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Alan Cowey

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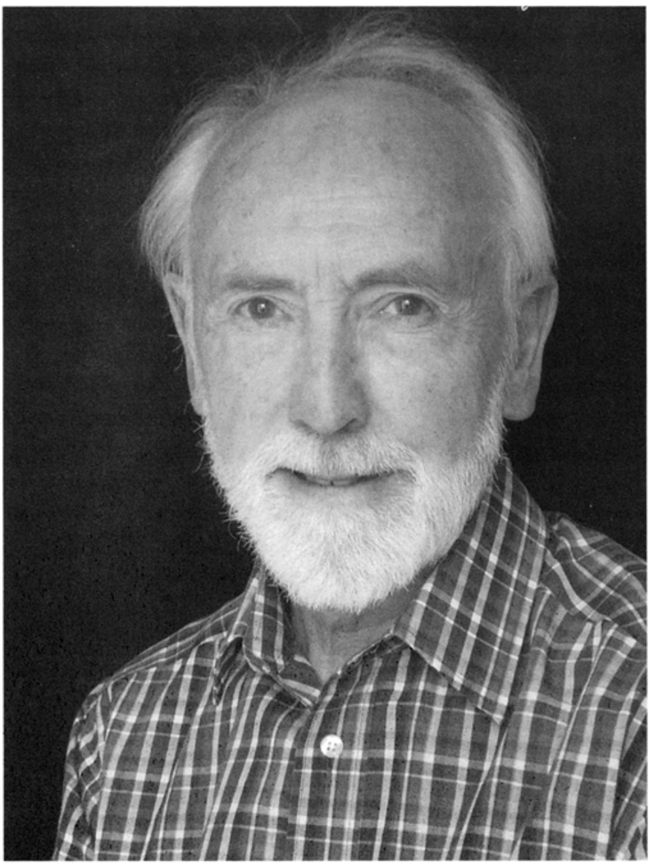

Alan Cowey

BORN:

Sunderland, County Durham, UK
April 28, 1935

EDUCATION:

University of Cambridge, B.A. (1957)
University of Cambridge, M.A., Ph.D. (1961)

APPOINTMENTS

Postdoctoral Fellow, Center for Brain Research,
University of Rochester, New York (1961,
Sponsor Robert W. Doty)
University of Cambridge, Demonstrator (1962)
University of Harvard, Visiting Fulbright Fellow (1966)
University of Oxford,
Senior Research Officer (1967)
Royal Society Henry Head Research Fellow (1968)
Reader in Physiological Psychology (1973)
Professor of Physiological Psychology (1980)
MRC Research Professor (1997)

HONORS AND AWARDS (SELECTED):

British Psychological Society, Spearman Medallist (1967)
European Brain and Behaviour Society,
President (1986–1988)
UK Experimental Psychology Society,
President (1990–1992)
Fellow of the Royal Society (1988)
Member Academia Europaea (1989)
Royal College of Ophthalmologists Medallist (1992)
Fellow Academy of Medical Sciences (1998)
Hon D.Sc., University of Durham (2000)
Royal Society Ferrier Medallist (2004)

Alan Cowey began his research by making perimetric measurements of visual field defects in monkeys with cortical or retinal lesions and showed that only the latter produced absolute blindness in the field defect. Later, he discovered and plotted cortical visual area V2 in monkeys. Subsequently he carried out behavioral experiments of visual acuity in monkeys and explained the effects on acuity of cortical lesions by studying the magnification factor of the retina in the thalamus and area V1 by anatomical and electrophysiological methods. He also studied the selective effects of a variety of brain lesions in monkeys and patients on form, motion, and color and interpreted their disorders by testing normal subjects with a combination of psychophysical, neuroimaging, and magnetic brain stimulation methods. He also combined studies on patients and monkeys to elucidate the neural basis of blindsight.

Alan Cowey

There are several reasons for writing an autobiography, whether it is a lengthy book or, like this one, a cameo. Common among them is "to set the record straight," which can be a disguise for settling old scores. Another can be to impress contemporaries with a catalogue of enviable and perhaps overlooked glittering achievements that, once acknowledged, will ensure the status of avatar. A third would be to take a last opportunity to ensure that one is remembered for as long as possible by providing a literary form of Last Will and Testament, for, as the much lamented playwright Arthur Miller said just months before his death, "I'll probably be forgotten completely. Most of the work in the world is forgotten completely—99.99 per cent of all art work is forgotten" (*UK Sunday Times,* October 2, 2004). I hope to avoid all three of these, which collectively amount to autohagiography. But I recognize that in attempting to present personal information and insights into "the causes of interesting things," which is the fourth reason and the one I hope to follow, there is a real danger of seeming to dally with the first three. And of course there is always the hazard in the elderly of confusing memory with imagination.

Ancestry

If developmental psychology, which I have never professionally studied but about which many of my friends and colleagues entertain and educate me, means anything at all it is that parents are important. They disagree about the relative importance and interaction of parental genes and the childhood environment (which can even include the absence of parents) but I have never heard anyone say that parents do not matter and I now recognize the role my own parents, however unthinkingly, played in shaping my career. Tearful winners at the annual Hollywood showbiz extravaganza called "The Oscars" often thank their parents (along with their dog or their manager or their hairdresser) for their success but do so without explanation. It is explanation that interests me.

I was born into a working class community in Sunderland, a town in the North East of England, in 1935. My mother was a practicing Roman Catholic but rather selective about the bits she practiced. My father was a nonpracticing Protestant but he never allowed his lack of practice to stop him protesting about my mother's religious life. She was born locally of parents who had emigrated from county Roscommon in Eire to seek employment in England in the late 19th century, like many of their contemporaries. Were it not for the European Union I suppose the present UK government might now call them illegal immigrants. My maternal grandmother, the only grandparent I met, became a laundry-maid in an agricultural college near Sunderland where she met and married my maternal grandfather, who had found work in the mining industry. He was a "shot firer," which means that he drilled holes in the coal face and filled them with explosive which broke down the coal face so that the hewers could then remove the coal into the pony-pulled carts that conveyed it to the lifts which took it to the surface. The mine was close to the seacoast and much of the firing and hewing was done under the sea; working conditions must have been deplorable. They had five children but my grandfather died in his early 40s of Bright's disease (chronic glomerulonephritis) when my mother was still a girl. In an era when social security was almost nonexistent my grandmother managed by taking in washing at home, which was in a miner's terraced house in the east end of the town and very much on the "wrong side of the tracks." As most young people at that time left school at the age of 13, my aunts and uncles already had jobs in the local factories and there was no destitution. But my mother was the youngest child and after leaving school she was not allowed to work in the local wire-mill with two of her sisters, which she wished to do. Instead she helped my grandmother with the washing and ironing and with anything that involved reading letters because my grandmother was illiterate; the only record of her hand that I possess is the birth certificate of one of my mother's sisters, marked by a cross where my grandmother had to "sign" it when registering the birth. I only discovered this as a young man when my mother mentioned it and explained that such things were not discussed because people were becoming ashamed of it. So I asked her about my father's parents and was told that *neither* of them could read nor write, which made her parents rather more distinguished!

Circumstances changed during the second half of the First World War, when so many men had been killed that women finally got to do what were previously and exclusively men's jobs. So she happily went to work in the local mill, which made ropes for the large local fishing industry. She met my father in 1919 after he came back from the war and they married in 1922. They could not afford wedding photographs so there is no pictorial record of the kind we now all take for granted. In fact I never saw a photograph of any of my grandparents.

Like my mother, my father was born in 1899 and went to the local elementary school. Being good at reading, writing, and sums he passed, at age 12, the exam that existed then and was normally taken at age 13 and which allowed the pupil to leave and seek a job. What a contrast with the present world where the smarter that people are the longer they stay in formal education! On the strength of his reading and writing he went to work in the town hall but was made to leave by his father, who insisted that as soon as he was old enough—14—he should have a proper profession like his own, i.e., learn a skilled trade in the shipyards. I have a group photograph of the shipwrights of Short's Shipyard; my father is the little boy sitting cross-legged on the ground at the front and holding a chalkboard saying "Short's shipwrights, 1914." He must have been 15 or nearly so at the time. Later that year and without telling his parents he enlisted in the army after presumably lying about his age. When he did tell them it seemed too late for parental interference. He joined the Hussars, did basic training, and was soon in France where his job was to transport horses to and from the front line. Although not widely known at the time the British army had lost so many men in the carnage of Flanders that tens of thousands of underage soldiers had been recruited and by the end of the war the total number of boy soldiers (including those who had died) approached 250,000. They are memorably described in *First World War,* by Martin Gilbert, 1995, and in the National Archives Learning Curve at www.spartacus.schoolnet.co.uk/FWWboy.htm. It happened again in Germany toward the end of World War II, when Hitler created the *Jungvolk* to help to defend the fatherland.

When news of the appalling casualty lists, including boy soldiers, began to filter through, my grandmother went to the local army office and demanded that her boy be discharged. I have his Certificate of Transfer, dated 30 October 1916. Rather than discharge him on the legal grounds of being too young to be in the army or too young to serve abroad (where the legal lower age limit was 19), the army transferred him—and thousands like him—to reserve regiments that were meant to be used solely in support work. As a result he ferried horses across the channel until he was deemed "acceptable" to join the front line again when he became 18. When I asked him 50 years ago what he learned to do in the army he said "smoke, drink, and sleep anywhere." He did the first two with enthusiasm and died at the age of 63 of chronic bronchitis and emphysema, caused partly by the lingering poison gas that he often encountered in the trenches. He was so unwell from his late 40s onward that he needed help to do the simplest manual jobs like sawing wood, sanding, climbing on to the roof, drilling, etc. I was that "help" and I became his apprentice at weekends and during the school holidays when he taught me his full range of manual skills. Often I would have preferred to be doing something else, like playing football, but without the instruction I would not have been able to tackle several scientific things years later. Without either of us knowing it at the time he shaped much of my outlook on how to deal with practical technical problems in life.

My parents married in 1922 and moved into rented rooms, close enough to the shipyard for my father to cycle to work and finish his training as a shipwright. My mother wanted to continue to work but unemployment was high after the war ended and she had no special training of any kind. She also gave birth to my brother in 1923 and at that time being a working class mother meant staying at home. Then the famous economic depression arrived in the mid-20s and my father was out of work. In fact much of the local population—which depended on shipyards, coal mines, and steelworks—was unemployed. My father decided that it was time to change his occupation and bought an old hand-drawn two-wheeled cart on which he transported his two shipwright's toolboxes (I still have one of them and its tools) and a set of long ladders round the streets in more affluent parts of town. He knocked on doors and managed to make a living repairing roofs (mostly retiling), replacing gutters and spouts, and doing joinery. He also learned how to hang wallpaper, do simple plumbing, and rewire the then primitive electrical systems. It was while doing repairs for a local doctor that the doctor offered him a job collecting the "doctor's money." This was a small sum, paid weekly to the doctor, either in part repayment for medical work already carried out or as an insurance for medical work that might be necessary. My father accepted and became a sort of debt collector or insurance agent. The practice grew and soon involved him in collecting for one of the then-named Friendly Societies that specialized in insurance against the cost of funerals, etc. My mother helped him by taking over some of the collecting and one of my earliest memories is of accompanying my mother in a pushchair on her rounds. In 1933 my brother was due to take the 11-plus exam but developed acute appendicitis and had his appendix removed instead of taking the exam. As a result he lost the opportunity to go to the only grammar school in the entire town. It seems that no one minded the missed opportunity and he remained in the elementary school until, aged 15, he left and went to work in a local shipyard. He started as an apprentice shipwright but really wanted to be a sailor. The Second World War provided the opportunity.

