



# The History of Neuroscience in Autobiography Volume 8

Edited by Larry R. Squire

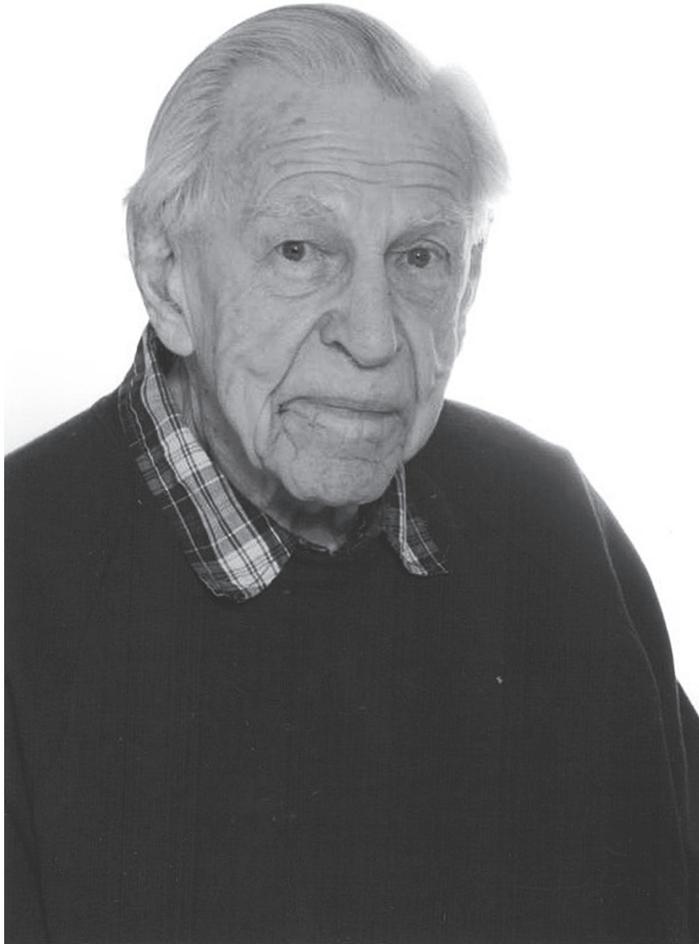
Published by Society for Neuroscience

ISBN: 978-0-615-94079-3

Peter M. Milner

pp. 290–323

<https://www.doi.org/10.1523/hon.008007>



# Peter M. Milner

**BORN:**

Silkstone Common, Yorkshire, UK  
June 13, 1919

**EDUCATION:**

Leeds University, U.K. B.Sc. (Engineering) (1941)  
McGill University, Montreal, Canada, Ph.D. (1954)

**APPOINTMENTS:**

Scientific Officer. U.K. Ministry of Supply (1941)  
McGill University (1955)

**HONORS AND AWARDS:**

Emeritus Professor, McGill University (1991)  
Canadian Psychological Society Gold Medal for Distinguished Lifetime Contributions to Canadian Psychology

*Peter Milner's first degree was in communication engineering, and he worked (during World War II) on the development of radar and nuclear energy. In 1947, as a result of reading Hebb's Organization of Behavior, he switched careers and trained as a neuropsychologist. In 1953, James Olds and Peter Milner, working at McGill University in the laboratory of Donald Hebb, found that electrical stimulation of a region rostral to the hypothalamus of the rat brain caused the rat to behave as if it had been rewarded. For several decades after the publication of this finding, many groups, including Peter Milner and his students, investigated the nature of this phenomenon.*

# Peter M. Milner

## History

I was born in 1919, the first child of David William Milner, a research chemist, and Edith Anne Marshall, an ex-schoolteacher, who everyone called Nance. My paternal grandfather had a corner grocery store near Leeds, where my father grew up. I heard that my great-grandfather Milner was a butler who ran the household for one of the gentry in North Yorkshire. Going back even further, to the eighteenth century, rumor among my paternal relatives has it that Joseph Priestley, the Unitarian minister who discovered oxygen and carbon dioxide, was an ancestor of ours. The daughter of one of my father's cousins, Dr. Thelma Rowell, who was a professor of psychology at the University of California at Berkeley for many years, heard the same story from her family. My belief in the rumor increased when I found that, amongst his many accomplishments, Priestley was a pioneer of neuropsychology. In 1775, he wrote a book entitled *Hartley's Theory of the Human Mind, on the Principle of the Association of Ideas; with Essays Relating to the Subject of It*. Hartley's theory was that sensations and ideas are the result of brain cell vibrations. In the introduction to his book, Priestley writes, "It will stagger some persons that so much of the business of thinking should be made to depend upon mere matter, as the doctrine of vibrations supposes. . . . But I do not know that this supposition need give any concern, except to those who maintain that a future life depends on the immateriality of the human soul."

My mother was a daughter of John Marshall and Elizabeth Mountain. In his younger days, John was an auctioneer and ran a pub in Boro'bridge, a North Yorkshire market town. Elizabeth did not consider a pub to be a suitable environment in which to raise daughters; so when my mother and her sisters began to appear, the family moved to a farm in the nearby village of Roecliffe. My grandparents still lived there when I was young, and a highlight of our visits, as far as I was concerned, was being met at Boro'bridge railway station (long gone) by my grandfather with his pony and pony cart. My mother was raised on the farm with her brother and two sisters. Her intelligence impressed the local parson, and he encouraged her to attend Teachers Training College in Ripon.

My father also trained as a teacher and because he did well in his science courses, he was persuaded to study for a bachelor's of science degree at Leeds University. This was a stroke of luck because when World War I started, shortly after he graduated, my father was sent to work in the laboratory

of an explosives factory instead of to the trenches. After the war, he was employed as chief chemist of a company that processed the by-products of the conversion of coal into coke. He never became a schoolteacher, though at one period he taught an evening class in organic chemistry at Barnsley Technical College.

## Early Years

Until I was about five, we lived in a small village in south Yorkshire, close to Barnsley. Our house had no gas or electricity, I needed a school, and my father's lab was in a suburb on the other side of Barnsley, so we moved into the town. I was enrolled in the infants' section of St. Mary's School and, after a couple of years, was promoted to St. Mary's Elementary School for Boys. Henceforth, as was the almost universal custom in England at the time, I was not distracted at school by the proximity of students of the opposite sex. Indeed, at the secondary level, my grammar school and the girls' high school were in different parts of town. Even when I reached the university, there were no female students in my engineering courses (though I believe that was not due to any official policy). Both my parents were trained teachers, so elementary school was only a minor part of my early education. My mother taught me how to read and write and tried, without success, to teach me how to play the piano. My father answered most of my questions about what things were for and how they worked. I also got further scientific information from regular installments of Arthur Mee's *Children's Encyclopedia*. In general knowledge, I was way ahead of most of my classmates.

My father liked making things; he fitted the Barnsley house with an electric doorbell powered by a homemade Leclenché cell, the wet forerunner of the zinc-carbon dry battery. He also built wireless sets. He gave me discarded components to play with, and I built pretend sets. Later, as I learned how receivers operated and I inherited functional components, I built sets that worked. When I was about ten or eleven, I built my first (unlicensed) transmitter that I, and no doubt our neighbors, could hear on our home wireless sets. I also built shortwave receivers and hoped one day to have an amateur transmitter's license. Rebuilding my sets, and finding new stations, took up a good deal of my time during secondary school. One of my teachers told me I could go far if I were not so lazy, but my apparent laziness was really an addiction to my hobby. After tea (the evening meal in Yorkshire), I rushed through my homework and stole time to scan short-wave radio bands for distant transmitters.

Television was not a problem; it did not exist. It is true that, as early as 1929, John Logie Baird and the BBC tested broadcasts of ultra-low definition TV, using the regular medium-wave transmitters after normal hours, but it could hardly be called entertainment. One of my father's former assistants, Ernest Woodcock, had a friend who built a television receiver, and

I once saw it working. A beam of light passed through a Kerr cell, where its intensity was modulated by the radio signal. A small square of the modulated light was scanned by viewing it through holes punched in a rapidly rotating disk. The image was about the size of a postage stamp and was accompanied by a strong smell of toxic nitrobenzene from the Kerr cell. An amazing technical achievement perhaps but not something anyone might be tempted to stare at all evening.

When I was about 13, we moved to a semidetached house in a suburb near my father's lab. The adjoining house was occupied by our friends the Copleys. Their son, Ronald, and I both liked to listen to late night music. This was long before the days of bedside clock radios. I had a homemade wireless set in my bedroom, but Ron had no such luxury. Our bedrooms were adjacent, so it was easy to sling a wire between the two windows to pipe the music to his room. My innovation was that I incorporated a relay into the receiver to switch it off when the transmitter closed down, usually around midnight. This gadget allowed me to fall asleep or, if I was awake, obviated the need for me to switch it off. As it turned out, these extracurricular activities were not a complete waste of time. They may have saved my life, just as my father's chemistry degree may have saved his, and they undoubtedly enhanced my quality of life a few years later.

## Higher Education

In my grammar school, after four years of general education, students intending to pursue postsecondary education continued to the sixth form for a two-year program specializing in either science or humanities. I, of course, chose science and because I wanted to go to university became more focused. It was not all science, however; German was compulsory. Mr. Noot our teacher, Dutch I believe, had spent the previous summer in Germany. He was favorably impressed by the changes there since Adolf Hitler took over, but he met only skepticism in school.

My favorite periods at school were the science labs. Our physics teacher, Mr. Cottingham, spent his spare time designing teaching tools, amongst which was a multipurpose overhead projector. As well as projecting the usual transparencies, it could, with a glass dish of water, equipped with electrically driven paddles for generating ripples, project wave interference patterns and other wave phenomena onto a screen for class demonstrations. Cottingham also constructed an oscilloscope, using a loudspeaker unit and a mirror drum. I, and some other sixth-form students, accompanied him to a Science Masters' Association Conference in Manchester to show off these toys.

