Memory

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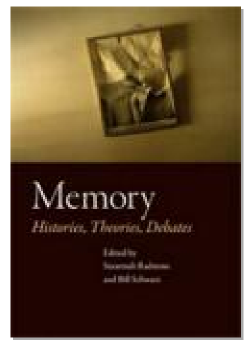

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15. Physiological Memory Systems

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The study of cultural memory depends almost without exception upon a prior physiological or psychological account of individual memory. Aby Warburg's influential studies of cultural memory, including his innovative *Mnemosyne* project of the mid- to late 1920s are rooted in his early work on energetic models of the physiology of memory,[1] contemporary with those that provided the point of departure for Freud's analyses of the pathologies of memory in the 1895 *Project for a Scientific Psychology* and for Bergson's 1896 *Matter and Memory*. Charting the relationship between cultural processes of memory and the formation of individual memory remains a challenge to memory studies, one that is often ignored or otherwise discreetly relegated to the sidelines. Yet the danger of a reductive account of memory threatens from both sides, as much from the social and cultural as from the physiological and psychological. In recent decades, however, developments in the neurophysioanatomy of memory suggest a radically new understanding not only of the formative processes of individual memory but also of those of social and cultural memory and, most importantly, of the inseparable relationship between them.

In an influential introduction to neuropsychology published in 1973, A. R. Luria described the "cerebral organization of memory" as one of the "least explored fields of psychophysiology," holding the promise of "a new and largely unopened chapter of neurophysiological science."[2] Yet in retrospect it is clear that the neurophysiology and anatomy of memory had already entered a phase of revolutionary development that would fundamentally change the understanding of the physical processes underlying or constituting memory. A number of diverse sources including advances in the knowledge of the function of neurons and their organization in the brain and nervous systems, the development of the discipline of immunology, and the clinical pathologies experienced by patients in the aftermath of brain surgery contributed to an enhanced understanding of the physical organization of memory. While many of the results of the neuroscientific exploration of memory are by now well established, the field is still in a phase of dynamic development and the interpretation of its findings open to debate.

One of the fundamental problems facing the investigation of memory is the proper point of departure: Should memory be approached structurally or functionally? The first approach, characteristic of the anatomical tradition of medical research locates the place of memory within the architecture of the brain, while the latter, more characteristic of the physiological tradition, would attempt to describe its function. Both approaches are complementary, but the precise relationship between the anatomy and the physiology of memory remains in question and subject to debate. The two Nobel Prize winners active in this field, the contemporaries Gerald Edelman (1929–) and Eric Kandel (1929–), illustrate this diversity of approach, with Edelman emphasizing the role of the architecture of neural group networks in the experience of memory and Kandel the electrical and biochemical processes that contribute to the plasticity of the synapse.[3] Although their work is clearly complementary, neither makes extensive or systematic critical reference to the work of the other: Edelman's "neural Darwinism" is attentive to the role of functional selection while emphasizing the structural stability of emergent neural networks, while Kandel focuses on the synapse and the role of electrical and biochemical function in shaping the architectural properties of the synapse. In awarding their prize to Kandel in 2000, the Nobel Committee was characteristically diplomatic, acknowledging his contribution to neuroanatomy as showing that "our memory may be located in the synapse" and to neurophysiology with the claim that "changes in synaptic function are fundamental in the formation of different types of memory."

The distinction between the anatomical and physiological approaches to understanding the body may be traced to the work of two important figures in the history of medicine, Andreas Vesalius (1514–1564) and William Harvey (1578–1657). Vesalius's *On the Fabric of the Human Body* (1543) systematically presented the visual architecture of the human body in seven books focusing on the skeleton, muscular organization, the venous and arterial systems, the brain and the nervous system, and the internal organs of the body. Based on close anatomical examination and motivated by the desire to describe visually the morphology of the body's organs and their spatial relationship with each other and with the whole body, Vesalius's book inaugurated modern anatomy as the precise and analytical description of the shape and place of the organs of the body. Harvey's *Anatomical Disquisition on the Motion of the Heart and Blood in Animals* (1628), while indebted to the advances made by Vesalius and the school of Padua where Harvey studied, nevertheless pursued a different inquiry. Harvey's point of departure was less the question of the shape and location of the organs of the body than their function. He was concerned primarily with the function of the heart, not with its architecture; his approach consisted in putting questions to the living body, formulating experiments that would disclose function. None of this would have been possible without the accurate descriptions of Vesalian anatomy, but the emphasis on the investigation of function rather than the description of structure was quite different from the approach pursued by anatomy. While the integration of structure and function would become the goal of research into the life of the body, the tension between the complementary approaches persisted in general medical research and specifically research into the brain and memory.