Life as a Young Boy

The War to end all Wars was followed in 1939 by World War II. I am aware of the existence of false memories and how difficult it can be to establish the veracity of childhood memories. Nonetheless, I trust my memories of the outbreak of war in 1939 when I was 4 and my mother cried, and neighbors and relatives suddenly became more friendly and outgoing and listened to the wireless in groups. My father was too unfit to be conscripted but had to return to the shipyard to replace younger men who were leaving in droves for the army. He lasted only a few months before being declared unfit to carry out hard manual work and returned to door-to-door collecting. In 1940 my brother, now aged 18, tried to join the Royal Navy but to his and my parents' shock he failed the medical exam. He had a serious heart murmur and was told that he would have to lead a quiet life. What a hope!

My father would have none of it and took him to see the aforementioned doctor who was still my father's employer. The doctor thought that the murmur might not be life threatening and, armed with a statutory signed form signifying that my brother was fit to be a sailor, he successfully joined the merchant Navy as a trainee ship's engineer. He joined the convoys that sailed across the Atlantic or from Scotland to Murmansk. I hardly saw him again for 5 years because shore leave was short and he had a girlfriend and soon a wife. His departure briefly changed my life because my brother and I, despite the age difference, had shared a double bed for the last 2 years (there was no third bedroom and no room for two single beds) and I regarded him as my "guardian," although he probably disliked having to share with a child. Years later I visited him on board ship in London docks in 1956 and we had our only conversation of note as two adults. He was puzzled and critical that I had chosen to become a student, which meant living on a small grant and doing "book-work," which he loathed. I failed totally to convince him that it was a good life, both enjoyable and worthwhile, and that the things he relished, like visiting exotic places, would happen to me in good time. After an uninterrupted career as a ship's engineer he died on board ship in Hamburg harbor in 1962, aged 39. The heart murmur had finally shouted. My brother taught me that one must not live in cotton wool in order to minimize risk. Hang the risk, he did what he wanted for 21 successful years.

School Days

My first school was a Kindergarden (sic), a nice misspelling of the German that I only appreciated many years later. The real reason I was there was to enable my mother to do more door-to-door collecting work and thus increase her income, presumably because it cost less to send me to preschool than the extra income she earned. The school was in an old terraced house only a short walk from where I lived and there were two classrooms, with about 10 children in each. The two sisters who owned and ran it believed in order, discipline, and learning but they were kind and I was happy there. When I left, aged 5, and entered the local elementary school I discovered that the education I had already received (starting to read and write, learn poetry by listening to it, do simple sums, recite the multiplication tables) gave me a head start. Much better than being trundled round town in a pushchair. The following 6 years were entirely run-of-the-mill, except that most of the school windows were shattered during one of the frequent night bombing-raids in 1942–1943; the explosion killed members of several families in the street next to the school but, echoing the emotional incomprehension of the very young, was briefly welcomed by the pupils because we all had an unexpected week-long holiday. But the less attractive outcome was that Morrison air-raid shelters were installed in local homes and

I spent the next 2 years sleeping on a mattress in a metal box frame with steel mesh sides to stop flying glass. My father was an air-raid warden, whose job was to go outside whenever the town siren sounded and check that people did not linger on the streets and, if it was dark, to make sure that their light-proof blinds were drawn. It is pointless to deny that for me it was an exhilarating experience. There was the constant hint of danger, the possibility of staying up after normal bedtime, the excitement of having to carry a gas mask and my father's spare shrapnel helmet, and, probably most important, the opportunity to listen to excited grownups shouting, arguing, and cursing. It nicely complemented my Kindergarden education. When I now watch TV shots of children taking part in dangerous demonstrations of all kinds throughout the world I am not surprised by their fearless enthusiasm.

When I was 11 years old I took the 11+ exam, the exam my brother had failed to take because of his appendicitis. The selected few (about 1 in 20) went on to the only nondenominational grammar school in town. I passed and moved on to Bede, named after the Venerable Bede who first translated the Bible into English. With the benefit of hindsight it was the first great change in my life. Although my parents were pleased, they were not overtly overjoyed and this was in keeping with their undemonstrative manner, which also meant that they had never put any pressure on me to work for the exam or suggested that not to pass would count as a failure. Bede school plunged me for the very first time into challenging academic studies, while encouraging sport. Being good at the latter protected me from the widespread physical and verbal bullying directed at academic pupils ("bookworms") so that my peers tolerated my success in exams. My greatest physical discovery was that I could control a ball, run fast, and jump high. As a result I became a games player: basketball, soccer, rugby, cricket, and athletics. It was athletics that briefly enlarged my life by allowing me to compete in local and then national events and to meet people so curiously different from me. At the age of 17 I believed that I could become a major athlete. It was not the only mistake I made as a young adult.

While flirting with the idea of a sporting life I encountered teachers whose dedication to academic things I initially had no time for. To a callow youth who loved football they were sad figures of fun. But some of them impressed me by their ability to mount an argument and even to listen patiently to what boys like me had to say. One in particular became an outstanding influence on my career. He taught biology but was also an accredited athletics coach, which made him more acceptable to young boys. But his passion was literature and the theatre and he directed the school plays. When I was about 15 he asked me what books I had read. With respect to novels the answer was "none" because I grew up in a household with only three books, one of them my mother's Bible and the other two about the Royal Family and the First World War in pictures

(I still have all three). So he gave me books that he said I should read. The first was George Eliot's *Adam Bede* (published 1859), a masterpiece of 19th century English literature, which I enjoyed without quite knowing why: something to do with the arresting and coruscating prose, and its ability to express through the lives of ordinary rural people the fate, sadness, and the strength of the human spirit. I am still mildly abashed that I read it without realizing that George Eliot was a woman and that she was one of the first English feminist novelists, something espied by Charles Dickens nearly 100 years before I discovered it. The second was Emily Bronte's *Wuthering Heights,* which he asked me to write something about. I wish I had kept a copy of what I wrote! My report was brief and he had the grace to say "that I had obviously read the book." I was clearly not destined for a career in English Literature. Fifty-five years later, I find that his comment often applies to writers of papers, books, and grant applications.

It was this schoolteacher's outlook on life that affected me for the rest of my own life. He thought that it was a mistake to concentrate on only one thing; that hobbies are as important as one's paid job; that literature informs us about human behavior; that failing to achieve is less important than having tried; and that no matter how many people believe something, it might be wrong. With respect to the latter it was he who weaned me off religious belief (something for which he might now be disciplined) and taught me that always thinking for oneself can be a lonely and even socially intimidating act. I have not a shred of doubt that this largely unremembered and often criticized schoolteacher was responsible for my conversion from a working class boy with a conventional predilection for football and comic books, which I still read at age 15, to someone ready for something different.

About 1 year before I was due to leave school I decided that I might go to University and study science. The obvious places were Durham or Newcastle because both were distinguished and almost on the doorstep, enabling me to live cheaply at home. But a different teacher, educated at Oxford, suggested that I should try for Cambridge because he thought it was the "best" UK university for science and that it might be a good idea to live away from home in order to gain experience. I duly applied, visited Cambridge for 5 days in early December to take the entrance examination [now abolished] and be interviewed, and was awarded a place on condition that I passed my A-level subjects later that summer, which I duly did. My Cambridge marks were modest and I think I was accepted because I was good at games and even then Cambridge was looking for promising if educationally undistinguished candidates from a working-class background. Unfortunately Cambridge, like Oxford, required all entrants at that time to have passed the "O" level exam in Latin, which I had never studied. To the rescue came a previous lecturer in classics at Cambridge who, having retired, did part-time teaching at my school. He assured me that I could learn the rudiments of Latin grammar in 6 months, in his and my spare time, and that I could memorize the set-book, Virgil's *Aeneid* Bk III, so that I could translate any section of it from Latin into English in an exam. He was right and the experience taught me two things. First, a normal and determined youthful mind can learn almost anything if it wants and needs to and, second, that anything acquired in this way is rapidly lost if not subsequently used. Just a few weeks after passing the Latin exam I forgot almost everything about Virgil and Aeneas. Cambridge University abolished its archaic requirement not long after.

What had my parents provided that I can now see to be so important? As long as I complied with a few basic rules concerning honesty, hard work, thrift, and respect for others, they let me be my own man from a very early age, rarely objecting to what I wanted to do. I had immense freedom, although I did not realize just how much at the time. When I was 16 they let me cycle to London and back with a group of three friends to see the Festival of Britain. They taught me, entirely by example, that nothing should be considered impossible until you have tried to accomplish it. Their own aims were modest but not because they were timid. Finally, they demonstrated that no one should feel inferior simply by being poor or ill-educated; at least in western society we can all overcome that.

University

I arrived in Cambridge in 1954 to study natural sciences at Emmanuel College. The culture shock was huge, as it must have been for many of us who had rarely spent more than a few nights away from home. The ancient and inadequately heated buildings, upper-class accents, seemingly effortless superiority of undergraduates from private schools [in England confusingly called public schools], and rituals like dining every evening while wearing a collar and tie and academic gown were alienating. But they were small beer when compared with what my parents had to deal with at the same age. It took only one term, lasting 8 weeks, to discover that Cambridge was an opportunity of a lifetime and I realized that the first stage of my life was over. Apart from visits to my parents and my girlfriend Pat, who became my wife, I never again lived in my home town. Cambridge was my new home.

Studying science at Cambridge was a revelation. For the first 2 years I had lectures, supervisions, and practical classes from 9 AM to 1 PM every day from Monday to Saturday and practical classes from 2 PM to 5 PM, three days each week. My subjects were zoology, botany, biochemistry, and organic chemistry. It sometimes seemed like a treadmill but for each subject I had a supervisor, with whom I and another student met each week to discuss the essay each of us had written. I got more from this weekly meeting than from all the lectures and practicals. It encouraged me to think critically, for as a schoolboy I had concentrated on regurgitating scientific facts or Virgil's Aeneid. Being asked for my opinion about a scientific problem was novel and, at first, intimidating. For one of my first botanical essays my supervisor (E.J.H. Corner, FRS) asked me to read "The Thalassiophyta and the sub-aerial transmigration" by F.H. Church and to write what I thought about it. I was mystified but grasped that its thesis was that the evolution of aquatic plants had reached an advanced stage *before* plants ever became terrestrial. It was probably the first time that anyone had suggested to me that received scientific wisdom might be wrong, something I now realize is common in neuroscience, for example that the adult human brain has no neuronal plasticity. My supervisor in zoology was A.J. Ramsay, also FRS, whose lectures and research involved chiefly invertebrates. He asked me to write an essay on why so-called higher organisms were evolutionarily more advanced than lower organisms. I made a complete hash of it because I thought the answer was self evident. "What is the evidence," he said, "that Amoeba ceased to evolve millions of years ago and is not still evolving?" But he said it kindly. I suppose this time at Cambridge is when I finally stopped taking things for granted. Another advantage of Cambridge is that it offered an optional 6-week fourth term in the summer. I opted to take this at the end of my first and my second years, first doing field work in biology and then histology. The latter was entirely practical and I learned to fix tissue, embed it in paraffin wax or nitrocellulose, section it on a rocking microtome, and stain it with a variety of vital dyes and with other methods including Golgi's, before examining, describing and drawing it with the aid of rather primitive microscopes without the aid of a drawing tube. I would like to be able to say that my specimens and drawings equalled in quality those of Cajal (of whom I had never heard at the time), but their inferiority was less important than the fact that I learned what was possible with my own hands. Ten years later it stood me in good stead.

