

# Neurobiology a century ago at the Marine Biological Laboratory, Woods Hole

Jane Maienschein

*Neurobiology was a central concern at the Marine Biological Laboratory (MBL), Woods Hole at the end of the last century, when the director Charles Otis Whitman set up a seminar for discussion of research and general issues in 'neurology', which took place annually from 1896 to 1900 and generated intense interest among MBL researchers. Although the emerging fields within neurobiology underwent changes, neurological concerns continued to play a central role. This article explores the activity at the MBL in the 1890s when the various studies had not yet unified to form the field of neurobiology.*

*Loligo pealei* is the most popular martyr to neurobiology at the MBL, and *Aplysia*, *Limulus* and a variety of other species also join the parade into the laboratory. It is not unexpected that neurobiologists should have joined cytologists and embryologists in making their way to the seashore for summer research. Nor is it odd that marine organisms should have turned out to be useful for the productive research programs designed around them. What does surprise most modern biologists, however, is that this pilgrimage is nothing new. Indeed, neurobiology first arrived at the MBL nearly 100 years ago.

Over the years, there have, of course, been significant changes. After all, science *does* progress. New techniques, equipment, different organisms, and a more narrowly focused set of questions have come to dominate neurobiology. Yet much remains the same, and much that is exciting in contemporary neurobiology traces its roots to work at the end of the last century. Perhaps the most important point is that then, as now, a few people in one time and place can crystallize diverse lines of research together into a shared, coherent pursuit – at least briefly.

The first formal discussion of neurobiology at the MBL occurred with Herbert Henry Donaldson's evening lecture in 1891 on 'Methods of Studying the Nervous System'. Donaldson's unpublished paper probably considered the latest advances from Europe, including modifications on the Golgi method of cell preparation and methylene blue staining. Perhaps he also expressed his caveats about the abnormalities that could occur, as he did a few years later<sup>2</sup>. He undoubtedly gave this lecture at the invitation of the first MBL director, Charles Otis Whitman (Fig. 1).

Whitman knew Donaldson from Clark University, where Whitman served as department chairman<sup>3</sup>. Whitman had willingly agreed in 1889 to become the first chair of biology at Clark because of its

research orientation, and the freedom that the founder, Clark, had promised his faculty. When, in 1892, Clark's perceived interference threatened their independence, Whitman, as well as most of the Clark faculty, including Donaldson, left for the newly founded University of Chicago<sup>4</sup>.

Donaldson's primary interest lay in neuroanatomy, specifically in the structure and growth of the human brain and the relative sizes of cranial nerves, which complemented Whitman's interests in leeches. In particular, Whitman had come to concentrate on questions about metamerism, examining especially the connections between central neuromeres and peripheral nerves and also their correlations with external features in *Clepsine*. Whitman set his students and colleagues to work exploring similar problems in a variety of organisms. Inspired by Whitman and also by work from Europe, several of Whitman's associates began to concentrate on the cranial nerves in particular. Oliver Smith Strong, for example, turned to the morphology and histology of cranial nerves in vertebrates, publishing a major paper in 1895<sup>5</sup>. This 130 page article appeared in the *Journal of Morphology*, which Whitman had started in 1887, and represented work begun at Princeton under MBL trustee Henry Fairfield Osborn. (Strong continued this work at Columbia University, still under the guidance of Osborn, and received his PhD from Columbia in 1895.) Presumably because of the close connection between Whitman and several of Columbia's leading biologists, Strong had also worked at the MBL and had discussed his ideas there with the growing group of interested researchers.

