The Life and Work of Donald Olding Hebb

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Abstract- In his book, The Organization of Behavior, Donald Olding Hebb introduced the concepts of synaptic plasticity and cell assemblies to provide a theory of the neurophysiological basis of behaviour. Hebb's ideas, as presented in this book and other writings, influenced all areas of psychology and neuroscience. Hebb was born in Chester, Nova Scotia, Canada and attended Dalhousie University (BA, 1925) and McGill University (MA, 1932). His PhD from Harvard in 1936 was supervised by Karl Lashley. Hebb worked with the neurosurgeon Wilder Penfield at the Montreal Neurological Institute for two years, taught at Queen's University in Kingston, Ontario, and was a research assistant with Lashley at the Yerkes Primate Labs in Florida before he became a professor of Psychology at McGill University in 1947. At McGill he taught the first year psychology course and wrote an introductory textbook in Psychology. Throughout his career, Hebb made many research discoveries, trained a number of researchers and won many honours. When he retired from McGill, he moved back to Nova Scotia, and became a Professor Emeritus at Dalhousie University. This paper reviews Hebb's life and work and the impact of his ideas in psychology and neuroscience.

Key Words: Biography, Hebb synapse, History, Organization of behaviour, Learning, Memory, Development, Perception

Acta Neurol Taiwan 2006;15:127-142

INTRODUCTION

Donald Olding Hebb's most influential book is The Organization of Behavior published in 1949[1]. Establishing a biological basis for psychological phenomena, this book introduced the concepts of synaptic plasticity and cell assemblies to account for the neural events underlying behaviour and these ideas revolutionized psychology. Hebb became a professor of Psychology at McGill in 1947 and head of his department in 1948. At McGill he taught the first year psychology course and wrote a unique and original introductory textbook in psychology[2]. Hebb was elected president of the Canadian Psychological Association in 1952 and the American Psychological Association in 1960 and became a fellow of the Royal Societies of Canada and England. Late in his career, he was the Vice Dean of Biological Sciences at McGill from 1964 to 1966 and the Chancellor of McGill University from 1970 to 1974. When he retired from McGill, he moved

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Received September 8, 2005.
Revised and Accepted October 4, 2005.
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back to Nova Scotia, where he was born, and became a Professor Emeritus at Dalhousie University from 1978 until his death in 1985. During this time he wrote his last book, Essay on Mind[3]. Hebb was inducted into the Canadian Medical Hall of Fame in October 2003. This paper reviews Hebb's life and work up to the publication of The Organization of Behaviour and the impact of his ideas in psychology and neuroscience. One paper on Donald Hebb has been published in Chinese[114].

1. Hebb's family

Much of what we know about Donald Olding Hebb comes from his published autobiography[4] but he also wrote an unpublished letter for his children and grandchildren that discusses his non-academic life[5]. Hebb's father, Arthur Morrison Hebb (1872-1959) received a BA in 1899 and an MD in 1902 from Dalhousie University and his mother, Mary Clara Olding (1870-1921) received an MD in 1896 from Dalhousie University, the third woman to do so[6]. Donald was born on July 22nd 1904, the first of four children (Figure). His brother Andrew (1905-2005) received a degree in law from Dalhousie in 1927 and was the founding chief executive of the Co-operators Insurance Company. Peter (1909-1955) received an MD in 1934 from Dalhousie and practiced medicine in Dartmouth, Nova Scotia. His sister Catherine (1912-1978) received a BA in Biology in 1932 and an MA in Pharmacology in 1933 from Dalhousie and a PhD in Physiology from McGill University in 1937. She studied the physiology of the digestive system with Dr. Boris Babkin at McGill and then taught in the Department of Physiology at the University of Edinburgh. Later she joined the Physiology Department of the Institute of Animal Physiology at Babraham, Cambridge, where she studied the biosynthesis of acetylcholine[7].