This formative period of my life lay between World War I and World War II. I was born after the armistice that halted the fighting in WWII, but before the signing of the Treaty of Versailles, which formally ended the war.

In 1933, in my third year of grammar school, Hitler took over a demoralized Germany with promises to restore territory and prestige lost in World War I. Canon Dick Sheppard thought that it might defuse the situation to demonstrate the strength of the anti-war feeling in Britain, so he organized a Peace Pledge renouncing war. One or two of my teachers, in subjects such as geography and history, were pacifist Quakers who recruited students, including me, to go door-to-door getting signatures for the Pledge. It received great support, of course, and probably gave much encouragement to Hitler, who had just sent his tanks with impunity into the Saar, a border region demilitarized by the Versailles Treaty.

In 1936, the Spaniards overwhelmingly elected a socialist-leaning government, triggering a revolt by some army officers, including General Franco. His army consisted mainly of troops airlifted from the Spanish colony of Morocco by the German air force, augmented by German and Italian “volunteers” from the two fascist powers in Europe. The Germans in particular used the ensuing Spanish civil war to rehearse the blitzkrieg techniques they were to use with such effect a few years later. Thanks to Picasso’s painting, their destruction of Guernica, a Basque town that was carpet-bombed continuously for three hours on a market day, is still remembered. By the time I graduated from grammar school in 1937, only incurable optimists were dreaming of peace. For most of us, it was just a question of what could be done to stop the fascists and how soon.

## Job Hunting

I must have thought better of becoming a ship’s radio officer at about this time. I attended an open day at Leeds University and found some of the demonstrations in the electrical engineering department very interesting. Before the results of my final exam for the Higher School Certificate were posted in July, my father may have had doubts about my getting into university, so I had an interview for a job in the Post Office telephone service. Before satellites and submarine cables, transatlantic and other intercontinental telephone services had to bounce shortwave radio signals from the unreliable ionized layers of the atmosphere to overcome the curvature of the Earth, so I might have found a job related to my hobby. My father and I also consulted the chairman of the electrical engineering department at Leeds University, and he strongly recommended that I apply to Metropolitan-Vickers for admission to their probationary college apprenticeship program. Metropolitan-Vickers (Met-Vicks), which started out with the name British Westinghouse around the turn of the century, was a large engineering firm located in Trafford Park, near Manchester. Their most visible activity was building power stations, but they also had a research lab that interested me. Each year they enrolled a few prospective engineering students in their probationary apprentice program. The apprentices spent a month or two

in different departments of the factory—such as the foundry, the turbine-assembly shop, and so on—learning what went on there. The candidates were supposed to return to Met-Vicks as fully fledged college apprentices after they graduated, with a good chance of subsequent employment. The Great Depression was still going on, so getting a job was a serious consideration.

## Metropolitan-Vickers

I made the short list of applicants invited to Manchester for an interview and, after a rather intimidating day in luxurious surroundings, I passed muster and became a probationary college apprentice (PCA), earning the princely sum of 17 shillings and 6 pence (about \$4.40 US in those days) per 48-hour week. The work was pretty strenuous, but during term time we were given Thursdays off to attend classes at Manchester Tech. I lived in a boardinghouse in Stretford with a couple of other apprentices, Struan Robertson (of Scottish-American background from Shanghai, whose father was an oil man) and Torfinn Oftedahl (a college apprentice from Norway). Recently, I read Torfinn's obituary in the *Washington Post* and discovered that he had entered the Norwegian diplomatic service in 1938; after 17 years in Washington, he was appointed as Norwegian ambassador in turn to Austria, Czechoslovakia, Canada, and Romania. In 1989, he died at the age of 80 in Baddeck, Nova Scotia, so he must have liked his spell in Canada. Our Stretford landlady was an excellent cook and housekeeper, whose invalid husband had fallen victim to mustard gas during the war. She served substantial evening meals, so I was able to economize with a light salad for lunch in the Met-Vicks refectory. Thus did I acquire the habit of eating my main meal in the evening. My fellow apprentices came from all parts of the UK, and a few, such as Struan and Torfinn, were from abroad. My year at Met-Vicks was my introduction to people with relatively sophisticated backgrounds.

We apprentices were circulated through a variety of workshops, usually for a month or two in each. I remember only a few of the places I worked; one was the assembly shop where they were putting the finishing touches to a turbine that may have been destined for Durban. I spent two months in the iron foundry, the first month helping to feed the furnace where the iron was melted, the second on the casting floor. In the machine shop, I helped to mill some small turbine blades. Probably the only reason that I still remember the job is that it was rumored that the blades were for an experimental gas turbine. A few years later fighter planes powered by jet engines began to appear.

During my time at Met-Vicks, the factory was visited by a team of efficiency experts conducting a "time and motion" study. They watched people work and recommended ways in which time and effort could be saved. Of course, building a power station is not the same as assembling a car or a

washing machine, but some of the jobs at Met-Vicks were repetitive. The exercise was not popular with the workers, but I thought the approach had some merit and it probably influenced the way I plan some of my activities.

## Leeds University

The first year in engineering at Leeds University was quite general; my specialty, communication engineering, was taught in later years. Math was mostly a repetition of the calculus, matrix algebra, analytical geometry, and so on that I had learned at school, relearned at Manchester Tech, and have spent the rest of my life forgetting. The dean of engineering was a heat engine man, so we received a thorough grounding in that. Possibly inspired by the rumor about the turbine blades that I milled at Met-Vicks, another student and I tried to apply theory that was well established for steam turbines to the design of hot air turbines, but I do not remember that it aroused much excitement among the faculty.

By the end of the school year, the war in Spain was over, with General Franco in control and the rest of Europe was waiting for Hitler's next move. I landed a summer job with the British Broadcasting Corporation (BBC)—a month at the Moorside Edge transmitter and another month at the other side of the microphones. The BBC had two 50-kilowatt medium-wave (about 300- to 600-meter) transmitters serving the north of England. They were located at a fairly isolated spot in the Pennines, the chain of highlands between Yorkshire and Lancashire. In 1939, the engineers—most of them ex-Navy men, were adjusting the frequency controls so that several BBC transmitters in different parts of the country could transmit on very nearly the same frequency. This made the signals difficult or impossible to use for navigation. Shelters and other preparations for air raids were also underway.

The daily routine at the transmitters was rigidly adhered to, and there was little for us summer students to do except in emergencies, such as a burned out transmitter valve, so I was looking forward to my month at the Manchester studios, which started in the middle of August. In fact, because I was assigned to outside broadcasts, I spent the first couple of weeks at various seaside resorts hauling and connecting sound equipment to broadcast music and variety shows. The next week I was due to move to the studios, but on Friday, Hitler invaded Poland and I was told that, in the likely event of Britain declaring war on Germany, I would not be allowed on the premises because I did not have a security clearance. Two days later, on Sunday morning, Neville Chamberlain announced the declaration of war, and my summer job was over. My parents came to take me back to Barnsley in the car. Nobody knew when the air raids would start, so a complete blackout was enforced, and we drove home over the Pennines with no lights of any sort. It was a scary ride. There were still a few weeks

before term started, so Ron Copley and I volunteered to help a local farmer with his harvest.

Engineering was considered an essential occupation by the War Ministry, and engineering students were allowed to complete their degrees before being drafted. We were, however, expected to join the Officer Training Corps (OTC). We were given uniforms and drilled once or twice a week, trained in the use of Enfield (World War I) rifles, and taught to disassemble, clean, and reassemble (but never fire) Bren light machine guns. Our degree program was also accelerated by eliminating the 1940 summer vacation.

Germany overran half of Poland very quickly and the USSR took advantage of the situation by grabbing the other half. Poland's allies decided against making a suicidal attempt to evict them. During the winter, all was quiet on the Western Front: the "phony" war. The Royal Air Force dropped propaganda leaflets on Germany; the Luftwaffe refrained from dropping bombs, or anything else, on England or France. Then in April 1940, Germany launched a surprise attack on Norway, a neutral country.

During World War I, the German Navy was bottled up in the Baltic Sea; this time they wanted Norway's Atlantic ports to avoid a repetition of the problem. I found out some years later that the Germans also wished to take over the heavy water plant at Vemork. This hydroelectric plant was the only source of substantial quantities of heavy water before the war, and Germany had imported a lot of it. The few people familiar with nuclear research at the time guessed that it was destined for research on nuclear energy and, eventually, bombs. The invasion should have ensured continuous access for the Germans, but in fact, because most Norwegians did not take kindly to the German presence, a large quantity of the heavy water went missing (much of it turned up eventually in Canada), and sabotage of the plant was so persistent that it was dismantled and taken to Germany, where it was never reassembled.

The success of the seaborne invasion under the nose of the British Navy was demoralizing, especially because it considerably increased the threat of submarine attacks on transatlantic shipping. But we had hardly taken it in before things took a more serious turn for the worse. Early in May, around exam time, a large and highly effective German army pushed through the Netherlands and Belgium, bypassing the strong defenses of the Maginot Line along the French border, and routed the French, Belgian, and British forces that were curiously ill-prepared for blitzkrieg tactics. The French collapsed, and the British raced the Germans to Dunkirk; in early June, thanks to thousands of small boats, 300,000 British troops escaped to England, leaving most of their equipment and supplies behind.

We all thought the Germans would not be long following them. Those of us in the university OTC were issued rifles and spent our nights guarding factories and sensitive areas in Leeds against possible parachute landings. Curiously, I do not remember that I ever considered the fact that someone

with a World War I-era rifle that he had fired only a few times would not stand much chance against a squad of well-trained commandos with automatic weapons. The whole thing felt very unreal, and in fact it was. The invasion never came. Hitler wanted to get control of the air first. He never got it, largely because the Germans underestimated the effectiveness of the British radar. In the attempt, Hitler lost a very large number of his bombers and their crews, and he decided Russia was a better bet; meanwhile, I started my third-year courses. In the communications classes, we learned about the design of transformers, amplifiers, telephone lines, and filters for a variety of functions.