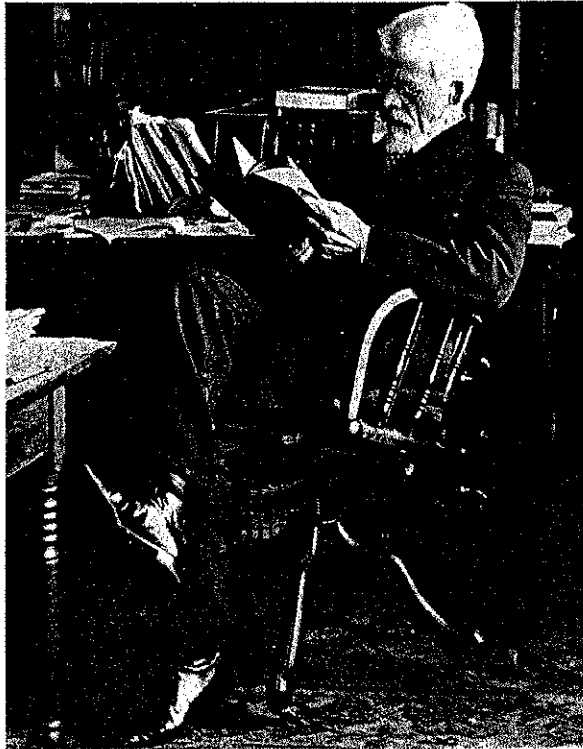
As a result of the increasing concern with nerve studies, Whitman organized a neurological seminar at the MBL. The research-oriented seminar was to serve 'for the benefit of investigators who were willing to report the results of unpublished researches on nerve-tissues, and to summarize and discuss the literature bearing on each problem thus reported'<sup>6</sup>. It was a closed seminar, not open to the public as Donaldson's lecture and other evening lectures were, and he asked Howard Ayers to serve as organizer.

A graduate of Harvard, Ayers had attended the MBL sessions as an instructor and investigator since the second year, 1889, when he had replaced Whitman as director of the Allis Lake Laboratory in Milwaukee, Wisconsin. With his lecture of 1890, 'The Ear of Man, its Past, Present and Future', he also began to develop his interest in neurobiology, extended in a study of brain cells<sup>7</sup>. In 1896, then at Missouri, he agreed to organize a 'neurological seminar' at the MBL.

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<sup>2</sup> For information about lectures at the MBL, including names and dates, see the *MBL Annual Reports*. On the evening lectures and their context, see also Ref. 1.

Fig. 1.  
Charles Otis Whitman  
at the MBL.  
(Photo from MBL  
Archives.)



The 1896 session had 19 speakers between 20 July and 10 August (see Fig. 2), with roughly 1 h long sessions twice a week. Most of the papers remained unpublished, but they were probably largely descriptive anatomical studies. In particular, the prime concerns lay with providing more detail in a larger range of species in order better to understand the relations between the parts of the nervous system.

Several papers did explore other topics, however, and these show the range of newly emerging neurological investigations. For example, a Radcliffe graduate student, Margaret Lewis, considered the 'Centrosome and Sphere in Nerve-cells'. She did not discuss the nucleus, as might have been expected but rather first showed that each of the ganglia cells in her annelid worm had a centrosome and sphere and then concluded that these are part of the cytoplasm<sup>8</sup>.

In his paper, William Patten began to discuss his far-reaching study of the *Limulus* nervous system. (Patten had received his PhD under Rudolf Leukart in Leipzig in 1884, shortly after Whitman had done so.) After two years of postdoctoral research at marine stations in Trieste and Naples, he served as Whitman's assistant at the Allis Lake Laboratory until 1889, when Whitman left for Clark and Patten went first to North Dakota and then on to settle at Dartmouth College, New Hampshire. Though he began his study of *Limulus* under Whitman at the Allis Lab, it was when Patten had his own graduate students at Dartmouth that he developed that work more fully. There, with William Redenbaugh, Patten published his studies of the nervous system of *Limulus polyphemus*, which established that each neuromere innervates one metamere, and that the

nervous system therefore parallels more general anatomical patterns of segmentation<sup>9</sup>. In his extensive series of papers, Patten suggested that researchers should get away from philosophical speculations, such as those about epigenesis or preformation and should instead concentrate on producing reliable information using careful preparations – a conviction that has helped to insure the continuing importance of his work<sup>10</sup>.

Only Charles Judson Herrick really addressed neurophysiological questions that first year with his discussion of 'Functional Changes in Nerve-cells'. Herrick had entered biology following the footsteps of his older brother Clarence Judson Herrick. Charles (or C. Judson as he was soon known) became a fellow and graduate student at Denison, Ohio, where his brother taught. When his brother became seriously ill, Charles took over for him in 1894. He assumed his teaching duties, while still a graduate student himself, and also became the managing editor of his brother's *Journal of Comparative Neurology*, begun in 1891 (changed to *Journal of Comparative Neurology and Psychology* in 1904). In 1896, Charles went to Columbia for a year to work on his PhD under Strong and Osborn, finishing his dissertation on the nerve components of bony fishes in 1900. This work always focused on correlating the CNS and specialized peripheral nerves with behavior.