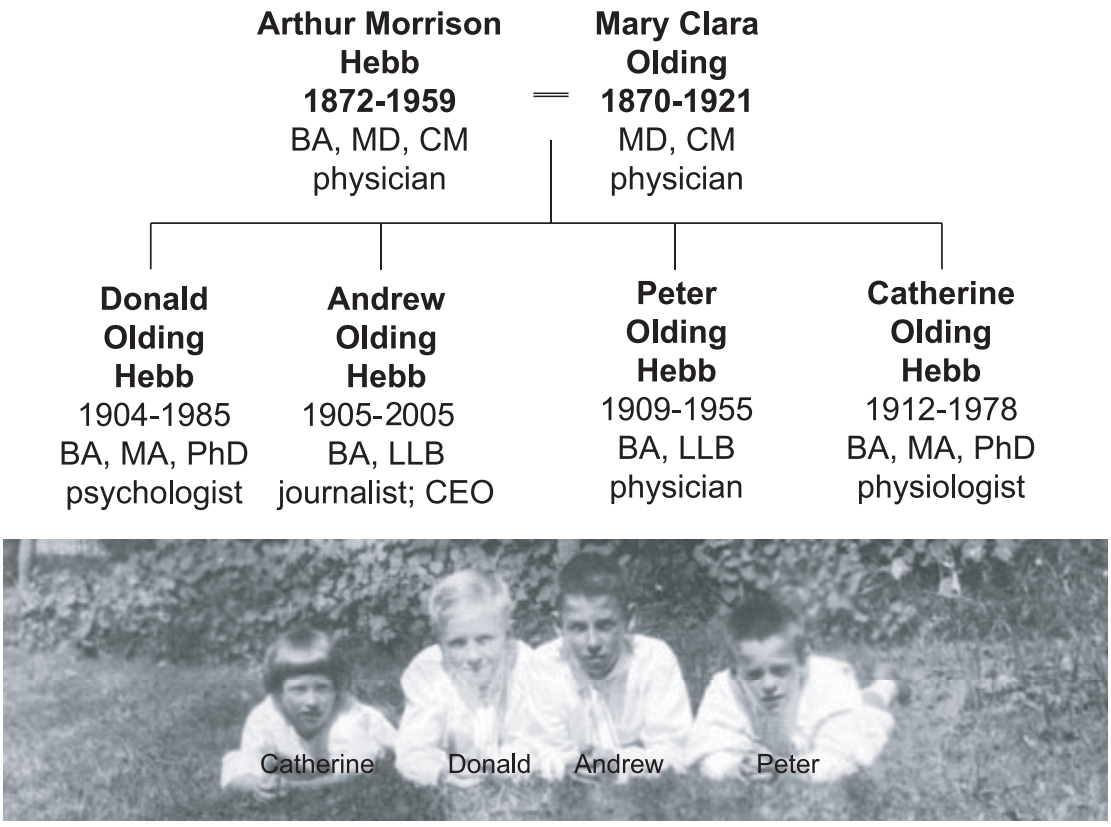

Figure. Hebb's family. From Gordon D. Hebb, with permission.

2. Hebb's student years

Donald was taught at home by his mother until he was 8 years old and entered the Chester School in the second grade. An avid reader, he advanced rapidly so that he reached the ninth grade at age 12[4]. He found that school came easily to him and, after winning a school spelling competition at age 10, he did little studying. As the result of lax teaching and poor study habits, he, and many of his classmates, failed the grade eleven provincial exams and had to repeat the eleventh grade. When he was 16, his family moved to Dartmouth, Nova Scotia, and both Donald and Andrew completed high school at the Halifax County Academy. They both entered Dalhousie University in 1921. Although his father wanted him to study math and physics like his uncle, Thomas Carlyle Hebb (the first head of the Physics Department at the University of British Columbia), Donald entered the Faculty of Arts, choosing to major in English and Philosophy with the intention of becoming a novelist[4]. After graduating in 1925, he took summer classes to obtain a teaching certificate from the Provincial Normal College in Truro, Nova Scotia, and spent a year as principal of his old school in Chester.

During the summer of 1926, Hebb worked as a laborer on a farm in Alberta, where it is thought that he contracted tuberculosis. In 1927 he moved to Montreal, where he returned to teaching at Verdun High School. During this time he began to read Freud and became interested in psychology. Hebb met Professor W. D. Tait, the head of the Psychology Department at McGill and in 1928, he attended his evening class in psychology for teachers. From 1928 to 1930, Hebb continued to teach in Verdun and studied as a part-time graduate student in Psychology at McGill under the supervision of Professor Chester Kellogg. During this time Hebb was appointed principal of Rushbrooke school and, with the help of Professor Kellogg and Professor Clarke from the McGill University Faculty of Education, he started his educational experiment. Hebb found that students of all intellectual abilities were failing at school. His experiment consisted in changing the school procedures in order to facilitate education and persuade the children that schoolwork was a privilege. Students were given no homework and were not punished for inattention. They were given more interesting classroom activities and those who disrupted the class were sent outside to play. Hebb published a short review of his educational experiment in 1930[8].

Hebb was bedridden between 1930 and 1931 with tuberculosis of the hip, which left him with a permanent limp. During this time, he convalesced at his father's home in Dartmouth, Nova Scotia, and was married[4]. While he was bedridden, Hebb studied Sherrington's Integrative Activity of the Nervous System and Pavlov's Conditioned Reflexes. He also wrote a theoretical MA thesis entitled Conditioned and Unconditioned Reflexes and Inhibition, which he submitted to McGill University in 1932[9]. This work is of interest because it contains Hebb's first thoughts on the nature of synaptic activity during conditioning[10]. The thesis was passed by two examiners, Professor Kellogg of the Psychology Department and Professor Boris P. Babkin of the Physiology Department, who had worked with Pavlov in St. Petersburg. After the completion of his MA thesis, Hebb worked in Babkin's laboratory, studying Pavlovian conditioning with Leonid Andreyev, another student of Pavlov's.

Hebb's teaching career continued while he was working on his PhD at McGill and from 1931 to 1934 he was the principal of Riverview School in Verdun. The year 1933-34, however, was not a good year for Hebb. The Protestant School Board of Montreal terminated his educational experiment[4] and, he became disillusioned with Pavlovian conditioning procedures and his graduate studies at McGill. Furthermore, Hebb and his wife were in a car accident and she died on his birthday in 1933. Following these difficulties, Hebb decided to leave McGill and complete his PhD elsewhere.

3. PhD research with Karl Lashley

Professor Babkin urged Hebb to apply to do a PhD with Karl Lashley at the University of Chicago. Lashley had published his book "Brain Mechanisms of Intelligence" in 1929[11] and his 1930 presidential address to the American Psychological Association outlined the state of the art in the physiology of behaviour[12]. In July

1934 Hebb was accepted to the University of Chicago and he became an important member of Lashley's research group. During the time that Hebb was in Chicago, it was the Centre of Functional Psychology with a focus on the biological basis of behaviour[13], an approach that Hebb was to take for the rest of his career.

