TIMELINE

The legacy of Donald O. Hebb: more than the Hebb Synapse

Richard E. Brown and Peter M. Milner

Neuroscientists associate the name of Donald O. Hebb with the Hebbian synapse and the Hebbian learning rule, which underlie connectionist theories and synaptic plasticity, but Hebb's work has also influenced developmental psychology, neuropsychology, perception and the study of emotions, as well as learning and memory. Here, we review the work of Hebb and its lasting influence on neuroscience in honour of the 2004 centenary of his birth.

Donald O. Hebb (FIG. 1) is best known for his neurophysiological postulate on learning (BOX 1, BOX2 and BOX3), which appeared in his book *The Organization of Behavior*[1], published in 1949. Stemming from the postulate, Hebb's name is increasingly used as an adjective, so that we have the Hebb synapse, Hebbian synaptic plasticity, Hebbian learning rules, Hebbian neural networks and even anti-Hebbian learning. The postulate forms part of Hebb's neural theory of perception, and much of our current understanding of functional neural connections is based on Hebbian concepts[2,3]. His book also contributed to many aspects of human neuropsychology, developmental psychobiology and cognitive neuroscience[4–7]. In this article, we trace the path that led Hebb to develop the theory that he presented and explored in *The Organization of Behavior*, and elaborate on the influence it has had on psychology and neuroscience.

Hebb's student years

Hebb's parents were both country physicians, and he was born in 1904 in the town of Chester, Nova Scotia in Canada. As a child he was a precocious and voracious reader. When he was 16, the family moved to Dartmouth, Nova Scotia, and the following year, Hebb entered the Faculty of Arts at Dalhousie University in Halifax (FIG. 2). He majored in English with the intention of becoming a novelist[8]. Hebb graduated with a B.A. in 1925 and taught at his old school in Chester for a year. This was not a success, and his novel writing did not progress.

Hebb spent the next year harvesting on a farm in Alberta, labouring in Quebec, and reading Sigmund Freud. This made him consider a career in psychology and he approached the chairman of the McGill University Department of Psychology, W. D. Tait, about doing graduate work. He was given a reading list and told to come back next year. To earn a living, he resumed his career as a schoolteacher. The following year (1928), he was accepted as a part-time graduate student at McGill. He was also appointed principal (headmaster) of a school in a working class suburb of Montreal, where there was a high rate of absenteeism and drop-out. With the help of two psychology professors, Kellogg and Clarke, from McGill University, he improved the situation by persuading the children that school-work was a privilege, giving the children more interesting things to do in class and sending any who disrupted the class outside to play[9].

In 1931, Hebb was bedridden with a tubercular infection of the hip. During that time, he studied Sherrington's *The Integrative Action of the Nervous System*[10] and Pavlov's *Conditioned Reflexes*[11], which had been published in English in 1927, and he wrote a theoretical M.A. thesis entitled *Conditioned and Unconditioned Reflexes and Inhibition*[12]. The thesis is of interest because it contains the seed of what was to become known as the Hebb synapse (BOX 1 and BOX 2). The thesis was passed *cum laude* by two examiners, one of whom was Boris P. Babkin, who had worked with Pavlov in St. Petersburg and Hill in London, and who, after a brief period at Dalhousie University, joined the Physiology Department at McGill. Babkin arranged for Hebb to conduct research on Pavlovian conditioning with Leonid Andreyev, who had also come from Pavlov's laboratory to pursue his research at McGill.

During 1933–1934, Hebb wrote an unpublished booklet entitled *Scientific Method in Psychology: A Theory of Epistemology Based on Objective Psychology* (Hebb, D. O., unpublished observations). Many of the ideas in it were later incorporated into *The Organization of Behavior* and *Essay on Mind*[13]. But by January 1934, Hebb had become disillusioned both with Montreal and McGill. His wife had died on his twenty-ninth birthday, after a car accident. Furthermore, his school reform experiment was, in his words, "defeated by the rigidity of the curriculum in Quebec's protestant schools"[8]. As for his graduate studies at McGill, most of the psychology faculty was engaged in educational psychology and intelligence testing, whereas Hebb was becoming increasingly interested in physiological psychology. He did not consider the Pavlovian conditioning experiments he was conducting to be true physiological psychology, and he was critical of the methodology.