The Cambridge Tripos system, where one studies several subjects for 2 years and then selects one for the final year is still one of the finest I know. How can we possibly know at age 18 what we really want to study? In my case I first wanted to be a Botanist, then thought it was Zoology, and finally decided it was what is now called Behavioral Neuroscience. I therefore changed from Zoology to Experimental Psychology for the last part of my Tripos and alongside it studied History and Philosophy of Science. My college at first resisted my last-minute move but it was probably a token opposition in order to make sure that I was changing for good reason. My tutor explained that I would need the permission of the Head of the Psychology Department. Being young and in a hurry I went to the Psychology Laboratory and asked if I could see the Professor about my proposed switch of subject. His secretary looked stern and dismissively explained that he was a very busy man and that he might be able to see me next week if I first wrote a letter of explanation. At that moment he came in from the adjoining room to see his secretary and, rather stiffly, asked what I wanted. I am still astonished and gratified that he invited me into his office, talked to me for half an hour, and agreed that I could join the course. His name was Oliver Zangwill, son of the socialist writer and painter Israel Zangwill, and although his interests were very wide indeed his personal research concerned the effects of brain damage on memory and spatial perception and how the normal brain controlled perception, memory, and action. I had met my first clinical and behavioral neuropsychologist. What a stroke of luck for me!

There were about 20 of us studying experimental psychology and we were taught by a staff of not more than 8 or 9, which provided a generous staff/student ratio but could hardly cover the entire subject satisfactorily. Wisely they did not try. Social, abnormal, educational, and individual psychology were hardly mentioned; instead the course taught in depth on learning theory, physiological psychology (Weiskrantz), perception (Gregory), attention (Broadbent), memory (Zangwill), human skills (Welford), information processing, and animal behavior (lectures in the Zoology Department by Thorpe and Hinde). There must have been more but this is all I recall. It was a golden time for me. I now had only one essay to write each week instead of three and my supervisor was Richard Gregory, who influenced me more than he can possibly know and subsequently became and remains a friend. The weekly tutorial was an opportunity to discuss a single topic that had been studied for a whole week. The topic could be narrow (What is the least amount of light we can see?) or broad (Is the brain just a complex machine?) and the almost complete absence of any detailed syllabus meant that the choice of topic was enormous. Choice? Yes, Richard would ask me and my supervision partner (Anne Treisman for one term) what we would like to think and write about. He would sometimes query our choice and make suggestions if we seemed at a loss but on the whole we picked the topic. It was a liberating if risky business but I learned much about myself and the nature of scholarship (reading original papers, thinking rather than accepting, having an open mind, not being overawed by reputation, only declaring an opinion if prepared to defend it, never dismissing an idea without examining the evidence, being prepared to differ even at the risk of offending a friend). One assignment suggested by Richard was to read Donald Hebb's *Organization of Behavior,* 1949. This stretched to three supervisions over 3 weeks (roughly 15% of the duration of the course just for one book) but I realize that it was an investment. When I subsequently became a supervisor of students at Cambridge and then at Oxford I modeled my approach on Richard's. In 1980 I was still asking tutorial pupils at Oxford what they would like to write about for the next tutorial. Regrettably, it would now be considered unacceptable. The teaching of science has become more regimented, lecture- and exam-based, constantly appraised, and accompanied by elaborate Power-Point presentations that must be accessible to the students whose knowledge and understanding are increasingly evaluated by essays and dissertations that include (and very occasionally consist entirely of) written work that has been pilfered or bought from the web. Plagiarism is on the increase although forbidden. It is we and our Universities, not our students, that are to blame for we have not been sufficiently alert to the rising tide of rewarded mediocrity, spoon feeding, stifling bureaucracy, mission statements, government insistence that all students must succeed, and the promotion of factual knowledge rather than understanding. "More formal training" is the cry; but it is not the recipe for independent thinking.

I must now turn briefly to another aspect of my life as a student because I was within a whisker of following a career that did not involve scientific research or university teaching. My genes made me good at school games and success at athletics might have tipped the balance when I applied to Cambridge. For 3 years at Cambridge I trained whenever I could at least 5 days each week by running, lifting weights in the gym, or pole-vaulting into a sand-pit that in the winter was occasionally frozen until anyone wanting to use it had dug over the sand. I am not sure how much good it did for my physical health (the necessary absence of alcohol was presumably good) but it was definitely an entrée to a life with a collection of heterogeneous sociable students from backgrounds different from mine. What we shared was a belief in testing oneself to the limits of physical endurance, helping each other, teaching our skills to others (for example by tours to schools in the summer break), and learning how to accept and deal with defeat. Athletics brought my first trip abroad, taught me my physical limitations, and made me many friends. Indeed it was so important at that time that I decided to become a school teacher and to combine teaching of games and science, like my mentor. I duly applied to Loughborough, the leading English establishment for physical education, and after an interview that included a hilarious set of physical tests that included back flips in their gymnasium, was accepted to study for a teaching diploma in education and physical education, neatly embracing both of my aspirations.

Luck and serendipity intervened again. My research project in my final undergraduate year involved attempting to measure eye position in observers whose head movements were restricted but not abolished. Measuring eye movements now is fairly straightforward if one has the equipment and software, but 50 years ago it was rarely attempted and most investigators just assumed that subjects in perceptual experiments were following instructions to fixate. By reading U.S. Air Force technical reports describing the filmed eye movements of pilots while they were taking-off and landing I learned that the pilots were often not looking where they were supposed to look. It was Richard Gregory who suggested to Larry Weiskrantz (my research project supervisor) and then to me that one might determine where the eyes were looking by taking advantage of the fact that specular reflections from a source effectively at infinity, like the sun or moon, do not change their relative position with respect to the border of the iris when the eyes continue to fixate but the head moves. But they do change their relative position to ocular landmarks when fixation changes. My job was to see how this held up with light sources much closer (1 meter). After calibrating the system by photographing the eyes while the subject gazed in turn at each dot in an array of 150 dots at 5-degree separations I found that head movements of up to 1 cm in any direction could be tolerated while still allowing any fixation to be correctly identified from the position of four specular reflections on each eye. With a maximum head movement off about 5 mm, easily obtained with head baffles, the accuracy was about 2 degrees. The entire experience of carrying out this research for a few months was the most intellectually rewarding and practically satisfying experience of my life as a student (Cowey and Wesikrantz, 1962) and many undergraduate students of my own in the past 45 years have said much the same thing: The research project can be the most important part of their scientific education. Larry suggested that the real challenge would be to do it with monkeys, where eye movements and visual fixation had never been assessed even though they were important in evaluating the results of experiments on their vision, and that I might like to stay on at Cambridge and make it part of a Ph.D. Oliver Zangwill nominated me for a Medical Research Council studentship and I withdrew from my postgraduate studentship in physical education at Loughborough. I have carried out research ever since.

A Graduate Student at Cambridge

I began my Ph.D. in 1958. My supervisor was Larry Weiskrantz and I shared a large office with Charlie Gross and several others. My project was to use the technique of monitoring eye fixation with monkeys while the monkeys were carrying out a visual detection task. The scientific rationale was to discover whether monkeys in which small parts of the primary visual cortex were surgically removed had a small island of induced total blindness (a scotoma) in the retinotopically corresponding part of the visual field, like neurological patients described by Holmes (1918) and many others. But the bigger intention behind the investigation was to test the theory of encephalization of vision, i.e., the idea that in evolution the visual striate cortex becomes progressively more important for vision until in humans it is entirely responsible for visual perception. So, would the monkeys have absolute or relative defects? I had never tested a monkey before and I had no apparatus. While waiting for the monkeys to arrive I built a perimeter, consisting of a plexiglas hemisphere with small bulbs embedded in it and four more powerful light sources top and bottom and at each side. The hemisphere was made by heating a Perspex sheet and bending it over a mold of plaster of Paris in the departmental workshop, an activity that would now be prohibited by diktat of the Health and Safety-at-Work police. The only photographic illustration, taken from my thesis, appeared in Cowey and Weiskrantz (1970). Facing the perimeter was a metal panel, contoured by panel-beating (which I learned to do at evening metalwork classes) to fit the face of an average macaque monkey and containing a contoured spy-hole that a monkey could peep through with its preferred eye. Adjustable metal plates meant that the monkey had to press its head into the face mask in order to look through the peep-hole. In the center of the perimeter was a plane mirror that provided a reflection of the monkey's own eye. To my relief, I found that monkeys like to look through a peephole and that the mirror attracted the monkey's attention, meaning that if I moved the mirror to different positions I could photograph its viewing eye over the entire perimeter. This allowed me to present brief flashes over the entire visual field and to photograph the eye with a cine-camera beneath the lower edge of the perimeter on each presentation. It all sounds easy but it took about a year to train the monkeys and to measure their detection thresholds and then to repeat the measurements after the striate cortex corresponding to the macula had been removed. The outcome was that each of the three monkeys had a macular field defect but that it was relative, not absolute. Only when the macular of the retina was subsequently destroyed by xenon-arc photocoagulation were they absolutely blind in the field defect. It now sounds old hat, but this was the first demonstration of perimetrically plotted residual visual sensitivity with a field defect caused by a cortical lesion in monkeys and it seemed to confirm that monkeys differed from patients and that the explanation was encephalization of function.

I have glossed over the problém of how to make retinal lesions that correspond in size to the retinotopic cortical lesions but it was one of the most fascinating parts of my research. Larry Weiskrantz and I contacted a leading ophthalmic surgeon at Moorfield's Eye Hospital in London and described what we wanted to do. He was enthusiastic and one Sunday—when there were no patients in the clinic—we drove to London with a van containing five monkeys, parked in the hospital car park, anesthetized them in the back of the van, and then took them, in turn, upstairs to the library. The library? Animals were not allowed into the operating theater so the xenon arc photocoagulator was brought into the library and the monkeys were in turn propped up with books and drapes on a library table for the procedure. It would all now be impossible. The retinal lesions produced absolute fields defects (Cowey, 1967; Weiskrantz and Cowey, 1967; Blakemore et al., 1968) and it was at last incontrovertibly clear that extensive residual visual processing still took place within field defects caused by visual cortical lesions in monkeys. But the apparent difference between the cortical organization of vision in monkeys and humans was even then not certain, and in our article in 1963 Cowey and Weiskrantz speculated that perhaps the difference was caused by asking patients whether they had seen anything whereas the monkeys were rewarded for responding appropriately, which is not the same thing. It is the difference, now widely acknowledged, between reports on phenomenal vision and forced-choice guessing, i.e., blindsight.

Three other aspects of being a research student in Cambridge in the 1950s deserve a comment. When I took up my studentship, Oliver Zangwill invited me to chat about it in his office, which was like being invited into the inner sanctum. Never an easy man, he seemed to wrestle with what should have been a perfectly straightforward occasion, not helped by his notorious inability to maintain eye contact for more than a fraction of a second except with his dogs. So painful was it for him to look straight at anyone that he would swing his head and eyes sideways or in an arc up and down. Even when confrontation was unavoidable he always managed to look into the far distance. His antipathy to eye contact was a particular problem when lecturing because he had to avoid a room full of eyes. I therefore found it difficult to pay enough attention to what he was saying, which was roughly how to be a successful research student and whether to register for a Ph.D. The latter confused me because I thought that it was at least partly the point of being a research student. No! He described the history of the Ph.D. and why it had only recently become a kind of union card (his term) that one might need in order to carry out research or take a post in North America. He himself did not have a doctorate; Richard Gregory, Donald Broadbent, C. Grindley, and Alan Watson, all well-known in the department, also did not have doctorates. "It used to be the case," he said "that one tried research and if it worked there was no need for the doctorate, and if it failed one gave up research and did something else, so there was no need for the doctorate." But he sighed and said that times were changing and I might find it desirable to have a doctorate for an academic post outside Britain.

The second memorable aspect of my 3 years as a research student was my interaction with Charlie Gross. Toward the end of his period as a graduate student working on the functions of the frontal lobes in monkeys he decided that in order to understand how our ideas about the frontal lobes and brain function in general had developed he needed to read original papers that were often cited but probably without being read. He moved back to the early part of the century (Fulton, Holmes etc.), then the 19th century (Ferrier, Goltz, Munk, Flourens), then 1000 years to the Arabian scientists (e.g., Alhazen), and finally to the Greeks (Hippocrates, Aristotle). I initially thought it was a waste of time but his enthusiasm was infectious and I now realize that he was the very first person to convince me that the present is inexplicable without an understanding of the past. His example was one reason why, aged 60, I opted to provide the opening course of lectures in the new Oxford M.Sc. in Neuroscience on the topic of the history of research on the brain.