The second year again brought 19 speakers, about half of whom had spoken in the first year. New subjects included a look at the lateral line system in several organisms, phosphorescing organs, and giant cells in vertebrates. Ulric Dahlgren's study of giant cells in the dorsal wall of the spinal cord of adult flatfishes, for example, suggested that the special cells were connected with the functioning of the dorsal and/or anal fins and showed interesting similarities to those of toadfish<sup>11</sup>. This season brought more reviews of work other than original research, perhaps because each participant had discussed his or her own work the year before and had not yet generated new results in this era of relatively few research opportunities.

The third year, 1898, brought changes. For the first time, the seminar went public and specifically invited researchers from the Fish Commission, across the street in Woods Hole, perhaps in an attempt to expand the range of subjects covered by adding new researchers with new interests. Perhaps, since 1897 had been a crisis year at the MBL both financially and psychologically, it was felt that the group needed to expand its base of support<sup>12</sup>.

So in this year, Ayers organized 29 talks. This allowed a wider participation certainly, and a broader range of topics, but it also required meeting for as many as five talks per day. Even with very short discussions, the summer must have been a bit exhausting for anyone who participated in everything. Ayers may have found it too much; certainly he did not return to the MBL thereafter.

The expanded session brought familiar topics certainly, but also new lines of inquiry. For 1898, we

have more information available since many of the papers were published in Herrick's *Journal of Comparative Neurology* (see Fig. 3). Evidently it had sometimes been difficult to get enough submissions in the early years, so this made-to-order collection probably suited Herrick nicely<sup>13</sup>. With a report on the session by Morrill, the section took up nearly 100 pages and included 19 reports. These reveal a continuing interest in the traditional subjects: new uses of the Golgi method especially for the study of cranial nerves, segmentation, giant ganglion cells in several organisms, or the network of peripheral nerve fibers.

In addition, the 1898 session brought a greater concern with physiology. One paper addressed the potential of functional nerves to be either active or inactive, and the role of the brain in determining a nerve's particular state of activity. Two papers drew opposite conclusions about the validity of 'neuron theory', which held that the nervous system is made up of separate, autonomous nerve cells. Clarence Fremont Hodge favored the neuron theory (see Ref. 14). Hodge, who had received his PhD from Johns Hopkins and then been a fellow at Clark while

Whitman was there, had remained at Clark after the mass exodus to Chicago. He advanced to an assistant professorship at Clark, where he conducted his studies of nerve cell physiology. In the late 1890s, he studied fatigue and aging in particular. His presentation in 1898 compared the nerve cells (specifically pyramid cells) seen in Golgi preparation, of sleeping and fatigued puppies – not specifically marine work obviously, but certainly neurobiological<sup>14</sup>.

Thomas Montgomery and George Howard Parker presented a set of slides prepared by the Hungarian histologist Stephen Apáthy to accompany an article on nerve fiber development<sup>15</sup>. Like most neuroembryologists at the time, Apáthy held that, contrary to the neuron theory, nerve cells all interconnect in a vast reticulum, with the cells literally passing through other cells to make up a functional as well as a structural whole. Apáthy's work offered strong support for the 'reticular theory'. The debate about nerve structure had moved to the embryological level, and it was thought that evidence about how the fibers first form would shed light on problems of neuroanatomy and physiology. Apáthy's work

MARINE BIOLOGICAL LABORATORY

REPORT ON THE NEUROLOGICAL SEMINAR

TITLES OF REPORTS.

1896.

