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Obituary - Nachruf

Peter H. Schiller (1931-2023) – Eminent neuroscientist

Peter H. Schiller

Peter Harkai Schiller, professor emeritus of Neuroscience in the Department of Brain and Cognitive Sciences at the Massachusetts Institute of Technology (MIT), died on December 23, 2023, at the age of 92 in Newton, MA. Berlin-born and of Hungarian descent, he was the last German-speaking faculty member in the department founded by Hans-Lukas Teuber, with Richard Held and Walle Nauta as core faculty.

Peter moved to the United States in 1947 from Budapest after surviving the Russian bombing and gory war experiences. Starting in 1953, he spent time at the Austen Riggs Center in Stockbridge, MA, where he interacted with David A. Rapaport, a Hungarian clinical psychologist, who mentored Peter in Freudian theory.

When Peter's father, Paul Harkai von Schiller, tragically perished in a skiing accident in 1949 on Mt. Washington, NH, his stepmother Claire moved to Gainesville, FL, to marry Karl Lashley. Lashley worked at the Yerkes Primate Laboratories and Claire several years later published a book entitled *Instinctive Behavior* (Schiller, 1957), which contained an introduction by Lashley and chapters by Konrad Lorenz, Jakob von Uexküll, Nicholas Tinbergen, and Paul von Schiller.

Peter obtained his bachelor's degree at Duke University (1955). From 1955-1957, he did military service in Frankfurt, Stuttgart, and Munich, Germany, interrogating Hungarian refugees, who had fled from the revolution. He then enrolled in graduate studies at Clark University (1959-1962) in Worcester, MA, where he did his doctoral work under Morton Wiener. The chairman of the department was Vienna-born Heinz Werner.

Wiener worked on subliminal perception, which was in fashion then, but Peter was more attracted to Werner's experiments on contour interactions, called metacontrast masking. When a disk and a ring were presented in a rapid sequence, with the contours of the inner portion of the ring and the preceding disk shared, the disk became invisible when the interval between the presentations of the two stimuli was between 60 and 100 ms.

Werner was a developmental psychologist who had written an influential book entitled *Comparative Psychology of Mental Development* (1940), and Peter took a strong interest in mental health problems and development. He even applied for a clinical internship at the Worcester State Hospital, where he saw patients and practiced psychotherapy daily. Sigmund Freud's books, most notably *The Interpretation of Dreams* (1899), became mandatory reading.

Peter took on a number of odd jobs to sustain his livelihood, among them driving a dump truck, administering the Stroop test to 240 children, testing discrimination in fish under the supervision of Greg Kimble, and directing canoe summer camps in Northern New Hampshire. Undeterred by his father's accident, Peter also undertook some daredevil mountain climbing on Longs Peak in Colorado, where he was almost killed. When he developed a longing for postdoctoral research, he turned to his father's friend, Hans-Lukas Teuber, who had just been called to MIT from New York.

I met Peter in the fall of 1964 shortly after my arrival at MIT, when he gave a seminar on backward masking. Using a 5-channel tachistoscope, he presented a large bright disk surrounded by a brighter annulus. When he presented the disk and immediately thereafter the annulus, the disk appeared completely dark, i.e., brightness masking. However, this worked only when both stimuli were presented to the same eye, suggesting a retinal origin. By comparison, metacontrast occurred also with interocular presentation (Schiller & Smith, 1968).

It so happened that I needed a strong and ultrashort light-flash to study the Hermann grid illusion at short exposure durations. Naturally, I asked Peter whether I could borrow his flash tube. ABSOLUTELY, he said and that was all. I quickly learned that Peter was brief, reliable, and fiercely independent. When something was wrong, he said it. Much later, when I was criticized for not mentioning Wolfgang Metzger's political past in the foreword to our translation of the *Laws of Seeing* (Metzger, 2006), he remarked "How are we to know, how we would have acted under these circumstances?"

It was his honesty, directness, and uncompromising presence, which may explain the small number of colleagues Peter called his friends. When Jack Werner and I proposed him for a coveted prize, he said, "I have fewer friends than fingers on my hand." Yet, despite his demanding demeanor, few vision scientists had as many graduate students and postdocs as he had, more than fifty in all. And excellent they were. Max Cynader, Shaul Hochstein, Anya Hurlbert, Fritz Koerner, Victor Lamme, Nikos Logothetis, John Maunsell, Stan Schein, Larry Squire, Michael Stryker, Rufin Vogels, and Karl Zipser are some of the people with roots in the Schiller laboratory, often publishing under their own names. Four of them became members of the National Academy of Sciences, to which Peter had been elected in 2007. A year later, he was inducted into the Magyar Tudományos Akadémia.

