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Recalling Lashley and Reconsolidating Hebb

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Abstract

Many of the foundational theoretical ideas in the field of learning and memory are traced to Donald Hebb. Examination of these ideas and their evolution suggest that Karl Lashley might have significantly influenced their development. Here, we discuss the relationship between Hebb and Lashley, and the parallels between them. Many now investigating the neurobiological basis of memory may be unaware both of Hebb's original descriptions, and the likely substantial contributions of Lashley. Many of their concerns remain with us today, and by clarifying the history we hope to strengthen the foundations of our field.

Keywords

cell assembly; phase sequence; equipotentiality; mass action; localization of function; memory

Introduction

Karl Lashley and Donald Hebb insisted that studies of the brain were critical to the domain of psychology, a position that now sounds so obvious as to not warrant mention, but which in their era was a debatable question. They were both searching for a solution to the related problems of *stimulus and response equivalence* that made sense biologically; how is it that a stimulus presented to different parts of the retina is perceived as the same thing? Or that two nonidentical stimuli are responded to in the same way. Lashley and Hebb agreed that the answer almost certainly involved some kind of internal "representation" of events, and states of the world, but they disagreed about how. Peter Milner (1999) put it this way:

> "Both men saw clearly that the popular notion of the brain as a collection of conditionable reflexes could not begin to explain the subtleties of mammalian behavior, and both tried to find alternatives, Lashley by discounting the influence of individual neural connections, and Hebb by postulating a more complex array of connections that permitted the brain to be active independently of sensory input."

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(Milner, 1999; p. vii)

For many decades, ideas attributed to Donald Hebb have served as key cornerstones in the study of learning and memory. A well-worn copy of *The Organization of Behavior* (Hebb, 1949, p.83) can be found on the bookshelf of many scientists searching for the neurobiological bases of cognition. Yet, Karl Lashley, who exerted significant influence on Hebb in the decade or so prior to the book's publication, felt that Hebb's magnum opus did little to advance the field. Lashley was certainly familiar with its contents, which included ideas about brain dynamics and plasticity that must have evolved from recurrent interactions between the two men.

One of the critical ideas, Hebb's notion of the cell assembly, ultimately propelled the investigation of behavior from psychology into the realm of neuroscience. Lashley's likely contribution to the development of this idea has not received much attention. While the reasons for this are unclear, one factor may be that Lashley was the "quintessential outsider", complete with opaque writing and a disinclination to defend any particular theory (Weidman, 2006). Another student of Lashley commented that he was a "theorist who specialized in disproving theories, especially his own" (Beach, 1961).

Lashley dismissed all analogy driven descriptions of the brain - hydraulic, telephone, electric field, and computers - as misleading:

> I suggest that we are more likely to find out how the brain works by studying the brain itself and the phenomena of behavior than by indulging in farfetched physical analogies. The similarities in such comparisons are the product of an oversimplification of the problems of behavior.
>
> (Beach et al., 1960, p. xix)

This made Lashley an antagonist to those in the cybernetics camp (led by figures such as Norbert Wiener, Warren McCulloch and Alan Turing; Fig. 1), demonstrating a generally negative attitude towards theories that implemented logic switches in the service of cognition (Dalton and Baars, 2004). This dramatic stance against theory and analogy left a gap that Hebb and *The Organization of Behavior* (1949) attempted to fill.

It is not widely known that early on Hebb offered Lashley co-authorship of his 1949 book. Lashley demurred, for reasons that remain unclear. Trying to answer that question was one of the things that drew us to look more closely at the relations between Lashley and Hebb. In so doing we came to understand that what Lashley and Hebb actually said are of more than just historical interest, as we hope to show in what follows.

Lashley and Hebb: Who Were They?

Karl Lashley (1890–1958; Fig. 2) was highly regarded as a researcher and theoretician. He was pensive and perceived by many as both inscrutable and as having a negative view of life. Jerzy Konorski referred to Lashley as an academic 'nihilist' (1968). Orbach commented that "as a critic, he was a demolition expert" (as cited in Bruce, 1996, p. 129). His tendency to find fault extended even to his own ideas, which he felt were inadequate. Donald Hebb (1904–1985; Fig. 3) was quite a different character. Although Hebb demonstrated intelligence at an early age, and was placed in a classroom with older children in his formative years (Orbach, 1998), his path to an academic career was indirect, starting with a degree in English and Philosophy at Dalhousie University in Nova Scotia, followed by a stint in teaching (Brown, 2006). A few years later Hebb shifted focus to psychology. While Lashley was pragmatic in his approach to psychology, potentially to a fault, Hebb ventured that big ideas were necessary to bridge the gap between biology and psychology. This focus on foundational ideas was readily observed by the psychology students required to take his first-year graduate seminar at McGill (including one of the authors, LN) and was a driving force behind his seminal book. While Lashley is often viewed as dedicated but quixotic (Josselyn et al., 2017; Orbach, 1998), and unable to find solace in his scientific endeavors, Hebb is seen as the genial father of a dozen scientific fields (Cooper, 2005; Klein, 2011). To what degree is this historical perspective on Lashley and Hebb fair? Are we justified in solely crediting Hebb for ideas about synaptic plasticity, cell assemblies and phase sequences, while dismissing much of Lashley's work? To what extent can the genesis of these ideas, typically attributed to Hebb, be traced to collaborative interactions with Lashley? And why does this matter?

History of Hebb and Lashley

In the 1930s, Hebb was working in Montreal in the laboratory of Boris Babkin, a student of Pavlov. Babkin advised Hebb to go to Chicago to work with Lashley, who was well-known by this time for his work on mass action and equipotentiality (see below) as well as for his attacks on behaviorism (and its proponents, including Babkin and Pavlov). While Babkin suggested that the opportunity to manipulate the nervous system in order to test psychological theories would be advantageous, he still cautioned that Lashley was incorrect in his theoretical ideas (Hebb, 1980). Specifically, Lashley's abhorrence of the "telephone switchboard" description of the nervous system placed him at odds with the behaviorists, such as Babkin, who were ascendant in the early part of the 20th century. In the end, Hebb did go to Chicago, and spent formative academic years under the tutelage of Lashley, first in Chicago, then at Harvard, where Lashley moved his laboratory in 1935.

Upon getting settled, Hebb started to work on the topic of *spatial orientation and place learning*. This project went slowly, and with Hebb needing to complete his degree, Lashley suggested he shift to an investigation of the effects on simple perception of rearing rats in darkness (Hebb, 1980). Following completion of his thesis in 1936, which essentially yielded a null result, Hebb worked for a year for Lashley as a research assistant. During this time Hebb immersed himself in a theoretical culture that sought to apply biological science to the mind. In 1937, Hebb returned to Montreal to work with Wilder Penfield (Hebb, 1980), before taking a position at Queen's University in Kingston, Ontario in 1939.

It would be roughly 5 years before Hebb and Lashley were reunited. In 1942, Lashley became director of the Yerkes Laboratories of Primate Biology, then in Florida and quickly became dissatisfied with his ability to recruit talented personnel - "North Florida was a cultural wasteland; and Orange Park itself was in the middle of nowhere" (Beach and Orbach, 1982, p. 23). An aggressive teaching load at Queen's was apparently enough for Hebb to consider and accept a full-time research appointment at Yerkes (Brown, 2006).

There, he planned to investigate the effects of lesions on primate learning, social interactions and overt behavior. However, the first surgery only occurred in Hebb's last month at Orange Park. In the interim, he studied chimpanzee behavior, paying attention also to their temperament, emotional displays, and apparent intentions, thereby obtaining considerable raw material for what would become *The Organization of Behavior* (Hebb, 1980). Perhaps more importantly, Hebb cited the weekly colloquia and persistent theoretical debate at the Yerkes Laboratory as critical in formulating his ideas (Preface to Hebb, 1949). Lashley was aware of Hebb's efforts, describing the early work on *The Organization of Behavior* in a 1947 annual report for the Yerkes Laboratories: "Dr. Hebb has been engaged in the development and elaboration of a theory of nervous integration which gives some promise of clarifying discrepancies between neurological and psychological theory. It will probably be published in book form" (as referenced in Orbach, 1998, p. 55; Fig. 4).

The Book that launched a field but possibly destroyed a relationship.

> *"In this book I have tried to bring together a number of different lines of research, in a general theory of behavior that attempts to bridge the gap between neurophysiology and psychology…"*
>
> (Hebb, 1949, vii)

As noted, Hebb offered Lashley the opportunity to co-author *The Organization of Behavior*, suggesting that it would help distribute the workload for a full length book, provide insights for the sections on perception, smooth over the theory and presentation, and finally, capitalize on Lashley's name in order to increase the book's visibility (Hebb, 1980). Why did Lashley decline?

Perhaps Lashley lacked interest in such a project. Perhaps he rejected Hebb's use of the word "connections" (Bruce, 1996). This was a loaded term for Lashley, as he had argued strongly against a passive switchboard model of the nervous system and disavowed the sequence chain hypotheses of the behaviorists (Beach and Orbach, 1982; Glickman, 1996; Lashley, 1951). Further, as Hebb received early training with Babkin, Lashley may have felt that - despite their time together - Hebb was still in the Pavlovian camp (Hebb, 1980). This perspective is supported by a lecture given by Lashley at the University of Rochester in 1957:

> …different theories have been proposed to account for the phenomena of stimulus equivalence. That of Hebb is most in accord with classical conditioned reflex theory. He assumes that multiple paths are developed by learning. Such learning is ruled out by a mass of evidence for innate discriminations and equivalences.
>
> (Karl Spencer Lashley Papers)

Finally, as noted earlier, Lashley abhorred speculation and may have felt that Hebb had not gathered adequate supporting evidence (Cooper, 2005):

> There have been, of course, other attempts to deal with the problem of organization, such as the resonance theory of Weiss and the lattice theory of Hebb. Each of these theories is also especially applicable to a limited series of facts and fails to account

> for other seemingly related ones. The field theory at present certainly best comprehends the perceptual data but is farthest removed from and least consistent with the data of neurophysiology.
>
> (Karl Spencer Lashley Papers; folder titled "The Objective Study of Perception")

Hebb's book was published and its impact was immediately felt. Reports from others who were there at the time, as well as Hebb's observations, suggest that Lashley's view was not all that positive. A former student of Hebb, Stephen Glickman, recounted comments made by Mark Rosenzweig, a student in a seminar run by Hebb at Harvard in the summer of 1947, who remembered,

> … *Lashley presenting a different, more caustic, view of the book to a group at an informal luncheon in New York (Rosenzweig, personal communication). Rosenzweig recalls Lashley saying that the ideas in the book were garbled versions of his (Lashley's) ideas that Hebb had misunderstood. The latter would certainly have been more in tune with Lashley's comments on the early manuscript and the tenor of his thoughts about such connectionist theorizing over the years. It is also the case that the precursors of Hebb's ideas can sometimes be found in Lashley (e.g., on the spontaneity of action in the nervous system), but, more often than not, Lashley had prematurely rejected the line that Hebb developed.*
>
> (Glickman, 1996, p. 259)

In a letter to Frank Beach, one of the founding fathers of behavioral neuroendocrinology, Hebb commented on his relationship with Lashley:

> All this time we were on excellent terms, somewhat distant; but friendly and good. He didn't approve of the Organization of Behavior at all when I was writing it (Perhaps I should say that when I first got interested in those ideas I went to him and suggested joint publication; he wasn't interested, and in fact it took five months to get him to look over a draft outline I left with him—because I had told him it was a theory of connections, and that word was one he couldn't stand). In his 1956 [Association for Research in Nervous and Mental Disease]paper… he published what is in effect my theory, using trace system as a term instead of cell assembly, and says it's "the theory of cerebral organization that I have dreamed up in the course of the years"— but omitting of course any reference to connections. Dirty word. "Association" is better. So he had come round quite a bit. (McGill University Archives)"
>
> (as referenced in Glickman, 1996, p. 259)

These quotes document the tension that developed between Hebb and Lashley, a rift discussed by Bruce (1996) at some length. Bruce suggests that Hebb's theories, relying heavily on synaptic connections, would have had difficulty getting beyond the "environmentally driven stimulus-complex response" issues raised by Lashley, as spelled out in his famous paper on the problem of serial order in behavior (1951). Moreover, Lashley staked his career on a dynamic memory system rather than localized storage in specific synaptic connections, as proposed by Hebb. With these caveats mentioned, near the end of his life Lashley moved towards a compromise on the general theory of the neural mechanisms that support behavior (Bruce, 1996).