It was not part of a formal course, but in our spare time two fellow students and I used the electronics lab to investigate and exploit a little-known property of the pentode valve. The early electron tubes had three electrodes: a hot cathode to emit electrons, a positively charged anode—to which the negatively charged electrons were attracted—and an interposed wire grid the voltage of which determined the electron flow. When the grid was at the same voltage as the cathode, it did not interfere with the flow of electrons to the anode, bringing the anode voltage to a minimum. A negative voltage on the grid reduced the flow of electrons and allowed the anode to go more positive. The grid and anode voltages thus go in opposite directions; an oscillator requires amplification without reversal of phase.

Pentodes have a second grid, held at a positive voltage, to eliminate capacity feedback between the anode and grid one, and a third grid usually held at the same voltage as the cathode, to catch electrons that might bounce off or be knocked from the anode onto the second grid. If this third grid is made negative, it reduces the current reaching the anode, but the repelled electrons go instead to the positively charged screen grid, reducing its voltage. Thus the voltage on the second grid goes in the same direction as that of the third grid. We used this characteristic to make an oscillator and discovered that the frequency of oscillation so produced could be varied by changing the voltage on the normal control grid (grid number one) of the pentode. By connecting that grid to the time base voltage from an oscilloscope, the frequency of the oscillator may be made to vary as a function of the horizontal position of the oscilloscope spot, so that the response of any circuit to a range of frequencies could be visualized on the screen. This application was the one that we emphasized in a paper we published in the *Leeds University Engineering Society Journal* (Burrell, Milner, Russell 1941), my first journal article.

Before the war, I had become interested in ultra shortwave radio and, possibly because of the pentode work, it occurred to me that at extremely high frequencies the time it takes an electron to travel from the grid of a normal triode to the anode could result in amplification with no phase reversal at extremely high frequencies. For example, if it takes a bunch of electrons 0.0005 microseconds to fly from the grid to the plate of a valve,

and part of the resulting drop in plate voltage is transmitted at the speed of light from the plate to the grid by capacity coupling, this negative voltage on the grid would cut off the flow of electrons, causing the anode and—by capacitive coupling—the grid to go positive and release another bunch of electrons. This process would recur every 0.001 microseconds, generating an oscillation at one gigahertz, corresponding to a wavelength of about 30 cm. I may have looked thoughtfully at various types of valves, wondering whether they were oscillating in the microwave range, but I had no way of detecting such oscillations, even less of modifying the structure of the valve. Thus it remained a theoretical concept.

After the war started, I was told that if I wanted a choice of military service I should volunteer before I was called up, so I volunteered for the Royal Air Force (RAF). My enlistment was put on hold because of my engineering degree courses, but I expected to hear from the military when I graduated. At Leeds University in the spring of 1941, Cedric Burrell and I were the only students graduating first class in electrical engineering (but Cedric got his only after an oral exam). After the results were announced, a representative of the Ministry of Supply visited the department, and Cedric and I were invited to Cambridge for interviews for positions in a radar research and development establishment. (It was called radio direction finding [RDF]; at the time, the name radar had not yet been coined.)

We were interviewed in Cambridge by the novelist C. P. Snow, who was also a physicist and fellow of Christ's College, and by John Cockroft, another Cambridge physicist, who, with Ernest Walton at the Cavendish Laboratory, had bombarded lithium with high-velocity hydrogen ions to achieve the first transmutation of one element into another that did not involve naturally radioactive material. (A lithium nucleus absorbs a proton and disintegrates into two helium nuclei.) In 1941, when he interviewed us, Cockroft was the director of the Air Defense Experimental Establishment (ADEE) of the Ministry of Supply. I do not remember much about the interview, but I do remember that my idea of using the time of flight of electrons to generate centimeter radio waves came up and Cockroft asked me if I had ever heard of the klystron. I later discovered that an electron tube working on that principle had been developed at Stanford University in 1939.

## Air Defense Establishment

Cedric and I were appointed experimental officers in the Ministry of Supply and told to present ourselves at ADEE, near Christchurch on the south coast. The ADEE had been set up during World War I to develop means to locate nocturnal intruding aircraft by sound, in order to guide searchlights. The intruders could then be tracked visually and attacked by anti-aircraft fire. Increasing speed and numbers of enemy planes made acoustic detection almost useless, but the discovery that aircraft reflect radio waves provided

a method of detecting them above clouds and at much greater distances, allowing time for fighter aircraft to reach operational height. It also held out the promise of providing a non-visual method of aiming anti-aircraft guns. But to achieve sufficient accuracy, very short radio waves were required; ideally less than a meter. A new laboratory for radio direction finding was built adjacent to a small airport at Somerford, a suburb of Christchurch, and ADEE moved to the site early in the war. Soon after Cedric and I arrived, the name was changed to the Air Defense Research and Development Establishment (ADRDE).

The surroundings were very attractive, close to the beach (unfortunately inaccessible) and not far from the New Forest. I was happy to be there, but a day or two later I learned that I would be going to Birmingham to work on transmitter valves. I expect this was the result of my discussion with Cockroft about klystrons. Fortunately, the workings of government departments are unfathomable, and the transfer never materialized. Possibly some bureaucrat was told that the newly developed cavity magnetron was excellent for centimeter wavelengths and no more research was needed. Cedric was assigned to a group working on centimeter-wave measurements. I was put in charge of developing a simulator for the new 10-cm Mark III radar that could be used to test the efficacy of different ways of displaying the returning pulses to the operators and to evaluate methods of steering the antenna. The simulator could later be used to train operators.

I worked on the equipment under the direction of Edward Shire, a physicist from King's College, Cambridge. My first design was an electronic circuit that simulated the changes in azimuth and elevation of an aircraft flying within range of the radar, but Shire did not like it. He argued that electronic devices were not robust enough for army use; he wanted something mechanical. We finished up with a massive steel contraption a couple of meters or more long in which a block, representing the target plane, was drawn along a metal track. As it moved, it turned a potentiometer to give a voltage corresponding to the changing azimuth of the simulated target. The operator turned a handle coupled to another potentiometer in an attempt to keep it in step with that turned by the simulated target. The operator had a display showing the error (i.e., the difference between the voltages from target and operator potentiometers). Equalizing the two signals sounds as if it would be easy, but in the real equipment the operator had to control the position of a large parabolic dish antenna perched on the roof of the cabin and exposed to the wind. Moreover, the strength of the reflections from the aircraft varied from pulse to pulse, due to the interplay of reflections from different parts of the fuselage as the plane moved, so there was a lot of "jitter" on the pulse display.

A motor-driven antenna controlled by the operator would need less effort, but the accuracy would suffer. When the operator notices an error and adjusts the speed of the antenna drive, overshoot almost always occurs. Trying to correct the overshoot is then likely to cause an overshoot in the

opposite direction—an outcome called “hunting.” Hunting can be minimized by linking a direct control of the antenna position with the velocity control. A motor turns the antenna to track the target, and the operator turns a handle that simultaneously corrects errors directly and makes slight compensatory adjustments of the speed of the motor drive. Our task was to find the best ratio of direct drive to motor speed control. This was not an area of expertise for engineers or physicists, but there was an operations research group in Cambridge that evaluated military equipment and procedures; Shire applied to them for help.

In due course, a young Cambridge psychology graduate named Brenda Langford arrived from her previous job of giving tests of sensory conflict to prospective air force pilots to decide whether they should go to bombers or fighters. She was well-versed in statistics and experimental methodology. She organized appropriate subjects and made suggestions as to what modifications of the simulator/trainer would be worth trying. Her main problem was that our prototype was not built with frequent modifications in mind, and I was kept busy changing displays and controls. As far as the jittery display was concerned, it was eventually determined that it was better to leave it alone and let the operators do the averaging in their heads. The pairs of pulses that had to be equalized were displayed side by side on a cathode ray screen. The operators then tried to keep the appearance of the two pulses as similar as possible.

In February 1942, British commandos raided a German radar station across the English Channel and brought back some important components and one of the German technicians. The significance of the fact that ADRDE was located on the south coast of England just across the channel from this event did not escape the War Office, and by April, our establishment had been moved lock, stock, and barrel to Malvern, near the Welsh border. ADRDE set up shop in a compound originally built to accommodate a government ministry, should London ever have to be evacuated. The compound was self-contained with barracks-style living quarters for unmarried staff—three to a room and common showers and washrooms for the men, somewhat less Spartan for women, with only two to a room.

Brenda continued to work on the operator interface, with technical contributions from me on occasions. My main job at the time was to develop a more sophisticated trainer, based on more realistic target trajectories recorded on film or tape. It was never finished. Anti-bomber artillery did not have a very high priority during the build-up for the invasion of Europe, and I never found out how useful our 10-cm Mark III proved to be against aircraft. According to Google, it was used to locate mortars during the invasion of France. Although the Mark III probably came too late to bring down many bombers, we learned a lot from it. It was the first radar to incorporate the new cavity magnetron; in fact, it was originally designed to work with a klystron, but the cavity magnetron was better.

In June 1944, the Germans started to launch their V1s (unmanned flying bombs) from the French coast against southern England. The V1, or buzz bomb as we usually called it, had a simple ram-jet engine and could fly faster than all but the latest jet fighters. After flying a preset distance (measured roughly by a propeller), its nose turned down. It was intended to dive to the ground under power but in the nose-down position, the fuel failed to flow to the combustion chamber, providing a brief warning period of silence before impact. I was assigned a new job, which involved plotting the paths of these bombs in the hope that they could be traced back to the launching sites, which could then be attacked. I spent a week or two at a radar station on the south coast, near Beachy Head, making measurements. Unfortunately, it turned out that multiple launching sites were hidden underground. Bombing proved futile, and the sites were destroyed only when the advancing Allied troops reached them.

