

## Profile of Peter H. Schiller

In a windowless laboratory on the sixth floor of the Brain and Cognitive Sciences Institute of Massachusetts Institute of Technology (MIT), neuroscientist Peter Schiller lines up visual stimuli on a computer screen. The stimuli are pairs of cues flashed side-by-side, such as horizontal and vertical lines, upright and inverted triangles, and the words “car” and “his.” As Schiller flashes the stimuli on his monitor, a volunteer observes them through a stereoscope, which presents one cue in a pair to one eye and the other cue to the other eye. The volunteer identifies the stimuli in order: a cross, the Star of David, and the word “chairs.” Then, the stereoscope displays groups of dots, some of which are shifted in position. To the volunteer, the shifting dots appear deeper than the rest. Through such experiments aimed at identifying people’s ability to combine visual cues and perceive depth, Schiller, who was elected to the National Academy of Sciences in 2007, hopes to determine the brain regions involved in binocular integration and depth perception. The findings from those studies could help pinpoint the precise time frame when corrective interventions can best help stereoblind people perceive depth. Beyond uncovering the neurobiological basis of vision, Schiller’s goal is to help restore sight to the blind someday.

Born in Berlin shortly before World War II, Schiller moved to Budapest, Hungary in 1934, when his father, a research psychologist, returned to his homeland after a postdoctoral stint at the University of Berlin. A German-speaking transplant in Budapest, Schiller at first struggled to memorize Hungarian poems in grammar school but soon mastered his mother tongue, devouring Hungarian translations of Jules Verne’s science-fiction books. Schiller’s boyhood years bear testimony to his budding scientific temperament. At the age of 12, he found a ball lost during play by using an identical one to retrace the path to where the lost ball lay hidden. As a teenager, he cobbled together a Morse code-based communication system to exchange surreptitious messages with his cousin, whom he was sometimes forbidden to see. When he was not devising science-based ploys for play, Schiller spent starlit nights in his uncle’s hilltop backyard with a map of the sky, gazing at constellations.

Growing up in war-torn Hungary, Schiller witnessed the ravages wrought by the Russian invasion of Budapest. Facing bleak prospects for a scientific career in a harsh political climate, Schiller’s father fled the country in 1947 for the United States, where he worked as a researcher at the Yerkes Laboratory, a primate research



Peter H. Schiller uses random-dot stereograms (on wall) to study depth perception.

institute then located in Florida. At the Yerkes Laboratory, where he joined his father months later, the adolescent Schiller helped his father carry out experiments in animal behavior. Those early forays into brain science research sowed the seeds of Schiller’s future scientific accomplishments.

Two years later, following the death of his father, Schiller went to Charleston, South Carolina to live with his father’s physician-friend James Anliker. With Anliker’s help, Schiller got a job in the anatomy department at Charleston Medical School, where his chores ranged from feeding monkeys in the animal facility to cleaning up after medical students dissecting cadavers. A meeting with Schiller’s color-blind high-school English teacher piqued Schiller’s early interest in vision. “When Mr. Gibbs told me he was pulled over by a cop for running a red light that he had presumed was green, I became intrigued—even more so when I learned that color blindness is more common among males than females,” Schiller says.

### Eye on Vision

Schiller struggles to pinpoint the precise point when he embarked on his decades-long career in vision research, but his undergraduate studies in psychology at Duke University are a good starting point. As an undergraduate, Schiller studied the ability of fish to see colors, his first formal attempt to study vision scientifically.

After graduating from Duke University, Schiller spent a year in Germany on military duty before enrolling in a graduate

program in psychology at Clark University in Worcester, Massachusetts. Under the tutelage of psychologist Morton Weiner, Schiller studied the phenomenon of subliminal perception, helping to debunk the then-rife myth of extrasensory perception by demonstrating that subliminal cues could trigger neurobiological processes underlying certain behaviors, such as people making a bee line to buy soda in movie halls when the message “Drink Coca Cola” was briefly flashed between movie frames (1).

While at Clark University, Schiller spent his summers at the Austen Riggs Center, an institution for psychotherapy, in Stockbridge, Massachusetts, where he met George Klein, a professor of psychology at New York University. At the center, Schiller and Klein conducted experiments on the development of visual interference in children. Working with more than 200 grade-school and college children, Schiller found that visual interference, which thwarts people’s ability to identify a color when its name is printed in a different color, wanes with age (2).

