



**VIKTOR HAMBURGER**  
(1900–2001)

## IN MEMORIAM

## Viktor Hamburger (1900–2001): A Remembrance

Viktor Hamburger, one of the outstanding developmental biologists of the 20th century, was born on July 9, 1900, in a small town in the Prussian province of Silesia, now part of Poland. Like many of us who now call ourselves developmental biologists, he was a junior naturalist, drawn to the study of nature and its wonders while still a child. After graduation from high school, he was drafted and served briefly in the German army at the end of World War I. He then enrolled at the University of Breslau, but left after a few months to go to the University of Heidelberg, where he studied with embryologists Curt Herbst and Hans Driesch. Finding the purely descriptive work in those labs not to his liking, he went to study with Hans Spemann at the University of Freiburg in southern Germany. Viktor believed that Spemann's experimental or manipulative approach, patterned after that of Wilhelm Roux, was better suited to revealing the mysteries of the developing embryo.

Viktor had the good fortune of being in Hans Spemann's laboratory when the experiments that resulted in the discovery of the organizer were being done. Hilde Mangold was a fellow graduate student in Spemann's lab during the spring of 1921. It was Hilde Mangold's transplantation experiments that confirmed earlier observations of Spemann demonstrating conclusively the ability of the dorsal lip of the blastopore to induce a secondary embryonic axis from presumptive belly tissue, which won Spemann the Nobel Prize in 1935. Aware of the reality that so many of us younger American scientists lack the foreign language training needed to read the original papers and correspondence leading to the discovery—these were of course written in German—Viktor wrote a monograph during the 1980s. That book, *The Heritage of Experimental Embryology. Hans Spemann and the Organizer*, was published in 1988. It describes Spemann's experiments leading to the discovery of the organizer and analyzes the intellectual environment in which ideas about the organizer's function were later developed and refined. It is typical of Viktor's intellectual commitment and breadth that he took the time and had the ability to write such a book which makes fascinating and instructive reading for anyone interested in embryo patterning and cell fate determination or in the history of science more generally.

Viktor's abiding interest in the phenomenon of neural induction reflected some of the range of his intellectual pursuits, but not his experimental activities. Spemann assigned to Viktor a thesis problem different from the major focus of his lab. Instead of working on some aspect of the

organizer, Viktor was to study the role of the nervous system on the development of limbs in amphibians. His experiments showed that limb development proceeded initially without influence from the nervous system, and his work brought him into contact with Ross Harrison, who was a friend and colleague of Spemann. Harrison encouraged Viktor's thinking and subsequent experimental work on the interdependence of limb and nervous system that emerges later in development. Harrison would spend some of each summer at Freiburg and Viktor viewed himself as much a student of Harrison as of Spemann. Viktor Hamburger received his Ph.D. from the University of Freiburg in 1925.

After a period of postdoctoral study in Berlin and Naples, Spemann hired Viktor as *Privatdozent* at the University of Freiburg. In 1932, Viktor received a Rockefeller Foundation fellowship to go to the University of Chicago where he was to work in Frank Lillie's Department of Zoology for what was intended to be a short sabbatical visit. Lillie had already published his first edition of the *Early Embryology of the Chick Embryo*, and Viktor was interested in applying the extirpation and transplantation techniques of the Spemann lab to the chick embryo. He did so successfully, and others who continue to use the chick embryo as a model system for developmental biology have adopted many of the experimental embryological techniques developed during those times.

Viktor's visit to Chicago proved to be a permanent cross-Atlantic transplantation, the consequence of a changed political climate in Germany. Because Viktor was Jewish, he was dismissed from his position at the University of Freiburg in 1933. Viktor left the University of Chicago in 1935 for a permanent faculty position at Washington University in St. Louis, where he spent the rest of his scientific career. Viktor viewed himself as an embryologist; when developmental neurobiology gained prominence in the 1970s, he became known as a neuroembryologist. He continued to live in St. Louis until his death, holding the title of Edward Mallinckrodt Distinguished Professor Emeritus of Biology.

Scientifically, Viktor is best known for his work on the development of spinal cord in the chicken embryo and for his studies showing the interaction between the nervous system and its peripheral innervation field. His early work on the regional patterning of the spinal cord demonstrated that changes in mitotic activity were the basis of the ventral to dorsal gradient of neuron production. Viktor also showed that early removal of a developing limb bud resulted in the virtual disappearance of motor neurons in relevant segments of spinal cord and also to a loss of sensory

neurons in the adjacent dorsal root ganglia. Together with Rita Levi-Montalcini, he showed that the absence of motor neurons was due to their death, not to a defect of proliferation or initial differentiation. Later work documented the occurrence of natural cell death among spinal motor neurons and showed that this loss could be delayed by enlargement of the peripheral innervation field. This body of work was important in establishing the general principle that neuronal death is a major and natural occurrence in the development of the vertebrate nervous system and that it can be regulated by interactions with peripheral tissues. The work has provided both a foundation of basic information about spinal cord development and a conceptual framework that remains relevant for contemporary investigators.