Two years after Hitler turned eastward for Germany's next lightning invasion, he was in deep trouble in the USSR. Furthermore, his failure to take advantage of the disorganization in Britain in 1940 allowed a build-up of Allied forces and air power on his doorstep. With the Allied landings in Normandy in June, the end seemed to be approaching. Things also seemed to be winding down at ADRDE. Our director, John Cockroft, was away in the United States for long periods, and it seemed clear that further developments in radar would be too late to affect the course of our war. The war in the Pacific was another matter.

## Tube Alloys

In the autumn of 1944, someone in the director's office asked me if I had any objection to going abroad for a year or two. I was not very keen on the idea, but I never refused new experiences in those days. My guess was that it would be to somewhere in the Far East such as Burma, where I had heard that they were having trouble using radar among the mountains. A few weeks later, after being sworn to secrecy, I learned that I would be going to Canada to work on atomic energy. In 1938, less than a year before the outbreak of war, two German scientists, Hahn and Strassmann, had reported that atoms of uranium broke up into lighter elements when bombarded by neutrons. That uranium reacted in a peculiar fashion to neutron bombardment had been known for some time, but Hahn and Strassmann—with some help from Lisa Meitner, a former colleague—identified the cause. Because the total mass of the fragments is less than the mass of the original uranium, it was clear from Einstein's famous formula  $E = MC^2$  that an enormous amount of energy must be released during the reaction. The implications of this discovery received surprisingly little publicity. In fact, I had never heard anything about the phenomenon before I learned I would be working on the attempt to harness this energy.

The project in which I had agreed to participate was code-named “Tube Alloys,” a joint British-Canadian enterprise. The British government was, of course, aware of the U.S. Manhattan Project, but it did not have the resources to prepare for the invasion of Europe and to develop nuclear weapons, or energy, at the same time. However, there were mobile resources in Britain, scientists who were no longer needed to develop armaments. With an eye to future commercial demand for atomic energy, it was decided to send a crew to Canada to learn the ropes and to form the nucleus for a post-war research establishment in Britain. I heard that our director, John Cockroft, was to become the head of this Canadian project, which explained his frequent absences. I was happy that Canada was the destination of the move, but there was a serious flaw in the arrangements; spouses were allowed to accompany the appointees but girlfriends received no mention, and I had a girlfriend.

Several factors had conspired to deprive me of much female company during my youth. The upshot was that my job at Christchurch was the first time I encountered a number of women of about my age. I had a few dates with Shire’s blond assistant but then she told me she was engaged and stopped seeing me. I was upset and assumed that my role had probably been to light a fire under the more fortunate suitor, a very good catch as I learned. This diversion into my love life may seem irrelevant to a history of neuroscience, but the sequel certainly is not. When Brenda Langford came to help us compare different settings of the machine/operator interface of my simulator, she rapidly became a dominant influence in my life. I was in some awe of her; she had an excellent Cambridge degree and was very competent in her work. We had a good friendly relationship, but I did not feel very competitive, especially after my recent bad experience. The establishment was overrun by brilliant Cambridge physicists so I did not think she would be interested in an engineer from Leeds. What I did not know was that somehow Brenda, the psychologist, had discovered that my vocabulary was slightly better than hers, tilting the playing field. She sensed that I might need some encouragement and gave me some. By the next summer, we were very close. There did appear to be a simple solution to the Canada problem, but I was not sure what Brenda would think of it. I was under the impression that she was looking forward to starting a new job in Cambridge after the war. Nevertheless, when we discussed the idea she seemed happy with it, so we got a special license, took it to the registry office, and were married in time to make the travel arrangements. We scrounged some stout wooden boxes that had contained radar parts and filled them with our books, which had to go to Birmingham for censorship and were shipped separately. In late October 1944, we boarded the *Queen Elizabeth* (then almost new) in Glasgow, along with war wounded and war brides. The North Atlantic was rough, and the zigzag course did not help. Brenda did not eat much on the journey, which seemed much shorter than I expected. We were supposed to land in

New York, but for some reason we disembarked in Boston. I remember being very charmed by the first words I heard on American soil from an American. The customs inspector told the lady ahead of me, “Don’t try to rush me ma’am. I got low blood pressure.” Not in accordance with my stereotype.

Our small group of scientists was taken to the Copley Plaza Hotel, through streets that seemed to us flooded with light, though they told us that it was their blackout. We had not seen such sights for five years. And there was planked steak for dinner. Boston was a good place to have landed because we had friends in the radiation lab of the Massachusetts Institute of Technology who had spent some time at ADRDE working on proximity fuses for anti-aircraft shells. One of our friends managed to get clearance for us to tour the lab. Another lent us some dollars. We had been allowed to take no more than five pounds sterling (about \$25 U.S.) out of England, and there were no such things as credit cards. I had a hard time paying him back because, to my surprise, sending money from Canada to the United States required a lot of red tape. After a couple of days of luxury, we took the train to Montreal; just as we crossed the border, it started to snow. It was November 5, Guy Fawkes Day.

When I arrived, the Tube Alloys group occupied one wing of the University of Montreal’s new building, which was still incomplete. I knew little of the history of the group except that it had originally consisted of some European scientists at the Collège de France in Paris, who had fled to England with precious heavy water and then moved to Canada for greater security. The significance of the heavy water derives from the fact that less than 1 percent of natural uranium consists of the isotope (U235) that is fissile, and the neutrons released during fission are too energetic to be captured by enough fissile atoms to maintain a chain reaction. They need to be slowed down before too many escape, and heavy water is an ideal moderator. I learned later that in 1940, one month before the Germans invaded Norway, a large consignment of heavy water was acquired from the Norwegian source by the Collège de France group. In May, when the Germans invaded France, the group—with their heavy water—escaped to England and later went to Canada, where they established a base in Montreal near McGill University. The group later became associated with the National Research Council of Canada and moved to more spacious quarters at the University of Montreal.

Tube Alloys had settled on building a heavy water moderated “pile” in a sparsely populated area that was easily accessible and that had a source of cooling water. Chalk River, about 150 km up the Ottawa River from Ottawa, was a favored location. Chalk River was hardly a town; it was just a watering stop on the Canadian Pacific Railway line through northern Ontario. The Trans-Canada Highway ran parallel to the river and the railway at that point, and there was plenty of water in the Ottawa River for cooling. Once settled in Montreal, my first proper job was to see how quickly scale

would build up on cooling pipes in the river. This entailed a number of trips to the vicinity of Chalk River. My memory of how I went about measuring the scaling is cloudy, but I do remember that one technique I tried involved nuclear magnetic resonance, a phenomenon that I had just read about. (Isidor Rabi received a Nobel Prize for its discovery in 1944.) This was a bizarre thing to try, and I can only assume I did so because I wanted to play around with nuclear resonance. I hoped to use it to measure the amount of scale without having to keep removing the test pipe from the river, but of course, I could not get it to work. I think I eventually just passed hot water through the submerged pipe and measured its temperature drop—the assumption being that it would lose less heat as scale formed. The scaling turned out to be negligible. Another of my jobs was to build an apparatus to measure the effect of an intense neutron flux on the mechanical properties of various materials used in the construction of the reactor. I was proud of the apparatus I built, but I left before the reactor managed to produce any neutrons, so I never found out how well it worked with “hot” samples.

In the meantime, Brenda, having ascertained that the psychology department of McGill University was in hibernation, found a job teaching comparative psychology (in French) at the University of Montreal, which at that time was a Catholic institution run by Dominican priests (Milner B, 1998). Brenda liked languages. She not only enjoyed French literature, but when she was working at ADRDE in Malvern, she found someone to teach her conversational French. This was in the middle of a war, when there was little chance that she would find herself in France and with no inkling that fluency in French might soon be essential for her job. After the privations of wartime life in England, life was much more comfortable in Montreal. But I think we both suffered some culture shock and began to look forward to the end of what we had been told would be about an 18-month mission. The war in Europe ended the next spring and in August, to the horror of many of us in the nuclear energy business, we heard that Japan had been attacked without warning by atom bombs. By the next month, the war was over. Work on the Chalk River site continued, of course, and I continued to work on my apparatus for measuring elasticity ultrasonically. Brenda and I moved to an apartment in Westmount and bought furniture. By the spring of 1946, the labs at the Chalk River site and the new residential village, Deep River, several miles upstream, were declared adequate and all the scientists and their equipment were transported there. Unfortunately, the nuclear reactor, which I believe was the first heavy-water moderated “pile,” was still far from being operational. All of us who were waiting for high levels of neutron flux had to find other things to do. In my case, I worked on part of the safety system that turned the pile off if the cooling water temperature rose too high. But I had a good deal of spare time, during which I read some of Brenda’s psychology books and learned to type.

Brenda stayed in Montreal to finish the course she was teaching and when she finally came to Deep River in the summer, she hated the place. It was deliberately chosen to be isolated so that if the pile got out of control, not too many innocent bystanders would be affected. Pastimes were pretty much limited to lying on the beach, boating, flirting, and listening to music. People brought their phonograph records to the Staff Hotel on Sunday evenings to give concerts. Though her father had been the *Manchester Guardian* music critic, and her mother a singer, Brenda has always been quite unable to recognize a tune or process any aspect of music other than its rhythm. She had been teaching at the University of Montreal for more than a year and was thoroughly enjoying it, so her visits to Deep River were short and infrequent that summer. There was good train service to Montreal, however, and I would often spend the weekend there.