- July 20, Professor A. D. MORRILL: The Terminations of the Auditory Nerve in the Sense-organs of the Ear.
- July 22, Dr. CORNELIA CLAPP: The Integumentary Sense-organs of Teleosts.
- July 24, Mr. J. F. SWEET: Nerve Terminations in the Tongue of the rabbit and Barbels of Catfish.
- July 27, Miss M. LEWIS: Centrosome and Sphere in Nerve-cells.
- July 28, Mr. U. DAHLGREN: On the So-called Transient Nervous System in Pleuronectes.
- July 29, Professor C. J. HERRICK: Functional Changes in Nerve-cells.
- July 30, Professor C. L. BRISTOL: The Nervous System of Nephelis.
- July 31, Miss F. E. LANGDON: On the Integumentary Sense-organs of Some Worms.
- August 1, Professor W. A. LOCY: Relations of the Cranial Nerves to the Primitive Brain Segments.
- August 3, Dr. O. S. STRONG: The Composition of the Cranial Nerves and Their Central Relations.
- August 4, Professor G. P. CLARK: The Anatomy and Physiology of the Otocysts in Some Crabs.
- August 5, Dr. S. PATON: The Central Relations of the Auditory Nerve in Man.
- August 6, Miss H. MERRILL: Some Features of Growth in the Sciatic Nerve of the Frog.
- August 6, Mr. J. H. GEROULD: The Nervous System in Certain Echinoderms.
- August 7, Dr. W. A. PATTEN: The Nervous System of Limulus.
- August 7, Mr. J. B. JOHNSTON: On the Application of Methylene Blue to Vertebrate Brains.
- August 8, Mr. J. E. PEABODY: The Integumentary Sense-organs in Elasmobranchs.
- August 8, Miss M. STURGES: The Giant Cell in Trematodes.
- August 10, Professor G. H. HOUSER: The Nerve Cells of the Shark's Brain.

1899.

- July 11, Dr. WM. A. LOCY: (Report of the Unpublished Work of Dr. Chas. Hill) Metamerism in the Head of the Teleost and Bird.
- July 20, Dr. M. M. METCALF: Relations of the Neural Gland and Ganglia in Tunicata.
- July 20, Dr. GEORGE LEFEVRE: The Origin of the Ganglia in the Budding of Perophora.
- July 25, Dr. F. S. LEE: Hearing in Fishes.
- July 25, Dr. E. P. LYON: Compensatory Movements in Insects.
- July 27, Mr. C. W. PRENTISS: The Innervation of the Otocyst in Crustacea.
- July 27, Dr. O. S. STRONG: Some Modifications of "Weigert's Method." With demonstrations.
- August 1, Professor C. JUDSON HERRICK: Some Problems Connected with the Theory of Nerve Components.
- August 1, Dr. CORNELIA M. CLAPP: A Comparison of the Lateral Line Systems of the Toadfish, *Amia* and the Cod.
- August 8, Professor G. P. CLARK: Pressure Sensation in the Human Skin.
- August 8, Mr. G. W. HUNTER, Jr.: Ganglion-cells in the Neural Gland of *Molgula*.
- August 8, Dr. E. L. THORNDIKE: Associative Processes in Teleosts.
- August 15, Mr. R. M. YERKES: Associative Processes in Turtles.
- August 15, Professor H. R. FLING: Demonstration of Some Points in the Nervous System of the Earthworm.

Fig. 2. Seminar lists for 1896 and 1899 as published in the MBL Annual Reports.