Viktor was also involved with Rita Levi-Montalcini and Stanley Cohen in the discovery of the nerve growth factor (NGF), which has a specific influence on sensory and sympathetic neurons. The experiments leading to the discovery of NGF arose from attempts to understand the relationship between neurons and the targets they innervate; many of the early NGF experiments were done in Viktor's laboratory. He correctly anticipated the interrelationships between cell death, neurotrophic support, and the formation of synaptic connections between neurons and their targets. Viktor also studied the development of motor behavior in chick embryos, using experimental embryological manipulations to demonstrate that the earliest movements are generated locally in the spinal cord and that they are not induced by sensory input but occur spontaneously. Viktor and his students were also among the first to study the underlying anatomical and physiological bases of embryonic motility. That work has been important for understanding the organization and ontogeny of vertebrate motor patterns.

Another of Viktor's well-known contributions was the publication of a staging series for chicken embryos. The Hamburger-Hamilton Staging Series published in 1951 remains one of the most cited papers in the literature. Viktor was proud of the fact that it has withstood the test of time and proven so useful to others.

Viktor Hamburger received a number of honors that acknowledge the importance of his contributions to our profession. Viktor served as President of the Society for Developmental Biology in 1950 and 1951 (when it was called the Society for Growth and Development). He was elected to the National Academy of Sciences in 1953 and to the American Academy of Arts and Sciences in 1959. He received the F. O. Schmitt Medal and Prize in Neuroscience in 1976 and the Wakeman Award in 1978. He received the R. G. Harrison Prize from the International Society of Developmental Biology in 1981, the Louise Gross Horwitz Prize in Cell Biology and Neurobiology in 1983, the Gerard Prize in 1985, the Fidia Award in 1987, the National Medal of Science in 1989, and the Karl Spencer Lashley award from the American Philosophical Society in 1990. He received honorary doctoral degrees from Uppsala University, the University of Freiburg, and Washington University in St. Louis. Many of his colleagues were disappointed that he did

not share the 1986 Nobel Prize that was awarded to Rita Levi-Montalcini and Stanley Cohen for the discovery of nerve growth factor. But as Viktor put it succinctly, "I know *exactly* what I contributed." He was presented with a Lifetime Achievement Award from the Society for Developmental Biology in 2000 for his many contributions to neuroembryology.

In addition to his contributions as a research scientist, Viktor was a dedicated and gifted master teacher, a fact appreciated by the generations of students who were enrolled in his courses at Washington University. He also participated in the Embryology Course taught at the Woods Hole Marine Laboratory for many summers. He was a model teacher-scholar even before the term became fashionable. He understood what the big questions were, and he encouraged his students to think of creative ways to uncover the embryo's secrets. English was Viktor's adopted tongue, yet anyone who has read his beautifully written papers knows that he was more than fluent. He believed that clear thinking and good writing are inextricably linked, and he provided his students with excellent examples to follow. After retiring from laboratory investigations in the 1980s, Viktor turned his attention to the history of neuroembryology, writing about a subject with which he was personally familiar, combining memoir and analysis in a most engaging manner. In both his experimental work and his more historical writings, as well as in conversation, Viktor knew how to tell a good story. He always set his ideas into an interesting context, providing enough details to make characters or data come alive, while never losing sight of the main themes or conclusions.

Those of us who had the privilege of working with Viktor found that he was extraordinarily generous with his ideas and his vast wealth of knowledge. He was supportive of his students and collaborators, always ready to offer constructive advice, which sometimes felt like criticism, but he also encouraged us to follow our own hunches and interests. Rita Levi-Montalcini was perhaps the first to benefit from this intellectual generosity as she continued her pursuit of the nerve growth factor with his blessings. Ron Oppenheim, Drew Noden, Anne Bekoff, and many others including myself also benefited from his encouragement of our independent pursuits growing out of his broad intellectual interests and the introduction he provided to the chick embryo.

Despite his imposing stature, formal European manner, and critical intellect, Viktor had a refined sense of humor and a frequent twinkle in his eye and was warm and loyal to his friends and associates. He was a gentleman in the truest sense of the word, treating everyone with fairness and courtesy, expecting others to play by the same rules in turn. Many of us will remain forever in his debt for his wise and kind mentorship. Viktor Hamburger will be missed but his many contributions will not be forgotten.

Margaret Hollyday  
Department of Biology  
Bryn Mawr College