The third aspect concerns intellectual freedom and independence. Charlie Gross and I were both supervised by Larry Weiskrantz who, as I discovered when talking to other graduate students with different supervisors, was the antithesis of autocratic. He suggested rather than ordered, explained rather than pronounced, and had an open-door policy with respect to his students. He was the best possible kind of supervisor for a young neuroscientist. While Charlie and I were respectively studying the frontal and occipital lobes of monkeys, the first articles on the anatomical basis of memory in *Planaria* (flatworms) appeared. They were so strikingly novel and seemed to be addressing the cellular and molecular basis of learning and memory that Charlie and I suggested to Larry that we should study the phenomenon. Larry provided the funds to allow us to make a water T-maze and assemble the apparatus to study conditioning to a light associated with a weak electrical shock, which made the planarian contract. We then cut the planarians in half and both halves regenerated, but there was no evidence that any of the regenerates remembered the task. What a pity that there was at that time no Journal of Unreproducible Results because I discovered years later that many other investigators had been similarly unsuccessful. But it was not time wasted, for I learned the hard way why published experiments should constantly be queried, in my case especially with respect to blindsight.

During the second of my 3 years as a research student Larry Weiskrantz took sabbatical leave to work with Hans-Lukas Teuber in New York. He left Charlie and me "in charge" of the lab and, as this was before e-mail or cheap telephone calls, it meant that rapid communication was out of the question. Oliver Zangwill was, as required by University regulations, appointed as my stand-in supervisor, but he explained that he had every confidence that I would be able to cope without his help but that I should consult him if there any serious problems. I took this to mean that I was really on my own and so it proved. I had a wonderful time doing what I wished and discovering that it often did not work. It was the best possible education.

During the final year Larry had returned and I was completing my perimetric study of field defects caused by removal of parts of striate cortex, V1. Why the defects were not absolute needed an explanation and the likely ones were that the retina also projects to extrastriate cortex or that some other noncortical pathway is responsible, like the superior colliculus. But the extrastriate cortex in primates seemed to be unresponsive to visual stimulation, at least under anesthesia (Talbot and Marshall, 1941; confirmed by Daniel and Whitteridge, 1961). I was therefore specially excited by the results being reported by Bob Doty (1958), which indicated widespread extrastriate visual activity in cats, even under anesthesia.

Larry suggested that I might like to become a postdoctoral fellow with Doty, whom I had never met, and he wrote to Doty and to the Rockefeller Foundation. Within a couple of months I had arranged to start work with Doty in Ann Arbor in September 1961, supported by the Rockefeller Foundation. I had to have my doctorate first, of course, and I started to write it on April 1, giving myself 3 months to complete it. I tested monkeys in the mornings, analyzed results and worked on figures and text corrections in the afternoons, and wrote fresh text at home in the evenings. My wife, Pat, typed what I had written or had corrected the previous day. Various people, notably Larry, read chapters and made comments and the revision of the first draft became the final version. I often wonder whether the development of word processing about 20 years later often holds up the production of a thesis by encouraging repeated but unnecessary revisions.

The regulations for appointing examiners at Cambridge at that time stipulated that the candidate should not know the identity of the two examiners until the thesis had been submitted, an arrangement preventing a thesis from being designed to please a particular examiner. But hints abounded and in my case Larry suggested during my writing that I should read the recent review by David Whitteridge of Giles Brindley's new book on the *Physiology of the Retina and Visual Pathways.* A nod is as good as a wink and I paid particular attention to what Whitteridge wrote for it was clear that he would be one of my examiners. I was wrong; Brindley, not Whitteridge, was the physiological examiner! But all went well.

Postdoctoral Science

I mentioned previously that I was set to travel to Ann Arbor to work with Bob Doty. Not long before being due to leave England he wrote to say that he was moving to Rochester, New York, to start a new group in the recently created Center for Brain Research, directed by E. Roy John, and that he would understand if I decided not to take up the Rockefeller Fellowship. Because it was Doty that I wanted to work with and I knew nothing about either Ann Arbor or Rochester, there was no problem in simply changing geographical direction. Pat and I sailed to New York early in September. Yes, sailed! In 1961 transatlantic air travel was expensive whereas autumnal ocean crossings on a relatively small passenger liner were cheap. So we had 7 days at sea. It should have been five and a half but one of the seasonal hurricanes swept up the northern seaboard and made life on board uncomfortable. That was when I found that, like my brother, I am not seasick. Decks were almost bare and dining rooms equally empty, and—to my dismay—the swimming pool had to be closed. So I wrote a scientific paper (Cowey, 1962) and pondered why about 1 in 20 people do not suffer from seasickness. I even thought that I might study it and that the explanation might be financially rewarding. Pie in the sky. It is still unclear why people are or are not seasick and I have also met several scientists whose amazing discoveries brought them little financial reward (Howard Florey and his team who found how to grow and extract penicillin, and Cesar Milstein, who developed monoclonal antibodies).

Understanding seasickness eluded me. But one lesson I learned from the voyage is that the best environment for writing a scientific paper is alone and far from colleagues and the telephone (I would now add fax and e-mail). Being instantly accessible at all times is creatively disruptive, like being a servant a century ago. You might smile, but modern life in a university means that we are increasingly required to be "on call" to administrators, managers, research evaluators, teaching assessors, editors, health and safety committees, the press, and even to government. It is all deeply regrettable but fortunately it is too late for anyone to fire me for saying so. About 15 years ago I was admonished by my University for calling, along with Ray Guillery, a meeting of neuroscientists to discuss how best to introduce a new course leading to an M.Sc. in Neuroscience. Apparently it was not my business to arrange such a meeting even though the conventional procedure had been slow and obstructive. The happy outcome is that Oxford, finally faced with incontrovertible evidence of the need and therefore the opportunity to teach neuroscience, finally introduced the hugely successful Neuroscience M.Sc. in 1991.

My time in Rochester was what a postdoctoral position should be: an opportunity to learn something new and useful, both practically and conceptually. Bob Doty showed me how to record from the dorsolateral visual cortex using surface silver ball electrodes or from deep cortex using penetrating bipolar electrodes. The equipment was state-of-the-art for that period, meaning that everything took place in a lead-shielded room and using banks of cumbersome amplifiers, preamps, and oscilloscopes. Projecting brief stimuli was a bit of a problem but I used an electroencephalographic (EEG) pen, with a cardboard flap glued to the end, to form an electromagnetic shutter in the light path from a projector. After passing through an iris diaphragm to provide brief small spots of light, the beam was reflected from a small adjustable mirror and could thereby be directed at any part of the wall in front of the animal. Although homemade, the device worked without trouble throughout my stay. The wall could be covered with large pieces of white paper so that "receptive fields" could be drawn on it during the experiment.

Doty had been using the midpontine pretrigeminal preparation, which provided an EEG characteristic of alertness, and I used the technique for several of the preparations. By sectioning the pons in the coronal plane just in front of the trigeminal nerves, having approached it from above and behind across the top of the cerebellum and under brief barbiturate anesthesia, the forebrain could then be kept in an alert aroused condition without any painful input via the trigeminal nerves. Other sensory nerves were infiltrated with local anesthetic and the eyes were immobilized by attaching the conjunctiva to a metal ring. This preparatory surgery took several hours and I then stimulated and recorded for about 12 hours. Once Bob was satisfied that I could do all this on my own, I spent the next 10 months plotting the topographic representation of the retina on occipital cortex and trying to discover how it arose. The first device for averaging signals was still some years away so the records were based on single trials, each evoked potential displayed on an oscilloscope with a long persistence phosphor so that it could be inspected, measured and if necessary photographed. Now that about 30 different visual areas have been described in monkeys (Felleman and Van Essen, 1991; Van Essen et al., 2001) it is probably difficult to imagine how excited I was when I discovered in the squirrel monkey that surrounding striate cortex was another band of cortex (V2), which was roughly a retinotopic mirror image of V1. By electrically stimulating striate cortex the connection between retinotopically corresponding points in V1 and V2 was revealed and this connection could be abolished by delicately severing the white matter along the border between them (Cowey, 1963). Just before leaving Rochester I was able to record from several macaques and found that here too the extrastriate cortex was visually excitable and retinotopically mapped. Why V2 had not been reported before in monkeys is still a puzzle but a likely explanation is the level and type of anesthesia. Discoveries often hinge on apparently small changes in procedures, like the pH of a neurohistological reaction.

Almost every neuroscientist I know has a story about just missing an important discovery and I am no exception. While recording from V2 in squirrel monkeys I sometimes moved the surface electrode further forward as a control for volume conduction. If I moved it over the caudal superior temporal sulcus I recorded a prominent evoked potential, which was even more conspicuous when I used a penetrating electrode in the dorsal bank of the sulcus. I noted this in several preparations but did not have time to explore its nature for the end of my post doc loomed. The mysterious activity was of course arising in area MT, so termed by Allman and Kaas (1971a,b) in their pioneering and influential studies on the extrastriate visual areas of the owl monkey, studies which arguably more than any others led to the explosion of interest in cortical visual areas. Had I stayed for a much longer period in Rochester, as temptingly suggested by Bob Doty and which I seriously considered, it was this source of mysterious evoked potentials that I would have worked on. My observations were far too inadequate to publish but in a—for me—particularly nostalgic moment during my Festscrift in 2002 my colleague and collaborator Paul Azzopardi showed slides of action potentials taken from my lab records of 1962. Cortical area MT—often called area V5 in Europe because when it was first described in macaque monkeys by Zeki (1971, 1974) it was not immediately recognized as being homologous to area MT—has since become one of the most intensively investigated cortical visual areas because of its central role in the perception of visual motion. If only—as everyone who kicks himself for missing an opportunity says—I had followed it up. The fact is that hardly anything that remains unpublished will be influential; when Charles Darwin was painstakingly working on his theory of evolution through natural selection there were others following the same scent, notably William Wallace. But Darwin published first and, rightly, got the credit. I do not lose sleep over area MT.

Back in Cambridge, 1962–1966

While in Rochester I was invited to apply for a Demonstratorship (roughly an Assistant Professorship in the USA) in Experimental Psychology in Cambridge. I applied and was appointed without being interviewed. It was too expensive for Cambridge to pay my travel costs, they already knew me, and the post was probably not widely advertised. I did have a curriculum vitae (CV), which I had to send by regular mail, for fax and e-mail did not exist, but I had published or had in press only three papers. Having served on countless appointing committees since then, especially in the past 30 years, I know how fortunate I was, for no one with my slim list of publications would ever be appointed now. I returned to Cambridge late in 1967 and immediately started a course of lectures and practical classes. But as Larry Weiskrantz was still there I was fortunate to be able to collaborate with him even though I did not have my own research grant. Without his support, life would have been much more difficult.

My job was to lecture and give practical instruction to undergraduates reading experimental psychology. As it was my first "proper job" it took most of my time. I also gave one-to-one supervisions (tutorials) for 6 hours each week, especially on topics in physiological psychology, animal behavior, and learning theory but also across most of the syllabus. It was a period when all University tutors were expected to be able to discuss any topic in their subject. That time is long gone and with detriment to our students. First, experts are often the worst instructors in their own specialty; we stupefy students with our expert knowledge. Second, in having to teach outside my own narrow research interests I learned a great deal about things whose relevance to my own interests I might otherwise never have encountered. Third, I met students whose mental agility was greater than mine and with whom a tutorial was as much of a challenge for me as for them. Michael Morgan, now Professor of Visual Psychophysics at City University in London, is a good example.