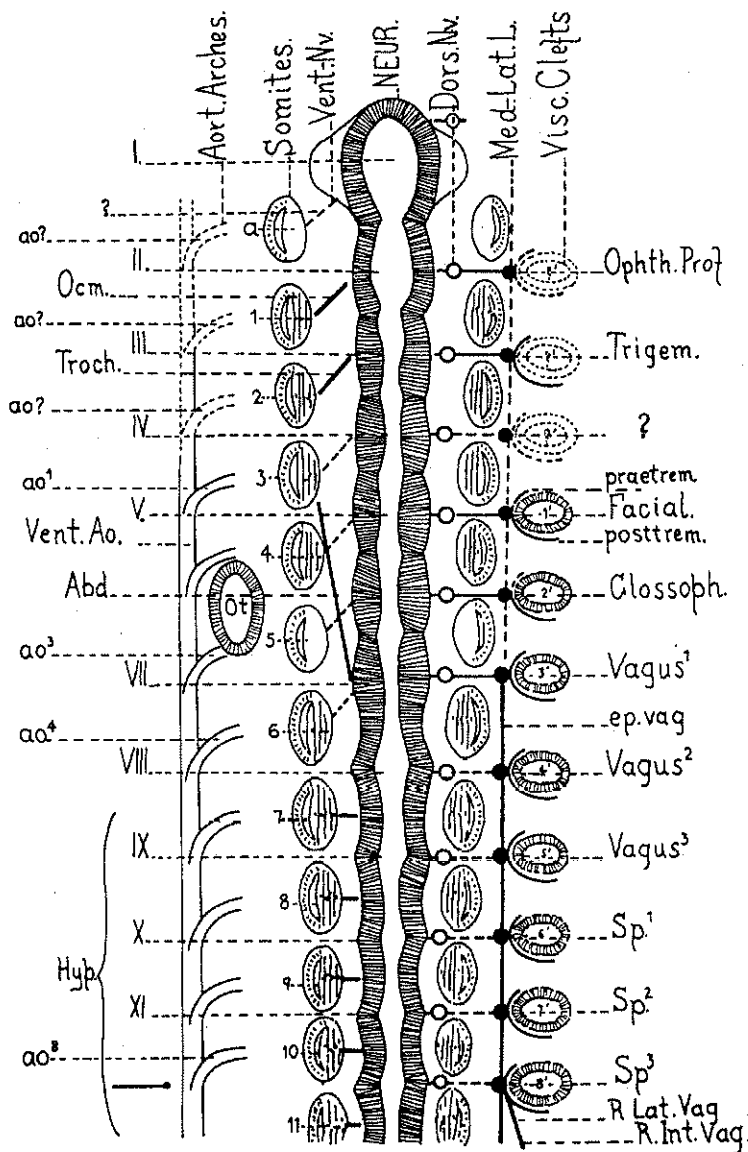


Fig. 3. Diagrammatic representation of the cephalic metameres in Selachii, showing the component organ systems and their relations to one another. (Redrawn from Ref. 22.)

would have been discussed eagerly, but perhaps not sympathetically by all present since several of the Americans had begun to support the neuron theory.

It is interesting to speculate whether Ross Granville Harrison attended the session on Apáthy's work. He was at the MBL that summer and had begun to work on nerve development. He later suggested that his early work on the histogenesis of the PNS, which led him on to his classic study of nerve fiber outgrowth, had been carried out in part at the MBL<sup>16</sup>. Perhaps he heard Apáthy's results and gained greater resolve to continue gathering evidence for the other side of the debate.

It is also surprising that Jacques Loeb seems to have been completely uninfluenced by the MBL's seminar, even though Loeb himself served as course director there up to 1895 and again in 1899. The book he published in 1900 reflects a similar set of

interests but does not refer to work at the MBL<sup>17</sup>.

In its last year, 1899, the seminar moved the group in new directions. Whitman's research had changed, and he probably encouraged the MBL group to move also toward study of behavior as part of neurobiology. The 1899 session of 14 talks (see Fig. 2) began with several, by now customary, reports on metamerism and neuromorphology. On 25 July, the group also heard two physiological papers. Columbia physiologist Frederick Schiller Lee discussed 'Hearing in Fishes' and argued that, in fact, there is none. Physiologist E. P. Lyon considered 'Compensatory Movements in Insects'.

Undoubtedly at Whitman's request and possibly at Wilson's or Osborn's suggestion, Edward Lee Thorndike presented a series of nine public lectures on animal behavior, instinct, learning and intelligence<sup>†</sup>. He contributed to the neurological seminar with his study of associated processes in teleosts and organized a course in comparative psychology at the MBL in 1899. Joined by Yerkes, who had begun graduate work at Harvard in 1899 with studies of reactions to light and who examined associations in turtles at the MBL<sup>18</sup>, Thorndike offered the course for two summers, 1899 and 1900. Each attracted just two students.