Ph.D. research with Karl Lashley

Having decided to leave Montreal, Hebb wrote to Robert Yerkes at Yale, and was offered a position to study for a Ph.D. Babkin, however, urged him to apply to Lashley if he wanted to learn about physiological psychology, and in July 1934 Lashley accepted Hebb to work with him at the University of Chicago[14].

Timeline | Life and work of Donald O. Hebb

- **1904** — Hebb is born in Chester, Nova Scotia on 22 July.
- **1921** — Enters Dalhousie University in 1921. Graduates with a B.A. in English in May 1925. Teaches in Chester, Nova Scotia from 1925 to 1926. Works on a farm in Alberta during the summer of 1926. Spends winter in Quebec as a labourer and reads Freud. Meets W. D. Tait at McGill University, who sends him to read James and Ladd & Woodworth. In Autumn 1927, he becomes a schoolteacher in Montreal.
- **1928** — Accepted as a part-time graduate student in psychology at McGill University in September 1928. Starts his 'learning as a reward' strategy in an elementary school. From 1930 to 1931, he is bedridden for a year with a tubercular hip. He writes his M.A. thesis in bed and submits it in April 1932.
- **1934** — Decides to study physiological psychology, and works with Lashley in Chicago for three academic terms. Moves to Harvard with Lashley in September 1935, and submits Ph.D. thesis in March 1936. From 1936 to 1937, he works with Lashley and E. G. Boring.
- **1937** — Fellow, Montreal Neurological Institute with W. Penfield from 1937–1939. Lecturer at Queen's University, Ontario from 1939 to 1941; Assistant Professor from 1941 to 1942. Involved in founding the *Bulletin of the Canadian Psychological Association* from 1940 to 1942.
- **1942** — Research Associate with Lashley at the Yerkes Laboratories of Primate Biology from 1942 to 1947. Officially employed as a Harvard University Research Fellow from 1945 to 1947. Professor of Psychology at McGill University from 1947 to 1970, and Chairman of the Psychology Department from 1948 to 1958.
- **1952** — Becomes President of the Canadian Psychological Association (CPA) in 1952. Becomes President of Division 3 of the American Psychological Association (APA) in 1953.
- **1956** — Becomes Chairman of the National Research Council (NRC) Experimental Psychology Committee. Awarded the Warren Medal by the Society of Experimental Psychologists in 1958.
- **1960** — Becomes President of the APA. Receives distinguished scientific contribution award from the APA in 1961, and an award from the Association for Research in Nervous Mental Disorders in 1962.
- **1964** — Vice Dean of biological sciences at McGill from 1964 to 1966. Nominated for the Nobel Prize in 1965 and awarded the Claude Bernard Medal from the University of Montreal in 1966.
- **1970** — Chancellor of McGill University from 1970 to 1974. Awarded gold medal from the APA in 1974.

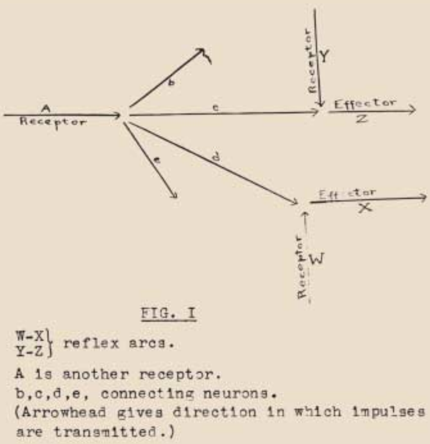
Hebb's Ph.D. thesis topic was 'The problem of spatial orientation and place learning', but before he had completed the research, Lashley accepted a position at Harvard. Hebb and two of his fellow students, Beach and Smith, were accepted as Ph.D. students at Harvard in 1935, but Hebb had to change his research topic. In Spring 1936, Hebb submitted a thesis on the vision of rats reared in darkness, and he received a Harvard Ph.D. For the next year, Hebb worked as a research assistant for Lashley, and also as a teaching assistant in introductory psychology at Radcliffe College, for E. G. Boring. He published his Ph.D. research[15] and completed the research that he had started in Chicago[16]. Informal discussions with Lashley and the members of his laboratory helped him to complete his psychological education.