Glickman provides yet another perspective, simultaneously acknowledging Lashley's influence on Hebb and how ideas among different scientists converge to the same logical outcome.:

> …it was Lashley's questions that set the agenda for Hebb's answers… In the more mature sciences, where the critical questions are clear to all, personal qualities of the scientist probably play a less significant role in terms of acceptance of findings and ideas. If Watson and Crick hadn't deciphered the genetic code when they did, Linus Pauling might have done so the next year, and the essential structure of DNA/RNA would have been identical. The problem that Hebb confronted was quite different.
>
> (Glickman, 1996, p. 250)

It is instructive to note that psychology at that moment in its history (the period between 1930 and 1950), had little concern for how biological processes in the brain could be responsible for core psychological capacities, and this is where the ingenuity of Hebb's leap resides. He insisted that to be a psychologist required also being a physiologist, and that physiology could indeed inform our understanding of perception, thought, memory, emotion, action and more.

There is one further consideration to be noted as we seek the origin of ideas that influenced Hebb's 1949 book. Already a decade earlier, Lashley referred to the work of Ramon y Cajal's last student, Lorente de Nó.

> The recent demonstration of recurrent nervous circuits, perhaps capable of infinite reverberation, by the anatomic and physiologic studies of Lorente de Nó, relieves us from the necessity of finding a peripheral mechanism to account for the maintenance of activity or for the dynamic tensions which are implied by the phenomenon of motivation
>
> (Lashley, 1938, p. 466).

Here is how Hebb describes his introduction to the same work:

> … *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 [(1940)] drew my attention to Rafael Lorente de Nó's work and led me to write The Organization of Behavior, which contained a theory quite different from any of my earlier ideas*
>
> (Hebb, 1980).

While Lorente de Nó clearly was a primary influence on both men (Fig. 5), these cited instances occurred after Hebb's departure from Harvard and prior to his arrival at Yerkes.

We cannot know whether Hebb borrowed this idea from Lashley or came upon it himself - but the reverberatory possibilities made clear by Lorente de Nó's work are at the core of Hebb's thinking about cell assemblies and phase sequences, and as such formed the basis of *The Organization of Behavior*. Was Lashley right in asserting that Hebb's ideas were poor recapitulations of his own, or was Hebb right in asserting that Lashley focused on critiquing his ideas, and then, later, rehashed Hebb's theory as his own? Shedding further light on this issue requires considering more closely what Hebb and Lashley said.

Lashley in Historical Context

To set the stage appropriately, we note that in the early portion of the twentieth century, when Lashley was a graduate student (Fig. 4; interacting with Watson, one of the fathers of modern behaviorism), there were effectively two competing theories about the brain: "field theory" (later, "mass action" as termed by Lashley) and "functional specialization" (broadly, Lashley generally agreed with field theory although rejected the neural interpretation by the Gestaltist; Lashley et al., 1951).

> "It is said that, historically, a swing of the pendulum tends to occur between these two positions. At one period the majority of informed opinion holds a localization theory, but a generation later this tends to be considered distinctly unorthodox."

(Tizard, *1959*, p. 132) (for a similar perspective, see Krech, 1963).

"Functional specialization" suggests that a particular brain region enables a particular psychological capacity, as captured in Franz Joseph Gall's theories of phrenology as well as in his methodological dissection of regions and circuits (Gall, 1835). Famous case studies taken to support this notion include Phineas Gage (see Damasio et al., 1994) and Henry Molaison (Scoville and Milner, 1957). On the other side of the argument was *field theory*, with some historical origins traced to Marie-Jean-Pierre Flourens (1794–1867), who set out to test the theories of Gall. Using what today would be considered quite imprecise techniques, Flourens concluded that there was little to no localization and introduced the idea of "cerebral equipotentiality" (for contemporary review, see Pearce, 2009):

> As long as not too much of the lobes is removed, they may in due time regain the exercise of their functions. Passing certain limits, however, the animal regains them only imperfectly, and passing these new limits it does not regain them at all. Finally, if one sensation comes back, all come back. If one faculty reappears, they all reappear…. This shows that each of these organs is only a single organ.

(Flourens,)

As elegantly covered by Tizard, evidence supporting localization slowly accrued. This wave, including the work of Francois Pourfour de Petit (1664 −1741), which demonstrated the lateralization of movement across hemispheres, that of Sir Charles Bell (1774–1842), which used the dissociation of nerve tracts to argue for distinct cortical functions, and Pierre Paul Broca (1824–1880), traditionally credited with the idea that a single lesion results in an inability to speak, concluded that the brain is potentially multiple groups of organs (although attribution to Broca is justifiably in dispute; see Thomas, 2007b). Despite some controversies, "…it seems reasonable to conclude that the physiologists of the last quarter of the nineteenth century interpreted their results as indicating the existence of local centers because of a prior conviction about the nature of the brain" (Tizard, 1959). Concepts resembling sequence chains were developed under the name "Associationism" by which complex ideas develop from the linking of simpler elements. However, the pendulum began to swing back towards field theory following the influence of William James (1842 −1910), who warned that simple neural connections representing associations will not be found in the brain:

> *If we make a symbolic diagram on the blackboard of the laws of association between ideas, we are inevitably led to draw circles, or closed figures of some kind, and to connect them by lines. When we hear that the nerve centres contain cells which send off fibres, we say that Nature has realised our diagram for us, and that the mechanical substratum of thought is plain. In some way, it is true our diagram must be realised in the brain, but surely in no such visible and palpable way as we at first suppose*"
>
> (originally published 1890, James, 2013, p. 81).

This history was not lost on Lashley, who recapitulated the history of Gall-Flourens through Broca as well as the discovery of motor, visual, auditory and sensory cortices in an unpublished manuscript (Karl Spencer Lashley Papers; *The Mystery of the Frontal Lobes*, Folder "May be part of Brief History of Psychology). His theoretical position reflected not ignorance, but rather a focus on the broader question we alluded to at the outset, namely 'stimulus equivalence':

> "How can a pattern of excitation occurring anywhere within a functional field give rise to a constant reaction? This question underlies every significant psychological problem."
>
> (Karl Spencer Lashley Papers, London Lectures).

As noted above, what led Lashley to these views included his own work; in particular that on relating the size and location of what he assumed were cortical lesions in the rat to performance on a series of spatial mazes of varying complexity.

Lashley was hardly the first person to search for the location of intelligence in the brain nor the first to use a broad lesion approach, but certainly among the vanguard in documenting his search (Fig. 6). His empirical tests of localization versus field theory included one of the earliest uses of statistics in neurobiological research. Following the work that lead to his principles of *Equipotentiality* (the notion that the brain functions as a single organ; "the capacity of any intact part of a functional area to carry out, with or without reduction in efficiency, the functions that are lost by the destruction [of the other parts]"; Lashley, 1929, p. 25) and *Mass Action* (".the efficiency of performance of an entire complex function may be reduced in proportion to the extent of brain injury within an area whose parts are not more specialized for one component of the function than the other" Lashley, 1929, p. 25; N.B. these definitions evolved over Lashley's career), Lashley clearly belonged in the "Field theory" camp. This camp was not without its detractors, as both Walter Hunter, who became president of the American Psychological Association, and Ivan Pavlov championed behaviorist perspectives (Hunter, 1930; Pavlov, 1941). Specifically, Lashley railed against Associationism, reflexes, and the chaining of simple associations to form complex thoughts. He believed that specific connections were less important than activity across circuits:

> Lorente (1934) has shown that each neuron may bear a hundred or more end-feet or separate synapses. However, considering the enormous complexity of the nervous activity involved in the performance of even the simplest of habit, it is doubtful that even the multiplication of cell number by a hundred fold will provide separate connexions that function only for single specific memories. The alternative to the theory of perseveration of memories by some local synaptic change is the postulate that the neurons are somehow sensitized to react to patterns or combinations of excitation. It is only by such permutations that the limited numbers of neurons can produce the variety of functions that they carry out. Local changes in the cell membrane, such that combined excitation by several synapse excite the cell, would provide a possible mechanism for such response to patterns, but speculation about this mechanism without direct evidence is likely to be as futile as speculation concerning changes in resistance in the synapse has been
>
> (Lashley, 1950, p. 26)

Traditional view of Hebb in the current context

Hebb is best known for three primary contributions. First is the clear formalization of the notion of association through synaptic plasticity, now often referred to as the Hebbian synapse. Hebb himself never claimed that the idea was original. In fact, he was puzzled by the credit he received for the “fire together-wire together” idea (McNaughton, 2003), as it can be traced at least to Lorente de Nó (see above), and probably to James (1890) as well. Similar ideas can also be found in Alexander Bain’s 19th century book, *Mind & Body*, in which a simple network of neurons could support associative memory through distributed activity:

> I can suppose that, at first, each one of the circuits would affect all others indiscriminately; but that, in consequence of two of them being independently made active at the same moment…a strengthened connection or diminished obstruction would arise between these two…
>
> (Bain, 1873, p. 119)

Moreover, as touched upon by P. Milner in correspondence with Orbach in 1996, the idea may even be traced back as far as the Greek philosophers (Orbach, 1998). Still, Donald Hebb has been credited with laying the theoretical framework leading to the discovery of “long-term potentiation” (LTP). One of the discoverers of LTP, Tim Bliss, was a graduate student at McGill in the early 1960s, working in the laboratory of the physiologist B.D. Burns. His dissertation work involved looking for sustained activity in slabs of neocortex - in essence a search for synaptic plasticity of the sort postulated by Hebb (Bliss et al., 1968; personal communication). Less than a decade later, Bliss found what he was looking for, and what Hebb had incorporated in his theory, not in neocortex, but in slices taken from the hippocampus (Bliss and Lomo, 1973).