Only a year after Hebb arrived, however, Lashley accepted a position at Harvard and Hebb moved with him to Cambridge, Massachusetts. In April 1936, Hebb submitted his PhD thesis on the visual abilities of rats reared in the dark[14] and received a Harvard PhD. For the next year, Hebb worked as a Research Assistant for Lashley, and as an instructor in Introductory Psychology for Professor E. G. Boring. During this year, Hebb published his PhD research[15] and completed the research on field orientation in rats[16] that he had started in Chicago. In 1937, Hebb married Elizabeth Donovan, his second wife, who had studied education and sociology at the University of Chicago. She was the mother of his two daughters, Jane and Mary Ellen.

4. Neuropsychology at the Montreal Neurological Institute: 1937-39

In 1937, Hebb began to study the psychological effects of brain operations on the patients of Wilder Penfield, the founder of the Montreal Neurological Institute (MNI). Penfield was the leading neurosurgeon of his day, and he specialized in surgery for epilepsy patients[17]. Hebb's work with Penfield's temporal and frontal lobe surgery patients initiated the scientific study of human neuropsychology. His most complete study was of patient KM[18], who had had a frontal lobotomy. Hebb tested this patient before and after his surgery and found little effect of the surgery on his scores on the standardized tests available at the time. Hebb concluded that the removal of large amounts of frontal lobe tissue either had no effect on the mental abilities of the patient or that the tests used were not sensitive enough to detect the effects of the surgery[18,19]. His experience in testing patients at the MNI led to a number of ideas about the nature of intelligence and how it should be tested[20,21]. With N. W. Morton of the McGill Psychology Department, Hebb began to develop two new tests, the verbal Adult Comprehension test and the non-verbal Picture Anomaly test[22]. Hebb also observed that lesions of different brain areas produced different cognitive impairments[23], that the age at which brain injury occurred was important in determining its effects on intelligence[24] and that intelligence was composed of two components, a fixed or innate component and a variable component that could be influenced by environmental experiences[24].

5. Hebb at Queen's university: 1939-42

In 1939, Hebb became a Lecturer in Psychology at Queen's University in Kingston, Ontario. Here he introduced a course in Experimental Psychology using textbooks written by E.G.Boring, and also had students conduct laboratory experiments[25]. Despite his heavy teaching load at Queen's, Hebb managed to publish work completed at the MNI on the frontal lobes[18] and on the effects of brain lesions at different ages[24] and to do some research projects with his students. With Kenneth Williams, he designed a variable path maze[26] for testing learning and memory in rats. This Hebb-Williams maze has since been used in a plethora of studies of comparative learning in animals and humans[27].

While Hebb was at Queen's, he was involved in founding the Canadian Psychological Association, which began in 1940. The first accomplishment of this group was the development of the M-test, an Army classification test for new recruits, developed primarily by N. W. Morton. The first issue of the Bulletin of the Canadian Psychology Association was published in October 1940. Hebb was the editor from December 1940 until he moved to Florida in 1942. Hebb's memory of his editorship of the Bulletin is that:

George Humphrey volunteered me to operate a newsletter for the membership. Instead of mimeographed sheets, I found a printer who would print an 8-page booklet for $25. Thus I became Editor of the Bulletin of the Canadian Psychological Association. I was also typist, proofreader, business manager and author of half of what appeared in it -though credited to someone else. In the year and a half of my editorship, nothing appeared that I had not begged for or written myself[28].

6. Hebb at the Yerkes Primate Research Laboratory: 1942-47

Lashley became the director of the Yale Primate Laboratories at Orange Park, Florida, in 1942 and he hired Hebb as a Research Associate (1942-45) and then as a Harvard University Research Fellow (1945-47). Hebb's research at Yerkes was on fear and anger in chimpanzees[29,30] and he related these findings to human emotionality[31,32]. In addition to his research on primates, Hebb studied the behaviour of dolphins[33] and continued his work on the development of rat intelligence. To determine the effects of early experience on learning, Hebb reared rats as pets at home, and showed that enriched experience during development resulted in improved maze learning in adulthood. Although these results were only published as an abstract at an American Psychology Association meeting[34], they formed the basis of many studies on the effects of environmental enrichment on behaviour and neural development[35], one of the most important concepts in developmental psychology, which still influences research today[36].

7. The Organization of Behavior, part 1: 1944-47

During his years at Orange Park, Hebb also completed the first five chapters of the manuscript of a book, eventually published under the title The Organization of Behavior, in which he outlined a new way of understanding behaviour in terms of brain function. In a 1959 paper Hebb explained how his theory of behavior came into being[37]. He states that his work on effects of brain lesions at different ages on intelligence[24] led him to the conclusion that "intelligence itself, and not merely the ability to do well on intelligence tests must be a product of experience'[4]. Hebb was then led to ask the question: "If concepts, modes of thought, and the way of perceiving constitute intelligence, what is a concept in terms of neural mechanisms?" In trying to answer this questions, Hebb recalled that:

... at this point my thinking stalled, partly because, like everyone else, I was still thinking of the brain as a through-transmission device and partly because of difficulty in reconciling the facts of learning (which must be localized in specific synapses) and the facts of perception (which, it seemed, is not localized). I had given up thinking about the problem for two years or so, when, in 1940, Hilgard and Marquis[38] drew my attention to Rafael Lorente de No's work and led me to write The Organization of Behavior, which contained a theory quite different from any of my earlier ideas[4].