Box 1 | Development of the 'Hebb synapse' postulate: 1932

The Organization of Behavior is still cited frequently, mostly referring to Hebb's neurophysiological postulate: "when an axon of cell A is near enough to excite a cell B and repeatedly and persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased." Neural network designers adopted this learning postulate, referring to it as the Hebb rule, and some years later neurophysiologists devised techniques for testing the postulate[55,56]. Synapses that conformed to the rule were eventually called 'Hebb synapses'[57].

Hebb's idea first appears in his M.A. thesis, *Conditioned and Unconditioned Reflexes and Inhibition*[12]. To follow his train of thought, it is useful to understand the climate in psychology at the time. The English translation of Pavlov's book *Conditioned Reflexes* was published in 1927 and created quite a stir. In 1928, Ariëns Kappers published his theory of neurobiotaxis[58], proposing that axons, regardless of whether they are being fired, grow towards active cells during development. In 1925, Sherrington had published a paper on reflex inhibition[59].

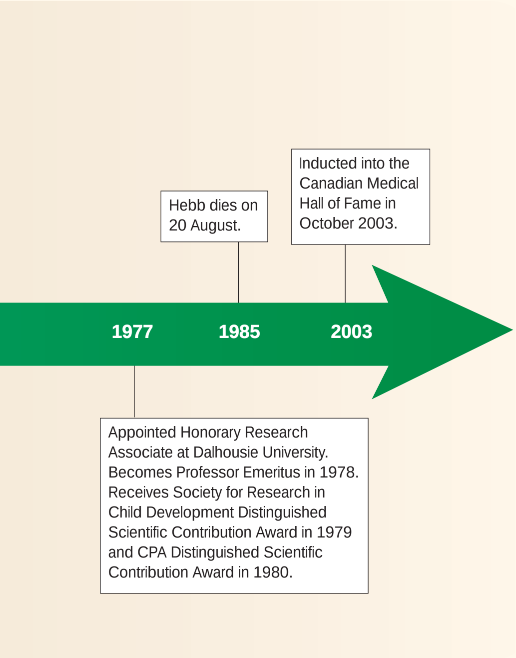
Hebb's M.A. thesis shows the influence of these publications. In this figure, he shows that axons fired by a stimulus during the elicitation of a reflex are attracted to the active effector and become able to fire it. Fired axons passing close to neurons that are not active during the reflex retreat from those neurons. Hebb's summary of this proposal in his thesis is: "An excited neuron tends to decrease its discharge to inactive neurons, and increase this discharge to any active neuron, and therefore to form a route to it, whether there are intervening neurons between the two or not. With repetition this tendency is prepotent in the formation of neural routes."[12]



Neuropsychology at the MNI

In the summer of 1937, Hebb's sister Catherine, then a Ph.D. student with Babkin at McGill University, told him that Wilder Penfield, founder of the Montreal Neurological Institute (MNI), was looking for someone to study the psychological effects of brain operations. Hebb, newly married to his second wife Elizabeth, applied for the job and was appointed a fellow of the MNI. Hebb's work in Penfield's surgery marked a turning point in the scientific study of human neuropsychology. Hebb was critical of both the Stanford Binet and the Wechsler intelligence scales for use with patients[17,18]. He observed that lesions of different brain areas produce different cognitive impairments, and he suggested that, rather than measuring overall intellectual change, one should seek specific aspects of intelligence that were affected by a brain lesion[19].

Hebb therefore assembled a battery of tests, including two new tests — the verbal Adult Comprehension Test and the non-verbal Picture Anomaly Test — which he was developing with N. W. Morton of the McGill Psychology Department[20]. Using the Picture Anomaly Test, he provided the first indication that the right temporal lobe was involved in visual recognition[17]. His most important papers from this period were those concerning



the functions of the frontal lobes[21,22]. Hebb showed that removal of large portions of the frontal cortex had little effect on intelligence, as measured by the standardized tests of the time. Hebb was most impressed by the patient K.M.[21], whose frontal lobes had been operated on by Penfield to remove epileptic foci. Hebb noted that removal of tissue constituting one third or more of each frontal lobe resulted in "a striking post-operative improvement in personality and intellectual capacity"[21], Hebb's theory that the frontal lobes are important only for learning during early life had an important influence on the view of the brain that he presented in *The Organization of Behavior*.