Back at Clark University, Schiller studied the basis of optical illusions. “Illusions are far more complicated than people think, largely because they could be generated in the retina or in various brain regions,” Schiller says. To determine where in the visual system illusions occur, Schiller had to present visual stimuli to experimental subjects in two ways: to each eye separately and to both eyes at once. To accomplish this, Schiller fashioned an optical tool called a five-field tachistoscope. The instrument helped reveal that many illusions, such as the Ebbinghaus illusion, in which identical circles appear different when surrounded by circles of different sizes, occur in the brain’s visual cortex rather than in the retina.

Extending his findings on illusions, Schiller trained his new tool on a phenomenon called masking, which reduces the visibility of an object shown to people milliseconds before a second object, known as a “masking” object, is shown. Vision researchers knew that masking could arise from differences in brightness, pattern, and contrast related to the two objects, but where in the visual system masking originates was a mystery. Schiller’s tachistoscope helped answer that question (3). “We found that brightness

This is a Profile of a recently elected member of the National Academy of Sciences to accompany the member’s Inaugural Article on page 17087 in issue 40 of volume 107.

masking occurred only when both visual stimuli were presented to the same eye, suggesting that it occurred in the retina, whereas pattern masking and metacontrast masking occurred even when different stimuli were presented to the two eyes, suggesting that it occurred in the brain," Schiller says. Schiller parlayed these wide-ranging studies into a PhD degree in psychology from Clark University in 1962.

### MIT-Bound

After a brief interlude of clinical work with mentally ill patients at Worcester State Hospital, Schiller began angling for postdoctoral research opportunities. Hans-Lukas Teuber, then recently appointed chair of the psychology department at MIT, invited Schiller to perform postdoctoral research on the mechanism of visual masking in the brain. There, Schiller mastered a method for recording electrical activity from individual brain cells in cats and monkeys by using varnish-coated tungsten microelectrodes that helped shed light on the mechanism of brightness masking. Later, in partnership with MIT psychologist Steven Chorover, Schiller studied short-term amnesia, a condition triggered by traumatic experiences. Their finding that electrical shock triggered a short bout of amnesia in rats helped other researchers study how brain cells consolidate memories (4). Schiller's diverse research pursuits led to an assistant professorship at MIT in 1964.

Schiller has since delved deeper into the dark recesses of the human visual system, illuminating its workings along the way. Notable among his contributions are studies on how the brain controls rapid eye movements, or saccades. Coined in the 1800s, the term "saccade" refers to a quick shift in gaze, guided by visual cues and controlled by the nervous system. People make nearly 3 saccades every second, or 170,000 saccades a day; each shift in gaze commands a concomitant movement of the eyes toward a target amid a welter of visual cues. "Animals move around, so to analyze the visual scene, they must fix the eyes periodically with reference to the environment," Schiller says. For example, when people recognize a face in a crowd, they use saccades to fix vision, directing the visual information to the fovea, a region of the retina that helps people see detail. To fix vision, the brain must decide how to direct the eye muscles with each saccade. Because the fibers of each eye muscle course uninterrupted through the length of the muscle, Schiller could use his recording technique to trace the firing of single neurons as the electrical signal rippled from the brain into the muscle. "These cells produce saccadic eye move-

ments by virtue of high-frequency bursts that rapidly contract the muscle; the duration of the burst defines the amplitude of the saccade," Schiller says. "That work led to a basic understanding of how the brain's oculomotor complex drives the eyes," he adds.

Soon thereafter, another brain structure driving the eyes became the focus of Schiller's interest. Dubbed the "superior colliculus," this many-layered nub of brain tissue serves as a source of saccades in primates. Schiller found that macaques without a superior colliculus were slow to execute saccades, whereas macaques with lesions in the frontal eye field had trouble selecting targets in a visual scene. Removing both regions scotched all saccades (5). These findings helped lay the foundation for an overarching scheme for the neural control of saccades (6): "There are two brain systems involved in generating saccades. One helps select targets in the visual scene to which the eyes must be directed, and the other generates saccades to sudden visual cues," Schiller says.

### Midgets, Parasols, and Toggle Switches

Schiller next unraveled how the eyes communicate with the brain. Central to this communication are retinal ganglion cells, which carpet the inner surface of the retina and transmit visual information from photoreceptors to the brain. Schiller's quest to study retinal ganglion cells led him and his postdoctoral fellow, Joseph Malpeli, to a brain region called the lateral geniculate nucleus, which receives visual input from the retina. First, Schiller and Malpeli found that two kinds of retinal ganglion cells—midget and parasol—send connections to different layers of the lateral geniculate nucleus. Then, by blocking either the midget or parasol cells with lesions in the corresponding layers of the lateral geniculate nucleus, they found that the midget cells process color and fine patterns, whereas the parasol cells process motion and depth perception (7).