Between 1933 and 1934, while still at McGill, Hebb wrote five chapters of a manuscript entitled Scientific Method in Psychology: A Theory of Epistemology Based on Objective Psychology[39]. These ideas stayed with him (as did his unpublished paper) as he began to formulate a neurophysiological theory of behaviour in 1944. Hebb's first notes for The Organization of Behaviour were outlined in a manuscript entitled "Precis: The Structure of a Set of Neuropsychological Speculations"[40], which was dated "March - July 1945". This precis outlined eight postulates whose aim was to provide physiological explanations for psychological processes such as attention, perception and learning. It is in these notes that Hebb worked out the basic propositions of his theory, which he states "is not merely a translation [of psychological data] into physiological terms, but does suggest the basis of considerable synthesis and makes possible an intelligible formulation of the problems of attention and thought, as a function of central processes"[40].

There were a number of problems that Hebb had to overcome in order to develop his neuropsychological theory and he mentions three of these in his notes: the inter-relatedness of psychological concepts; the assumption that behavior is under sensory control; and the lack of neurophysiological data. He dealt with these problems by developing a set of postulates which became the building blocks of his theory. These were that perception required learning; that synaptic change could account for learning; that neural activity could be separated from sensory input; and that both perception and learning could be accounted for through the development of cell assemblies.

The idea that perception required learning was stimulated by the work of von Senden[42,42a] on the development of visual ability in congenitally blind people after

surgical operations which enabled them to see for the first time. Hebb used the case studies in this book and the work of Riesen[43] on monkeys reared in the dark to argue that perception relied on learning. It was only after he developed the idea of perceptual learning that Hebb returned to his own PhD thesis and understood how he mis-interpreted his results. Hebb[15] had concluded that visual ability of rats was innate as rats reared in total darkness could discriminate between two figures, but in proposition H of his Precis[29], he realized that his rats reared in darkness took much longer to make this discrimination than rats reared in the light as they had to undergo a period of perceptual learning once they were removed from the darkness[30]. Although Wertheimer[44] disagreed with Hebb's interpretation of von Senden's results, they were crucial to Hebb's development of the concept of the cell assembly and the idea that perceptual organization occurs through a process of learning. This allowed Hebb to critique Kohler's field theory and Lashley's theory of equipotentiality and to consider attention and the development of perception in his neuropsychological theory.

Hebb relied on two books for his background information on learning theory and the physiology of behaviour[38,50], both of which explained the synapse and neural connections as described by Lorente de No[41]. These references determined how Hebb thought that synapses functioned. When Hebb was developing his ideas about the neural basis of behaviour in 1944 and 1945, there were no textbook descriptions of chemical transmission in the CNS and thus no neurotransmitters to discuss. Hebb, like everyone else, was working only with the idea of electrical transmission in the cortex. This meant that the brain was envisioned as a series of electrical circuits. Changes in "bio-electric fields" were thought to underlie learning[38]. The neurochemical synapse was not formally acknowledged until Eccles published his seminal paper[48] and it was only in 1954 that Eccles came to believe that synaptic transmission in the CNS could be chemical as well as electrical. Thus, Hebb's idea that synaptic change accounted for learning came from the ideas in these papers. He did not claim that the "Hebb synapse" idea was his own.

Hilgard and Marquis[38] focused on Lorente de No's[41] theory of recurrant (Reverberating) nerve circuits, and it was from these that Hebb developed his idea of "lattices" (later changed to "cell-assemblies"). The concept of the cell assembly, with its reverberating circuits, meant that neural activity could continue in the absence of an external stimulus. Eccles had developed the idea of inhibitory synapses[51] but Hebb did not incorpaorate the concept of inhibition into his theory; it had to wait for Milner's[52] revision. The cell assembly theory provided a neural explanation for perceptual processes and learning as both relied on external input to develop a mental image (cell assembly). The concept of the phase sequence allowed cell assemblies to communicate and thus provided the neural basis for thought and other higher order mental processes.

Hebb wrote the first three chapters of The Organization of Behavior in Florida between 1945 and 1946 and sent them to a number of his colleagues for comments. E. G. Boring at Harvard sent Hebb six pages of comments and advised him to be briefer, more positive, kindly, gay, friendly, and less defensive and sober. Boring's detailed comments discussed each page of Hebb's manuscript. Hebb gave his manuscript to Lashley, who replied with two pages of comments in February 1947, and was not impressed with the manuscript. Hebb asked him to be a coauthor, but he declined, telling Hebb that it was very weak with no value because it was so and vague. Despite Lashley's negative opinion, Hebb submitted the first five chapters of his manuscript to Thomas Publishers in 1947. Henry Nissan was sent the manuscript to review, and between March and September 1948, he sent Hebb many letters with comments on each chapter.

8. Harvard and McGill: 1947-48

Edwin G. Boring, now the Chairman of the Psychology Department at Harvard, offered Hebb a teaching position during the summer session of 1947. Hebb taught a class in physiological psychology, and a graduate seminar for which Boring suggested "you can try out your book on them", which he did. This draft of the book, however, included only the first five chapters.