John Maunsell, now at the University of Chicago, recalls: "Peter was the boldest experimentalist I've ever known. Once he engaged with a question, he was unintimidated by how exacting, intricate, or extensive the required experiments might be. Over the years he produced an impressive range of results that others viewed as beyond reach."

Michael Stryker at The University of California San Francisco comments: "Peter combined skepticism, rigor, and technical advances in vision science to a degree equaled by few. He was merciless in his criticism of weakly supported conclusions, whether by students or by major figures in the field. He demanded good data, real measurements, no matter how hard they were to make."

And Anna Roe-Wang, Zhejiang University, remembers: "Peter was so precise and creative, in both science and art. He contributed hugely not only to systems neuroscience but also to the field of brain-machine interface. He and Ed Tehovnik produced some of the most careful and quantitative work in vision. Peter was a great mentor because he was exacting, with no patience for sloppiness. Direct, honest, insightful. He also had a big heart. After my last visit, he sent me a copy of his book *Vision and the Visual System*. It brought tears to my eyes."

Peter applied the same high standard to his work on the neural systems that underlie vision, visual perception, and the control of visually guided eye movements. In doing so, he successfully integrated the methods of psychology, neurophysiology, pharmacology, and anatomy to solve fundamental problems in each of these areas. His work is original, elegant, and innovative and has had a far-reaching impact.

Studies in Eye Movement Control

The major aim of this work has been to identify and characterize the neural structures involved in the generation of visually guided saccadic eye movements. Using single-cell recordings, electrical microstimulation, and lesions in the superior colliculus, Peter studied visually guided saccadic eye movements in the alert rhesus monkey.

Specifically, he outlined two parallel neural pathways for guiding our eyes to a target in the visual scene. According to this idea, the frontal eye fields (together with other visual areas) select the target, while the superior colliculus executes a saccade so that the gaze falls onto the target. This is done by computing a vector code that specifies the location of the receptive fields of the visually activated neurons relative to the fovea. Peter confirmed this idea experimentally, by demonstrating that an electrically stimulated neuron in the intermediate and deep layers of the colliculus elicits an eye movement, which shifts the gaze to the center of the receptive field of that neuron (i.e., foveation). Both systems have an orderly topographic representation of saccade direction and amplitude, which ensures the accuracy of the eye movement. Peter and his team also confirmed the finding by Burkart Fischer and Rolf Boch (1983) from the Freiburg laboratory that there is a bimodal distribution of saccadic latencies when monkeys made eye movements to single, conspicuous targets – so-called *express saccades*. Express saccades have a latency of 80-125 ms. They occur when a gap is introduced between the offset of the fixation point and the onset of a target anywhere in the visual field.

Peter's later work further clarified the complementary roles of the superior colliculus and frontal eye fields. He showed that express saccades are eliminated by removal of the colliculus, whereas a lesion of the frontal eye fields severely impaired target selection. When both the superior colliculi and the frontal eye fields were surgically ablated, monkeys could not make visually guided eye movements at all; their eyes appeared fixed in the orbit looking straight ahead. This work established the essential roles of the colliculus and frontal eye fields (FEF) in the generation of visually directed rapid eye movements and complemented findings on the contributions of many other cortical areas to the generation of various types of eye movements, among them areas V1, V2, LIP (lateral intraparietal cortex), and MEF (medial eye field).

Studies of Vision and Visual Perception

Here, Peter studied the role of two sets of parallel channels in the visual system, the On- and Off-channels and the midget and parasol channels. The earlier studies of Kuffler, Hubel, and Wiesel had shown that On-cells in the retina and lateral geniculate nucleus respond to onsets of light and bright spots on a dark ground, whereas Off-cells respond to offsets of light and dark spots on a bright ground. Both On- and Off-cells use *excitation* to signal brighter and darker, respectively, in space and time. This is because the Off-bipolars in the retina are sign-conserving while the ON-bipolars are sign-inverting, thereby making it possible to send excitatory signals into the visual brain for both light increments and decrements. The On- and Off-pathways remain largely segregated from the retina to the striate cortex.