## McGill Psychology

Meanwhile, McGill's psychology department was beginning to come alive again. The ailing absentee chairman died and was eventually succeeded by Robert MacLeod, a well-organized experimental psychologist who had spent the war in army intelligence. He set about establishing a laboratory and collecting a new department. He was an excellent teacher of traditional psychology, and Brenda was able to arrange her lectures so that she could attend a graduate seminar he gave. Like most English academics of that era, she did not have any post-graduate degree. Two of MacLeod's recruits, Donald Hebb and George Ferguson, arrived on the scene the next year, 1947. Both were raised in Nova Scotia, both attended Dalhousie University—Hebb in the 1920s, Ferguson about ten years later. As an undergraduate, Hebb did well in science, but because he was set on becoming a novelist, he majored in philosophy and English. After graduating, he went back to his old school as a teacher, hoping to write a novel in his spare time. That did not happen, however; so after a few years, he returned to academic work and received a master's degree in psychology from McGill and a PhD from Harvard with Karl Lashley, the most important American physiological psychologist of the time. Then, after a fellowship with the neurosurgeon Wilder Penfield at the Montreal Neurological Institute, he spent some time teaching psychology at Queens University in Ontario. Next followed a five-year fellowship in Florida, with Karl Lashley again, studying chimpanzee emotion, after which he was invited to McGill by MacLeod. Ferguson had obtained an excellent degree in Latin at Dalhousie, earning a scholarship to Edinburgh, where he was granted a PhD in psychology. He spent the war in the army, developing tests for soldiers, and was then recruited by MacLeod to teach statistics at McGill. The next year, MacLeod moved to Cornell University, and Hebb took over as chairman of the McGill psychology department.

Hebb must have really liked teaching because, until he retired, every new graduate student had to attend his weekly seminar, and every psychology undergraduate had to take his elementary course, which most years occupied at least two of the largest classrooms linked by video. He had a good fund of chimpanzee anecdotes. His graduate seminars were as much concerned with communication as with research. Timing of student presentations and pronunciation were carefully monitored, and Hebb's stopwatch and pencil-tapping were legendary. When he came to McGill, Hebb brought the manuscript of a book titled *The Organization of Behavior*. It was not published until 1949, but he used the manuscript in a graduate seminar that Brenda attended. Oliver Zangwill, her supervisor at Cambridge, studied patients with brain lesions so Brenda already knew something about the role of the brain in behavior, the theme of Hebb's book. She found Hebb's seminars exciting and sent me some extracts from his manuscript. I became particularly interested in Hebb's speculations about the circuitry of the brain.

This situation unfolded at a critical time for me. The British government was now prepared to enter the business of nuclear energy and offered research positions to the pioneers they had sent to Canada. I had the alternative of becoming a Canadian and continuing at Chalk River with the Canadian National Research Council or going back to England. The situation in Britain was not at all attractive. Two or three years after the war, food and fuel were still in short supply and were rationed. Many towns were still suffering from the results of enemy bombing. On the other hand, I had no desire to spend the rest of my life in Chalk River as an engineering physicist. Hebb's manuscript suggested another more radical alternative; I could try to persuade Hebb to let me pursue the brain-behavior relationship with his supervision. I think I had an idealistic impression that professors sat around concocting and publishing theories that students would then take to the lab and test. So in the spring of 1947, on one of my visits to Montreal, I arranged to meet Hebb and asked him if it would be possible for me to do graduate work with him. After checking my qualifications, he told me I would have to take some psychology and physiology courses in a qualifying year. If I passed, he would take me on as a graduate student. I was lucky that the department was still small and somewhat disorganized, and that Hebb was new to the job of chairman. A few years later, there would have been much more red tape; the chairman would have had to consult his executive committee before accepting a graduate student, for example.

One of the regular visitors to the nuclear site at Chalk River was John Stuart Foster of the McGill physics department. He was in charge of the McGill Radiation Laboratory where a large synchro-cyclotron was being assembled, so the next thing I did was to visit him and ask if any part-time help was needed. There was a job for me; it was to build an ion source. Foster had the specifications used in the synchro-cyclotron built by Ernest Lawrence at the University of California, Berkeley, but they were for a hot-cathode source,

which did not work well in our machine. I converted it to a cold-cathode source, which was an improvement. I also had to design and construct a transformer to deliver pulses to the source, which sent me back to my Leeds textbooks. The rest of the time I took courses in psychology, physiology, and statistics. One of Hebb's graduate students, Herb Lansdell, taught me how to operate on a rat brain. At the end of the year, my exam results apparently satisfied Hebb, and I was accepted into the graduate program.

## Graduate Student

I became an acknowledged graduate student in the fall of 1948. This qualified me for a job as an assistant, which in my case involved getting to the lab at the crack of dawn and cleaning out the dog cages. I also had to decide on an experiment for my master's of science thesis. Hebb had settled in as chairman and renewed his contacts with people at the Montreal Neurological Institute (Neuro) with whom he had worked during his fellowship, 10 years earlier. Probably because of my background, he suggested that I follow up on Penfield's use of electrical stimulation of the cortex or perhaps record cortical electrical activity. Accordingly, he sent me to the Neuro to learn how to implant cortical electrodes in dogs. (Hebb used dogs for much of his animal research.) In human patients, Penfield was able to interfere with speech by electrical stimulation of the cortical speech areas. I started to look for stimulation-produced interference of learned behavior in the dog but gave up due to technical difficulties. Dogs are less tolerant of being wired-up than rats. Also, the cortical electrodes either fell out or got infected. It became obvious that I could not finish the experiment within the allotted time, so I looked for something that required no surgery and used rats.

In his book and lectures, Hebb suggested that animals must learn what food is good for them. I decided to test this hypothesis for my master's research. I deprived weanling rats of potassium, and then gave them a choice between dilute potassium chloride and magnesium sulphate solutions. The results were clear; the deprived rats immediately chose the potassium salt much more often than did the undeprived controls, making it improbable that the preference depended on a beneficial aftereffect of its consumption. Some learning was observed, however. After the preference trials, rats of the deprived group were fed the control diet for six days and given unrestricted access to the potassium salt. In subsequent preference trials, they showed an even greater preference for the potassium solution than they had done in their earlier, deprived trials. This suggests that the reinforcing effect of the potassium on the deprived rats established a long-lasting liking for the taste of potassium salt that became independent of deprivation. I was intrigued by the implications for motivation of this finding. The master's thesis was accepted in the fall of 1950, and I advanced to the PhD. Some of the experiment was repeated later by one of my students (Milner and Zucker, 1965).

As mentioned earlier, Hebb still had links with the Montreal Neurological Institute. He knew many of the staff and sent several of his graduate students to participate in their seminars. Francis McNaughton taught us human brain anatomy (we made models using colored Plasticine), and Herbert Jasper discussed recent information about the brainstem and other neurophysiological findings. Jasper was a man of wide interests extending from philosophy through biochemistry to electronic engineering. He was a pioneer of electroencephalography (EEG) and, with Carmichael, published the first U.S. paper on the relation of the EEG to the level of arousal. His use of the EEG to localize epileptic foci played a vital role in Wilder Penfield's surgical treatment of epilepsy. When I attended his seminar, Jasper had recently discovered that electrical stimulation in part of the brainstem of anesthetized cats produces cortical activity resembling that of an alert cat. The next year, Moruzzi and Magoun (1949) localized the effect to the brainstem reticular system. The relation of the reticular system to sleep, waking, and arousal was a subject of much investigation during the late 1940s, and we heard a great deal about it during the seminars. Seth Sharpless, a philosophy student from the University of Chicago and fellow graduate student, who like me was attracted to McGill by Hebb's *Organization of Behavior*, did his doctoral research on sleep and wakefulness in Jasper's lab (Sharpless and Jasper 1956).

Seth and I spent a lot of time discussing Hebb's cell-assembly theory. Like his mentor Lashley, Hebb was good at identifying problems but handicapped in their solution by the primitive state of neuroscience. In his book, Hebb refers to the problem of motor equivalence, the ability of animals to reach a goal in different ways depending on circumstances. Although the main emphasis of the *Organization of Behavior* is on the visual system, Hebb argues strongly in favor of better understanding the motor system. Sperry (1952) wrote an article in which he pointed out that the sensory systems evolved to enhance the effectiveness of the motor system, further focusing my interest on response mechanisms.

In most learning situations, the goal is the source of a reward; therefore, an association with the goal is also an association with the reward system. Seth and I speculated that there must be a component of the reward system that goes to the motor system and attempts to find a learned intention to approach the goal and, if successful, to boost it until the responses become overt. We called this facilitator the "go" pathway. I recently discovered the following sentence in the "theory" section of my master's thesis: "The alternative seems to imply that there are separate structures, or overall patterns of cerebral activity, subserving pleasure sensations, or the facilitation of some general concept of approach" (Milner 1950). Apparently, I had already been thinking along these lines before starting my doctoral research. The behavior of a rat at the choice-point of a T-maze provides

a simple illustration of the proposed reward feedback mechanism. Before training, the choice-point responses are random, but, if a hungry rat finds food after turning left, it soon acquires an association between the neural intention to make a left turn and a neural representation of food. Food is rewarding to a hungry rat, so its association with an intention to make a left turn must trigger the reward system, amplifying the intention until the rat actually makes a left turn. The reticular arousal system we were hearing about from Jasper sounded as if it might be a promising candidate for our postulated “go-system.”

My doctoral research involved subcortical electrical stimulation of rats, and some of the rats had electrodes in the reticular pathway. Seth and I decided to use these rats to test the notion that stimulating their reticular activating systems could influence their behavior in a maze. We found that it did but not in the way we had hoped. The only clear outcome was that almost all the rats responded as if they had been punished by the stimulation. They avoided the places where it had occurred. Electrical stimulation of sensory pathways is usually aversive so it was not too surprising to find that nuclei receiving sensory input respond in the same way. We abandoned the experiment for the time being, and I went back to my official thesis research, which was investigating the neural mechanism for estimating short time intervals. I was intrigued by the way estimates of the passage of time seemed to depend on attention. On the evidence of the “watched pot never boils” phenomenon, I guessed that attention speeded up a neural clock, making an objectively short time interval seem longer. I thought it might be possible to exert some control over time estimation in rats by stimulating their arousal systems. I used shock-avoidance conditioning in a shuttle box to measure the ability of the rats to estimate time. (Thinking about it now, it was probably not a good idea to use foot shock to train rats for an arousal experiment.) The rats learned to avoid shock by jumping the shuttle box partition at about 12-second intervals; when they were shuttling regularly, the shocks were turned off and the effect of stimulating the arousal system observed.