In the time remaining, and chiefly in the vacations, I returned to the problem of the nature of the surviving visual sensitivity following damage to the primary visual cortex. When I went to Rochester I had left behind in Cambridge a macaque monkey with a cortically induced macular field defect, whose extent and threshold sensitivity I had plotted in Cambridge. When I returned a year later I found that the defect had remained unchanged but that with renewed repeated testing its size gradually diminished and the residual sensitivity within it improved (Cowey, 1967). At that time the accepted wisdom was that the brain showed no genuine repair of damage and that impairments of perception or movement or language were permanent once the more-widespread immediate effects had diminished. The evidence that repeated practice improved visual sensitivity within cortical field defects, especially at the edges, prompted my own subsequent investigations on rats (with Hugh Perry) into the nature of visual development and the importance of the age at which brain damage occurs in influencing the extent of any recovery. However, the paper in 1967 was cautious in its interpretation of the nature of the recovery with practice, acknowledging that spontaneous but late recovery can occur in some patients and that "the shrinkage of the defect with time may reflect the animal's increasing ability [with practice] to detect such a [weak] stimulus near the edge of the defect." I am intrigued to see that nearly 40 years later the effects of training on visual recovery within areas of cortical blindness or within regions of motion blindness are still being vigorously pursued along similar lines (e.g., Williams et al., 2004; Huxlin and Pasternak, 2004) and that the existence and interpretation of any recovery remains as controversial as ever (Reinhard et al., 2005; Horton, 2005; Sabel, 1999).

While in Cambridge I also supervised my first research student, Richard Latto. Richard chose to work on the frontal eye-fields (FEF) in primates, using the monkey perimeter that I had built and following up much earlier and pioneering work by Margaret Kennard (1938, 1939), who demonstrated that unilateral lesions centered on Brodmann's area 8 (FEF) in monkeys produced a prominent contralateral neglect, which gradually resolved. Together Richard and I discovered three new things. First, in a perimeter the defect appeared to be no different from a field defect produced by unilateral damage to V1. Why, given that there was no damage to what was then regarded as the cortical visual system? Second, sensitivity within the field defect increased with practice but the defect could still be demonstrated over a year later. Third, a bilateral lesion produced a bilateral defect, showing that the initial unilateral defect was not simply unilateral neglect caused by the now dominant and inhibitory role of the FEF in the undamaged hemisphere. Although many distinguished experiments involving single unit recordings from neurons in FEF of behaving monkeys were carried out in the 1960s and 1970s there was a clear slackening of interest thereafter for about 20 years, arguably because the FEF seemed to be no more than motor cortex for the eyes and the earlier behavioral results remained inexplicable and were increasingly ignored and even forgotten. Several developments restored interest in the FEF in the 1990s: Functional brain imaging indicated their top-down role in visual search; renewed single cell recordings indicated that the FEF respond to visual stimuli far sooner than previously thought, as soon as cells in V2 (Bullier, 2001a,b; Nowak and Bullier, 1997; Schmolesky and Wang, 1998); transcranial magnetic stimulation (TMS) applied to FEF changes the regional cerebral blood flow not only in the eye-fields themselves but also in the posterior parietal cortex (Paus et al., 1997); the timing of the effect of TMS over FEF indicates that it exerts its effects on visual search by this downward projection to parietal cortex (O'Shea et al., 2004). From being motor cortex for the eyes the FEF have been promoted to having a major top-down role in visual attention and visual search. Hardly surprising that their removal makes primates visually inattentive. At last we can understand Margaret Kennard's early findings.

Despite teaching duties, this period was scientifically productive for me. In addition to the research mentioned above I met two outstanding undergraduates who carried out their final year research projects with me. I hesitate to say that I supervised their work because even at that stage they were even then outstandingly independent. Their names were Colin Blakemore and Edmund Rolls. Colin chose to study the basis of the recovery from the misreaching that follows retinal damage to the macula or damage to its representation in V1 in both human patients and monkeys. Is it mediated by surviving macular projections to other parts of the brain (aberrant projections to remaining V1, visual cortex outside V1, or the midbrain visual centers) or is it independent of them? He addressed this by studying monkeys with retinal lesions, where all projections from the macula have been destroyed. The recovery from the initial "past-pointing" was indistinguishable from that of cortically induced past pointing, neatly disproving a hypothesis (Blakemore et al., 1968). The result certainly affected my thinking about the nature of visuomotor recovery from brain damage and I hope that it provided a modest nudge to his subsequent distinguished career in neural plasticity.

Edmund Rolls opted to study the relationship between the variation with retinal eccentricity of the density of ganglion cells and retinal cone receptors in macaque monkeys and squirrel monkeys and their relationship to cortical magnification factor and to visual acuity of the two species with respect to eccentricity, which I had been studying behaviorally. Edmund's investigation was entirely neurohistological and he and I independently made the cell counts. Fortunately we obtained the same result (Rolls and Cowey, 1970), namely that magnification factor correlates closely with cone and ganglion cell density in both species and that it provides a satisfactory explanation for the variation in visual acuity with retinal eccentricity. This result has stood the test of time with one major and important exception, namely that the fovea of the retina, is *overrepresented* in V1, i.e., its magnification factor *cannot* be predicted from the density of ganglion cells concerned with the fovea (Perry and Cowey, 1985, 1988). The latter became a contentious issue in the 1980s and 1990s because it contradicted the simple and attractive principle that the amount of primary sensory cortex devoted to the peripheral sensory surface faithfully mimics the receptor density at the latter and that this is true for all modalities. Instead, the foveal projection is preferentially elaborated in V1, which necessitates more neurons and therefore more space. But this preferential cortical elaboration closely corresponds with psychophysical results that showed a variety of previously anomalous visual thresholds at the fovea itself (Jüttner and Rentschler, 1966, 2000; Strasburger and Rentschler, 1996; Strasburger, Rentschler, and Harvey, 1994). This special status of the representation of the fovea in human V1 has never been directly demonstrated but a good bet is that it might be resolved by functional neuroimaging (e.g., Engel et al., 1994) as long as we can trust the available measurements of ganglion cell density and its variation with retinal eccentricity so that they can be related to the topography of the functional activations in V1 produced by localized retinal stimulation. I am constantly reminded how long it can take to establish something beyond reasonable doubt.

Not long after taking up my Demonstratorship in Cambridge, Oliver Zangwill invited me to dinner in King's College, where his professorial fellowship was based. I imagined that the occasion, in one of the finest Gothic dining halls in Cambridge and close to what hordes of tourists regard as the finest perpendicular Gothic chapel in Europe, was simply a friendly and totally informal occasion. Instead I discovered that Zangwill intended to gently "instruct" me about things that every young university teacher should know, especially getting the right balance between teaching, research, and administration. He explained that doing a stint of administration was not just useful to the community but could be a comfort at times when research was not going well. In later years I often wondered whether he was reflecting on his own research career! Perhaps I took him too seriously because in the space of 4 years I had become a Fellow and Tutor at my old college (Emmanuel), was secretary of the college residential building committee at a time when the college was designing and constructing a new set of buildings, was academic librarian in the Psychology Department, and was secretary of the faculty board, a job that was little more than being a scientific amanuensis. I had too often said "Yes" when I should have said "No." But I was entitled to sabbatical leave and arranged to work with Charlie Gross at Harvard for most of 1967. Freed from these duties I did little but research for the entire time. Hans Kuypers and his colleagues had recently published the first systematic anatomical study of the forward cortical projections of V1; Mishkin and his colleagues had shown that temporal neocortex was necessary for normal visual object processing in macaques, and Brenda Milner and others had drawn attention to the importance of the temporal lobes for object perception in man. Charlie and I accordingly compared the effects of what we called foveal prestriate lesions (roughly areas V4 and TEO) and more rostral inferior temporal lesions (area TE) on the aquisition and retention of visual pattern and color discriminations in macaques. We found a double dissociation in the effects: Prestriate lesions impaired perception whereas TE lesions impaired visual memory (Cowey and Gross, 1970). Our collaboration had been so close that we decided on the order of authors by tossing a coin. At the time, I doubt whether either of us realized that the analysis of the role of different occipitotemporal visual areas would occupy visual neuroscientists for at least a further 30 years.

With the benefit of hindsight I can now appreciate that we were working in the heyday of analyzing brain function by making lesions and studying their effects, using the reasoning, if not the precise techniques, of giants like Ferrier, Lashley, Pribram, Chow, and Mishkin from 80 to 20 years earlier. This single-method approach has almost died with the end of the last century. By making reversible lesions with local anesthetics, recording from and stimulating single cells in awake behaving monkeys, applying specific neurotransmitter agonists or antagonists to clusters of neurons, obtaining high resolution structural magnetic resonance (MR) scans of experimental lesions, and studying the effects of lesions by modern neurohistological methods, the number of monkeys used has decreased as the amount we learn from each one has increased. However, it is commonly asserted that we no longer need such studies at all because computers can simulate behavior and show us how it is mediated; I have not yet encountered a single example of computer simulation of memory, perception, emotion, or consciousness that tells me how the brain brings about these things.

Oxford

Not long before I was due back in England I received the good news that Cambridge had promoted me to Lecturer, which meant that I had a tenured University post and a College Fellowship to the retiring age of 67. But almost at the same time I learned from Larry Weiskrantz that he had accepted the Chair of Psychology in Oxford and that he would like me to join his department there and help in setting up a new laboratory for studying primate behavior. He made clear it that he could not offer me a permanent University appointment but that he would attempt to create such a position once I was there. It was a straight choice between a secure post in Cambridge, with an attached College Fellowship, and a new start in Oxford at a lower salary, without tenure or a College fellowship but with the prospect of better facilities. At the same time I received a telephone call from the Senior Tutor at Lincoln College Oxford, followed by several letters, who explained that he had heard via Larry that I might be taking up a post in Oxford and that the College would be pleased if I could give tutorials in Psychology to their Psychology/Philosophy undergraduates if I decided to move. That a small medieval Oxford college (founded 1427 and mostly built in that century) would take such trouble to find a part-time tutor in a minor subject surprised and intrigued me. I have never regretted taking the riskier option. I resigned while still at Harvard, we sold our house in England without ever setting foot in it again, and had our possessions moved to Oxford. I wrote to say goodbye to lots of friends in Cambridge who, on the whole, were puzzled and lukewarm. To paraphrase one of them "Why resign from a 'real job' in the best university in the world for science in order to take a soft-money position in an undistinguished psychology department in a medieval university that barely tolerates real science?" With that kind of stinging comment on my mind I arrived in Oxford with my family 1 week before starting a new career there. How wrong they were!