One of the students in this class was Mark Rosenzweig, who wrote:

I took a graduate seminar with Donald O. Hebb at Harvard in the summer of 1947 where the text was a mimeographed version of Hebb's influential book The Organization of Behavior which appeared in print in 1949. (I wish I had had the foresight to save that 1947 version.) Hebb's creative suggestions revitalized theorizing and research on learning and memory, and I benefitted directly from them and from further contacts with him[45].

When his summer at Harvard was over, Hebb took a position as Professor of Psychology at McGill University, where his teaching load was as heavy as it had been at Queen's University five years before. Much of his teaching was with graduate students. He taught courses in Comparative Psychology and Physiological Psychology, but much of his teaching was with graduate students.

9. The Organization of Behavior, part 2: McGill 1947-49

During his time at McGill, Hebb was able to consider Henry Nissen's comments on his manuscript. Nissen suggested that Hebb "tone down the criticism" and set "a less argumentative tone". In a letter written on 19 May 1948, Hebb invited Nissen to share authorship of his book. The reasons he gave were that Nissen had already contributed "more than you would be likely to realize", and that Nissen had a number of ideas that were "quite relevant to the main argument." In order to complete the book, Hebb planned to re-write the chapters already critiqued by Nissen, and to complete three more chapters, on emotion, clinical deviations of emotion, and human intelligence.

Nissen wrote back to Hebb on 23 May 1948 and told him that he should complete the book himself, with help from Nissen and from others at Orange Park. He attributed Hebb's request for Nissen to co-author the book to over-reaction to Lashley's criticisms, a failure to realize how good the completed chapters were, and an unrealistic feeling of inability to complete the book within a reasonable length of time. Between May and September 1948, Nissen sent Hebb comments on chapters 8, 9, 10, 11. Austen Riesen, Robert Blum and many others also sent Hebb comments, and on 29 September 1948, Hebb mailed the final manuscript to Thomas Publishers under the title On Thought and Behavior. But Thomas returned Hebb's book, stating that he had a number of other books to publish and did not want to delay the publication of Hebb's book. With the help of letters from Frank Beach and Henry Nissen, John Wiley & Sons agreed to publish the book. On March 18th 1949, James Helming, the Psychology Editor at Wiley, wrote to Hebb that the Editor-in-Chief wrote that:

This is by far the best-written manuscript that has come my way in some time. The exposition is lucid, persuasive, and also lively - the author need have no misgivings about the propriety of his humorous touches; they are distinctly refreshing. Unlike most factual manuscripts this one has a definite appeal on literary merits alone.

And so the book, now entitled The Organization of Behavior was finally published in the fall of 1949. Wiley reported to Hebb that the book sold 1321 copies by February 1950 and 3288 copies by January 1951.

10. The Organization of Behaviour: The basic premises

In his book, Hebb examined the issues concerning psychologists in the 1940s and showed how these problems might be dealt with through a set of neurophysiological postulates. He proposed two concepts, synaptic plasticity and cell assemblies, which have since become central tenants in neuroscience[46]. Hebb devised a way to integrate the research and theories of the most prominant psychologists of the time (Lashley, Kohler, Tolman and Hull), through a common neurophysiological process. Hebb also reinterpreted his own previous research on Penfield's neurosurgery patients, on intelligence and how it develops, on animal models of intelligence, and his work on emotions in chimpanzees and on fear in humans, integrating them all into his theory.

Hebb managed to take 'mental' processes such as attention that had been rejected by the behaviourists, and to relate these psychological concepts to neurophysio-

logical activity. He was critical of the Pavlovian stimulus-response (S-R) association model, on which Hull's learning theory was based, and put emphasis on Tolman's stimulus-stimulus (S-S) associations. Hebb was also critical of the Gestalt School's field theory explanation of generalization in the visual system. Gestalt theory could not explain how recognition of the field was acquired. Behaviourist theory could explain the learning but was vague as to how a pattern falling on different receptors could reach the same learned recognition structure. Hull had suggested it was by "afferent neural interaction", but did not explain how that process might work[47].

11. Hebb's view of the synapse

The neurochemical synapse was not formally acknowledged until Eccles published his seminal paper in 1954[48]. Before this, it was generally believed that synapses in the Central Nervous System were electrical. Thus, in 1945, when Hebb was developing his ideas about the neural basis of behaviour, he did not discuss neurotransmitters as chemical transmission in the CNS was unknown. Hebb had been at the Montreal Neurological Institute while H. H. Jasper was developing the electroencephalograph to study the electrical activity of the cortex[49]. Like everyone else, Hebb was working only with the idea of electrical transmission in the cortex, and he envisioned the brain as a series of electrical circuits. Changes in "bio-electric fields" were thought to underlie learning. Hebb's main references, Hilgard and Marquis[38] and Morgan[50], focused on Lorente de No's[48] theory of recurrant (reverberating) nerve circuits, and it was from this theory that Hebb developed his idea of "lattices", which he later called "cell-assemblies". Eccles had also developed the idea of inhibitory synapses[51] but Hebb did not incorporate the concept of inhibition into his theory; it had to wait for Milner's[52] revision.

Nevertheless, Hebb employed the neuroanatomical and neurophysiological knowledge of the day to develop his ideas of synaptic change, cell-assemblies, and chains of cell-assemblies linked by the neural activity, that he called phase-sequences. Hebb envisioned phase-sequences as neural representations of images and concepts. Hebb realized that his theory would need revision in the light of new discoveries, but the fact that much of his theory remains intact today is a tribute to his intuition. The progress in the development of the neurosciences has justified the acclaim that Hebb's theories have enjoyed since 1949.