Shying away from credit for the notion of synaptic plasticity, Hebb found his other theoretical postulates more interesting. Chief among them was the concept of the cell assembly. As noted, Hebb cited Lorente de Nó as the primary inspiration behind the concept of the cell assembly. As initially described by Hebb, cells with activity within a certain temporal window would undergo a shared growth if this activity is repeated. Energy propagation could be self-sustained through recurrent projections. The net effect of recurrent activation would be the development of a spatiotemporal pattern among the members of the assembly that would be readily re-activated should the initiating event occur again in the future. Hebb noted that the description was not fully developed: “This then is the cell-assembly. Some of its characteristics have been defined only by implication, and these are to be developed elsewhere, particularly in the remainder of the chapter *(~4 pages)*, in the following chapter *(“Ch. 5 Perception of a Complex: The Phase Sequence’)*, and in Chapter 8 (see pp. 195–197 *; reference to section titled “Metabolic Factors Disturbing Behavior’)”* (italacize portions ours, Hebb, 1949).

Note that the way ‘cell assemblies’ are now discussed within neuroscience and psychology diverges in several ways from what Hebb proposed. Hebb’s assemblies were designed to capture temporal associations physiologically, by strengthening the link between neuron A and neuron B whenever activity in A is followed by activity in B. The focus was on sequence, but without dependence on sensory input, since the recurrent nature of the network would allow it to maintain its activity in the absence of such input. While Hebb’s definition made no mention of neurons of an assembly needing to be temporally synchronous, such synchronicity is assumed in more modern versions (Abeles, 2011). Moreover, Hebb’s original model was predicated solely on excitatory recurrent connections, as inhibitory synapses had not yet been firmly established. Both excitation and inhibition are part of current attempts to physiologically define cell assembly membership (Harris et al., 2003; Maurer et al., 2006). Indeed, we now know that such networks can even be comprised solely of inhibitory interneurons. The meaning of the term cell assembly is hence fluid and dependent upon its contextual use (Abeles, 2011).

Hebb also made a very important assumption about how a memory, in the guise of enhanced synaptic efficacy in a cell assembly, is formed in the brain. He suggested that the reverberation occurring within a cell assembly, initially triggered by some external input, can temporarily maintain the memory. Over time, these reverberations will initiate structural changes in the same set of synapses, and this will now constitute the permanent memory. The idea that short-term memory and long-term memory occur within the same circuits was discarded early on, as notions about systems-level memory consolidation emerged (e.g., Squire et al., 1984). We will return to this important thread in Hebb’s thinking below, as there is now considerable evidence that he was on the right track here.

What was actually original in Hebb’s notion of the cell assembly? His description of it as “a closed solid cage-work, or three-dimensional lattice, with no regular structure” is akin to the “nerve nets” suggested by McCulloch and Pitts (originally published in 1943; republished 1990). The concept of reentrant processes among the networks of the brain - something Hebb said was inspired by Lorente de Nó - was already prevalent in the literature (Hilgard and Marquis, 1940; Lashley, 1938; Lashley, 1942; McCulloch and Pitts, 1943). One could even imagine that Bain was onto this idea in 1873, in considering the ability of a network to support multiple functions by propagating activity through the same network, but toward two distinct outcomes:

> If each set of sensory fibres had one definite connection with motory or outcarrying fibres, we should have always the same movement answering to the stimulation of the same nerves, as in the reflex system; the fibre a could do nothing but affect the movement x. It is necessary to the variety and flexibility of our acquirements, that the fibre a should at one time take part in stimulating x, and at another time take part in stimulating y, the circumstances being different. The stroke of the clock will stimulate us at one time to set in one direction, and at another time in another direction, according to the ideas that it co-operates with.
>
> (Bain, 1873, p. 109)

Here, prior even to the neuron doctrine, Bain provided a connectionist idea of how the brain supports flexible behavior (Wilkes and Wade, 1997).

Hebb's critical insight would seem to be his assertion that these recurrent neural networks were modifiable by experience. While others talked about synaptic plasticity and still others talked about recurrent networks, it was Hebb who saw the power of putting these two things together. Doing so lead to Hebb's third major contribution: the idea that a trained neural network, complete with recurrent connectivity, would be capable of self-sustaining activity and effectively functioning as a closed system. While this concept of a "phase sequence" is often attributed to Hebb's 1949 book, the etiology of the idea can be found in earlier works:

> Behavior is directly correlated with a phase sequence which is temporally organized (Beach, 1942), in part by the inherent properties of the system (the constitutional factor) and in part by the time relations of various afferent excitations in the past (the factor of experience). The spatial organization of each phase, the actual anatomical pattern of cells which are active at any moment, would be affected by the present afferent excitation also. Subjectively, the phase sequence would be identified with the train of thought and perception.
>
> (Hebb, 1946, p.269)

Interestingly, Hebb referenced Frank Beach and his investigations of the organization of courtship and copulation in the male, noting that many actions appear to be innately organized in the rat while, in the primate, there is an interaction between what is modified by experience and what is inherited. Through this, Beach concluded that "the circuits for organization of the motor acts may be subject to facilitative impulses from higher brain centers" (Beach, 1942). As Beach was also a student of Lashley, along with Hebb, it seems likely that they all shared discussions of how behavior seems to be both organized and adaptive – the major theoretical advance the "phase sequence" provides.

Hebb noted how the architecture set forth by Lorente de Nó could establish either stable, reinforcing dynamic patterns, or – perhaps challenged by fluctuation – result in an unstable, unpredictable pattern. Finally, Hebb stated in this early manuscript that learning would increase "cerebral organization" and hence more effectively organize behavior. Current understanding of the notion of a phase sequence invokes the concept of an assembly that assumes simultaneity of cellular activity (“fire together, wire together”), linking each assembly together in a chain through associative plasticity. By this conventional understanding, chains of cell assemblies equal a phase sequence. This formulation probably falls short of capturing what Hebb had in mind because it fails to properly emphasize two concepts: 1) reentrant loops provide a mechanism for self-sustaining activity and 2) cell assemblies can propagate activity through alternate anatomical pathways in a way that distributes the “engram”. This latter point is particularly crucial, as it allowed Hebb to argue that memory is indeed not localized in specific synapses, but in the trained neural network pathways through which activity moves.

It is worth noting that, based on his pedagogical training from Lashley, Hebb would most likely reject the contemporary definition of the phase sequence as it evokes descriptions of sequence chains and chaining. Following on from behaviorism, “chaining” is the idea that complex behavior is constructed through a series of smaller sequence-response events. Once learned, a stimulus can evoke a cascade of responses. Its shortcomings, as described by Terrance (“Intelligent behavior is greater than the sum of discrete conditioned responses” (2005)), echoed back to Karl Lashley, in his comprehensive attempt to capture the failings of the chaining theory which was most-likely prevalent in Lashley’s thoughts when working with Hebb; Lashley published his ideas in 1951. In describing complex movement, Lashley states:

> Sensory control of movement seems to be ruled out in such acts. They require the postulation of some central nervous mechanism which fires with predetermined intensity and duration or activates different muscles in predetermined order. This mechanism might be represented by a chain of effector neurons, linked together by internuncials to produce successive delays in firing. In some systems the order of action may be determined by such a leader or pace setter.
>
> (Lashley, 1951, p. 123)

Lashley drew evidence from a patient who most-likely suffered a spinal cord transection (dorsal column likely) but remained capable of moving his leg. The patient’s ability to initiate precise movements in the absence of proprioception showed that sensation is not necessary for appropriate responses. Second, Lashley noted that hand motions, such as that of a skilled pianist, occur faster than proprioceptive elements can be relayed back to the brain. Music at the arpeggio pace was far too fast to achieve sight reading or register the feedback sensation of the last moment to cue the next. A pianist, fingering at the rate of 16 key strokes per second, has coordinated movement that outpaces the reaction time of the visual system (Lashley 1951). Based on this evidence, Lashley rationalized that the brain must “chunk” information, taking in large blocks of written chords and translating them into a sequence of events to be executed with a predetermined intensity and duration. Lashley’s third objection to pure stimulus-response mechanisms, was that errors in motor or speech were often related to a higher cognitive process, involving anticipation or over correction. Lashley related his own typing experience -- a typo in which he accidently omitted a letter resulted in an overcompensation shortly thereafter, adding one too many of the ‘lost’ letter somewhere else. From this, Lashley deduced that thought and motor execution must be independent. Further, he suggested that "conflicting impulses may distort the order", which we interpret as Lashley suggesting that higher cognition can influence lower dynamics.

Lashley had a fourth reason to dismiss any form of connectionism – his own research on the impact of brain lesions, and of disconnecting various regions, on behavior, and in particular on perception, learning, and memory. These are the primary data that led Lashley to his talk about mass action and equipotentiality, for which he has been derided and ultimately ignored. But this is a mistake. Though some believe Equipotentiality and Mass Action to be theories put forward by Lashley, they "…were not the explanation he sought, but rather summary statements of observations which themselves needed explanation" (Hebb, 1959, p. 149). It is the data that need explaining, and this is not the place to do that job. Suffice it to say here that the methods in use at the time (lesions, etc) were not specific enough in their effects to support the conclusions that Lashley drew from them. Newer techniques have made it possible to track down particular "memories" to specific brain regions, even as they have shown that for the kind of memories of greatest interest to humans – our life's events – it takes a network to get it done. But that is a topic for another time.

All these reasons put together led Lashley to dismiss sequence chaining as a mechanism of higher-cognition. He moved irrevocably away from the concept of a stable "engram" carried by a fixed series of connected neurons firing in a specific order. Hebb, too, was well aware of the shortcomings of the sequence chain hypothesis and noted that his own theory "is evidently a form of connectionism, one of the switchboard variety, though it does not deal in direct connections between afferent and efferent pathways: not an 'S-R' psychology, if R means muscular response". This conclusion almost inevitably shares a common etiology with Lashley.

Lashley and Hebb on Connections

The mention by Hebb that his theory was a form of connectionism may seem strange to the modern reader. This likely shows the direct influence of Lashley on Hebb. More to the point, this caveat echoes a statement that came years prior:

> I have objected to the kind of psychology which formulates its theories in terms of S and R, where S represents an environmental situation and R a product of muscular activity, and which assumes that S wholly determines R (or many S's many R's), believing that because its diagrams are simple, neural processes must be equally so. The traditional reflex arc of three neurons is alone inadequate to explain even the simplest known reflex without the postulation of contributory sensory and integrative processes which are as little established
>
> (Lashley, 1931, p. 16)

Therefore, Hebb's use of hedge words in his theory, "…evidently a form of connectionism…", may signal genuflection towards Lashley (Boden, 2006), and it is important to reiterate that Hebb did not portray his theories as an absolute rejection of field theory. This deference from Hebb to Lashley necessitates serious consideration of the question posed by Glickman, "[What was the degree to which]…Lashley's questions.set the agenda for Hebb's answers…?" (Glickman, 1996). From the above quote, it can be inferred that Lashley required more evidence in support of the idea that local synaptic plasticity was the basis of memory (Orbach, 1998). The resurrection of synaptic plasticity as a memory mechanism can be readily credited to Hebb, whether he wanted the credit or not. To address Lashley's concerns, Hebb offered his concept of the cell assembly, which used local synaptic plasticity to achieve some of the functions Lashley thought only a field theory could address. Importantly, both Hebb and Lashley built on the recurrent framework, drawn from the anatomical drawings of Lorente de Nó, as their starting platform. This framework has a traceable connection from Lashley to Hebb, even if indirect (Orbach, 1998). Lashley appreciated this anatomical architecture in 1938. Moreover, he sought an 'in-person' connection to Lorente de Nó notably during the time in which Hebb and Lashley were working together at Yerkes and three years prior to the publication of Hebb's book (Fig. 7). Nevertheless, it was Hebb's ingenuity that connected recurrent anatomy to synaptic plasticity as the physiological basis by which spatiotemporal patterns could be formed.