Oxford Collegiate Life

I was in Oxford to carry out behavioral neuroscience on monkeys. But I also had a duty to teach undergraduates for Lincoln College. The first time I dined there the Senior Tutor, who had in a sense recruited me while I was at Harvard, asked me to sit next to him in dinner. He was the historian J.B Owen and we did not talk about science. I asked him how old the dining hall was and he said, in a matter-of-fact, rich, New Zealand voice, "Oh, finished about 1440, the oldest unspoiled dining hall in Oxford." He was not exaggerating and I have since dined there more than a thousand times. So what? Who cares? Why does it matter? It matters because a self-governing community of like-minded academics whose statutory duties are not only to engage in teaching and research but also to govern the institution—its finances, buildings, teaching, selection of students, staff, and mode of operation—is the best model I have yet met for dealing effectively with education, research, and academic community life. I also appreciated working with academics from almost every other subject than my own and from the scientists I learned a great deal about other subjects than mine: anatomy, pharmacology, physiology, cell biology, biochemistry; but it was establishing friendships—not just the much vaunted "contacts"—with scientists in these fields that proved so helpful to my neuroscience. I was elected to a senior research fellowship in 1968 and am now an Emeritus Fellow. When elected I discovered that I was a "penicillin fellow," funded by the bequest from William Morris (subsequently Lord Nuffield and founder of Nuffield college) to provide College Fellowships for the three members of the team that, under the direction of Howard Florey, had first shown the dramatic therapeutic effectiveness of penicillin (Chain et al., 1940) and discovered how to culture the mold and produce its antibacterial product in sufficiently large quantities to treat infections. I got to know Norman Heatley well (he died aged 93 in 2004) and am constantly amazed that those who oppose research on animals on the grounds that the results are not applicable to man continue to deny that antibiotics (which have saved hundreds of millions of lives) did not arise as a result of Heatley's experiments on mice. He gave to three groups of mice, all inoculated with *Streptococcus pyogenes, Staphylococcus aureus,* or *Clostridium septique,* either penicillin or a placebo. Whereas all 73 mice given a placebo died, 66 out of 73 treated mice survived. It was a momentously important medical experiment, one of the greatest of the 20th century, yet its significance is still dismissed on the grounds that "animals are just different from man." Talking to Heatley (who was not first author of the paper because *The Lancet* listed them alphabetically) for just 5 minutes would disabuse anyone of that astounding prejudice. But why was I a "penicillin fellow"? The simple answer is that by 1968 the great period of the biochemical development of antibiotics had ended and the college no longer needed three Research Fellows dedicated to just that. I was therefore appointed to teach psychology on the grounds that it was biomedical, the College had no Fellow in that increasingly popular subject, and, at that time, psychology could only be studied with either physiology or philosophy, in both of which the college was strong. It was another stroke of luck for me that I was on hand at the right time.

The Department of Experimental Psychology in 1967 occupied a Victorian villa, next door and in the shadow of the magnificent but bogus classical façade of Rhodes House, home of the Rhodes Trust and Rhodes scholars. Further down the road a large hole in the ground marked the footprint of the new Psychology/Zoology building. Another fortuitous event had precipitated this initially uneasy partnership. The new Linacre Professor of Zoology, John Pringle, had wanted a slim 25-story, 260 feet high, Zoology skyscraper, built on the edge of the University Parks where it would dominate the science area and the Oxford skyline. The architect's portrayal of his grand design, described as like something from San Gimignano, can be found in the exquisite and revealing book called *Unbuilt Oxford,* by Howard Colvin (1983). The democratic Congregation of the University rose up and resoundingly voted against the scheme. Instead, the present 5-story Ziggurat structure was built and although Pringle got the total square footage he desired the University awarded one third of it to Psychology, which also needed to expand. So the psychologists got what they wanted on the coat tails of Zoology and the firm promise of these new premises was an important factor in attracting Larry Weiskrantz, me, and many other psychologists to Oxford. However, I had to spend the first 2 years in the Victorian villa, where we established laboratories and a colony of monkeys in the back garden. It would now be impossible: security was slight; the now strict mandatory temperature and humidity controls for the animals did not exist—just as they do not exist in the wild!—and unlike now the animals could even look out of windows. There was no surgical suite but David Whitteridge generously allowed us to use the facilities in the Physiology Department, some of which were probably created and used by Sherrington. The problem was that the two departments were on opposite sides of a major public road through the science area. This was solved by anesthetizing the monkey in Psychology, wrapping it in a blanket in a cardboard box, and carrying it to the Physiology Department. Thirty years later a similar but slightly longer journey was needed to take monkeys to the MRC imaging center in order to obtain structural images of their cortical lesions. This required written permission from the UK Home Office, a formal addition to my animal research license, and transporting the anesthetized animals in a locked metal box while in an authorized University vehicle without windows. It's called progress.

A year after arriving in Oxford I became the Henry Head Research Fellow of the Royal Society, solving any problems of a salary for 5 years. It was not a post I had applied for because at that time there was no application procedure. Instead one had to be proposed by a fellow, with the support of the head of the host department. The culprits turned out to be David Whitteridge and Larry Weiskrantz. Fergus Campbell, at that time one of the world's best known visual psychophysicists and author of the article in *Scientific American* on "Taking the Psycho Out of Psychophysics"—pointed out that it was the best scientific job in Britain because the holder was known as the head fellow of the Royal Society and had no other duties. If only! Although I continued to teach for 6 hours each week, I spent the 5 years working with Larry Weiskrantz to develop a neurohistology lab, proper surgical facilities, automatic behavioral testing methods, and a program of research on various aspects of visual perception and memory.

With respect to neurohistology I was helped enormously by meeting Tom Powell in Oxford and Brian Boycott in London, although this was tricky because neither liked the other. Tom Powell was notoriously prickly but before coming to Oxford I had several times met Walle Nauta at MIT, who said that I should approach Powell if I was serious about introducing experimental neuroanatomy in the Psychology Department. I doubt whether Powell would have agreed to see me had I not had this slight connection with Nauta. As a result I went to Powell's lectures, got to know his young colleagues and learned how to perform autoradiography, the Golgi technique, and the Fink-Heimer methods for staining degenerating nerve preterminals. I realized that Powell had decided I was a serious scientist when he invited me to be the internal examiner for several of his doctoral students and he asked whether I might have a job for his youngest histologist, Caroline Healy-Yorke, after his current grant ended. I did have a post and she worked with me in psychology for the next 20 years, producing histology—and scientific gossip—of the highest quality. I owed a lot to Tom Powell.

It seemed strange to some colleagues in Oxford that the Psychology Department had a group of experimental neuroanatomists and—at its peak—three full-time histologists. I remember having the same feeling when Hans-Lukas Teuber became head of the Psychology Department at MIT in the 1960s and promptly appointed one of the world's leading neuroanatomists, Walle Nauta from Switzerland, to lead a rapid expansion of what was then called physiological psychology and that included Emilio Bizzi, Peter Schiller, Ann Graybiel, and Gerry Schneider. It exemplified the young subject of neuroscience, where understanding how the nervous system controlled behavior benefited from methods and ideas that were hitherto traditionally and strictly segregated. I have continued to use anatomical methods to solve, or illuminate, behavioral problems and at present count have published 57 articles whose primary techniques were anatomical. Naturally I did not do this on my own and although there are too many to list I should highlight Hugh Perry, Ben Reese, Glen Jeffery, Rafael Linden, and Peter Somogyi. Peter deserves special mention for several reasons. I met him about 1980 while he was in Oxford, developing his technique of revealing how several neurons in a chain of neurons could be followed, now called microcircuitry. In order to get as close as possible to the human brain, he wanted to study thalamocortical and intracortical connections in monkeys that had sustained small geniculate lesions or intracortical injections of tracers. I was able to provide and operate on monkeys that were going to be perfused for other purposes and, as a result, we carried out our investigations without involving additional animals.

Peter Somogyi's work attracted international recognition and the then recently appointed Professor of Pharmacology, David Smith, with whom Peter had first come to work in Oxford, proposed to the Medical Research Council that it should set up a new MRC Unit to investigate anatomical neuropharmacology. The time was ripe, Peter was clearly outstanding, and both I and Charles Phillips (then the Head of the Anatomy Department) were members of the MRC Neurosciences Board. Council debated the proposal and asked Phillips and I to seek international opinion about its merits. We divided the work and I contacted Walle Nauta, Janos Szentagothai, and Max Cowan. Everyone contacted was enthusiastic and the MRC ANU was officially opened in 1985. I attended its 20-year celebrations in March 2005, where its leading role in European Neuroscience was evident and had already been recognized by the election of Somogyi to the Royal Society in 2001. He is another scientist with whom I have been lucky and privileged to work.

Jim Gowans, head of the MRC cellular immunology unit in Oxford until he became head of the MRC in 1977, once said to me that it was a good idea for every scientist to change direction every 10 years or so. "It makes one young again, with no laurels to rest on." I think he meant a sea change rather than a slight veer and he had done just that by taking on the job of running the MRC and doing it again when he became Secretary General of the Human Frontier Science Program in 1989. It was during the latter period that he was visiting the Psychology Department in connection with HFSP support for a workshop on blindsight. His words touched a chord because I liked doing new things, even at the risk of being criticized—as I have been—as a scientific butterfly. In 1985 I began two new lines of research that seemed risky at the time but have proved to be hugely gratifying, at least for me. The first was work on cortical color blindness with my friend and colleague Charles Heywood. We were both interested in prosopagnosia (agnosia for faces) when Freda Newcombe offered us the opportunity to examine the color blindness of one of her prosopagnosic patients. Twenty years on, patient MS is still densely prosopagnosic but he also remains completely color blind in the sense that he cannot reliably name a colored surface or pick out the odd color in three surface colors. It took us another 10 years to establish that his brain is nevertheless still processing information about hue and wavelength and that he is an outstanding example of how differences in hue can be used to generate the perception of contour (and therefore shape) and motion of contours even though the hue itself is invisible (for review see Heywood and Cowey, 2004). Expressed more generally, MS shows that the brain can use sensory information to generate a percept even when there is no phenomenal experience of the attribute usually attributed to that sensory information (in this case color); MS is a particularly striking example because he can paradoxically perceive chromatic contours in the absence of color perception. Several such examples have since come to light but it is still a challenge to show exactly how the brain achieves this.

An unforeseen outcome of the work on cortical color blindness is that it became embroiled in an ongoing international disagreement about the properties and functional role in perception of V4 in monkeys and man. There is no disagreement about the position of extrastriate area V4 in macaques but little consensus about whether the properties of its cells indicate that it should be regarded as an area concerned primarily with wavelength, color constancy, form perception, visual selective attention, visual search, or all of these. It would not be an exaggeration to describe some of the views expressed about V4 as arousing passionate indignation. But they seem mild when compared to declarations about the anatomical position of human V4 and whether it corresponds to the region of maximum change in regional blood flow when subjects are performing perceptual tasks involving color as opposed to a variety of form discriminations and whether the lesion that leads to cortical color blindness corresponds to human V4 or to nearby more rostral areas. When something so apparently straightforward arouses such passions it usually indicates that different methods, criteria, terminology, prejudices, or all of these are responsible. Anyone interested would get a good impression of the quarrelsome altercation by consulting Heywood and Cowey (2003); Bichot, Rossi, and Desimone (2005); Tootell et al., (2004); and Zeki (2003). I suspect that the dispute will outlast me.

The second example concerns blindsight. Although I had worked for many years on residual visual sensitivity after damage to V1 in monkeys I was not initially involved in the subsequent work on blindsight in patients with similar brain damage. Such patients showed highly significant forced-choice discrimination of visual stimuli presented in their field defects despite denying that they had seen anything (Pöppel et al., 1973; Weiskrantz et al., 1974). At the time it was still believed—not unreasonably—that damage to V1 had different effects in monkeys and humans and that so-called evolutionary encephalization of function was the explanation. The new work with patients showed that patients and monkeys were not that different after all and that studying the biological basis of the residual discrimination in monkeys and any changes in it with time or practice might be helpful in evaluating and treating patients. Blindsight also demonstrated that the perceptual effect off sensory cortical damage depend on how one assesses it: asking subjects to say yes or no about visual stimuli indicates blindness whereas forced-choice guessing uncovers good, sometimes almost perfect, discrimination. My interest in impaired color vision introduced me to the work on residual color processing in blindsight by Petra Stoerig (1987) and, after discussing it at a conference, we decided to collaborate and to study residual visual processing in patients and monkeys contemporaneously and, where possible, to combine it with neuroanatomical investigations. This was my second major change in research in the 1980s and it exceeded all initial expectations. After publishing 26 jointly authored papers I think we understand much more about not only color processing in blindsight in both patients and monkeys but also motion, contour, and the nature of awareness (for reviews see Stoerig and Cowey, 1997; Cowey, 2004). Twenty years ago I would never have guessed that a chance meeting with a young German behavioral neurobiologist would lead to such a productive scientific collaboration.