12. Reviews of Hebb's book: 1949-2004

Response to The Organization of Behaviour came in the form of published reviews and private letters. The published reviews were uniformly positive, even when they were critical. Manford H. Kuhn stated that "this book will probably come to be regarded as a landmark in psychological theory"[53]. W. J. Brogden wrote that "the neural theory is admittedly gross, and probably impossible to test, but its presentation results in provocative discussion"[54]. Fred Attneave[55] stated that "I believe The Organization of Behavior to be the most important contribution to psychological theory in recent years." In a lengthy review, Leeper[56] wrote that, "there are so many respects in which Hebb's book is so high in quality and is so delightfully written that it will have an assured status in psychology". Although Wertheimer[44] critiqued Hebb's views of the importance of learning in perception, Allport[57] devoted a chapter entitled "The Association Approach, Cell Assembly and Phase Sequence" to a discussion of Hebb's ideas on perception.

Many of Hebb's colleagues wrote to him about their impressions of the book. In November 1949, Lashley wrote to Hebb:

My best thanks for the copy of your book. Although I am still unconvinced by your arguments and disagree with many of the conclusions of the first part, I feel a real admiration for the book. It is an exceedingly thoughtful and stimulating treatment with a broad outlook and a literary style that I envy. Hearty congratulations on an outstanding achievement.

In April 1950, Neal Miller wrote from Yale that "My class found your book most stimulating" and in a four page letter, he listed fourteen questions for Hebb to answer in his upcoming seminar at Yale. Hebb wrote replies to these questions, which he presumably commu-

nicated to Miller's students.

Hebb's book lived up to the reviewer's predictions and became one of the most important contributions to psychology in the 20th century. At the 50th anniversary of its publication, there were almost as many reviews of The Organization of Behavior as when it was originally published[58-60] and the impact of this book has been compared with that of Darwin's Origin of Species[61]. Because the 1966 paperback version of The Organization of Behaviour was out of print, Peter Milner and I had it republished in 2002 with a Foreword about the importance of the book and a bibliography of Hebb's work[10]. This reissue has also been reviewed[62]. Hebb's ideas of synaptic plasticity and cell assemblies have now become fundamental concepts in psychology and neuroscience[46,63-66] and Posner and Rothbart[67] have argued that Hebb's ideas provide the basis for an integration of the disperate sub-fields of psychology. We have examined the origins of The Organization of Behavior[10] and Cooper provides a history and commentary on the Hebb synapse and learning rule[68].

13. Hebb's evaluation of his own book

When Hebb[37] discussed the development of his theory and its impact in psychology, he said that he aimed to "deal with set and attention and perceptual generalization and learning in one theoretical framework, not have one approach for thinking, another for learning, and a third for perception-- the position in which the members of the Gestalt group found themselves". He states that:

My theory is the only one that attempts to do this, and in my opinion, to be quite frank, is consequently the only realistic attempt to deal theoretically with the problems of behavior. Skinner of course has avoided theory; Tolman and Guthrie have proposed approaches to the problem of constructing a theory, but both have remained, essentially, programmatic. Hull's is the only real alternative to mine; and the course of development of his ideas from 1937 to 1951, has shown a narrowing of the range of phenomena dealt with, an increasingly clear set of difficulties to be encountered even in the narrow range with which his theory does deal, and an increasing concern with minor modifications of postulates as defensive measures to meet the attacks of critics. ...Mine, in short, is the only attempt to deal with the thought process and perception in the framework of a theory of learning. It has serious defects, but no real competitor. This fact I see as the major "evidence for the system", together with the body of research that it has, directly or indirectly, stimulated (pages 638-639).

Hebb's retrospective focuses on the importance of Lashley and Kohler in the development of his ideas and the importance of the work of von Senden for helping him understand the role of learning in perception. In the discussion of the value of his theory for stimulating research, Hebb focused primarily on the work of his students[37].

14. Hebb's students and their research: 1947-54

Once Hebb became Chairman at McGill, he began to develop a graduate program in physiological psychology that attracted very high quality students. Between 1933 and 1939 there had been four PhDs awarded in Psychology at McGill. After Hebb arrived, there were 39 PhDs awarded between 1949 to 1958 and 82 between 1959 and 1968. Thus, Hebb had a remarkable influence on the training of graduate students in Psychology at McGill.

Once Hebb had written The Organization of Behavior, he saw his own previous research in a new light and he set his colleagues and students to repeat and extend his old experiments in light of his new view of psychology. Hebb was not a co-author on any of these papers, but is usually mentioned in the acknowledgements. Thus, to understand how Hebb's research was influenced by his theory, one must look at the work of his students. For example, Rabinovitch and Rosvold[69] developed a standardized procedure for the Hebb-Williams maze and tested rats with cortical damage and rats reared in a "free environment". Other students used the Hebb-Williams maze to test the effects of electroconvulsive shocks[70], environmental experience and lesions[71], thalamic stimulation[72], the effects of blindness and early rearing experience[73] and the effects of environmental enrichment[74] on learning and memory.

Other students repeated the studies on the effects of

lesions on intelligence that Hebb began with Penfield. Rosvold and Mishkin[75] looked at the effects of prefrontal lobotomy on intelligence as Hebb had done in 1937; Forgays[76] looked at the development of cognitive dysfunction after surgery and Milner[77] looked at the intellectual function of the temporal lobes as Hebb had done in 1939.

