mammalian species. *J Comp Neurol* 1999;413:305–326.

Marlow J. *Captain Boycott and the Irish*. London: André Deutsch, 1973.

Maurois A. *A history of France*. London: Jonathan Cape, 1949.

Medawar PB. *Memoir of a thinking radish*. Oxford: Oxford Univ. Press, 1986.

Melzack R, Wall PD. *The challenge of pain*, 2nd ed. Harmondsworth, Middlesex, UK: Penguin, 1996.

Milner B. Brenda Milner. In L. R. Squire, ed. *The history of neuroscience in autobiography*, 2nd ed. San Diego: Academic Press, 1998:276–305.

Mori K, Nagao H, Yoshihara Y. The olfactory bulb: Coding and processing of odour molecule information. *Science* 1999;286:711–715.

Peichl L, Gonzalez-Soriano J. Morphological types of horizontal cell in rodent retinae: A comparison of rat, mouse, gerbil and guinea-pig. *Vis Neurosci* 1994;11:501–517.

Peichl L, Wässle H. Morphological identification of on- and off-centre brisk transient (Y) cells in the cat retina. *Proc R Soc London B* 1981;212:139–156.

Phillips JL. *The bends: Compressed air in the history of science, diving and engineering*. New Haven, CT: Yale University Press, 1998.

Polyak SL. *The retina*. Chicago: Chicago University Press, 1941.

Raviola G, Raviola E. Light and electron microscopic observations on the inner plexiform layer of the rabbit retina. *Am J Anat* 1967;120:403–426.

Squire LR, Kandel ER. *Memory: From mind to molecules*. New York: Scientific American Library/Freeman, 1999.

Stellar E. Physiological psychology. *Annu. Rev. Psychol*. 1957;8:415–436.

Strausfeld NJ. *Atlas of an insect brain*. Berlin: Springer-Verlag, 1976:1–300.

Tinbergen N. *The study of instinct*. Oxford: Clarendon, 1951.

Toni N, Buchs PA, Nikonenko I, Bron CR, Muller D. LTP promotes formation of multiple spine synapses between a single axon terminal and a dendrite. *Nature* 1999;402:421–426.

Valenzi M. *Reinhard Dohrn 1880–1962*. Berlin: Springer Verlag, 1983.

Wässle H. Parallel pathways from the outer to the inner retina in primates. In Gegenfurtner KR, Sharpe LT, eds. *Colour vision: From genes to perception*. Cambridge, UK: Cambridge University Press, 1999:145–162.

Wässle H, Riemann HJ. The mosaic of nerve cells in the mammalian retina. *Proc R Soc London B* 1978; 200:441–461.

Wells MJ. *Octopus: Physiology and behaviour of an advanced invertebrate*. London: Chapman & Hall, 1978.

Young JZ. *The anatomy of the nervous system of Octopus vulgaris*. Oxford: Clarendon, 1971.