This was also a period during which cognitive neuropsychologists increasingly studied the effects on perception, usually measured by reaction times, of unseen stimuli. With respect to blindsight the usefulness of the approach was first demonstrated by Marzi et al. (1996). An unseen target in the blind part of the visual field affected reaction time to seen targets in the normal field. Sure enough, when Petra Stoerig and I tried this with monkeys (and other patients) it worked; stimuli delivered in a hemianopic region a few 100 ms before a target in the normal hemifield significantly and prominently delayed reaction times to the latter (Cowey, Stoerig, and LeMare, 1998).

But one piece in the jigsaw was missing. Before we could be certain that the work on monkeys provided a means of studying blindsight we had to show that the monkeys were like patients in not having any visual percept of visual stimuli that they could discriminate by forced-choice responding. In other words we needed a yes/no task. Petra and I resolved this by training monkeys to touch real visual stimuli but to respond in a different way on trials when no visual stimulus was delivered. The result could hardly have been clearer. The same stimuli that could easily be detected and localized by forced choice guessing were categorized as blank trials, ie., "no," when the yes/no task was used (Cowey and Stoerig, 1995, 1997). By a simple adjustment of the way in which monkeys were tested, a long-standing paradox disappeared and as a bonus the work already carried out on the anatomical consequences of removing V1 in monkeys was instantly relevant to work on humans. For example the retrograde transneuronal retinal degeneration known for many years in monkeys (van Buren, 1963; Cowey, 1974) and confined to the color-opponent retinal ganglion cells (Cowey et al., 1989) showed why some stimuli were much more easily discriminated in blindsight and which anatomical pathways were probably responsible (Cowey, 2004).

One of the major planks of critics of work on animals, at least in the UK, is that it is scientifically irrelevant to human disorders. This accusation has often been leveled at me, by telephone calls in the middle of the night, pamphlets distributed in the center of Oxford, noisy demonstrations outside my department, and the systematic vandalizing of my car outside my home. It would be a comfort to know that at least some of my research is effective in refuting the accusation but I doubt it, for a particularly depressing aspect of the antivivisection debate is that there is no proper debate. It mostly amounts, by *both* sides, to a well-worn and almost ritualistic exchange of insults, clichés, and prejudices. In 40 years I have on only a few occasions witnessed or read an account of a genuine, open-minded, intellectually honest debate about the ethics of research on animals. I have read accounts of events leading up to and during the infamous but unsuccessful, criminal prosecution of David Ferrier in London in 1881, brought under the Cruelty to Animals Act, and it has an astonishing contemporary ring, as if no progress had occurred in more than a century. It has become a political, emotional, violent, and social problem rather than an intellectual and ethical one and I am less confident about the outcome than almost anything else in neuroscience.

Why Anatomy Matters

I wish I could remember which one of two eminent visual neurophysiologists in a lecture I attended in Oxford many years ago declared that "Physiology without anatomy is impossible," meaning that we could never properly understand physiological results on the receptive field properties of cortical visual cells until we understood the anatomical microcircuity underlying them. It did not take long for my surprise to become agreement for I realized that I would never understand the residual vision, now known as blindsight, without some idea of where and how the brain processed the underlying sensory information. I will give just a single example but more can be found in Cowey (2004). There are 10 known pathways from the eye into the brain (see Stoerig and Cowey, 1998), the two most numerous being to the superior colliculus (about 1.5×10^4 fibers in the macaque monkey) and the dorsal lateral geniculate nucleus (dLGN) of the thalamus (at least 10^6 in macaques). When V1 is removed there is almost complete retrograde degeneration of projection neurons in all six principal layers of the dLGN (Michailovich et al., 1975) and it is usually assumed that the other pathways are unchanged and that they must be mediating the visual processing that underlies blindsight. The truth is rather different, for the interlaminar layers of the dLGN do *not* degenerate, or at least not conspicuously. These cells are part of the koniocellular, or K, projection (for review see Hendry and Reid, 2000), thought to arise from bistratified retinal ganglion cells and to signal information about wavelength (Dacey, 1994, 2000). The fact that they survive destruction of striate cortex almost certainly reflects the fact they also project to extrastriate areas such as V2, V4, and inferior temporal cortex and, as recently shown by Sincich et al. (2005), to the motion area MT. Their numbers have never been accurately assessed but they seem to be as common as magnocellular (M) cells, i.e., as many as 10^4on each side of the brain. This is as many as all ganglion cells in an animal like the rat, which seems to see quite well! The next step is surely to use diffusion tensor imaging (DTI) to trace surviving pathways in the human brain now that it has been shown that DTI can reveal the entire pattern of thalamocortical projections noninvasively (Behrens et al., 2003). Francis Crick often argued passionately for more, not fewer, anatomical studies on macaque monkeys as a means of understanding how billions of neurons give rise to perception, memory, awareness, etc. (Crick and Jones, 1993). He is right, but perhaps DTI will provide some answers with respect to long pathways in discrete bundles.

Transcranial Magnetic Stimulation: Panacea or Delusion

My last major technical change of direction occurred in 1995, when I read an article about reversibly disrupting cortical neurons—and visual perception—by applying a brief magnetic field above the occipital skull and inducing a similarly brief electrical field in the tissue beneath (Amassian et al., 1989). It seemed that the technique, known (strictly speaking wrongly) as TMS, must surely be useful in investigating a wide range of perceptual and cognitive functions. I purchased my first, single pulse, TMS machine speculatively and the first qualitative results were disappointing.

Using myself as a subject the best I could do was produce a faint smudge of light (phosphene) in the center of my visual field by stimulation delivered above the occiput. It was while wondering what to do next that my colleague Vincent Walsh asked if he could use the equipment and try something more cognitive. Our first paper (Ashbridge, Walsh, and Cowey, 1997) demonstrated that a single pulse of TMS applied above the right parietal cortex about 100 ms after presenting a visual search array impaired performance on serial (conjunction) search but not on parallel (pop-out) search. The effect disappeared once the task had been mastered but reappeared as soon as new stimuli were used (Walsh, Ashbridge, and Cowey, 1998). We were also joined by Eric Corthout, who extended Amassian's findings by showing that there were at least four time periods between –100 and +200 ms of the presentation of a 4 ms foveal letter target at which a single TMS pulse impaired identification of the letter, indicating that TMS could be used to disentangle the contributions to perception of cortico-fugal, feed-forward and reentrant events (Corthout et al., 1999a,b; 2000a,b; 2001; 2002; 2003). From these small beginnings about 20 people were using TMS in the Oxford Psychology Department by 2005 and similar developments occurred worldwide.

TMS has been used to study many aspects of sensation, perception, learning, awareness, priming, voluntary movement, top-down planning, mood, and recovery from brain damage (Cowey, 2005). Yet it remains a controversial tool. Quite apart from the important issues of safety, it has been suggested that the exact site of action of TMS, whether it affects excitatory or inhibitory neurons or both, and how long the effects of one pulse last are all unknown or uncontrolled. These are all valid points but some have already been successfully addressed (Cowey, 2005). It is important to remember that TMS is just a tool and that it can be used well or badly, as my father taught me. It is also proving to be especially useful when used in conjunction with other techniques, notably EEG, and structural and functional MRI. It is neither panacea nor delusion but behavioral neuroscience would be poorer without it.

Helping to Administer Neuroscience

A common complaint is that there is too little time for research because "there is too much admin." But there is good and bad administration of science. The bad includes rampant petty bureaucracy, needless and tedious inquiries whose results disappear into untraceable filing cabinets, micro-management by administrators, unnecessary mission statements, unrealistic and overspecified goals, and strategic planning by nonscientists or failed scientists. The good includes the difficult business of creating and preserving the best possible scientific environment. When I was young

I imagined that if something was scientifically desirable it would just happen. I had to learn that things only happen if people work hard to bring them about and that doing so actually helps one's own science.

My first involvement in promoting neuroscience occurred just after coming to Oxford. Following a meeting in 1967 called by the Organisation for Economic and Cooperative Development (OECD) to consider which areas of interdisciplinary research to encourage, a small group of neuroscientists led by Larry Weiskrantz and including Konrad Akert, Hans Kuypers, and (I think) Otto Creuzfeld lamented the fact that European brain scientists from different disciplines and countries rarely met professionally, let alone collaborated. They agreed that a new international society was needed, not just more funds for existing national organizations. I subsequently joined the group and, as the youngest member, incautiously agreed to be its secretary. Following many letters to major neuroscientists in western Europe, we formed a steering committee consisting of Akert, Cowey, M. Frankenhaeuser, Kuypers, Paillard, Ploog, Scherrer, van Hof, and Weiskrantz. We prepared and circulated an announcement of our intention to start a new international and interdisciplinary Society subsequently called the European Brain and Behaviour Society, or EBBS. The steering committee arranged a meeting of about 30 brain scientists in Rotterdam in April 1969 to plan the organization of the society (aims, rules, membership, etc.) and EBBS was formally started on April 15. Larry Weiskrantz and Elizabeth Warrington were appointed President and Secretary, respectively. The first annual meeting, hosted by Jacques Paillard, took place in Marseilles 6 months later. I have glossed over how much work was involved but the outcome was gratifying, with one dramatic and painful exception. Jan Bures had been an enthusiastic and polite but outspoken member of those assembled in Amsterdam in 1969. He continued to support EBBS but his views about international science were not welcomed by the governing regime in Czechoslovakia following the Russian invasion of 1968 and he was progressively stripped of his scientific stature within his own country together with some of his facilities. Naturally he simply became even more famous in the West but for 18 years he was unable to travel to any western country to lecture or even just to attend meetings. These events are movingly described in his autobiographical chapter in volume 4 of this series (Bures, 2004).

EBBS held its 37th annual meeting in 2005 in Dublin and a glance at the program shows that its core is still behavioral neuroscience. At the first annual meeting the committee met representatives of IBRO, who were concerned that EBBS might be trying to take over some of IBRO's responsibilities. It was an uneasy meeting but much helped by the fact that one of the IBRO representatives was Han-Lukas Teuber, who knew many of the EBBS committee and who proved to be a skilled negotiator and adroit mediator. One reason for mentioning these events is their extraordinary resemblance to those occurring in the United States at about the same time (Doty, 1987). As Doty points out, in 1965 a group of brain scientists "came to recognize the diffuseness of neuroscience, a part of many disciplines but lacking a focus of its own." A new society was needed, "But what kind of society should it be?" After several meetings of the group, the Society for Neuroscience was formed in July 1969, just 3 months after EBBS. As in Europe "There was significant sentiment against forming a new society...from the more established scientists already satisfied with their professional ties." Given that the reasons for establishing EBBS and SfN were so similar, why has the latter been so much more successful in terms of membership and prestige? With the usual benefit of hindsight and a little insight it is not difficult to see why. First, the SfN decided to have its own journal—the *Journal of Neuroscience*—whereas EBBS voted *not* to have a journal despite overtures from both *Brain Research* and *Behavioural Brain Research.* I think the decision was a mistake for neuroscience in Europe although it was finally rectified by the creation of the European Neuroscience Association a few years later and, shortly thereafter, the *European Journal of Neuroscience.* Second, the SfN boldly decided to cover the gamut of subjects under the umbrella of neuroscience, both in its annual meeting and its journal, whereas EBBS initially emphasized the behavioral component. I recall Hans Kuypers protesting at the policy of EBBS in refusing to allow anatomical contributions to the annual meeting unless they made reference to their relevance to some behavioral problem. For anatomy also read pure physiology, pharmacology, biochemistry, and neurochemistry. Fortunately the mistake was finally recognized by the formation of the Federation of European Neuroscience Societies (FENS), which is about as close as one could get to the SfN while still preserving the independence of the component organizations. I learned a lot about people and their scientific politics by my association with both EBBS and EJN. From 1986 to 1988 I was President of EBBS and at that time the trickiest part of the job was still its relationship with ENA!