Peter found that by infusing the eye with 2-amino-4-phosphono-butyrate, he could selectively block the On-pathway while leaving the Off-pathway unaffected. As a consequence, monkeys could no longer detect a light spot on a gray background but had no problem in detecting the appearance of a dark spot on the same background. Correspondingly, cortical cells that normally respond to increments and decrements of light lost their responses to light increments while their orientation, direction, and spatial frequency selectivity were unaffected.

The second channel, the midget and parasol cells, connects the retina to the parvo- and magnocellular layers of the lateral geniculate nucleus of the thalamus and via the primary visual cortex to regions further upstream including visual area V4, which receives input from both types of cells; and visual area MT, which is driven predominantly by the parasol cells. Midget cells have small receptive fields and process color, fine pattern detail, form, shape, and stereopsis. In comparison, parasol cells have large receptive fields and play a central role in the processing of low contrast stimuli, high velocity motion, flicker, and motion parallax for depth perception. Many cells in V4 are contextual, implying that their response can be modulated by stimuli from outside their classical receptive fields. This is due to top-down projections from higher areas. The upshot of this research is that the midget channel mediates high visual resolution that includes color vision, and the parasol channel mediates low spatial and high temporal resolution and emphasizes the detection of motion.

Feature Detectors vs. Multi-Function Analyzers

Next, Peter showed that individual neurons in the primate visual cortex are multifunctional and not just feature detectors, as has long been claimed. The same cells also carry out complex, interactive oculomotor and visual tasks rather than just the processing of color, form, motion, depth, texture, and shape. For example, neurons in area V4 engage in view-independent object recognition, visual learning, spatial generalization, visual attention, and stimulus selection. Surprisingly, when both V4 (a major color area) and MT (a major motion area) were removed, perception of color, shape, motion, and stereoscopic depth were only moderately compromised. This is consistent with V1 projecting to several other visual areas in addition to V4 and MT.

Looking back at Peter's career, he was a prime example of a dedicated neuroscientist who looked at visual function from the perspective of visual perception to neuronal mechanisms, linking the two in the tradition of Mach, Exner, and Hering. No wonder that he once exclaimed that the Freiburg conference proceedings on the *Psychophysik und Neurophysiologie des Visuellen System*, edited by Jung & Kornhuber (1960), was the most important book to usher him into his later career.

Personal life

Peter was an ambitious sailor, racing his *Thistle* on many a weekend off the shores of Boston or on the Charles River opposite MIT. He also enjoyed skiing, mountain climbing, swimming, and canoeing. He was a superb tennis player and loved playing the piano and guitar. Visiting him was always a pleasure as he was cordial, hospitable, communicative, and brilliant. Visitors to the laboratory were quickly prompted to sit down next to a chinrest to see the latest visual phenomena, he had created. Based on Bela Julesz' random-dot stereogram, Peter was able to present disparity, motion parallax, and shading cues (separately or together) to human and non-human primate subjects as their visual cortices were imaged, which demonstrated his great technical expertise. I also admired his demonstrations of the Ternus motion quartet, for which he pitted the Gestalt laws of similarity, proximity, and smooth continuation against each other. It was like a homecoming. A highly acclaimed neurophysiologist who had done single cell work for 40 years, returned to the psychophysics and holistic phenomenology of his father and Max Wertheimer. Next to his science, which he pursued well into his eighties, Peter also delighted in producing sculptures and other sophisticated woodwork (www.richfieldstudios.com).

The last time I saw Peter, he had an office in MIT's emeritage, which did not make him very happy. I had vainly tried to spend three months in Boston to attend his last classes. It was not to be. The entire course was recorded and can be accessed on MIT's website (Schiller, 2005). This also applies to all chapters of his book *Vision and Visual System*, published together with Edward J. Tehovnik, which brilliantly summarizes the state of knowledge of the visual system. Readers of this remembrance may want to also read Peter's own account of his life, which appeared in Larry Squire's *History of Neuroscience in Autobiography* and MIT's obituary https://bcs.mit.edu/news/professor-emeritus-peter-schiller-pioneer-researcher-visual-system-dies-92.

In the hallway next to his office, Peter had posted a collage of 114 photos of noted neuroscientists to which he affixed a red label when one of them had died. None of us expected Peter to receive a red label so soon.

R. I. P.

Lothar Spillmann, Freiburg

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