The research that was reported in my thesis was hardly more than a pilot study. Only about 20 rats completed the trials, and their electrodes were distributed widely through the brainstem. The duration, frequency, and voltage of the brain stimulation were also scattered. Brief stimulation caused a statistically significant, but unexpected, slowing of response rate in almost all the subjects. Continuous low-level stimulation during the animal’s responding caused a significant rate increase in the group of rats that had the most posterior electrodes, but most of the others continued to be slowed by the stimulation. The best part of my thesis was the introduction, which was a very exhaustive review of the reticular arousal system.

## Reward

Obviously, the doctoral study should at least have been followed up by a more systematic investigation of the caudal mid-brain tegmentum, but fate stepped in. One day in the fall of 1953, Hebb brought a young man to my lab and introduced him as James Olds, a new “postdoc” from the Harvard Department of Social Relations. In spite of his provenance, he was interested in motivation and learning. He had just written a paper on Tolman’s sign-Gestalt theory and, influenced by Hebb’s *Organization of Behavior*, he wished to develop a neural version of the theory. He had obtained a post-doctoral fellowship to do so with Hebb. Jim had no experience with animals or the brain, so Hebb asked me to show him the ropes. I do not know whether Hebb knew at the time about my experiments and speculations concerning the reticular activating system and motivation.

I gave Jim a rat brain atlas and told him to learn some neuro-anatomy. By the end of the week, he knew the rat’s brain map better than I did. Next, we tackled electrode implantations. After my bad experience with infections in dogs, I had adopted an electrode design used in monkeys by José Delgado at Yale. Two insulated, stainless steel wires were glued together and, using a stereotaxic instrument, inserted into the target area through a small hole drilled in the skull. The electrode was then fixed to the skull with dental cement. When the cement had hardened, the electrode was released from the stereotaxic instrument and the emerging wires were passed under the scalp, brought out through the back of the neck, and provided with a small socket.

I showed Jim this technique and watched as he practiced. After a few days, he felt ready to perform an implantation on his own, intending to put the electrode into the reticular activating system. He probably chose that target because it was the system that everyone was interested in at that time. He may also have been talking to Seth, who was somewhat reluctant to accept the negative results of our earlier attempts to guide rats to a target by stimulating the reticular activating system. Although our experiment consistently yielded negative results, most of the subjects were still alive, so we did not know precisely where their electrodes were located.

When Jim’s rat had recovered from the operation, he tested it. As it wandered about on a bench top, Jim stimulated it using a handheld switch. He noticed that after a bout of stimulation the rat sniffed around the region where it had occurred and would return there if displaced. Jim got very excited and told Seth and me that the rat was being rewarded by the stimulation. We, who had stimulated that region before, were somewhat skeptical. I told Jim we would believe it if the rat would work for stimulation in a Skinner box. The McGill psychology department may have been the only one in North America at that time that did not possess a Skinner box, so I had to build one. The rat passed the Skinner box test rapidly and convinc-

ingly. I next tried to replicate the effect, using the coordinates that Jim said he was using, but without success. We then began to have doubts about the location of the electrode. The Donner Building, where our lab was located, was mostly occupied by the department of experimental surgery. They had an X-ray machine, and we persuaded the operator to X-ray the rat's head. It was immediately obvious that the electrode had not gone where it was supposed to go. Its tip appeared to be in the vicinity of the septal area. We guessed that the dental cement had not completely set when Jim bent the external part of the electrode back to go under the scalp, forcing the business end to move in a rostral direction. Unfortunately, by the time we reluctantly sacrificed the rat, its brain had become too infected for autopsy. After we had more self-stimulating rats, we recognized that the rat's behavior had been similar to that of rats with electrodes in or near the nucleus accumbens or the medial forebrain bundle.

The next priority was to obtain enough data for an acceptable paper as quickly as possible. Jim was a very energetic and efficient person, and he knew this was a big deal. He planned to collect data from many rats, so he designed a battery of Skinner boxes with large floor level "levers" that the rat could hardly help stepping on. This raised the unrewarded operant level high enough for it to be possible to measure aversive as well as rewarding stimulation. He also designed electrodes that were easier to implant. He had been reading Hess et al. (1953), who inserted electrodes into the brains of cats, mounting them on a small platform screwed to the skull. Jim designed electrodes embedded in small, rectangular plastic blocks that could be secured to the skull with jeweler's screws. In some rats, Jim left the skull around the electrode open, and to my astonishment, they did not get infected. Hank Macintosh, the chairman of the physiology department, heard about this and remembered a story that, in colonial days, people who had been scalped in the Indian wars often developed infections and died. But then a French surgeon started to bore small holes in their skulls and the fluid that oozed out spread over the bone, coagulated, and protected it from infection.

A reporter for the *Montreal Star*, D. Macfarlane, routinely roamed the McGill campus, and Hebb steered him in our direction. As a result, the *Star* for March 13, 1954, had a front-page banner headline "McGill Opens Vast New Research Field with Brain 'Pleasure Area' Discovery" and in slightly smaller print "It May Prove Key to Human Behaviour" and "Anglo-American Achievement Has Fantastic Possibilities." It must have been a quiet day for news because the story was copied around the world. Jim and I thought some of the report was a bit over the top; in any case, it was unorthodox to have the work evaluated by a newspaper reporter before it was submitted to a journal and peer reviewed so we sent a letter to the *Star* to that effect. Nevertheless when our paper, "Positive Reinforcement Produced by Electrical Stimulation of Septal Area and Other Regions of Rat Brain,"

was eventually published in December (Olds and Milner 1954), it certainly boosted Hebb's efforts to persuade psychologists to take the brain seriously.

At the time, I doubt whether there were many other psychologists who had tried unsuccessfully to find a brain system that facilitated goal-directed responses, so fate must have had a good time sending us someone to show us how to do it. Fate chose the right person to send; it would be difficult to imagine anyone better qualified for tackling the awesome task of thoroughly investigating the phenomenon. Most of the valuable early research on the anatomy and pharmacology of the reward system was carried out by Jim and Marianne (Nickie), his wife. I was as excited by the discovery as Jim but could not completely abandon my thesis research.

After confirmation of the reward effect, one of the first questions to be studied was the relation between brain stimulation reward and more conventional rewards, such as food. Hebb gave Jim a graduate student, Rolphe Morrison, who investigated the effect of food deprivation on self-stimulation and the effect of self-stimulation on feeding (Morrison 1955). Jim and Nickie worked all-out, mapping the brain for reward and punishment sites (Olds 1956; Olds and Olds 1963). They left McGill in 1955 and were given every resource to continue their investigation of the reward system at the Brain Research Institute of the University of California, Los Angeles. In 1957, Jim was appointed assistant professor at the University of Michigan. I returned to my research, finished my doctoral thesis as best I could, and it was accepted. Hebb then treated me rather as Lashley had treated him, appointing me as a sort of postdoc and giving me some teaching to do. I also became an IBM consultant.

## Artificial Intelligence

I was working in the field of nuclear energy when I first read Hebb's account of the cell assembly in the copy of his manuscript that Brenda sent to me in Chalk River. My previous impression of physiological psychology had been that it was a piecemeal attempt to discover the function of the brain by studying the effects of different brain lesions in animals and human patients. Hebb's synthetic model, which used the properties of neural elements in an attempt to explain function, appealed to me as being more like other sciences, though adequate knowledge about neurons was still lacking. I thought Hebb's model was a step in the right direction, but my work with nuclear reactors alerted me to a serious flaw in the basic component of his model, the cell assembly.

Nuclear reactors depend on a chain reaction, and I recognized the cell assembly as a neural version. In Hebb's model, when a cortical neuron fires, it delivers excitatory stimulation to similar neurons with which it synapses. As a result, some of those neurons fire (especially any that are being facilitated by sensory input) and randomly excite other cortical neurons. In

a nuclear reactor, when an atom of uranium 235 absorbs a neutron and undergoes fission, it sprays neutrons at random. Some of them penetrate neighboring atoms of uranium 235, causing them to undergo fission and to emit further bursts of neutrons. Chain reactions such as this are fundamentally unstable; if the fission of one atom causes an average of more than one other atom to undergo fission, you very soon have a bomb. But if an average of less than one fission is triggered, the action fizzles out. To deliver controlled energy, the average fission must result in exactly one new fission. Fortunately, there is a slight reduction in efficiency as the neutron flux increases, reducing the probability of neutron capture. Small fluctuations, therefore, do not start an avalanche. Unfortunately for Hebb's hypothetical cell assembly, however, a small increase in firing of cortical neurons, as might be caused by increased sensory input, would result in increased synaptic summation, leading to a further increase in cortical firing. Hebb's learning rule, which also increases the number of other neurons fired by the average cortical neuron, would exacerbate the problem. Without inhibition, the classical cell assembly would grow exponentially until every cortical neuron fires full time.

One way to avoid this outcome would be for cortical neurons to inhibit each other via inhibitory neurons. An increase in cortical firing would then turn off some cortical neurons but never enough of them to stop cortical firing altogether, for that would also eliminate the inhibition. Hebb avoided the use of inhibition; it was incompatible with the prevailing idea of electrical transmission of neural activity and was deemed to be impossible by influential neuro-physiologists. Chemical neuro-transmission was demonstrated at about the time Hebb's book went to press (Eccles 1953). Another problem I had with Hebb's account of the cell assembly concerned the way one cell assembly was supposed to become associated with other assemblies. It was not clear why, if two assemblies were active at the same time, they did not combine into a bigger cell assembly, so that eventually the cortex would be just one giant cell assembly. I suggested that cortical neurons that received synaptic input from an active assembly, but did not fire because of simultaneous inhibition, might start to fire when a new assembly starts up, thus becoming incorporated into the new assembly and forming a link between the two assemblies.