Therefore, while it appears that Lashley believed Hebb was misrepresenting the original ideas (see Rosenzweig's account above), it seems more reasonable to argue that Hebb provided the logical extension of Lashley's ideas (Glickman, 1996). In terms of similarity, Lashley favored the use of the word "trace" which shared a great deal with Hebb's cell assembly:

> The billions of neurons in the cerebral network are organized into a large number of systems. Each system consists of the traces of a number of habits or memories. Knowledge of the moves and games of chess would constitute one such system. Memories of neural anatomy another, and so on through all of the individual's varied interests. The traces or engramata in any system are more closely connected with one another than with other systems. The systems are not anatomically separate and the same neurons in different permutations may participate in many systems. For brevity I shall call these 'trace systems.'
>
> (How the Brain has a Mind, Karl Spencer Lashley papers)

Neurons, organized into the recurrent networks of Lorente de Nó, would generate a broad pattern of activity when excited, propagating like a wave (Lashley, 1942). This concept was later expanded on with parallels to Hebb's phase sequence. Certain traces, supporting different functions such as memory or knowledge, can become active via external input and sustain their activity through recurrent projections. Moreover, one "trace" can activate another and "partial traces" can exist (Lashley, 1951; 1958).

The differences between the approaches are that Lashley (1) denied the relevance of specific synaptic connections and pathways, (2) strongly emphasized dynamics and (3) pushed a broader mechanism of reduplication through reverberation:

> Briefly, the characteristics of the nervous network are such that, when it is subject to any pattern of excitation, it may develop a pattern of activity, reduplicated throughout an entire functional area by spread of excitations, much as the surface of a liquid develops an interference pattern of spreading waves when it is disturbed at several points (Lashley, 1942a). This means that, within a functional area, the

> neurons must be sensitized to react in certain combinations, perhaps in complex patterns of reverberatory circuits, reduplicated throughout the area.
>
> (Lashley, 1950, p. 28)

Thus, although there were similarities between Lashley and Hebb, this stands as clear evidence that theoretical differences could be identified as early as one year after the publication of Hebb's book, and quite likely existed beforehand. Hebb's inspiring framework, even in the absence of rigorous derivation (cf. MILNER, 1957) drove the field of neuropsychology forward. Noting that the initial definition of cell assembly was limited in terms of its description and drawing parallels between the assembly and a precious situation in a fission reactor, Milner introduced inhibition to the model (1957). He also added the use of simultaneous firing to identify neurons as part of a cell assembly, binding these cells into a group, and distinguishing them from those neurons that are not firing (Milner, 1957). Hebb took note and modified his own theory in 1982 to include inhibitory interneurons:

> In **The Organization of Behavior** I proposed that the function of recurrent circuits was to maintain firing…For repetitive firing I thought that [a neuron] would have to be restimulated, and this was the function of the closed circuit. But it seems instead that a neuron fired once tends to fire several times at least, and I am now inclined to think that those circuits may be predominantly inhibitory and serve the purpose of promptly shutting off a cell-assembly once it has performed its function of firing, or taking part in firing another
>
> (Hebb, 1982, p. 486–487)

Some Implications of Lashley's Views

> The conclusion is justified, I believe, by such considerations and is supported by electrical studies, that all of the cells of the brain are constantly active and are participating, by a sort of algebraic summation, in every activity. There are no special cells reserved for special memories.
>
> (Lashley, 1950, p. 26)

Perhaps in light of his views on mass action, Lashley may have argued that, although correlates exist, there are no special cells devoted to specific encoding tasks, say of faces, time or space. For example, with respect to hippocampal place cells, it is likely that Lashley would have argued that time and space are correlates inherent to a dynamic system:

> Since memory traces are, we believe, in large part static and persist simultaneously, it must be assumed that they are spatially differentiated. Nevertheless, reproductive memory appears almost invariably as a temporal sequence, either as a succession of words or of acts. Even descriptions of visual imagery (the supposed simultaneous reproductive memory in sensory terms) are generally descriptions of sequences, of temporal reconstructions from very fragmentary and questionable visual elements. Spatial and temporal order thus appear to be almost completely interchangeable in cerebral action. The translation from the spatial distribution of memory traces to temporal sequence seems to be a fundamental aspect of the problem of serial order.
>
> (Lashley 1951; p. 128)

Lashley viewed the perception of space and time as interchangeable (Nadine Weidman, personal communication) and thought that the act of moving activity across the brain is what is necessary for higher-cognition and memory. Both Hebb and Lashley felt that the system effectively creates its own time in that, similar to a pendulum, activity that returns via recurrent pathways to a particular population can define time with each volley of activity. While humans often consider time and space as independent entities, individual cells might have little to do with the encoding of these parameters. Rather, Lashley reasoned that reentrant processing - input spreading through recurrent connections in a series of repeating volleys - was the foundation of the brain as a dynamic system. Operationalizing this in terms of a mechanism that could support higher-cognition, Lashley weakly ventured that:

> To illustrate such a mechanism I have used the analogy of interacting inters on [sic] the surface of a lake. The ripples from a breeze give a basic oriented pattern-direction in the space coordinate system. The cross waves from a bobbing log impose a rhythmic pattern like the time sequence of action. The bow waves from a speeding boat sweep across the surface, as the effects of an external stimulus. All these surface waves combine to a compound wave which can sweep with little distortion around obstacles, as the nervous organization gets past partial sections of the tissue. The waves finally reach the shore and shake the reeds there into patterns of movement, the motor responses. The organization and transmission is not dependent upon preformed pathways, but upon the permutations and combinations of transmitted excitations.
>
> The analogy is far-fetched but I believe a closer representation of the events in the nervous system than is the classical notion of stable reflex paths. Multiple recordings [sic] of electrical potentials from different parts of the brain, as in Gray Walter's demonstration of widespread synchronies of driven Alpha rhythm and John Lilly's picture of organized waves of activity sweeping the cortex, is giving data which lend at least a little plausibility to the concept of neural integration by means of interference patterns of waves of neural activity.
>
> (Lashley Papers, University of Rochester Lecture, Nov. 1957 UF Archives).

Lashley mulled this theory for many years with a description published as early as 1942:

> The action should be somewhat analogous to the transmission of waves on the surface of a fluid medium. Interference of waves in such a system produces a pattern of crests and troughs … which is reduplicated roughly over the entire surface … The analogy with wave motion in a homogeneous liquid cannot be applied seriously to the cortical activity, since the cortical tissues have inherent characteristics as a transmitting mechanism quite different from those of a fluid. The analogy is presented only to give a picture of a reduplicated system which may serve as a starting point for a more adequate conception of the structure of the memory trace.
>
> (Lashley, 1942, p. 313–314)

This theoretical position was highlighted in the University of Rochester lecture in which Lashley described his research using low resistance conductors placed over the visual cortex in an attempt to distort the perceived visual input, along with experiments by Sperry, who implanted mica (an insulating medium) into the cortex. If the electrical field were important, this manipulation should "short" the potential between regions, presumably with negative consequences.

> The experiments seem to rule out electrical fields as the basis of cerebral organization. Nevertheless, the visual data seem to demand some sort of field theory; some over-all influence which groups and combines the activities of individual neurons into organized patterns. There is no present clue to the nature of such a mechanism
>
> (Lashley Papers, UF Archive).

Perhaps these results led Lashley to refine his position. In an unpublished, undated manuscript, Lashley suggested that the wave analogy is illusory yet extended it to biological observations:

> I can only refer again to the analogy of interweaving waves on the surface of a lake as a graphic representation of the activity in the cortex. The efferent cells whose fibers descend from all parts of the cortex to influence the motor cells of lower centers might be likened to so many bobbing cork, firing when lifted high on a wave. The pattern of wave motion causes the corks to bob up in definite patterns, the patterns of motor control. The analogy is anschaulich, comprehensible, but misleading in some respects, for it is not waves but patterns of reverbatory circuits which sweep over the cortex and their mode of interaction is not that of a wave.
>
> (Karl Spencer Lashley papers, folder marked "II").

Distilled to its core, Lashley felt that interacting, reentrant loops of the nervous system generated patterns of neural firing that provided the basis for perception, cognition and action. Nonetheless, as the perpetual critic, Lashley conceded that his formulations and attempts to address these issues were not fully developed, applying to his own theory the same criticisms he levelled at Hebb. For his part, Hebb pointed out the limitations of the reverberatory mechanisms that Lashley was describing:

> It might be supposed that the mnemonic trace is a lasting pattern of reverberatory activity without fixed locus, like some cloud formations or an eddy in a millpond. But if so it seems that the multitudinous traces in the small confines of the cerebral cortex would interfere with one another, producing a much greater distortion of early memories by later ones than actually occurs.
>
> (Hebb, 1949, p. 12–13)

Moreover, Lashley's implementation of analogy runs counter to his stance on the use of 'farfetched' equivalences as noted above. It is of interest to note that the analogy Lashley chose is neither digital nor man-made, but reflective of analog dynamics seen elsewhere in nature.

In addition to his promulgation of the notions of mass action and equipotentiality, Lashley is also known for his failed 'search for the engram'. Lashley, however, did not believe he failed to find the engram as a consequence of lesioning the wrong brain region, but instead because the 'engram' itself might be a good deal more abstract than what had been thought, a very modern idea:

> In describing the effects of removal of the temporal lobe of monkeys I pointed out that, although it may result in the loss of discriminative habits, the memory traces are not actually destroyed, since the habits come back spontaneously after training in other tasks. What is the nature of the disturbance produced by this operation? … These experiments introduce a concept of the function of the association areas which, although I can express it only vaguely, seem to me essential for understanding of the organization of thoughts and behavior. It is the formation of schemata of action; generalized plans or types of organization into which the specific acts or elements of thought are fitted.
>
> *(Lashley papers, unpublished manuscript "An* interpretation of Cerebral Localization")

It is now commonplace to note that brains have evolved in order to adapt and predict in the service of survival and reproduction (for recent examples, see Buzsaki, 2006; Buzsaki, 2013). The simplest mechanism to achieve prediction, as seen in lower organisms, is a single stimulus-response loop. Higher order animals have multiple, layered loops with connections that allow complex network interactions. Patterns of activity through these networks are self-organized, long-lasting and adaptive.