The difference between the two approaches may be expressed in terms of whether memory can be specifically located somewhere in the brain or whether it consists in a global mental function akin to consciousness. If the former, then the question arises of where is it located and what shape it assumes; if the latter, that of how it functions and its effects. The answers to such questions presuppose some understanding of the constitution of the brain itself. The recognition that the brain possessed well-defined internal articulations along with attempts to locate discrete mental functions in terms of these articulations formed part of the legacy of ancient Greek and Roman medicine. Yet the recognition that the constituent parts of the brain possessed a specific cellular structure—the neuron—was the much-disputed discovery of Santiago Ramon Cajal (1852–1934) in the 1890s. The anatomical properties of the neuron were the subject of a famous dispute between Cajal and Camillo Golgi over whether the filaments issuing from the nerve cells (axon and dendrites) were discrete or linked in a global network. The anatomical dispute had drastic implications for the understanding of the function of the brain. Cajal's position, which prevailed, focused physiological research on the function of the neuron as an individual part of a signaling system, concentrating specifically on the functioning of the terminals that input and output signals from the neuron. The points of proximity between the terminals of neurons—named synapses by Charles Sherrington (1857–1952)—thus became a major focus for physiological research into the functioning of the brain and nervous systems.

The history of this research is largely a twentieth-century achievement, with a number of extraordinary discoveries all of which contributed to the late twentieth-century revolution in the understanding of memory. The neurons were functionally and structurally distinguished according to whether they were involved in transmitting sensory signals to the brain, motor signals from the brain, or interconnecting neurons within the brain. Their function as a signaling system was achieved by a combination of electrical and biochemical properties (their precise character remained in dispute until after the Second World War). The synapse formed an electrical potential that was either maintained or dramatically altered by means of the transfer of chemoelectrical charges—ions—by means of the opening and closing of protein gates across the synaptic cleft. The drastic electrochemical changes associated with the "action potential" or the inequality associated with the arrival of an electrical signal at the presynapse combined with the "synaptic potential" or local inequality of the postsynapse in effecting communication between neurons.

The explanation of the experience of memory in terms of the neuron doctrine poses a number of particular and fascinating problems that may be approached architectonically or functionally. At the root of all the specific problems is the more general one of accounting for the persistence of neural structure or function over time—precisely the problem of memory. This problem is complicated by the contribution of the third great tradition of modern medical inquiry alongside anatomy and physiology, namely, pathology. Pathology, or the study of dysfunction and structural anomaly, has until recently played a prominent role in the study of the link between structure and function in the brain. Nineteenth-century neurology was dominated by the pathological method, proceeding from the location of lesions within the brain to allegedly corresponding mental dysfunctions. The inaugural step in this direction was Pierre-Paul Broca's 1861 association of aphasia with a lesion in the left frontal lobe of the brain.[4] This suggested that the function of speech was indeed localized within a specific area of the brain. The key clinical case in the pathological study of memory was Brenda Milner's (1918–) studies of HM, a patient who underwent brain surgery in the attempt to alleviate devastating symptoms of epilepsy. Surgery removed the inner surface of the medial temporal lobe and, crucially, the hippocampus. The symptoms of epilepsy were relieved, but at the cost of a severe and very idiosyncratic memory disorder. HM possessed full memory of the time before the operation, a good short-term memory measured in minutes and a procedural memory but suffered the complete inability to form long-term memories of events after the surgery. This pathology suggested that it was important to distinguish between different types of memory as well as pointing unequivocally to the localization of these types within discrete parts of the brain. Milner's work showed that loss of the inner temporal lobe and hippocampus directly compromised the ability to form long-term memory.