Hebb was also interested in continuing the studies of fear and emotionality that he had started at the Yerkes Primate laboratories. Instead of chimpanzees, however, he now used pure-bred Scottish terriers. The dogs were first tested in studies of early rearing experience (enriched and isolated) as Hebb had done with rats reared at home[78,79], and then on studies of emotional behaviour[80-82], and the development of social behaviour[83].

During the 1950's, work from Hebb's lab was often reported in Montreal newspapers. The work of Olds and Milner, for example, 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[84]". The work on sensory deprivation[85] 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". Hebb[37] explained that his theory stimulated:

...the studies of visual perception of Mishkin and Forgays, Orbach, Heron, and Hunton; the effects of perceptual isolation by Bexton, Heron, Scott, and Doane; the role of the infant environment in mental development by Hymovitch, Forgays and Forgays, Clarke et al., Thompson and Heron, Melzack, and Mahut; and the reexamination of the mass-action and equipotentiality conceptions by Lansdell and Smith. Apart from these studies, the theory as far as I can see had its effect by raising rather general questions and promoting argument in the laboratory".

15. Two important Conferences in Montreal

Hebb's arrival at McGill in 1947, in combination with the MNI made Montreal a world centre for brain research and attracted two major conferences in the early 1950s. The first was the Brain Mechanisms and Consciousness Symposium held in Ste-Marguerite, Quebec in August 1953. In the Foreword to the published volume, Delafresnaye[86] states that:

...the symposium was planned around the general theme of 'Brain Mechanisms and Consciousness'. Research workers in the fields of neuroanatomy, neurophysiology, neurosurgery, psychology and psychiatry were invited to review the functional significance of the brain stem reticular system which was typical at the time.

This meeting brought the top neuroscientists from all over the world to Quebec. These included H. W. Magoun, who presented a review of the ascending reticular activating system and wakefulness, and G. Moruzzi, who reported on the physiological properties of the brain stem reticular activating system. Walle Nauta, W. R. Hess, Mary Brazier, and E. D. Adrian (later Lord Adrian), all gave presentations, as did Wilder Penfield, W. Grey Walter and Herbert Jasper. Hebb spoke on the problem of consciousness and introspection through a discussion of his experiments on sensory deprivation. Lashley spoke on dynamic processes in perception and Lawrence Kubie (from Yale) spoke on psychiatric and psychoanalytic considerations of the problem of consciousness.

The second meeting, the 14th International Congress of Psychology, was held in Montreal in June 1954. It was presided over by Edward C. Tolman, the President of the America Psychology Association and Edward A. Bott, the President of the CPA. Hebb was on the Organizing Committee and was the chairman of the Local Arrangements Committee, along with other McGill faculty[87].

16. Hebb's writings after The Organization of Behaviour

With the completion of The Organization of Behaviour, Hebb had become a major theorist in the field of physiological psychology. Hebb reviewed the field of animal and physiological psychology for the first Annual Review of Psychology[88]. In addition to discussing his student's work, he reviewed the work of the

European ethologists Tinbergen and Lorenz, Beach's work in Hormones and Behavior, Harlow's primate research and the primate studies from the Yerkes labs, the work of Teuber on brain-injured soldiers and the work of Moruzzi and Magoun on the reticular activating system. In "The Role of Neurological Ideas in Psychology", Hebb[89] compared his theory of behavior to the theories of Tolman, Krech, Hull and the Gestaltists, and presented evidence showing the relevance of his neurological approach to the theory of personality. Hebb's[90] presentation at the Association for the Study of Animal Behaviour meeting in London, England, focussed on the problem of separating genetic and environmental components of behaviour. It is in this paper that he states that asking what percent of behaviour is due to heredity and what percent due to environment "...is exactly like asking how much of the area of a field is due to its length, how much due to its width." He also criticized the ethologists for attempting to study innate behaviour before studying learning, saying that such studies are logically impossible because all forms of behaviour involve some form of learning.

Hebb's presidential address to the Canadian Psychological Association, entitled "On Human Thought", focused on the idea that human thought is the central problem for psychology, even though its importance had been denied by S-R behaviorists such as Thorndike, and not explained by the Gestaltists[91]. Hebb then gave a brief discussion of how his cell assembly model could deal with the concept of thought. At the end of this presentation, Hebb used poetry as an example of the complexity of human thinking, and quotes from some of his favorite works. In his symposium paper on the problem of consciousness and introspection, Hebb's used the idea of cell assemblies to explain the neurophysiology of consciousness and presented data from his ongoing studies of sensory deprivation to illustrate that environmental stimulation is important for normal consciousness. He suggested that "The higher animal" "continually behaves in such a way as to seek an optimal degree of disturbing stimulation" to maintain his arousal level.

In the Handbook of Social Psychology, Hebb and Thompson[93] examined the social significance of animal research for human behaviour. This chapter focussed on the influence of animal studies on intelligence, social behaviour, communication, cooperation, emotion, and related these to human behaviour. Here Hebb made use of his research on the emotional behaviour of chimpanzees and on his new work with dogs and the importance of environmental experience. He argued that emotionality and psychopathology result from breakdowns in cell assemblies.