For various reasons, some of the most impactful aspects of Lashley's and Hebb's work have been largely ignored. First, self-sustaining, reverberatory activity through reentrant processes is what defines "cell assemblies", which serve as the building blocks of phase sequences, which in turn subserve complex behavior and higher cognition. While there is an allure to having a population code by which multiple neurons associate through plasticity, causing them to fire simultaneously, this was <u>not</u> part of Hebb's original definition. Neither Hebb nor Lashley intended to describe a mechanism of how memories are stored - they were focused, as noted at the outset, on the more general issues of how neural mechanisms support coordinated behavior and the fundamental problems of "stimulus and response equivalence". Second is the idea that activity in one loop, connected via synapses, can induce patterned activity in other loops. As Hebb invokes this, the patterned activity in other regions would effectively be anticipatory or predictive of what was about to occur in the environment following learning. One could say that this constitutes memory, and can be equated to modern ideas about pattern completion. Lashley, however, avoided ideas that placed emphasis on single cells or synapses. Rather, he saw the recurrent flow of activity as akin to waves and would most likely have taken a more dynamical perspective. Similar to Rayleigh–Bénard convection, Lashley's approach suggests "pattern formation", by which activity takes similar paths through recurrent networks, but in a manner significantly more malleable than the index theories that currently hold sway amongst hippocampal aficionados (Teyler and DiScenna, 1986). Recall that Lashley viewed the nervous system and its activity in terms of "statistical accuracy" (Lashley, 1957).

Third, as noted above, current theories of learning and memory invoke Hebbian synapses, diverging yet again from the original Hebbian concept. Hebb, like Lashley, diminished the importance of individual synapses:

> In a single system, and with a constant set of connections between neurons in the system, the direction to which an entering excitation will be conducted may be completely dependent on the timing of other excitations. Connections are necessary, but may not be decisive in themselves; in a complex system, especially, time factors must always influence the direction of conduction.
>
> (Hebb, 1949)

Though there is an attraction to the causal nature of "fire together, wire together" by which associations are encoded in synapses, both Lashley and Hebb were reluctant to suggest that cause-and-effect are easy to uncouple in the nervous system. Rather, their perspective suggests that neuroscience should seek to uncover the rules that govern how the nervous system is predisposed to respond to inputs.

Finally, it is worth noting that Lashley was explicitly addressing a central question at the crux of the NIH BRAIN initiative: "Today we know that neurons fire and we know that they are connected. We don't know how they act in concert to govern behavior, the essential question in treating neurological disease and mental-health disorders" (Allen and Collins, 2013). Lashley's comments seem prophetic and anticipatory:

> Research on the brain has revealed a network of cells, organized in various structures and systems, subject to constant excitation from the sense organs, and capable of developing and maintaining a great variety of patterns of activity. On the physical side the phenomena can be described, and although the picture is far from complete, the essential elementary processes for the production of behavior have been defined. In contrast, the conception of mind has been extremely vague and has not provided a basis for asking meaningful questions about its relations to the neural events.
>
> (Lashley1958, p. 13–14)

Re-evaluating Memory from the Lashley-Hebb Perspective

Although mostly associated with the ideas of cell assemblies, phase sequences, equipotentiality and mass action, Lashley and Hebb provided theoretical foundations that remain critically relevant to one of the central goals of modern neuroscience: understanding the mechanisms of cognition. Hebb never abandoned the questions that Lashley set-forth concerning serial order and how recurrent networks could lead to higher-level cognition. For instance, Hebb revisited Lashley's *The Problem of Serial Order in Behavior*, replacing the pianist with a violist capable of making 16 finger movements per second (Hebb, 1958). Hebb agreed that the rate of sensory feedback was too slow to support a chaining model that drives the next response, but it could be received at the initiation of the 4th or 5th response down the line (Fig. 8, top). And while Hebb acknowledged the importance of internal processes, he believed that they occurred simultaneously with sensory information being integrated:

> In a single rapid series of skilled movements, highly practiced, it is possible that behavior may be momentarily without sensory guidance – but only momentarily. With this possible exception, it is clear that sensory guidance is essential to any organized series of actions. Mediating processes are fundamentally a means of modifying the way in which sensory controls act, not an absence of it.
>
> (Hebb, 1958. p. 63)

Hebb's pictorial schematic invoked multiple reverberatory loops of different sizes that are capable of interacting and, as later noted, "predicting" (Buzsaki, 2013). Furthermore, it is here that Hebb offers a lifeline to the "waves of Lashley". Hebb noted that, within the re-entrant pathways of the brain

> "…*excitation might theoretically continue for an indefinite period, 'chasing its tail,' and not leave the circuit until some other excitation came along with which it might combine to produce a motor effect that neither could produce alone"*
>
> (Hebb, 1958. p. 56).

Lashley's notion of reduplicated waves interacting and interfering with each other among reentrant loops until they finally flow into one of many possible pathways for an output is operationalized by Hebb in a description of what occurs between sensation and response (Fig. 8, bottom):

> With one activity going on in the brain, a particular stimulus arouses one response; with another central activity, exactly the same stimulus arouses a different response
>
> (Hebb, 1958. p. 56–58).

Importantly, this is the "cell assembly" theory that Hebb emphasized in 1949 (Fig. 5). It is not the synapses nor the active neurons that form the fundamental basis of behavior; rather *it is the pathway that the activity flows through*. This may appear to be an inconsequential distinction relative to how the engram and cell assembly are currently understood but there are clear ramifications for the field of learning and memory. Consider the generic and widely accepted two-stage model of encoding and consolidation (Fig. 9). In this model, during the "on line" state, sensory information activates neurons in the primary sensory cortices, then in higher association cortices, and eventually in the hippocampus. The population of active cells in the hippocampus is said to have formed an engram or "index" of the co-active cortical elements. In a later, "off-line" period, the neurons of the hippocampus reactivate, driving the regions in the lower hierarchical regions including elements in the primary sensory cortices that were activated by the initial experience. Following numerous such reactivations, neurons in the primary cortices are assumed to form cross-linkages, thereby providing the brain with the ability to reconstruct the initiating event in a hippocampal independent manner.

While models of this type often cite Hebb and Lashley as providing theoretical foundations, aspects of this type of memory model are in fact opposed to the concepts that Lashley and Hebb formalized. Lashley vehemently argued against a "switchboard" model of brain function; a role seemingly played by the "index" in the two-stage model.

Similarly, Hebb avoided implementing hierarchical structures in favor of recurrent circuitry and noted that cognition is not localized to synapses. Both Hebb and Lashley emphasized that the important factor was the manner by which activity flowed through neural circuits. Similar arguments have been made in which the connectome is necessary, but insufficient to understand the brain, as it neglects neural dynamics (Cook, 2015). The two-stage model ascribes specific stages of information processing to specific brain regions, suggesting that a hard line can be drawn between regions that support perception and those that support memory. This stands in direct contrast to Hebb's notion that STM and LTM are instantiated in the same networks. Unambiguously, Hebb found theories that placed specific psychological functions within an isolated region or circuit objectionable:

> There is a trap here, however, that the student must be warned about. No psychological function can exist within a segment of cortex by itself. We commonly say that vision is localized in the visual area, a part of the occipital lobe; but this does not mean that the whole process of seeing (or even of visual imagery) can occur in the occipital lobe. What it means is that an essential part of the process occurs there, and only there. As we shall see shortly, speech is "localized" in the cerebral cortex on the left side (for most persons). This again does not mean that the mediating processes of speech can occur in that tissue alone; it does mean that their organization depends on it. Injury to this area of cortex can abolish speech (and certain other abilities to some extent), whereas larger destructions in other areas have no such effect.
>
> (Hebb, 1958, p. 83)

This comment by Hebb is a theoretical "tip-of-the-hat" to Lashley's "equipotentiality" and "mass action". As Hebb had the capability of maintaining a level of honesty and respect towards Lashley posthumously (Fig. 10), it stands to reason that Lashley's ideas would be enveloped into Hebb's theories.

Conclusions re Credit

An electrophysiological recording without reference makes it difficult, if not impossible, to sort the signal from the noise. Fortunately, the written records of Lashley and Hebb make it possible to recalibrate our contemporary understanding of their contributions. Donald Hebb currently receives more attention than Karl Lashley. We have argued here that Lashley and Hebb had an extensive working relationship, with Lashley likely providing the framework for Hebb to succeed. The major driving force behind the theories of both men was the recurrent nature of neuronal networks as first described by Lorente de Nó. The importance of these networks was that activity in the brain could be maintained in the absence of any input or reflex arc as championed by associationist theories.

Lashley assailed the popular theory of localized function within the brain, believing it did little to advance our understanding of how a pattern of activity within the brain leads to complex behavior (Lashley, 1929). He developed the insight that learning, while clearly a consequence of the neurons active during the original behavior, might also alter synapses on neurons that were silent (Lashley, 1924). To this end, Lashley exhibited immense intuition, understanding that changing the resistance between two neurons in an activity dependent manner could also affect neurons not directly participating in the task. The brain as a whole is inevitably changed by experience. Should a memory trace exist, it would take a distributed form. Given that these ideas remain current, it is hard to see why so little credit is given to Lashley:

> Lashley's book [Brain Mechanisms and Intelligence], similarly, is remembered only as reporting that there is no localization of function in the rat's cortex, and that large lesions affect learning more than small lesions. 'Equipotentiality,' and 'mass action.' Full stop… But this, of course, is not a true picture of Lashley's research… In the first place, he did not deny, but rather emphasized, the existence of cortical localizations of function, in rat as well as in man. What he did deny was that localization is all that it has been thought to be… Lashley concluded, in general, that equipotentiality and mass action may both hold over the whole cortex for one function, such as learning a complex alley maze; but that in another situation, such as the elevated maze, vision becomes more important and equipotentiality disappears or is diminished.
>
> (Hebb, 1963, p. xii-xiii)

One possible reason for the imbalance in credit between Lashley and Hebb could be that Lashley was acknowledged to be a difficult, complex personality. As described by one of his former students, "Lashley was always impersonal in his dealings with his students and associates. I do not believe that he had the capacity for a real close friendship with anybody" (excerpt from Beach, 1961). Moreover, Lashley had a sort of scientific imbalance, capable of assailing the theories of others without having one of his own to defend (Hebb, 1959). Finally, stated simply, Lashley did not suffer fools gladly. Directly speaking to his attitude, near the end of his life, Lashley responded to a request for an autobiography to be used in a seminar:

> *This is my first and, I hope, last attempt at autobiography. [Henry] Murray has pointed out, apparently with surprise, that a great many psychologists are not interested in people. I am one of that sort and would be a lot more interesting to myself if I could develop a good visual agnosia or other trait related to my problems. But then I should probably object to an immediate autopsy and so be as useless as other human subjects. You will find numerous contradictions in my work. I make no apology for* them; interpretations were based on the facts available and later experiments changed the picture. Recent [evidence] on lack of effect of transcortical connections… may knock all my theories cockeyed. This may mean some progress. Mixed wishes for your course
>
> (pg. xviii, Beach and Orbach, 1982).

We tend to downplay these personality factors as critical here, partly because Hebb also refused to suffer fools. He was tough, but ultimately supportive.

A second possible reason that Lashley's contribution has been diminished is that his writing tended to be opaque. Comparing *The Problem of Serial Order in Behavior* (Lashley, 1951) to *The Organization of Behavior* (Hebb, 1949) is to compare jargon to enthusiasm, respectively. Lashley may have been aware of his short-coming and the disparity between writing styles. In a personal letter to Hebb regarding *The Organization of Behavior*, Lashley is quoted "Although I am still unconvinced of your arguments and disagree with many of your conclusions… I feel a real admiration for the book. It is an exceedingly thoughtful and stimulating treatment with a broad outlook and literary style I envy." (p. 55, Orbach, 1998). The communication of ideas is significantly easier when the reading is pleasurable. Moreover, Lashley apparently believed that book writing is for those who could not or would not conduct scientific research. The success and enormous impact of Hebb's book would seem to put that argument to rest.