In 1976 I began to serve on MRC Committees and had I realized from the outset how many years I would serve I might have declined the initial invitation. I was a member of the Neurosciences Grants Committee for 5 years and chairman for 2 years. It was followed by 4 years on the Neuroscience Board, which looked after the more long-term program grants, MRC Units, and scientific policy in the neurosciences. I was chairman of the board for 2 years. Finally, for 4 years I served on council, which dealt with MRC policy (which included long-term planning) for much more than just neuroscience. The grants committee provided an unparalleled opportunity to discover who was doing what in UK Neuroscience, the Board made it possible to meet many of them on subcommittee visits to MRC establishments, and the council taught me why and how to prioritize. As there were never enough funds to cover all grant applications, or all proposals for radically new lines of work, awarding funds necessarily reflected both scientific excellence and medical importance, which often seemed not to be highly correlated. This is all familiar to those who have followed this path but I still meet colleagues who do not understand why science funding works the way it does.

With respect to my own neuroscience in Oxford I was especially helped by having served on MRC official bodies. In the late 1980s Larry Weiskrantz and I asked to see the, then, head of the MRC, Dai Rees, about how best to promote interdisciplinary behavioral neuroscience in Oxford. We were not proposing that people should be *made* to collaborate, which does not work but is increasingly required by the misguided policy of some funding organizations that earmark funds for projects that involve scientists from different disciplines in different countries. We simply wanted to make it much easier for those who wanted to collaborate to do so. The MRC was already considering its own scheme to create and fund a small number of Interdisciplinary Research Centres (IRCs) and Dai Rees suggested that Oxford should put in an application. A small committee of the usual suspects (Blakemore, Cowey, Guillery, Rolls, Stein) agreed to coordinate the attempt to get over 100 neuroscientists to agree on a final proposal that was based on suggestions from the entire community and was agreeable to the University, which was initially suspicious about a new supradepartmental group in a conservative and rigidly compartmentalized university whose science was organized along departmental lines. It took over a year—an eyeblink in a university that is 700 years old—but the IRC in brain and behavior officially began in 1990. I was the first director, with Colin Blakemore and Edmund Rolls as codirectors. By longstanding agreement this changed with the renewal in 1996 when Colin became the director until 2002. Many of us, including some on the founding committee, were anxious about whether this center without walls would work but it was a gratifying success. Its funds allowed us to appoint scientists whose interests and skills (optical imaging, computational neuroscience, confocal microscopy, neuroimaging, software development) crossed the old departmental boundaries and to purchase capital equipment that was not readily affordable by any one department. Many neuroscientists from outside Oxford became members of the IRC by virtue of collaborating with it and within a few years we had about 300 members and a portfolio of projects that would have been unthinkable without the IRC. In the early 1990s Colin Blakemore spearheaded a similar application to the McDonnell-Pew Foundation for funds to create a Centre for Cognitive Neuroscience in Oxford. The membership was little different from that of the IRC but its intellectual focus was less cellular/molecular and more systems/philosophical. Colin was its director but several of us served on the boards of both centers. The McD-Pew Board introduced network grants to cover the costs of travel and accommodation for international collaborations and there were about 10 of these at any one time. They proved to be a remarkably cheap and efficient way of pump-priming international collaborations in neuroscience. For example they funded my own collaborations with Petra Stoerig in Germany and Lucia Vaina in Boston. Together, the two centers also organized and largely funded the annual Oxford Autumn School in Neuroscience, under the direction of Edmund Rolls. There have now been 12 such schools, each one covering four topics and with more than half of the lecturers from outside Oxford. About 300 graduate students and post docs attend, many from abroad, and for some of them it is their first taste of neuroscience. I believe that the IRC and the McD-Pew Centre flourished because they were created and managed entirely by the scientists whose needs and aspirations they served.

What's In a Name?

There is still no undergraduate degree in neuroscience or a Department of Neuroscience at the University of Oxford, despite the fact that the number of neuroscientists is as high or higher than at any other UK university. Colleagues and students often comment on this anomaly. Does it matter? I think it does. Prospective undergraduates have heard of neuroscience but cannot find it listed as a degree subject. The closest they can get to something resembling a degree in neuroscience is to take the joint honors School of Physiology, Psychology, and Philosophy (PPP) and opt to take only the first two of the Ps. But this still omits whole swathes of neuroscience. Other UK universities swiftly recognized the problem and that the solution does not necessarily require new buildings—the dread of university treasurers and accountants. It does require more than a self-service smorgasbord of parts of existing subjects but in truth the extra work is fine-tuning rather going back to the drawing board. Perhaps Oxford takes literally the idea that "if one can't be first it is better to be last."

Things are much better with respect to formal postgraduate teaching of neuroscience. In 1988 several Oxford neuroscientists, led by Ray Guillery (then Professor of Anatomy), proposed that the University should introduce a taught M.Sc. in Neuroscience. The chief justification was that postgraduate research in neuroscience required both knowledge and practical skills that many prospective research students lacked. I have already mentioned that the University of Oxford was displeased when, exasperated by the tardiness of the University and on behalf of my colleagues, I arranged a meeting of neuroscientists to discuss the issue and also invited members of the central administration. I now realize that the administrators were probably infuriated by such unilateral action. Happily, the pressure to introduce the Neuroscience M.Sc. was irresistible, although the University rightly insisted that any postgraduate course must never consist of a collection of undergraduate lectures; it must be genuinely postgraduate. The outcome, after much planning, was a 12-month course in neuroscience that consists entirely of new lectures, practical classes, and research projects. In advertising the course, it was stressed that we welcomed applicants whose first degree was not in neuroscience. As a result we received applications from students with a background in subjects as diverse as engineering, math, zoology, computation, and social psychology. As there were, and still are, more than 100 applicants each year for about 20 places, the chosen few are a pleasure to teach and most have gone on to successful careers in neuroscience. If I had to help again in designing such a course I would make very few changes. With respect to myself, the requirement that the new course must not consist of a rehash of existing lectures meant, as one of the organizers, that I had to lecture on new topics. I decided that after 35 years of lecturing on perception I would instead teach the history of neuroscience, starting with the Greeks whose ideas had inspired my friend Charlie Gross 40 years earlier (Cowey, 2001). With respect to teaching, it was my last major innovation and I discovered that the vast majority of young neuroscientists have not the faintest idea of the history of their subject and, therefore, the reasons why they are studying particular phenomena. Perhaps it is just my age; as Hans Lukas Teuber once said at a conference, when asked by Karl Pribram why he always talked about the past, "How else can I be original?"

Functional Neuroimaging

At a Winter School in Switzerland in 1990 I met Per Roland, who described the exciting discovery, shown by positron emission tomography (PET), that specific brain regions increase or decrease their blood flow according to what the person being scanned is doing. Per was studying the brain regions concerned with language, movements, and thought. I suggested that we collaborate on a study of the cortical regions activated (or inhibited) when subjects were discriminating shape or brightness or color or motion or depth-from-retinal disparity. The outcome was a collaboration, involving several colleagues in Stockholm and Oxford, in which we attempted to reveal the occipital and temporal cortical areas activated during a task in which the subject had to indicate which of three stimuli was different from the other two but where the odd-one-out was defined only by shape or brightness or color or texture or motion (Gulyas et al., 1994a,b; 1998). I still believe that the paradigm is one of the best for revealing functional activations associated with specific sensory attributes. However, PET could not provide the spatial resolution needed to distinguish between adjacent or overlapping functional visual areas and it was not possible to study the same subject repeatedly because of the restrictions on the amount of radioactivity that could be delivered each year. After I was first scanned by PET I was disconsolate to discover that it could not be repeated for a year. Something else was needed, namely functional magnetic resonance imaging (FMRI).

FMRI is now such an established technique that it is extraordinary to recall that as recently as 1994 the regional changes in cerebral blood flow that it seemed to reveal were sometimes dismissed as artefacts caused by head movements. As a member of an MRC visiting committee to the MRC functional imaging unit at the Hammersmith Hospital in London I listened to a distinguished physicist declare that FMRI was a waste of time and money. He was right to say what he believed but the world now knows that he was wrong. Fortunately the chairman of the visiting committee was George Radda, then Director of the MRC Magnetic Resonance Spectroscopy Unit in Oxford, who was convinced that the signals were not artefacts. A couple of years later he and I and John Newsome-Davies (Professor of Clinical Neurology in Oxford and my successor as chairman of the MRC Neuroscience Board, which meant that I knew him well) got together to discuss how best to introduce FMRI to Oxford. We usually met in the MRS Unit at 7:30 AM or early evening so that we could get on with other things as usual during the rest of the day. It took about 2 years to plan the new unit and to raise the funds from a variety of sources. At a crucial stage the University agreed to lend us the final million pounds (now repaid) and Paul Matthews, then at McGill, agreed to be the first Director. Nine years on and under his direction, Oxford's center for functional brain imaging is a leading international center of research in cognitive neuroscience (especially pain, recovery from stroke, visual attention, intersensory perception, top-down processing), image analysis, using diffusion tensor imaging to study anatomical pathways, and the physics of magnetic imaging. However, from an autobiographical point of view I want to stress that none of this would have happened without a concerted effort from a group of friends who shared experience and contacts in the national administration of biomedical neuroscience. All those hours in London bore fruit yet again.

On a slightly different point, no one appointed to a scientific position in FMRIB was more than 40 years old and, given the choice, I would always go for the younger candidates. To do so is becoming more difficult in UK universities as they vie with each other to excel in the farce called "research assessment exercise" by trying to attract aging stars whose publication record and grant income inflate the score and therefore boost the funds awarded to the university from central government. A young Charles Darwin would have difficulty in getting a job nowadays because his publication record would be too poor!

Coda

Our lives often appear to follow a straight course, like time's arrow. Any perturbations get smoothed out and many of them are mental and never observed by anyone else. But when I reflect on my own life I can see how nonlinear it can be. I have changed my aspirations, beliefs, preferences, methods, and skills many times in response to changing circumstances, and never more so than in science. I started as a botanist, changed to zoology, then to psychology (with a preference for animal learning theory) and finally to systems neuroscience, although the term did not exist then. Within the latter I was initially interested in the phenomenon of perceptual consciousness and awareness in monkeys (Cowey and Weiskrantz, 1963), put that to one side for more than 20 years, then returned to it after 20 years. If accused of dabbling or spreading myself too thin I might have to plead guilty. But science needs dabblers and especially in a subject as broad as neuroscience. To return for a moment to interdisciplinary research, it is often assumed that it will successfully take place as long as funds are provided for it and given to a group of investigators who say, because they want the funds, that they will collaborate even though they are widely dispersed. But at some point interdisciplinary thinking has to go on inside one head. Dabblers help here.

Another factor that is often not apparent in a scientific career is the element of luck. I did not plan my career in any detail at any point, following instead a very broad interest in the brain and how it controls behavior and taking opportunities as they arose. It was not a random walk but there was no road map either. I was fortunate to meet several outstanding students, post docs, and colleagues with whom I collaborated or from whom I learned things. If I had never met Richard Gregory, Larry Weiskrantz, Walle Nauta, Charlie Gross, Hugh Perry, Peter Somogyi, Petra Steorig, Charlie Heywood, or Vincent Walsh (to name only a few), my career would probably have been very different. Free will certainly exists but acting on it is constrained by luck.

Finally, I have always been struck by the extent to which science is, almost everyday, a social activity. I expect the solitary scientist still exists but I have never encountered one. For me one of the greatest pleasures in a life of science is interacting with students, technicians, and colleagues. They have shaped my career but there are too many of them to mention here. The most influential of all is my wife Pat, but as she is not a scientist her huge influence on my life will have to wait for a different kind of autobiography.

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