Hebb never studied patients again after he left the MNI in 1939, but after he returned to McGill in 1947, he collaborated with Penfield through his students and colleagues. These included Mortimer Mishkin and H. Enger Rosvold, who followed up his ideas on the frontal lobes[23], and Brenda Milner, who extended Hebb's ideas and techniques to further explore the effects of temporal lobe lesions[24], most famously with patient H.M.[25].

Developmental psychobiology

Inspired by his theory of the changing role of the frontal lobes with age, Hebb began working on the development of rat intelligence. At Queen's University, where he was appointed to a teaching position in 1939, Hebb and a student, Kenneth Williams, designed a variable path maze[26]. The Hebb–Williams maze has since been used in a plethora of studies of comparative learning in animals[27].

To determine the effects of early experience on learning, Hebb used this and other mazes to test rats blinded at different ages, and rats reared as pets at home versus rats reared in laboratory cages. He showed that enriched experience during development resulted in improved maze learning in adulthood[28], and he concluded "there is a lasting effect of infant experience on the problem-solving ability of the adult rat." These ideas formed the basis of one of the most powerful concepts in developmental psychology, leading to the establishment of 'early start' programmes to enrich the experiences of underprivileged children in reading, writing and mathematical abilities, and in music, sports and art (Head Start)[29], and studies on the effects of environmental stimulation on neural development[30]. They still influence research today. He also showed that the effects of brain damage on the development of intelligence depended on the age when the damage occurred[31].

The Organization of Behavior

In 1942, Lashley moved to Orange Park, Florida, to replace Yerkes as Director of the Yerkes Laboratories of Primate Biology, and he invited Hebb to join his team to investigate chimpanzee behaviour. Hebb's role was to develop tests of emotion that could be used with normal and brain-lesioned animals. Lashley was to investigate learning, but he found chimpanzees more difficult to teach than rats, and no chimpanzees were operated on during the five years of Hebb's fellowship. Hebb did, however, develop several tests for fear and anger expression in intact chimpanzees[32].

The research proceeded slowly, but the intellectual climate was stimulating. By the end of his five-year fellowship, in addition to several papers on emotionality[32,33] and dolphin behaviour[34], Hebb had completed the manuscript of a book, eventually published under the title *The Organization of Behavior*. In this book, he outlined an entirely new way of relating brain and behaviour, based on the conviction, not then prevalent among psychologists, that the only scientific way to explain behaviour was in terms of brain function.

Hebb summarized with great clarity some of the problems confronting psychologists in the middle of the twentieth century, and outlined his solutions for them. The first problem concerned 'mental' processes, such as attention and determining tendency, that were generally acknowledged to be important, but that had been declared off-limits for psychologists by the dominant school of neo-Pavlovian behaviourists. Hebb was critical of the Pavlovian stimulus–response (S–R) association model, on which behavioural learning theory was based at that time. He attributed its adoption to an overzealous attempt to avoid the 'little man in the head' fallacy. Hebb's theory lays great emphasis on stimulus–stimulus (S–S) association.

Figure 1 | **Chester, Nova Scotia.** Donald O. Hebb at his summer home in 1942, with daughters Jane at his side and Mary Ellen on his shoulder. Photo courtesy of Mary Ellen Hebb.

A second important problem involved perception. It is clear that visual recognition does not depend on the excitation of a specific group of receptors. Circles of different sizes and retinal position are all readily recognized as circles, although they cannot be stimulating the same receptors. Similar generalization takes place in other modalities. This is difficult to reconcile with the evidence that the traces that are responsible for recognition are structural, involving, for example, changes in synaptic strength of specific neurons. Separate neural structures for the recognition of every object at every size and position would require more neurons than we possess.