Hebb's writing remains pleasurable nearly 70 years later. Hebb understood the short-comings of his ideas when he put them on paper, but ventured them anyway. *The Organization of Behavior* provided a framework within which to think about neural computation and representation, and later modelers and theoreticians had to pick up where he and Marr (1971) left off and operationalize these ideas (one cost of all of this was that the assembly idea has morphed into several different ideas). Nonetheless, the issue of priority and the failure to recognize Lashley's recognition to the field of cognition - despite altering the field of motor control (Bruce, 1994) - are issues that should be revisited and resolved. Misattribution has the potential to lead to misinterpretation.

Conclusion re Ideas

> In any scientific investigation, one must start with the accepted knowledge and current explanatory hypotheses. These set the problems and determine the direction of research. One can best understand the present status of the problems of neural organization by tracing them from some of the older conceptions.
>
> (Lashley, University of Rochester Lecture, UF Archive)

In seeking to get credit assignment right, we uncovered a number of ways in which both Lashley and Hebb should have been taken more seriously. Consider these words of caution from Hebb, holding up the virtues of Lashley's early research:

> In the preceding decades it was possible to debate the question seriously, whether consciousness was due to an impulse passing high resistance at the synapse, or low resistance. It was still possible to put single memories into single brain cells, like little jewel cases, each with its own jewel… The stock-in-trade of physiological behavior theory had been synaptic resistances, detailed localizations of cortical function, and new paths from point to point in the cortex for new habits. Now, suddenly, it appeared from Lashley's work that such ideas were fantasy, not science.
>
> (Hebb, 1963, p. v-vi)

We have seen how Hebb proposed to account for Lashley's findings in a way that retained the importance of specific neurons, but only as replaceable parts of cell assemblies and phase sequences. In this day of claims about highly specific "engram cells" (e.g., Kitamura et al., 2017), these concerns need to be taken seriously (cf., Hardt and Nadel, 2017).

One surprising result of our looking closely at what Lashley and Hebb actually said concerns the issue raised briefly already: the idea, posited by Hebb, that temporary and permanent memory is stored in the same circuits. This idea, which was rapidly ignored, now looks more appealing. Put most succinctly, the emergence of the idea of systems consolidation, coupled with what has been called the "standard model" of consolidation, led inexorably to the notion of a so-called medial temporal lobe memory system, that played a time-limited role in LTM, and had no role in perception or STM (e.g., Squire, 1992). Recent data from a variety of sources suggest that this perspective is wrong and that Hebb was on the right track in linking both STM and LTM to the same assemblies. The emergence of multiple trace theory (Nadel and Moscovitch, 1997), and its emphasis on the effects of reactivation, harkens back to the ideas that Lashley and Hebb grappled with over 75 years ago. While it is beyond the scope of the current effort to explore these connections in more detail here, we hope to take them up in a subsequent paper.

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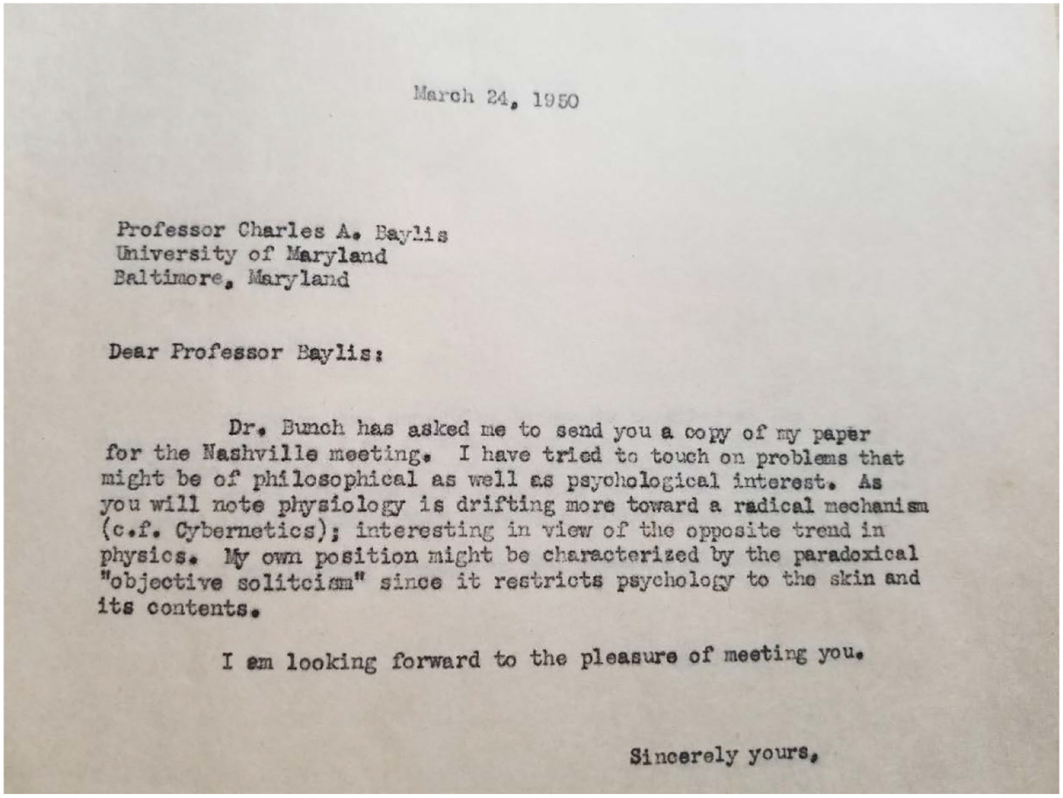


March 24, 1950

Professor Charles A. Baylis
University of Maryland
Baltimore, Maryland

Dear Professor Baylis:

Dr. Bunch has asked me to send you a copy of my paper for the Nashville meeting. I have tried to touch on problems that might be of philosophical as well as psychological interest. As you will note physiology is drifting more toward a radical mechanism (c.f. Cybernetics); interesting in view of the opposite trend in physics. My own position might be characterized by the paradoxical "objective solitcism" since it restricts psychology to the skin and its contents.

I am looking forward to the pleasure of meeting you.

Sincerely yours,

Fig. l:

In Lashley's own words, he summarily dismisses cybernetics, a field on the rise at the time which found utility in operationalizing logic switches in the service of cognition. The word "soliticism" is most likely a misspelling of "soliticism", the theoretical position that one is only certain that their own mind exists. This position is clarified in a later publication, in which Lashley rejects Descartes classic "I think, therefore I am". "The only conclusion that can be derived from experience is that thought exists…*There are neither empirical nor logical grounds for assuming that the existence of consciousness implies a distinct entity which is in the relation to it, a knower or do-er*" (Lashley, 1958). Put simply, the implementation of cybernetics necessitates the implementation of a "reader" that transcends the other processes.

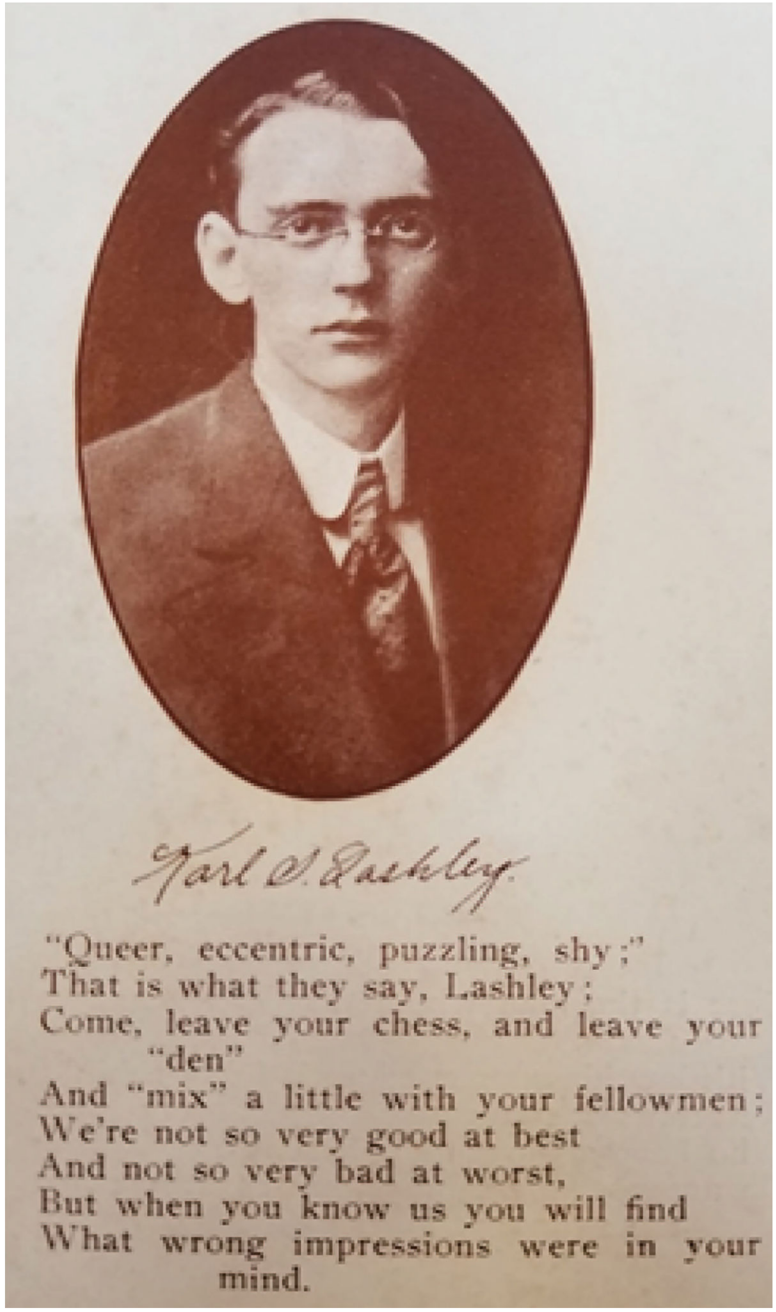


Fig. 2:
Early photograph of Karl Lashley (University of West Virginia Year Book1910)