Whitman's own work on animal behavior began with a public lecture and a classic paper in 1898 at the MBL<sup>19</sup>. There he addressed questions about the nature of animal intelligence, suggesting that much is based on instinct that is strictly inherited and adaptive, but that some learning takes place as well. Pigeons can, under some conditions, make simple associations and act on them. This work, which appeared just as Thorndike was completing his study, must have underlined their mutual interests. For a short time, the MBL became a center for leading work on the comparative psychology and biology of behavior. Herbert Spencer Jennings (a young instructor at Dartmouth in 1898-1899, where Patton taught) also arrived to discuss behavior in unicellular organisms, which he had begun to study during a year at Jena and Naples in 1897-1898<sup>20</sup>.

Yet this interest did not last long at the MBL. Whitman found it too difficult to haul his pigeons from Chicago to Woods Hole each summer. Thorndike and Yerkes evidently decided that simple marine organisms did not make the best organisms for studying animal intelligence and moved on to others. Work in behavior diverged into ethology on one hand, and primate research on another.

The bold enthusiasm for a 'neurological seminar' in 1896 had evidently run its course and given way to the reality that there was not a unified discipline of neurobiology - yet. The diversity of problems, organisms, questions, techniques and traditions of the researchers made it difficult to sustain long-term interchange. 'However', as the second director of

<sup>†</sup> MBL's Annual Reports give the titles of papers by E. L. Thorndike. See especially his dissertation, *Animal Intelligence* (1898) Columbia University.

the MBL, Frank Rattray Lillie, put it, 'the interest in neurological work has never disappeared at the Marine Biology Laboratory'<sup>21</sup>. In fact, we could trace many major trends within neurobiology by following the changes in research and organisms used at the MBL through the century.

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## Brain maps and parallel computers

Mark E. Nelson and James M. Bower

*It is well known that neural responses in many brain regions are organized in characteristic spatial patterns referred to as brain maps. It is likely that these patterns in some way reflect aspects of the neural computations being performed, but to date there are no general guiding principles for relating the structure of a brain map to the properties of the associated computation. In the field of parallel computing, maps similar to brain maps arise when computations are distributed across the multiple processors of a parallel computer. In this case, the relationship between maps and computations is well understood and general principles for optimally mapping computations onto parallel computers have been developed. In this paper we discuss how these principles may help illuminate the relationship between maps and computations in the nervous system.*

Historically, descriptions of brain function tend to be cast in terms of the most sophisticated technology of the day. For example, early Greeks, influenced by the technology of aqueducts, described mental processes in terms of the flow of bodily fluids, Descartes framed nervous function in terms of machines and mechanical forces, and Sherrington used the analogy of a telephone switchboard. Today, brain function is most often described in terms of circuits and computations, reflecting the modern influences of electronics and computers. Although technology-based metaphors eventually become obsolete, they can serve a useful purpose by providing new conceptual frameworks for generating ideas and posing questions concerning brain function. In that spirit, we will draw on the emerging technology of parallel computing in an attempt to gain new insights into parallel processing in the brain.

Recent progress in the field of parallel computing has demonstrated the practicality of harnessing large numbers of modest processors together to achieve remarkable levels of computing performance<sup>1,2</sup>. Parallel computers have been shown to be

capable of solving difficult problems in a wide variety of scientific and engineering fields including computational neuroscience. In fact, our own initial involvement in parallel computing arose primarily from our interest in carrying out large-scale simulations of biological neural networks<sup>3,4</sup>. However, while learning to use parallel computers for this practical purpose, we became aware that some of the parallel processing issues we were facing seemed to have closely related counterparts in neuroscience. In particular, the question of how to map a computation optimally onto multiple processors seemed to be a fundamental issue, whether the individual processors were silicon chips or neurons. In this paper, we address this question by describing how optimal maps are constructed on parallel computers and discussing how the principles that have emerged from this effort might apply to maps in the brain.

#### Parallel computer maps

In principle, a parallel computer has the potential to deliver computing power equivalent to the total power of the processors from which it is constructed: a machine with 100 processors can potentially deliver 100 times the computing power of a single processor. In practice, however, the performance or computational efficiency that can be achieved is always less than this ideal value. For a given computational task, one of the factors that most influences this efficiency is how the computation is mapped onto the available processors<sup>5</sup>. In parallel programming, the efficiency of a particular parallel mapping is analysed in terms of two potential sources of inefficiency referred to as 'load imbalance' and 'communication overhead' (see Box 1 for mathematical description). Load balance is a measure of how uniformly the computational work-

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