The existence of proof for the localization of the functions of memory and the need to account for the persistence over time of neural structure or function poses problems for the understanding of memory that have been met in fascinating ways. It is necessary to account not only for the persistence of neural structure or function but also for its clustering or concentration in particular parts of the brain. The approaches to these problems of memory have adopted complementary but still not fully convergent methodologies. One approach, associated with Gerald Edelman's "neural Darwinism" departs from the premise that the brain is to be understood as a *population* of neurons that conform to the rules of selection elaborated for population biology. The cerebral cortex alone has a population of a hundred billion neurons, each possessing on average a thousand synapses, thus indeed constituting a vast population. Edelman's scientific background is in immunological memory research, where the "memory" of an antibody is not something recalled by a cell when facing attack but rather the property of a number of specialized cells that form members of a vast population of cells waiting to reproduce when confronted with a recognizable threat. The emphasis on the properties of populations informs his views of the selective emergence and maintenance of neural networks for memory in general. Connections between neurons enter a process of natural selection that produces neural architectures and distributions unique to each brain. Much of the approach of Edelman and his school consists in identifying dynamic mappings and the properties of feedback or reentry that ensure their reproduction, yet the stabilization of such global mappings supposes a physiological account of the persistence and repetition of networks at the level of the individual neuron:

> Global mappings provide a necessary substrate for relating categorization to memory. This relationship cannot generally be accounted for by the activity of any one small neural region, for, by their nature, global mappings must include large portions of the nervous system. Within a global mapping, long-term changes in synaptic strengths tend to favour the mutual re-entrant activity of those groups whose activity has been correlated across different gaps during past behaviour.[5]

The phenomenon of memory and its localization is thus explained by means of the reiteration of global mappings, but this in turn is a process in which synaptic strength plays an important role.

If Edelman's work departs from the population of neurons, that of Kandel has its point of departure in the individual synapse. His work on the neurons of the invertebrate *Aplysia* showed the plasticity of the synapse and the changes in its structural and functional properties that took place in response to activity. Kandel's extremely sophisticated physiological research, motivated by an early and enduring fascination with Freud and psychoanalysis and the oft-stated desire to extend the "talking cure" to the individual neuron, details the genetic and biochemical factors involved in the production of enzymes and specific proteins in response to the excitation of the synapse. It gives an account of the process of the structural change of the synapse that leads to morphological change that adapts it to the repeated connections that characterize memory. These findings are often linked in the literature with a suggestion by Donald Hebb in his 1949 *The Organisation of Behaviour: A Neuropsychological Theory* cited by Kandel: "When an axon of cell A . . . excites cell B and repeatedly or persistently takes part in its firing, some growth process or metabolic changes take place in both cells so that A's efficiency is increased."[6] This property of the neuron, later known as LTP or long-term potentiation, is central to explaining why certain connections are repeated. Experiments in disrupting LTP in specific synapses seem to result in compromising memory, while its augmentation leads to the growth of memory. The discovery of LTP in certain synapses of the hippocampus seems to move in the direction of an explanation for the important role of this part of the brain in the formation of long-term memory.

The various approaches to the physical understanding of memory have generated a number of findings and perhaps an even larger number of questions. Memory is increasingly recognized as a physically dynamic system far removed from any mechanical analogies of storage and retrieval, such as those suggested by the operation of computers. The different kinds of memory appear to obey a rule of localization, with long-term memories associated with the cerebral cortex, procedural or routine memory with the putamen, traumatic and unconscious memory with the amygdala, and instinctual memory with the caudate nucleus. The process of memory formation also seems to obey complex rules of temporal and spatial distribution, with the formation and retrieval of semantic memory associated with the cortex, and event memory initially focused in the hippocampus and then over a period of sometimes years repeatedly distributed by means of neural networks to specific areas of the cortex where the potential networks are established and form part of the explicit memory system.

The anatomy and physiology of memory are much more fully understood now than even twenty years ago. The macro- and micro-neural approaches of Edelman and Kandel to the problem of memory seem in many ways complementary and even logically, if not historically, dependent upon each other. The accounts of the neural structures and functions that add up to the experience of memory are increasingly inseparable. They form the background to understanding an increasing number of specific and identifiable properties of memory, a process aided by the emergence of sophisticated brain research and diagnostic technologies. While the physical account of memory remains incomplete and fragmentary and may or should always form but a part of a broader understanding of cultural and historical memory, the progress this field of memory studies has made since the 1970s is remarkable, not only for an understanding of the physical basis of remembering but also for diagnosing and potentially treating devastating diseases and pathologies of the memory.

The implications of this work are only beginning to be explored in the fields of sociology and cultural analysis. The new models of memory, although located at the level of the synapse and the physioanatomy of the brain, far from being reductive explanations, emphasize the role of experience and education in the formation of the brain and its memory. This dynamic and interactive approach points to new ways in which to explore the relationship between physiological, social, and cultural memory that will need to be considered in future work in the broader field of memory studies.