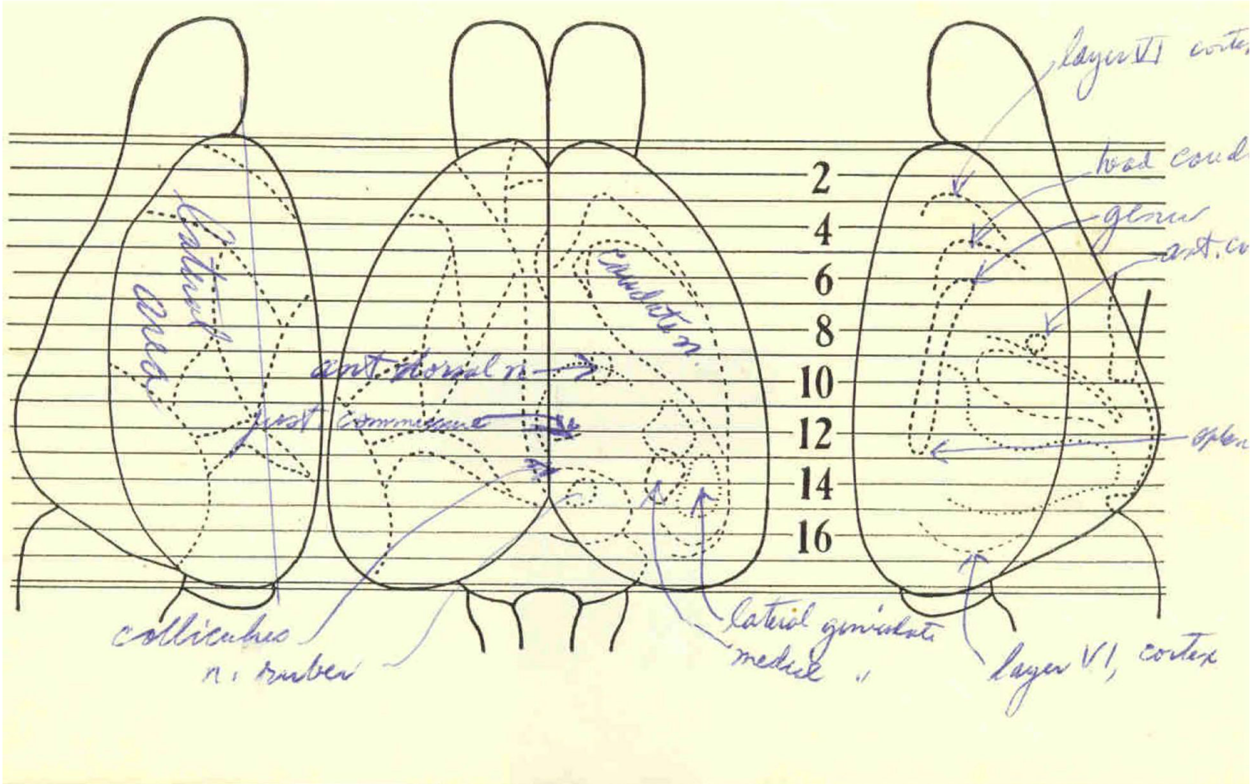
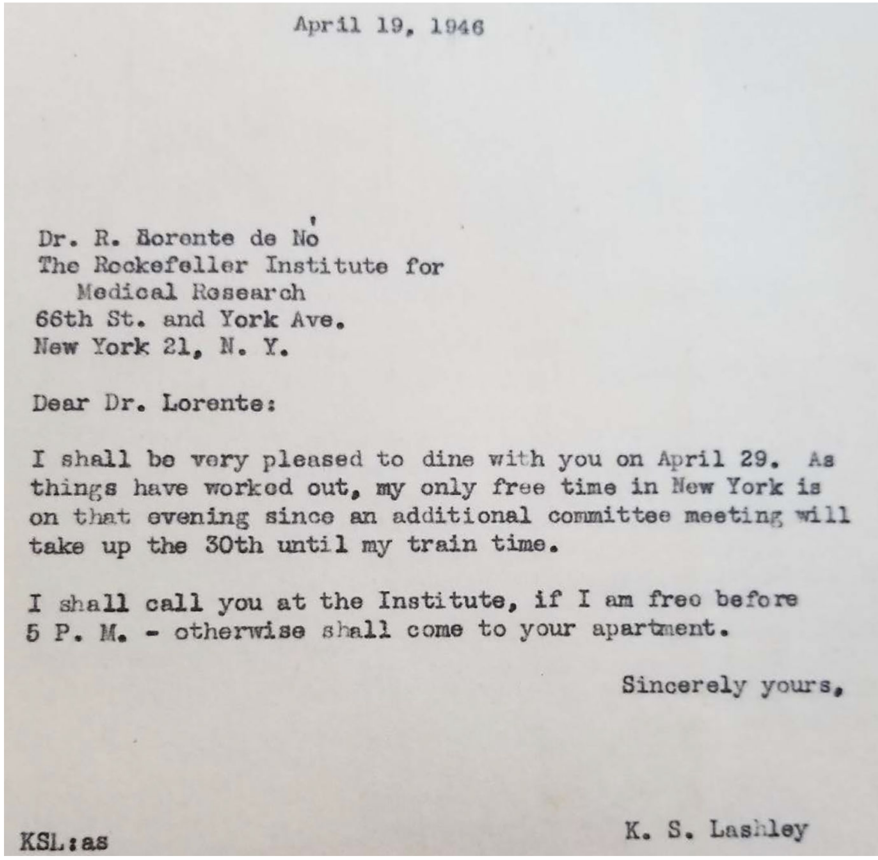


Fig. 3:

Photograph of Donald Hebb taken around 1922 at Dahlhousie UniverisityPhoto courtesy of Mary Ellen Hebb.” (see Brown and Milner, 2003)



April 19, 1946

Dr. R. Lorente de Nó
The Rockefeller Institute for
Medical Research
66th St. and York Ave.
New York 21, N. Y.

Dear Dr. Lorente:

I shall be very pleased to dine with you on April 29. As things have worked out, my only free time in New York is on that evening since an additional committee meeting will take up the 30th until my train time.

I shall call you at the Institute, if I am free before 5 P. M. - otherwise shall come to your apartment.

Sincerely yours,

K. S. Lashley

KSL:as

Fig. 4:

Timelines of Karl Lashley and Donald Hebb. Their academic careers intersected twice, first during Hebb's graduate education and then again at the Yerkes Primate Institute.

December 9, 1958

Dear Don Hebb:

Thank you for your note, and for your sympathy. Truly, I need it. And yours means a good deal. For I know that, despite your divergent theories, you and my dear had much in common, among other things, a mutual respect. Why else would he have insisted that you be approached first about the directorship of the Labs? Then, too, controversy was the breath of life to him and, to his mind, to science and its progress as well.

January 12, 1959

Dear Don Hebb:

Thank you for letting me see your biography of Karl. It was truly generous of you, and I feel privileged and honored.

You need have had no misgivings. I realize that a statement such as this must, from its very nature, be to some extent unfeeling and critical. Certainly he would not have it otherwise. I even had a wicked thought upon reading your letter for the second time: wouldn't it be typical if even the memoirs of him were to arouse a controversy? But I can sense the affection and respect, too. And with your successful attempt to make him live in at least three dimensions I concur wholeheartedly.

I would not worry about being suspected of over-valuation, if I were you. To me, of course, he is a genius - a most unscientific term with no explanatory value - and that not only because I love him so completely. He was one of the only two men living to whom I have known Paul, my first husband, look up admittedly (the other being Köhler). I am confident that, as you say, he will only grow in stature with the passing of time, and come to be seen in the light of greatness which some of us even today feel is his.

Some day, when you are all finished with this, and if it is not asking too much, I should like to read all the material that you managed to collect, just to round out my own picture of my beloved over the years. I hope, too, that our paths may cross again, and that you will tell me lots more about him from the time before his and mine.

Thank you once more, for everything.

Yours sincerely,

Mrs. Karl S. Lashley

McGILL UNIVERSITY
MONTREAL

January 5, 1959

Mrs. Karl S. Lashley
Fiddler's Cove
3936 McGirts Boulevard
Jacksonville 10, Florida

Dear Mrs. Lashley:

With some misgivings, I enclose a copy of my labors. Unfortunately I miscounted in having copies made, and this is my own working copy; could you let me have it back when it is convenient? I will certainly see that you get a reprint when the report appears in March.

My misgivings are because this may seem unfeeling and critical to you, though in fact it is written with affection and great respect. I have tried to do two things: to make Lashley live in the mind of the reader, as a lively, vigorous, fun-loving and adventurous human being rather than a cold, two-dimensional still-life; and secondly, I have tried to avoid giving a picture of scientific perfection, again in order to picture him in three dimensions with the intention of stimulating the reader to go back again and look at his work (especially when the volume of selected papers appears). As a former student I will be suspected of over-valuation; I hope to avoid this by a critical note, and so hope that my over-all evaluation (which is very high) will be taken at face value.

You refer to differences of theory between him and me, but these never bulked large in my mind—instead, my work seemed to me to grow directly out of his; though he himself did not see the matter in that light, there was certainly nothing personal in the differences of opinion. I went deep in debt to work with him in the first place (instead of going to work with Yerkes, who would have provided an assistantship), and I have never seen any reason to doubt

page 2, Mrs. Lashley, Jan. 5/59

the wisdom of that early decision. He was, in my mind, the best psychologist of this century, and one of the great ones in any century.

So, read any critical remarks in the paper as being part of a description of a man who was too big to be insulted by a white-washing and—I hope—helping to persuade the reader that I am not doing so, that my high appraisal in other respects should be taken seriously and not as the adulation of a former student.

Most sincerely,

Don Hebb

D. O. Hebb,
Department of Pschology

Fig. 5:

(**Left**) A figure from Lorente de Nó (Lorente de Nó, 1938) outlining the recurrent circuits of the hippocampus. Even earlier, Cajal was engaged with similar ideas of connectivity and plasticity, as evident in his Croonian lectures: *"In a continuous, well-established network – represented as a grid of telegraphic cables, where no new stations or new cables can be created – the network is something rigid, unchangeable, and unalterable, which unfortunately shows that the thought organ has certain limits, but it is malleable and can be perfected during the stages of development with the use of well-directed mental gymnastics. If we do not fear abusing comparisons, we would defend our conception by saying that the cerebral cortex is a rich garden with innumerable trees, where pyramidal cells have an* *intelligence of multiplying their branches and insert increasingly deeply their roots. The pyramidal cells produce diverse fruits and flowers, each time more delicious"*. (Cajal, 1894) (**Right**) Hebb's original schematic of the assembly emphasizing a path of reverberation, rather than a population of simultaneously active cells, as the means to organize higher-cognition and behavior (Hebb, 1949).

Fig. 6:
Plate of lesion localization method with anatomical notes written by Lashley. Although Lashley was not the first to implement the lesioning approach, he was among the vanguard in terms of applying a rigorous method of localization. This image was provided courtesy of Roger K. Thomas, via his PhD Major Professor, Lelon (Lee) J. Peacock. In 1954, Peacock wrote Lashley and requested advice on mapping rat brain lesions. Lashley wrote about a 1.5 single spaced typed letter describing his method. He stated in the letter that he had never published on his method. Lashley included with the latter the hand-labeled diagram and a few blank diagrams. (Roger K. Thomas, personal communication; Thomas, 2007a)

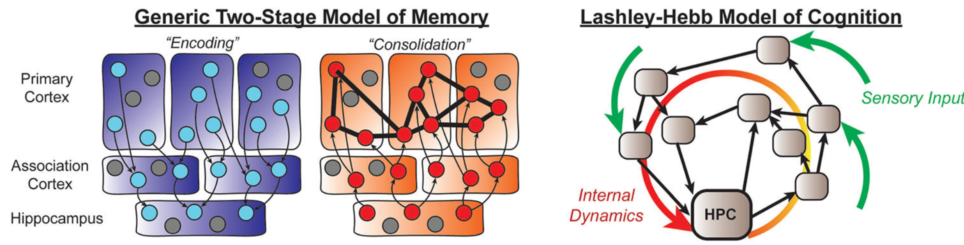


Fig. 7:

Letter of correspondence between Lorente de Nó and Karl Lashley from 1946, demonstrating a professional and possibly personal relationship.