Regarding the first problem, Hebb points out that neo-Pavlovian learning theory, although officially non-physiological, was in fact based entirely on an out-of-date anatomical map, in which receptor organs, such as the eye and the ear, feed input to the brain, and paths leading from the brain deliver its output to muscles and other effectors.

Classical learning theory attempted to formulate what happens to the information during this journey. Because neurons conduct in only one direction, the route was misguidedly assumed to be 'one way'. Furthermore, the entire transmission path was postulated to be passive, adding nothing to the input signal. This made it difficult, if not impossible, for the theory to take account of mental processes like intention or desire, should such 'heresy' ever be contemplated.

Hans Berger's announcement, in 1929 (REF 35), that the brain exhibits continuous electrical activity changed all this. Simple equations could no longer be considered as realistic representations of the S–R relationship in living organisms; the intrinsic activity of the path must be taken into account. For Hebb, this meant that psychologists could no longer pretend that the biology of the organism is irrelevant. If, as seems obvious, behaviour is affected by variables like attention and set, psychological theory cannot ignore them. The phenomena must be related to neural activity, and if current neural data cannot explain them, the only scientifically acceptable conclusion is that current data are wrong or incomplete. Hebb pointed out that electroencephalic data clearly demonstrated the inadequacy of the physiological data on which classical behaviourism rested. This was Hebb's justification for adopting a neural theory based on more current neurophysiological data.

Generalization in the visual system was the main issue that was tackled by Hebb in *The Organization of Behavior* (BOX 3). The Gestalt school of thought for the explanation of generalization was that sensory input establishes a field, perhaps electrical, in the brain. The form taken by the field was stipulated to depend only on the pattern of the stimulus, and not on the specific location of the stimulated receptors, so similar patterns always gave rise to the same field. Gestalt theory could not explain how recognition of the field was acquired, however. When this question arose, the Gestalt answer was that recognition took place in the mind. The rival behaviourist school of thought, on the other hand, could explain the learning but was vague as to how a pattern falling on different receptors could reach the same learned recognition structure. Hull[36] suggested that it was by "afferent neural interaction", but did not explain how that process might work.

Hebb thought that these problems could be solved by the application of up-to-date neural data, and he claimed that his theory did just that. Unfortunately, however, the anatomy and physiology of the 1940s was only marginally better than that of the 1920s. Little was known about the structure and connections of the neocortex, and even less was known about the anatomical connections between and within subcortical and brainstem nuclei. Synaptic transmission was still believed to be electrical, making inhibition, the action of psychoactive drugs, learning, neural effects lasting for longer than a few milliseconds and many other neural mechanisms much more difficult to understand than they are today, now that we know that most synaptic transmission is chemical.

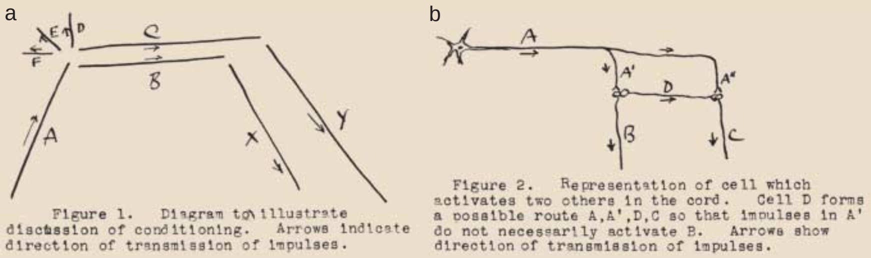
Figure 2 | **Dalhousie University.** Donald O. Hebb at Dalhousie University, circa 1922. Photo courtesy of Mary Ellen Hebb.

Even some of the psychological data that was available to Hebb proved to be unreliable. Lashley was convinced, on the basis of his 1929 rat maze experiments, that the non-sensory cortex is equipotential for learning[37]. Present-day imaging methods show this to be far from the case. Hebb also believed that perceptual learning developed slowly, whereas we now know that infants can recognize some objects by sight within a few hours of birth, and might learn about some sounds even before birth.