Schiller continued to probe the retina in still finer detail, revealing surprising insights on the evolutionary origin of a system of toggle switches in the eyes. In the early 1960s, neuroscientist Haldan Keffler Hartline discovered that the retina houses cells that constitute an ON/OFF toggle switch: cells that fire when light comes on, cells that fire when light is turned off, and cells that fire in both situations. The discovery, which earned Hartline a Nobel prize, left in its wake the mystery of the evolutionary origin of the toggle switch. Contrary to then-popular theories about why the ON/OFF system evolved, Schiller proved that the system plays a role in rapidly

responding to rises and drops in the amount of light. Objects absorb and reflect different wavelengths of light, altering the number of photons of light entering eyes trained on them. The ON/OFF system, Schiller found, helps the eyes perceive changes in light intensity (8). "We did experiments that selectively blocked one channel and found that the ON channel responds to light increment, whereas the OFF channel responds to light decrement," Schiller says. Those seemingly mundane findings underlie revelatory "Aha!" moments when applied to real-world scenarios. Thanks to the OFF channel, people can read print, which usually contains dark characters on a light background; reading dark characters in succession signals light decrement to the retina. Thanks to the ON channel, a fish in the ocean can spot its predator in murky waters through the light bouncing off the predator's body; the reflection signals light increment to the retina. "The ON/OFF system is crucial for survival for virtually every species, except maybe for largely nocturnal animals," Schiller says.

These days, Schiller's mind is preoccupied with how people perceive depth. Thanks to their ability to reconstitute 3D visual scenes from the 2D images falling on the retina, most people can perform with ease a range of tasks that rely on depth perception, from threading needles to driving cars. However, at least 5% of the population in the United States is stereoblind, unable to estimate depth with reasonable accuracy. Schiller has sought to pinpoint brain regions where depth cues are processed. Researchers have long known that depth perception partly depends on phenomena called stereopsis and motion parallax. Stereopsis refers to a natural disparity that occurs when observing an object in a scene; converging neuronal signals from each eye arise from slightly different locations in the scene, causing the brain to compute a depth cue from the disparity. Motion parallax stems from differences in the velocities of moving objects in a scene; the difference provides a depth cue. Schiller found that blocking the midget cells of the retina affects stereopsis, whereas blocking the parasol cells affects motion parallax (9). "We are now combining behavioral studies and functional magnetic resonance imaging to determine how the brains of stereoblind individuals are different from those of people with normal depth perception," Schiller says. Those efforts, he says, could lead to corrective measures that would restore depth perception to stereoblind people.

## Vision for the Future

Schiller's forays into vision research have no doubt unearthed a wealth of basic insights into how people see, but his long-cherished goal is to restore sight to the blind, possibly via an implantable visual prosthetic device. Some researchers have successfully constructed retinal implants for people with retinitis pigmentosa, age-related macular degeneration, and other defects of the retina. Other approaches, based on gene therapy, stem cells, and artificial retinas, are in various stages of development. However, so far, a device that would restore sight by direct electrical stimulation of the visual cortex remains a distant dream. Schiller and his collaborators hope to lay the groundwork for such a device by performing a feat of technological wizardry: developing a camera that captures and transmits visual images to an array of electrodes implanted in area V1 of the visual cortex.

The electrodes would stimulate the area and yield information about shape, motion, and depth. An algorithm would integrate the camera and the electrodes (10). To test this idea, Schiller conducts noninvasive experiments on people with normal vision by mimicking electrical stimulation with a camera that converts visual images into displays on a computer screen. Those findings, Schiller says, could help reveal the feasibility of developing a device based on actual electrical stimulation, inching closer to an implantable prosthetic.

However, that path is riddled with roadblocks. Unlike cochlear implants, whose runaway success has restored hearing to thousands of deaf people, visual prosthetic devices face a formidable challenge. Whereas the neuronal projections from the cochlea to the central nervous system number in the tens of thousands, more than a million nerve fibers wend their way from

each eye to the brain. "Vision is a much more complicated problem, which is further compounded by the need for depth perception," Schiller says. To prove useful, electrode arrays implanted in the brain must last years, if not decades, placing limits on the kinds of electrodes that can be used. That is partly why an implantable prosthetic based on electrical stimulation of the brain is hardly around the corner.

Whether or not such a visual prosthetic becomes a reality before the end of Schiller's scientific career, his contributions to vision research have already earned him recognition among his peers. True to his scientific temperament, Schiller says pursuing his research goals has proved to be almost as satisfying as achieving them—an outlook that might keep him busy at the laboratory bench for many years.

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