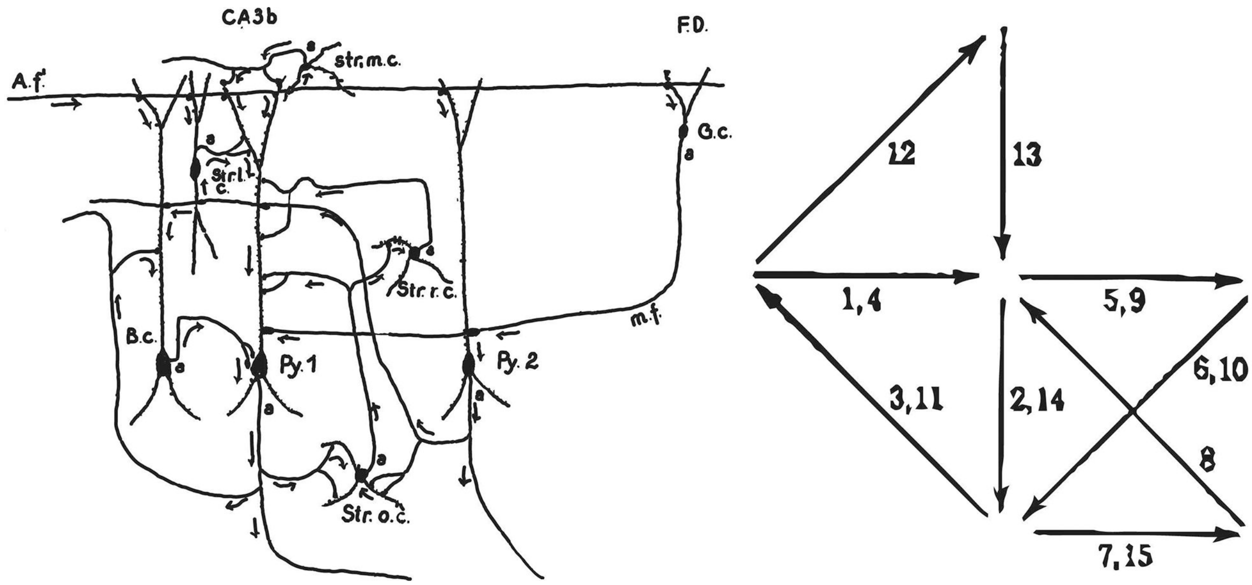


Figure 8:

Top. Sensory input arrives into the central nervous system triggering what Hebb referred to as a trace – a holding mechanism in which activity in one loci volleys outward only to return at a later timestep (small arrow circles). This sequence of conditioned responses ("C") forms a basis for serial ordered behavior. As a solution to the chaining problem as described by Lashley (1951), Hebb offers the idea that a longer loop, initiated by the first response and influencing the 4th, can potentially be used to organize complex behavior (Fig. 20 from Hebb, 1958). Bottom. *"Diagramming a possible mechanism of a set to add. The excitation from the prior stimulus, 'add', is held in a reverberatory loop. The second stimulus, (8,2), is connected with two motor paths and can evoke '10' or '6'; but the reverberatory activity supports only one of these, and the response is '10'. If the prior stimulation had been 'subtract," a different reverberatory circuit would have been active and would have determined the response '6.' Needless to say, this diagram is entirely schematic (any resemblance to neural tissue is entirely coincidental)"* (Fig. 18 from Hebb, 1958, p. 57).

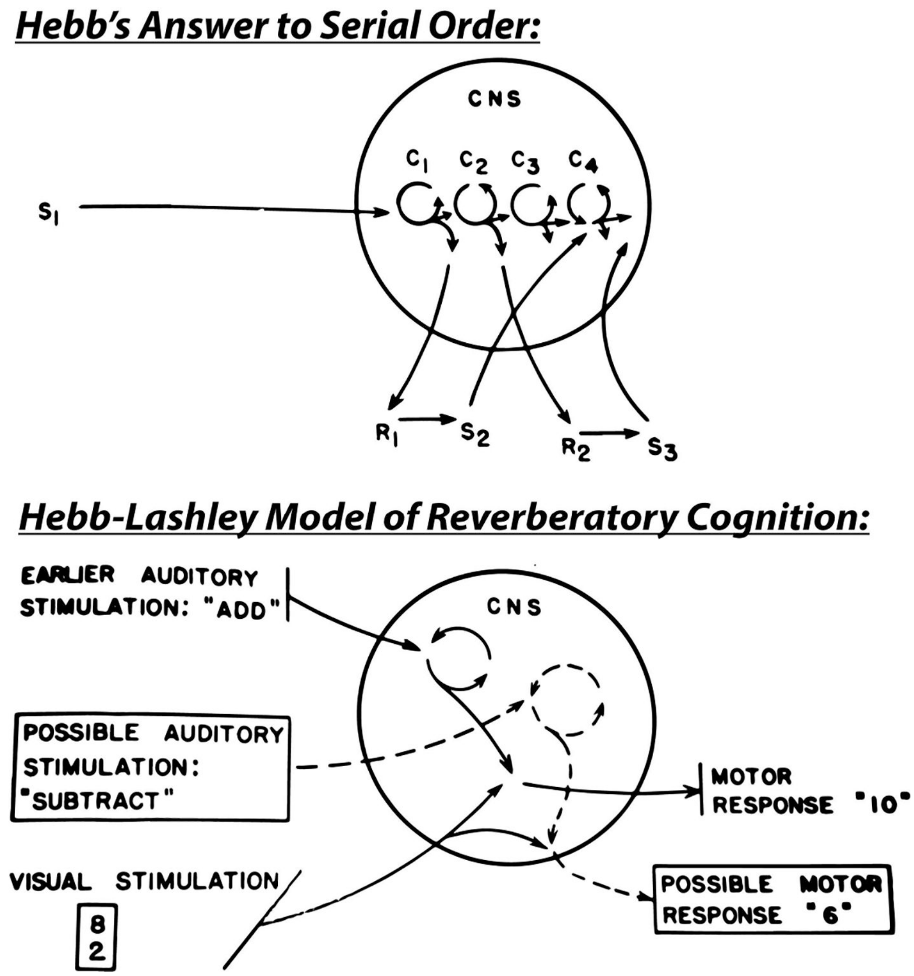


Figure 9:

Cartoon depiction of the generic memory consolidation model versus a reentrent Lashley-Hebb model. Important distinction between the generic consolidation model (GCM) and the Lashley-Hebb model (LHM) is that the GCM is hierarchical in construction and consists of two divergent processing states ("encoding" versus "consolidation"). In the GCM, during acquisition, sensory stimulation is relayed from the primary cortices to towards the hippocampus (or the prefrontal cortex, depending on the model), acquiring an abstract representation which is importantly, orthogonal to other previously stored memories. In a later offline period, the population of neurons within the hippocampus involved in encoding are replayed, reinitiating the patterns in the primary and association cortices. Through multiple replay events, the cortex becomes capable of retaining the associations independent of the hippocampus. The LHM model differs notably in the emphasis of reentrant loops and the manner by which activity moves through the circuits. From their perspective (e.g., serial order of behavior), activity will inevitably travel through these recurrent networks with sensory input potentially altering the manner in which it travels. Finally, *note bene* that the LHM avoids localizing memory to a single region but emphasizes that the flow across multiple, recurrently connected regions form the larger mediating processes.

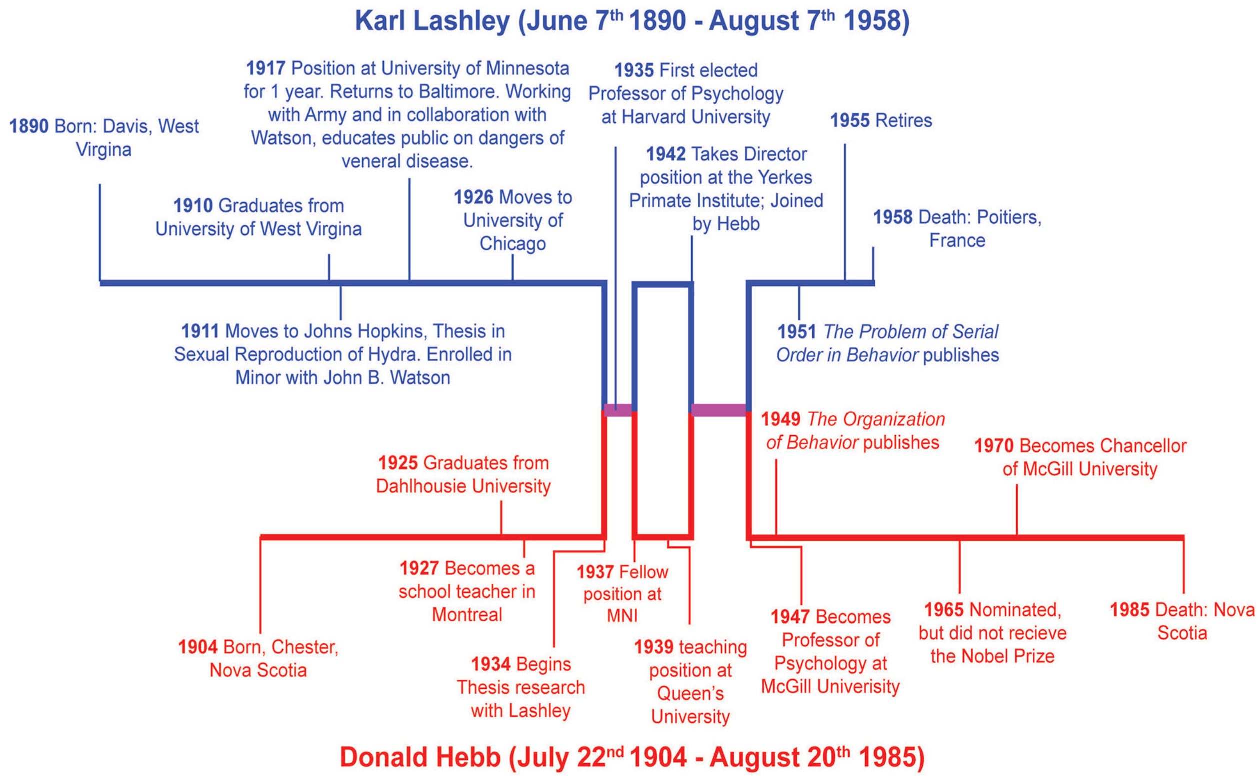


Fig. 10:

Correspondence between Claire Lashley and Donald Hebb following Karl Lashley's death, August 7th 1958. The interaction touches on the topic of a memorial piece that Hebb is constructing, but of notable interest is that Hebb was potentially offered the director position at the Yerkes Laboratories and the theoretical differences between Karl Lashley and Donald Hebb. Note that this side of Lashley, seen by Claire, hints at a person seemingly unknown to either Lashley's students or contemporaries (Claire Imredy Schiller Lashley Papers).