My decision to do graduate work at McGill was influenced by a desire to follow up on the ideas I had to bring Hebb's model more up to date. I thought Hebb might want to be involved, but he considered the running of a very understaffed department, with lectures all day and seminars in the evening, more urgent than fiddling with his book, which was enjoying far greater success than he expected. He was kind enough to comment on a paper I wrote introducing inhibition into the cell assembly model, so the paper, titled "The Cell Assembly: Mark II," was eventually published (Milner 1957).

Nat Rochester, who helped to design IBM's digital computer 701, the first digital computer to be made available commercially, thought Hebb's cell assembly might be used to make his computer think for itself. He and his group at the Poughkeepsie lab of IBM had tried to adapt the cell assembly for the task and had encountered the predicted instability. They cured this by weakening inactive synapses whenever active synapses were strengthened, but repeated identical sensory input still did not generate cell assemblies, so Rochester consulted Hebb. Hebb sent him to me, so presumably he accepted my tinkering with his model. I told Nat about inhibition and gave him a draft of the Mark II paper. He then made some rather drastic changes to his "Conceptor" model, and eventually was able to obtain cell assemblies. (Rochester et al. 1956). They still could not get them to associate with each other, however, even when they moved to a later model computer, which was bigger (with a RAM of just over two whole kilobytes!) and allowed them to model a (very slow) cortex of 512 neurons. I visited Poughkeepsie a few times to observe progress but was unable to help. I thought more work had to be done on the neural model. During this period as an IBM consultant, I was invited to a meeting of computer scientists and information theorists at Dartmouth College. Most of the time I had no idea what they were talking about, but the Dartmouth Conference is now considered to be the birthplace of artificial intelligence. Due to criticism from some IBM shareholders, who thought artificial intelligence was a waste of research funds, Nat's program was abandoned shortly afterward.

## Lecturing

The next year, 1956, I was appointed assistant professor to replace Haldor Rosvold, who had left to start an animal behavior division at the National Institutes of Health in Bethesda. I took over his physiological psychology course, which in the next year or two occupied much of my time. The textbook I inherited was not entirely suited to my plans for the course, so I supplemented it with printed lecture notes. I subsequently updated and added to the notes and, after a few years, they were collected in book form and sold by the McGill bookstore. Several publishers then invited me to turn them into a textbook, which I started to do.

By this time, in the early 1960s, I had plenty of distractions. I was still trying to extend Hebb's brain model. In March 1959, I presented a theoretical paper in a current trends in psychology series at the University of Pittsburgh (Milner 1961a) and a somewhat different paper later in the same year, at a conference on self-organizing systems in Chicago (Milner 1960). I was a research associate of the Carnegie Institute in Washington from 1960 to 1964, site-visiting labs in the United States and Europe where research on brain modeling was being carried out. From 1963 to 1967, I was a consultant for the Rand Corporation and spent the summer of 1963 helping design the

“brain” of a robot vehicle that may have been intended for the moon or some planet. Between 1963 and 1973, I spent a number of years on the granting agencies for the National Research Council of Canada and the U.S. National Institute of Mental Health. Reading the applications was a lot of work but it kept me up to date on the latest trends in physiological psychology, and I enjoyed meeting all the famous psychologists. During the school year, I gave the usual undergraduate lectures, graduate seminars, organized research, and wrote papers and grant applications; progress on the textbook was slow.

It was eventually published in 1970, and for a few years, it dominated the market. It was translated into several languages, including Portuguese, Italian, and Russian. I like to think its popularity was partly because the factual material was spiced with snatches of speculation. As it aged, I was under considerable pressure from the publisher and others to prepare a second edition, but I write slowly and neuroscience progressed very fast. After a couple of years, I stopped trying to keep up and went back to supplementary lecture notes. Some of my students are dispersed all over the world, teaching and doing research.

## Research

I chose to do graduate work at McGill with the idea of developing Hebb's theoretical model, but after I completed my PhD and Hebb appointed me to a research position, brain-stimulation reward was the obvious topic for me to take up. Jim and Nickie Olds had, by then, completed a monumental mapping of reward and aversive stimulation sites in the rat brain, and after the publication of the first stages of that study in 1954, research on the phenomenon was quickly taken up by other groups. There were many avenues to explore. The original mapping revealed that the sites had different properties. Some required little or no practice; the rat pressed the lever enthusiastically within seconds of the first accidental press. Other sites needed several hours of stimulation before the rat responded spontaneously. It was also found that rats would not bar-press for less than a train of at least four or five pulses of current, no matter what their strength. The effect apparently required temporal summation. Most rats, even those that appeared most vigorous once started, ignored the lever the next day when they were returned to the Skinner box; they still needed to be “primed” before they would return to the lever. It was also noticed that rats terminated the stimulation after a few seconds when given control over its duration. They soon learned to turn off the stimulating current if it were turned on by an experimenter. Apparently, stimulation rapidly becomes aversive. Perhaps it is aversive from its onset, but as soon as the current train ends, the rat seems compelled to turn it on again.

Mapping reward sites does not demand accurate measurement of the intensity of reward, but as the emphasis turned to other characteristics of

the system, several researchers found that rate of bar-pressing, or speed of running down an alley, were not reliable measures of reward strength. Increasing the stimulating current beyond a certain level reduces rates of response, but in a choice experiment, the rats nevertheless choose the source of higher current. In an effort to circumvent this measurement problem, I designed a stimulator with feedback that automatically adjusted the current to maintain a constant response rate. The current was then a relative measure of reward. Deutsch (1964) thought that self-stimulation must involve two neural circuits, one for drive and the other for reinforcement, and tried to distinguish them by measuring the refractory periods of the neurons involved. I tried to identify the participating neurons by plotting strength-duration curves, varying pulse duration and noting the change in current to maintain constant rate of pressing.

These, and other experiments conducted by the many groups working on self-stimulation problems during the decades after its discovery, indicated that the medial forebrain bundle was important for reward, but that it consisted of many different paths. The physiological measurements suggested that the path stimulated during self-stimulation consisted of thin myelinated fibers. Pharmacological tests implicate dopamine, which uses unmyelinated fibers. The myelinated path descends to the midbrain nuclei and the dopamine path goes in the opposite direction, to the basal ganglia. Attempts to clarify the functioning of the reward and reinforcement systems continued for many years and were reviewed in detail (Milner 1991). More than 75 of these papers were published by my students from McGill or by their students.

## Problem-Solving

When I began to study psychology, the major theories were mainly concerned with visual perception and learning. Reading Hebb (1949) and Sperry (1952) made me realize that the motor system, the source of overt behavior, was relatively neglected. Lecturing and writing a textbook also made me aware that understanding behavior requires knowing how the whole brain works. What goes on in the chicken's brain before it crosses the road is a fundamental neuropsychological question.

By analogy with the sensory system, it seemed that the motor cortex should be a storage place for action engrams. Established theories, based on Pavlovian reflexes, held that a response engram was selected by external sensory input, but that certainly was not true most of the time. People do not enter a room in daylight and turn the light on because they happen to see a switch. In the dark, you may try to find a light switch even if there is no light switch in sight. Most of the time, the action is selected by a need. Conventional learning theory might have attributed the choice of potassium solution by the deprived rats of my master's research to some sensory

characteristic such as its smell, ignoring the fact that the characteristic had no effect on rats that did not need potassium. The problem was to find out how need selected a behavior that ensured satisfaction.

One hypothesis was that a state of need, either innately or through learning, facilitates motor engrams for reaching a satisfier. These motor engrams then facilitate the sensory engrams of objects they have found useful in performing their responses. If any of the helpful stimuli are present, their engrams receive facilitation from both need and the environment, strongly activating them to inform the motor system about the location, size, and so on of the needed object. This was roughly the model that Seth Sharpless and I had in mind when we did the failed reticular-formation stimulation experiment. When Jim Olds appeared on the scene, I discovered that his reading of Tolman (1932) and Meehl and McCorquodale (1951), Tolman's interpreters, had led him to a somewhat similar model, though expressed in less neural terms.

During the 1930s, psychologists dealt with learning mostly in terms of Pavlovian conditioning. The conditioned stimulus was usually auditory or, sometimes, a light; it could vary in intensity, but the neural response was much the same from trial to trial. When psychologists began training animals to respond to visual stimuli, however, it was no longer possible to assume a simple relationship between the stimulus and the neural response. The visual stimulus from an object has many degrees of freedom: location, size, color, and so on. Attention or relative position of the observer and the stimulus can profoundly change the neural activity elicited by the stimulus. For some time, learning theorists continued to assume that responses become associated with what they called the stimulus, ignoring the fact that the association must often be transferred from one neural version of the visual stimulus to a completely different one. For example, a large triangle does not stimulate the same retinal receptors as a smaller triangle, but a rat trained to approach one for food will also approach the other.

Theorists who worried about this problem thought that the brain could somehow convert the different neural activities into engrams with common properties that could be associated with the rewarded response. Köhler (1940), who was a Gestalt psychologist, suggested that equivalent stimuli might evoke similar electric fields in the cortex. Lashley (1942) postulated that a shape gives rise to similar brain wave interference patterns, no matter what its size, orientation, or retinal location. No evidence supported these rather vague suggestions. I first learned about this problem from Hebb's monograph (1949), where he cites convincing evidence that eye movements are important for perception and proposed that they enable stimulus-equivalence learning in infancy. He postulated that cell assemblies (engrams) for a shape are sequential, such as the sounds and letters in the engrams for words, consisting of a series of visual traces separated by eye movement traces. Thus, after a lot of experience, a large number of closely

associated cell assemblies would represent all neural versions of a shape. I had my doubts about this theory, partly because complete learning of a new shape would be very slow, even for adults, and the peculiar perceptual difficulties of anyone who had not yet learned all possible versions of the stimulus would be obvious and widespread.