Nevertheless, Hebb employed this unpromising material with great ingenuity to conjure up cell-assemblies and chains of cell-assemblies, linked by the neural activity accompanying eye movements that he called phase-sequences. Hebb envisioned phase-sequences as neural representations of images and concepts. Many psychologists were disillusioned by the rarefied philosophy of the neo-Pavlovians, so these constructs were received with great enthusiasm. The Hebb of 1945 would not have recognized the nervous system of 2003, but if it had been accessible to him when he was writing his book, who knows what a wonderful psychological theory he would have woven from it?

Hebb acknowledged that his theory would need revision in the light of new discoveries. All theories are built on the shifting sand of experimental data, and the sand on which Hebb built shifted unusually quickly, partly as

Box 2 | Development of the 'Hebb synapse' postulate: 1934



As a Ph.D. student at the University of Chicago in 1934, Hebb re-applied his ideas in a paper for his anatomy class, entitled 'The interpretation of experimental data on neural action'. One of the figures from this paper (panel a) illustrates the Hebb synapse principle. A represents an afferent axon excited by the stimulus to be conditioned, and X and Y represent efferent tracts leading to the active reflex and to other less active reflexes. The co-incidence of excitation in A and reflex activity in X would lead to the formation of a route A–B–X and to the discontinuance of other routes, such as A–C–Y, A–D and A–E. So, to explain the acquisition of conditioned reflexes, Hebb modified the neurobiotaxis theory in two ways: 1) only active axons would grow towards active target cells, and 2) active axons would be repelled by inactive cells. Another figure from this paper (panel b) expands this concept to an axon A with two terminal branches A' and A" activating B and C. With greater activity of B, the route A'–B will be strengthened, but if there is an interneuron D, which is activated by A', the route A'–D–C will be strengthened.

a consequence of his own activities. The fact that a large part of his structure remains intact today is a tribute to his intuition. He knew better than the physiologists what sort of brain would be needed to produce the behaviour he observed. Though the material he used was primitive and faulty, he lashed it together into something that served his purpose, which was primarily to promote the idea that the future of psychological theory lay in the arms of the neural sciences. In this, he succeeded far beyond his expectations.

In 1949 Hebb stood at the crossroad, pointing out the new road called neuroscience, which psychologists and biologists with an interest in the nervous system and behaviour could take together to reach their common goals. The enduring value of Hebb's writing stems from this vision. Few people today would defend the nuts and bolts of Hebb's neuropsychological theory of perceptual learning, but it provided a goal towards which psychological theory should move, and showed what could be done as anatomical and physiological knowledge expanded. The ensuing progress in that direction more than justifies the acclaim that Hebb's speculations have enjoyed for the last half-century.

Hebb as teacher and administrator

During the 1950s and his later years (FIG. 3), Hebb's name was associated less with research papers and more with theoretical reviews and administrative and educational issues. At McGill, Hebb taught introductory psychology classes, wrote a textbook of psychology[38] (which was reprinted four times), and taught a graduate research seminar. Hebb developed an idiosyncratic philosophy of graduate education[39], in which he stated that you cannot train students to do research, but you can set up the conditions for them to do research. For example, you can encourage them to start research projects early in their career; prevent them from taking too much coursework or formal examinations; help them in choosing a research problem and in making a success of their project, and train them to write. He believed that students should be evaluated on their intelligence and motivation to do research, and their ability to think and do, rather than to memorize the work of others.

Hebb defined psychology as a biological science[40] and stated that it should be studied by objective methods, rather than by introspective, humanistic or subjective methods that are more suited to literature and the arts. Like Lashley, Hebb saw the subject matter of psychology as the mind and the capacity for thought, and he defined thought biologically, as the integrative activity of the brain. Hebb's focus on the biological bases of behaviour and his methods for training students turned McGill into the foremost centre for physiological psychology (behavioural neuroscience) in the world. The success of Hebb's educational methods are reflected in the success of his students, including Bernard Hymovitch, Donald Forgays, Mortimer Mishkin, Brenda Milner, Peter Milner, Ronald Melzack, Seth Sharpless, Woodburn Heron, Helen Mahut, Gordon Mogenson, Case Vanderwolf and legions of others who attended his introductory psychology class and graduate seminar and were motivated to pursue biological psychology as a career.