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 Division 3 of the American Psychology Association, Hebb[94] discussed the concept of motivation in terms of the CNS (Conceptual Nervous System). Hebb wrote this paper in response to B.F. Skinner[95,96], who wrote that "the letters CNS be regarded as representing not the Central Nervous System, but the Conceptual Nervous System". Skinner argued that "Many theorists point out that they are not talking about the nervous system as an actual structure undergoing physiological or biochemical changes but only as a system with a certain dynamic output."[96]. Following a historical review of the concepts of motivation, Hebb presented data on the perceptual isolation studies in his lab, the work of Moruzzi and Magoun on the brain stem arousal system and the results of Olds and Milner's studies of reward by electrical brain stimulation to point out the inverted U shaped curve for the optimal arousal of behaviour. He also pointed out the need for comparative studies of different species and the need to study the cortical or cognitive components of motivation.

In his presentation to the American Psychiatric Foundation, Hebb[97] again discussed the importance of environmental stimulation during development which he had studied in dogs and rats and the effects of sensory deprivation in humans, and he related environmental stimulation to levels of adjustment at maturity. In particular, Hebb pointed out to an audience of psychiatrists

that "a short period of deprivation of normal sensory input produces personality changes and a clear loss of capacity to solve problems" (page 829).

17. The Extentions of Hebb's Theory

Hebb extended his cell assembly theory to many areas of psychology, but he was not the only one to do so. For example, Paul Benoit applied Hebb's ideas to the study of learning disabilities in children with mental retardation[98,99]. Frank Fish applied Hebb's theory to clinical disorders, including manic depressive illness and schizophrenia[100]. Arthur Stein attempted to use Hebb's model "as a unifying explanatory dynamism for psychoanalytic theory" by translating Rapaport's psychoanalytic model into Hebb's theory[101]. None of this work, however, seems to have had much of a lasting impact in the field of psychology, as they are few reference citations to these papers.

Two areas of Hebb's research that had a major impact on psychological research were the studies of the effects of environmental enrichment in early development and on sensory deprivation. Beach and Jaynes reviewed the literature on the effects of early experience on the behaviour of animals and stated that:

The most recent increase of interest in the effects of early life experiences upon the behavior of adult animals is traceable to theories that stress the importance of perceptual learning in infancy upon subsequent performance in tests of learning. A leader in this field is Hebb, whose The Organization of Behavior (1949) has been directly or indirectly responsible for a number of experiments reported in psychological journals during the last two or three years[102].

Hebb's work stimulated research on the effects of early experience on problem solving, neuroanatomy and neurochemistry[103]. His ideas further helped to facilitate the development of 'head start' programs using environmental enrichment for poor children[104]. Hebb's studies of sensory deprivation also started an entire field of research[105].

18. Hebb as teacher and administrator

Through his experience teaching at McGill, Hebb[106] developed an idiosyncratic philosophy of graduate education in which he stated that you can not train students to do research, but you can set up the conditions for them to do research. He suggested that students be encouraged to start research projects early in their career; not take too much course work or formal examinations, and learn to write. He believed that students should be evaluated on their intelligence and motivation to do research and on their ability to think and do, rather than on memorizing the work of others. Hebb was involved in the 1958 Colorado conference on the teaching of psychology[107] which proposed a plan of action for the education of psychology students.

Hebb was the chairman of the Psychology Department at McGill from 1948 to 1958 and the 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, including the Warren Medal from the Society of Experimental Psychologists in 1958, the Distinguished Scientific Contribution Award from the American Psychological Association in 1961, and an award from the Association for Research in Nervous Mental Disorders in 1962. He was awarded the Claude Bernard Medal from the University of Montreal in 1966, the Gold Medal from the APA in 1974, the Society for Research in Child Development Distinguished Scientific Contribution Award in 1979 and the Canadian Psychological Association Distinguished Scientific Contribution Award in 1980. He was given honorary doctorates by fifteen Universities and was nominated for the Nobel Prize in Physiology and Medicine in 1965.

Hebb also worked tirelessly for the support of research in psychology in Canada. He lobbied the National Research Council to create a grant for research in psychology and became the Chairman of the National Research Council of Canada Experimental Psychology Committee in 1956.

19. Hebb retires to Nova Scotia

In 1977, Hebb retired to a house that his father had built in Marrot's Cove, Nova Scotia, only a few miles

from where he was born in Chester. He became a Professor Emeritus at Dalhousie University and commuted to Halifax once a week for lunch with colleagues including Graham Goddard, Lynn Nadel, Ray Klein and their students, who included Carol Barnes, Bruce McNaughton and Rob Douglas. Hebb always enjoyed sailing and went out in his boat, "The Raven," whenever he could. During his retirement, he wrote his third book, Essay on Mind[3], a summary of his ideas on the biological basis of mind.

20. The legacy of Hebb's work

Hebb died on 20 August 1985, following complications from surgery. Numerous obituaries were published which described his legacy to psychology and neuroscience[108-110]. 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, long-term potentiation[111] is the experimental analysis of Hebbian synaptic plasticity and the work of Hubel and Wiesel on neural plasticity of sensory system development[112] derives from the first five chapters of The Organization of Behavior. There are very few areas of Behavioural Neuroscience today that have not been influenced by Hebb's work and the field of computational neuroscience is largely based on Hebb's ideas[113].

ACKNOWLEDGEMENTS

I would like to thank the McGill University archives, University of Chicago, Harvard University and Queen's University for access to Hebb's files. Also special thanks to Mary Ellen Hebb and Jane Hebb Paul for access to family photographs and letters and to Gordon Hebb for access to unpublished Hebb family genealogical research.

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