These tentative suggestions from some of the brightest neuropsychologists of their time underlined the need for more research. Relevant experiments had to await the introduction of micro-electrodes capable of recording the activity of single cortical neurons. Hubel and Wiesel (1959) performed such experiments, though their relevance to the stimulus-equivalence problem was not fully appreciated at the time. This may have been because the advent of affordable digital computers had led some theorists (e.g., Minsky and Papert 1969; Rosenblatt 1958, 1962) to believe that an algorithm could be found to account for stimulus-equivalence. I like puzzles, so I thought about this problem from time to time but never got far beyond the criticism of existing theories. In 1971, my textbook was safely launched, and I was due a sabbatical year. I heard that some interesting experiments on the neural mechanisms of vision were underway in Cambridge University, so I went there. The physiological studies of vision were not very enlightening from the stimulus-equivalence viewpoint. But I looked again at the Hubel and Wiesel experiments, and it occurred to me that they might have a key to the solution. I was sure that others must have had the same idea, but I had seen no mention of it. Hubel and Wiesel describe two classes of neuron in the primary visual cortex (V1), simple and complex. A simple cell responds to the sum of inputs originating from a line of retinal receptors; complex cells respond to visual stimulation from any of a group of parallel lines. It was assumed that the complex cells respond to synaptic input from any one of a group of simple cells fired by parallel lines. In other words, the key to generalization was convergence. If a complex cell responds to parallel lines in only a part of the visual field, a number of such complex cells fired by lines in different small fields could converge on another complex cell, causing it to respond to lines in a larger field. Cells fired by the convergence of outputs from two complex cells representing lines of different orientation would detect angles. I also worked out neural circuits to calculate length ratios of lines, making it possible to generalize size differences. Objects can thus be recognized whatever their size and location, but if we want to make a response to them, these generalized engrams are useless because they do not tell us where the objects are; their origins are hidden by repeated convergences. Only retinal receptors provide completely reliable information about the location of a visual stimulus in relation to the body, and the only way to access this information is by selectively amplifying it with top-down attention from the engram of the relevant object.

How is that particular engram chosen as the target of attention? This is a question that I had already addressed when dealing with need

and motivation. An experienced animal will already have learned that the target engram represents a satisfier of the current need. Water, for example, rapidly becomes attractive to a thirsty animal. The attraction to water is shared with objects frequently present at the time. This means that the cortical engrams for water, and any associated stimuli, receive input from the need for water. Henceforth, thirst facilitates water engrams, even when no water is around; but if water is present, the engram receives facilitation from both the need and water, so it fires vigorously. The aroused activity travels back along a reverse path to the eye and increases activity in the receptors receiving light from water and objects related to water. When the output of the visual receptors is selectively intensified in this way by the top-down attention, it is intensified in all the neural representations of the object in the ventro-lateral visual recognition path, and to the motor system via the dorsal visual pathway, which is separate from the recognition path. (The dorsal visual path found by Ungerleider and Mishkin [1982] was unknown when I wrote my first account of this theory [Milner 1974], but there is a direct path from the retina to the superior colliculus to keep the eye focused on, and directed toward, the attended object. I suggested that it might also convey the location of the desired object to the rest of the motor system.)

I thought that I had found a neural model of the stimulus-equivalence phenomenon that was at least plausible. I published my version of the model (Milner 1974), but it aroused little interest. Probably the few psychologists who were aware of the problem assumed that it had been dealt with by Lashley or Hebb. I thought that if I wrote a computer program based on the model, it might attract more attention. Before Windows arrived to complicate things, I could still write C-programs, and I succeeded in writing a program that could name a figure (up to pentagons) at every location and orientation the program could accommodate. It could also answer questions as to whether a particular figure was present, even if it was part of a larger figure (e.g., a triangle in a rectangle with a diagonal). I put it on my Web site but never published it. I still have a copy of the program, but modern processors do not recognize the code. These days, when practically every camera or mobile phone has face locating capability, I can only conclude that the mechanism of visual stimulus-equivalence is no longer a mystery.

Lashley (1951) was also puzzled by the memory for serial order—an ability essential for most learned responses, especially speaking and writing. Lashley said it was “both the most important and the most neglected problem of cerebral psychology.” I tried to provide an answer in 1961 with a paper, “A Neural Mechanism for the Immediate Recall of Sequences,” which turned out not to work because I made some bad guesses about synaptic change. I made what I think was a more plausible attempt to explain it many years later, when I was writing *The Autonomous Brain* (Milner 1999). One difficulty is that the trace of the first member of a series is presumably the

one that has become most weak by the time the series must be recalled. My solution was to work with fading inhibitory synapses that suppress active traces. The problem is of prime importance for language neuropsychologists, an ingenious group whose work I have not been following closely, so possibly they have discovered a better solution by now.

After I retired from teaching, I indulged my devotion to puzzles in my spare time by polishing some of my speculations and assembling them in a book, *The Autonomous Brain*, published in 1999 (the fiftieth anniversary of Hebb's book). It is basically my attempt to provide Hebb's theory with a more up-to-date nervous system, the goal I set myself when I chose to study with Hebb about a half century earlier. That task is by no means complete, but it provided me with a sort of closure.

## References

- Burrell CM, PM Milner, KA Russell. Negative transconductance characteristic of pentodes. *Leeds University Engineering Society Journal* 1941;1:18–22.
- Deutsch JA. Behavioral measurements of the neural refractory period and its application to intracranial self-stimulation. *Journal of Comparative and Physiological Psychology* 1964;58:1–9.
- Eccles JC. *The Neurophysiological Basis of Mind*. Oxford: Clarendon, 1953.
- Hebb DO. *The Organization of Behavior*. New York: Wiley, 1949.
- . Drives and the C.N.S. (conceptual nervous system). *Psychological Review* 1955;62:243–254.
- Hess R Jr., WP Koella, K Akert. Cortical and subcortical recordings in natural and artificially induced sleep in cats. *EEG and Clinical Neurophysiology* 1953;5:75–90.
- Hubel DH, TN Wiesel. Receptive fields of single neurones in the cat's striate cortex. *Journal of Physiology (London)* 1959;148:574–591.
- Köhler W. *Dynamics in Psychology*. New York: Liveright, 1940.
- Lashley KS. The problem of cerebral organization in vision. In H. Klüver (ed). *Biology Symposia*, Vol. 7. 1942; 301–322. Lancaster, PA: Cattell.
- . The problem of serial order in behavior. In LH Jeffress (ed). *Cerebral Mechanisms in Behavior*, 1951; 112–136. New York: Wiley.
- McCorquodale K, PE Meehl. *Edward C. Tolman*. In AT Poffenberger (ed). *Modern Learning Theory*, 1954; 177–266 New York: Appleton-Century-Crofts.
- Meehl PE, K McCorquodale. Some methodological comments concerning expectancy theory. *Psychological Review* 1951;58:230–233.
- Milner B. *Brenda Milner*. In LR Squire (ed). *The History of Neuroscience in Autobiography*, 1998; 276–305. San Diego: Academic.
- Milner P, I Zucker. Specific hunger for potassium in the rat. *Psychonomic Science* 1965;2:17–18.
- Milner PM. A study of the mode of development of food preferences in rats (1950). (M.Sc. Thesis). McGill University Library.

- . The cell assembly Mark II. *Psychological Review* 1957;64:242–252.
- . Learning in neural systems. In MC Yovits and S Cameron, (eds). *Self-Organizing Systems*, 1960; 190–204. New York: Pergamon Press.
- . The application of physiology to learning theory. In Patton, RA (ed). *Current Trends in Psychological Theory* 1961a. PA: University of Pittsburgh Press. 111–133.
- . A neural mechanism for the immediate recall of sequences. *Kybernetik* 1961b; 1:76–81.
- . *Physiological Psychology*. New York: Holt, Rinehart, Winston, 1970.
- . A model for visual shape recognition. *Psychological Review* 1974;81:521–535.
- . Brain stimulation reward: A review. *Canadian Journal of Psychology* 1991;45:1–36.
- . *The Autonomous Brain*. Mahwah, NJ: Erlbaum, 1999.
- Minsky M, SA Papert. *Perceptrons*. Cambridge, MA: MIT Press, 1969.
- Morrison GR. The relation of rewarding intracranial stimulation to biological drives (1955). (Unpublished master's thesis). McGill University Library.
- Moruzzi G, HW Magoun. Brain stem reticular formation and activation of the EEG. *Electroencephalography and Clinical Neurophysiology* 1949;1:455–473.
- Olds J. A preliminary mapping of electrical reinforcing effects in the rat brain. *Journal of Comparative and Physiological Psychology* 1956;49:281–285.
- Olds J, P Milner. Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. *Journal of Comparative and Physiological Psychology* 1954;47:419–427.
- Olds ME, J Olds. Approach-avoidance analysis of rat diencephalon. *Journal of Comparative Neurology* 1963;120:259–295.
- Priestley J. *Hartley's Theory of the Human Mind, on the Principle of the Association of Ideas; with Essays Relating to the Subject of It*. London: Johnson, 1775.
- Rochester N, JH Holland, LH Haibt, WL Duda. Tests on a cell assembly theory of the action of the brain, using a large digital computer. *Transactions on Information Theory, IBM* 1956;3:80–93.
- Rosenblatt F. The perceptron: A probabilistic model for information storage and organization in the brain, Cornell Aeronautical Laboratory. *Psychological Review* 1958;65:386–408.
- . *Principles of Neurodynamics*. Washington, DC: Spartan, 1962.
- Sharpless S, H Jasper. Habituation of the arousal reaction. *Brain* 1956;79:655–680.
- Sperry RW. Neurology and the mind brain problem. *American Scientist* 1952;40: 291–312.
- Tolman EC. *Purposive Behavior in Animals and Men*. New York: Appleton-Century, 1932.
- Ungerleider LG, M Mishkin. *Two cortical visual systems*. In DG Ingle, MA Goodale, RJW Mansfield (eds.) *Analysis of Visual Behavior*, 1982; 549–586. Cambridge, MA: MIT Press.
- Zucker I, P Milner. The effect of amphetamine on established hoarding in the rat. *Psychonomic Science* 1964;1:367.