During the 1950s, work from Hebb's laboratory was often front-page news in the Montreal newspapers. For example, the work of Olds and Milner was reported on the front page of the Montreal Gazette on 12 March 1954, under the headline "McGill opens vast new research field with brain 'pleasure area' discovery." The work of Bexton, Heron, Scott and Sharpless on sensory deprivation was reported in the Montreal Gazette of 14 January 1954 under the headline "See, hear, feel nothing research shows bored brain acts queerly: isolation tests at McGill pay human guinea pigs $20 a day — but few can take it." The same research was treated more harshly in the New York Times of 15 April 1956, which linked Hebb's sensory deprivation experiments at McGill to brainwashing. The Montreal Gazette of 26 April 1956 ran a front page headline "Brainwashing defense found" and a second article entitled "McGill discovery will benefit military", which explained how the Defense Research Board of Canada had contracted the experiments on sensory deprivation to study "so-called brainwashing ... used by opponents of western powers." This was at the time of the Korean War (1950–1953), and the introduction of the term 'brainwashing' in Edward Hunter's book *Brainwashing in Red China* (1951) led to the fear of communist brainwashing of captured soldiers.

Box 3 | Development of the 'Hebb synapse' postulate: 1949

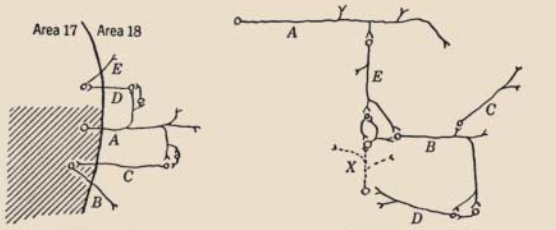


FIGURE 8 FIGURE 9

FIGURE 8. Cells *A* and *B* lie in a region of area 17 (shown by hatching) which is massively excited by an afferent stimulation. *C* is a cell in area 18 which leads back into 17. *E* is in area 17 but lies outside the region of activity. See text.

FIGURE 9. *A*, *B*, and *C* are cells in area 18 which are excited by converging fibers (not shown) leading from a specific pattern of activity in area 17. *D*, *E*, and *X* are, *among the many cells with which* A, B, *and* C *have connections*, ones which would contribute to an integration of their activity. See text.

In the late 1940s, Hebb was confronted with the problem of how a random collection of neurons could be organized by visual stimuli to allow the subsequent recognition of the stimuli. Once more he resorted to his learning postulate. Possibly because the neurobiotaxis idea was strongly criticized during the intervening years, the 1949 postulate differs in two respects from that of his thesis. First, Hebb introduced metabolic change as a possible alternative to growth as a means of changing the effectiveness of a connection. Second, there is no mention of the withdrawal of axons from inactive neurons. This second aspect of the theory has been criticized because it only predicts increases in synaptic strength. Ironically, recent research[43] shows that if neuron A of Hebb's postulate, instead of contributing to the firing of neuron B, fires after B has already fired, the connection between A and B is weakened, as Hebb originally proposed. The figure illustrates Hebb's hypothetical cortical circuit to explain how his learning postulate was involved in the growth of cell assemblies[1].

In 1973, Bliss and Lomo[60] reported long-term potentiation (LTP) of synaptic transmission in hippocampal neurons after tetanic stimulation of an afferent path. This could have been the result of a diminished synaptic resistance, but in 1994 Lin and Glanzman[61] showed that if a cell was hyperpolarized to prevent it from firing during stimulation of the afferent path, it showed no LTP. So, nearly a decade after his death, it was confirmed that at least some neurons behaved in accordance with Hebb's neurophysiological postulate. Figure reproduced, with permission, from *The Organization of Behavior* © Mary Ellen Hebb.

Figure 3 | **Montreal Neurological Institute.** Donald O. Hebb delivering the Hughlings Jackson Lecture in 1958. Photo courtesy of Mary Ellen Hebb.

Although aspects of Hebb's sensory deprivation experiments are still classified as secret, most of the results have been published, including a summary in *Scientific American*[41].

Hebb's belief that the biological basis of the mind is the proper study of psychology, combined with his conceptual focus on the synapse and the cell assembly, allowed him to apply his ideas on the biological basis of behaviour to social and clinical psychology, motivation, perception, thought and the study of consciousness. In his presidential address to the Experimental Division of the American Psychological Association[42], Hebb incorporated the newly discovered reticular arousal system into his theory to explain optimum levels of arousal for different tasks, and in the *Handbook of Social Psychology*, Hebb and Thompson[43] examined the social importance of animal research for human behaviour as an approach to the biological basis of behaviour.

Hebb's 1980 book *Essay on Mind*[13] is a summary of his ideas on the biological basis of mind. It is also a sequel to *The Organization of Behavior* and a completion of the unfinished book he started to write in 1933, in which the first chapter was entitled 'The conception of mind' bringing his writing full circle from 1980 back to 1933.

Hebb was the chairman of the Psychology Department at McGill from 1948 to 1958 and Vice Dean of biological sciences from 1964 to 1966. After his 'retirement', he was elected Chancellor of McGill University from 1970 to 1974. Throughout his career, Hebb received many honours (TIMELINE). He was given honorary doctorates by 15 universities and was nominated for the Nobel Prize in Physiology and Medicine in 1965.

Hebb's legacy

The legacy of Hebb is found in every area of psychology and neuroscience. Modern neuropsychology is based on Hebb's work with Penfield, the study of environmental effects on development derives from Hebb's pet rats reared at home in an enriched environment, and computer models of the brain are based on Hebb's ideas of the synapse and cell assembly. Also, the physiological bases of learning and memory are based on Hebb's ideas of multiple memory systems, and long-term potentiation (LTP) is the experimental analysis of Hebbian synaptic plasticity. Hebb's frequent emphasis on the effects of the timing of neural impulses on brain function is in keeping with the recent discovery of spike-time-dependent synaptic plasticity[44,45], and the work of Hubel and Wiesel on neural plasticity of sensory system development was inspired by the first five chapters of *The Organization of Behavior*. In addition, studies of the neural bases of emotion, motivation, reward and pain derive from Hebb's ideas and the research of his students.

Hebb's ideas have stood the test of time and have become the central tenets of psychology and neuroscience. Although a 2002 study[46] ranked Hebb as only the nineteenth most eminent psychologist of the twentieth century, a greater awareness of what we owe to Hebb should increase this ranking substantially. Interestingly, the fiftieth anniversary of *The Organization of Behavior* stimulated more reviews[2,44,47–49] than appeared in the years just after the original publication[49]. Hebb's ideas are the basis of special issues of the *Canadian Journal of Experimental Psychology* (March 1999) and *Biological Cybernetics* (December 2002). Four papers on the Hebb rule and Hebb synapse appeared in the February 2003 issue of *Canadian Psychology*[50–53]. But the greatest tribute to Hebb was probably paid by Adams[54], who stated that "Two of the most influential books in the history of biology are Darwin's *On the Origin of Species* (1859/1964) and Hebb's *The Organization of Behavior* (1949)."

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Competing interests statement

The authors declare that they have no competing financial interests.

Online links

FURTHER INFORMATION
American Psychological Association: http://www.apa.org/
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CORRECTION

MYELIN-ASSOCIATED INHIBITORS OF AXONAL REGENERATION IN THE ADULT MAMMALIAN CNS

Marie T. Filbin

Nature. Rev. Neuroscience **4**, 703–713 (2003)

In box 2, the second sentence of the second paragraph should read "how can this be the case when sialic acid-dependent binding seems to be non-essential for Mag to bring about inhibition?"

CORRECTION

THE HIGH-CONDUCTANCE STATE OF NEOCORTICAL NEURONS *IN VIVO*

Alain Destexhe, Michael Rudolph and Denis Paré

Nature Rev. Neurosci. **4**, 739–751 (2003)

In Figure 6b, the abscissa should read "Input frequency (Hz)". The legend to figure 6b should read "The right panels show examples of interspike interval (ISI) histograms for stimulation at 4 ms and 12 ms interstimulus intervals, for the quiescent (bottom) and high-conductance (top) states."