Biography of Charles R. Gallistel

sychologists have long been interested in the study of learning and memory. Central to the basic understanding of learning is a concept called "the learning curve," which is used to mathematically describe the emergence of a learned behavior. Visually, the learning curve is depicted by plotting the magnitude or frequency of the conditioned response as a function of the number of reinforcements. Some reinforcements are positive, such as food, whereas others are negative, such as a short electrical shock to the footpad. Despite a lack of supporting basic research, psychological dogma has held that learning is a gradual process, with behavior changing slowly over time, according to Charles R. Gallistel, professor of psychology and cognitive science at Rutgers, The State University of New Jersey in New Brunswick. "You would think that determining what the learning curve actually looks like would be about as basic as you could get, and that they must have done that 100 years ago," Gallistel said. "But, in fact, no one ever did."

Gallistel and his colleagues are doing fundamental research on the learning curve, and their findings indicate that learning is not gradual at all. Rather, they say the learning curves for individual subjects show abrupt, often step-like, increases going from a naïve initial level to a final learned level with 1–10 trials. Gallistel's Inaugural Article (1), "The learning curve: Implications of a quantitative analysis," published in this issue of PNAS, addresses the abrupt nature of learning and suggests that the learning curve cannot be estimated from a group average. If an individual subject's progress during learning is indeed stepwise, averaging several subjects will smooth out the rapid transitions and indicate a gradual increase. Gallistel's research could have profound implications in the field of cognitive psychology by allowing researchers to more accurately describe the learning process.

The pursuit of understanding the basis of learning and memory has led Gallistel to a distinguished career spanning both U.S. coasts. His honors include election to the National Academy of Science in 2002 and fellowships in the American Association for the Advancement of Science, the Society of Experimental Psychologists, and the American Academy of Arts and Sciences. He is currently codirector of the Center for Cognitive Science at Rutgers.



Charles R. Gallistel

Seeking Motivation

Gallistel's interest in psychology began early in his undergraduate studies. In 1959 he enrolled at Stanford University in Stanford, CA, with the intention of becoming an engineer like his father and both of his grandfathers. Disappointed with the rigidly structured nature of the engineering curriculum, Gallistel decided to pursue social psychology to satiate an interest he had developed growing up at the end of World War II. Thousands enlisted in the military despite the natural human instinct for self-preservation. "Huge masses of people flung themselves into death in World War II," Gallistel said. A desire to understand the psychology behind this phenomenon motivated Gallistel to learn more about the behavior of people in large groups. Although his early coursework provided little insight into this mass psychology, Gallistel was exposed to the work of Clark Hull, a former professor of psychology at Yale University in New Haven, CT, who attempted to give mathematical formulations of the laws of learning. This quantitative approach to psychology captivated Gallistel and helped him focus his research: "I was fascinated by the idea that you could have a mathematical theory of the mind," he said.

Gallistel tried to apply a mathematical approach to psychology by joining the laboratory of Stanford Professor J. Anthony Deutsch. In Deutsch's lab, Gallistel explored motivation in rats through experiments using electrical self-stimulation of the brain—a system whereby an animal can perform various tasks, such as pressing a lever, to stimulate its own brain via electrodes inserted into the hypothalamus. Because the stimulation was physiologically rewarding to the animals, the rats would often repeatedly perform the task leading to the stimulation. "It was a very robust phenomenon," Gallistel said. "They'd stimulate their own brains all day long and all night long." Through this work, Gallistel and his team discovered both a motivational effect and a rewarding effect of stimulation. The rewarding effect lasted indefinitely but depended on the rat's memory of the place, the amount of stimulation obtained, and the task performed. In contrast, the motivating effect was a transient aftereffect of stimulation; the magnitude of the motivating effect depended only on the stimulation itself and not on the rat. These two effects would form the basis of Gallistel's research for most of the next 30 years.

Gallistel was profoundly influenced by working in Deutsch's lab and taking one of his classes. Gallistel's first publication (2), a review of the implications of electrical self-stimulation of the brain, was originally written for an undergraduate class taught by Deutsch. At the urging of his professor, Gallistel submitted the paper to the Psychological Bulletin and was surprised to learn that it was accepted for publication. "I got something back that I thought was a rejection," Gallistel noted as he recalled the editor's criticisms of the paper. "Deutsch said, 'It isn't a rejection; it's an acceptance letter!' I followed his advice, revised it, and sure enough it got accepted." Gallistel finished his undergraduate studies at Stanford with a B.A. in psychology coupled with a deep interest in physiological psychology.

For his graduate studies, Gallistel was drawn to Yale University by the work of Neal Miller and Robert Galambos, both of whom were doing exciting work in the field of physiological psychology. From his first day at Yale,

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This is a Biography of a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 13124.

Gallistel had his research goals clearly planned out: "I probably could have written a research proposal the day I enrolled as a graduate student," he said. He attributes this focus to his rigorous research track as an undergraduate. Not surprisingly, his vision was to explore the basis of motivation through electrical self-stimulation of the brain.

In pursuit of his research goals, Gallistel started working with Miller, but he ultimately found a better fit working in Fred Gault's laboratory, where he had more discretion in his research track. Just 3 years after arriving at Yale, Gallistel finished his Ph.D. His thesis demonstrated that behavior was driven by a motivating effect, which could be distinguished from a rewarding effect. Using rats, Gallistel also found that the motivation to perform a task did not last long in the absence of the reward. After just half a minute without stimulation, the motivation to repeat the action dissipated. Gallistel published his thesis in two parts, the first appearing in the Journal of Comparative and Physiological Psychology in 1966 (which included parts from his undergraduate honors project) (3) and the second in 1967 in Psychonomic Science (4).

Organizing a Career

After finishing his doctorate, Gallistel went directly to an assistant professorship in the department of psychology at the University of Pennsylvania in Philadelphia. He was excited by the opportunity to work with Philip Teitlebaum, Alan Epstein, and Eliot Stellar, three prominent physiological psychologists who would be among his colleagues. "The Penn department was justly regarded as a very intellectually exciting department, so it was easily my first choice," Gallistel remarked.

While at the University of Pennsylvania, Gallistel and members of his laboratory used a psychophysical approach to analyze parts of the brain that were stimulated during the electrical selfstimulation experiments. Focusing on the tradeoffs between two different parameters of the stimulation (current, pulse frequency, pulse duration, or pulse pairing), Gallistel found that a balance existed between the two parameters being tested. For example, different stimuli could elicit the same behavioral effect by adjusting one parameter while controlling the second. Gallistel describes the process as being akin to a chemical titration where different variables are manipulated to produce the same effect. He and his team were then able to infer electrophysiologically measurable properties of the neural system, such as the recovery time necessary between stimuli

(5). Gallistel's interest in the neurobiology of motivation led him to put together an influential book of classic readings—with extensive commentary which established motivation as the highest level of organization in the action hierarchy (6).

Gallistel met his wife, Rochel Gelman, also a well known psychologist, when she was hired by his department in 1967. They were married 2 years later, but they first had to petition the provost to relax strict rules at the University of Pennsylvania, which barred married couples from working in the same department. Gallistel fondly recalls the provost saying, "The University of Pennsylvania does not want to be responsible for you living in sin," before abolishing the rule. Gallistel and his wife went on to work together, eventually coauthoring The Child's Understanding of Number (7), a book that addressed the development of mathematical and scientific thinking in preschool children.

During his tenure at the University of Pennsylvania, Gallistel was also involved in teaching at both the graduate and undergraduate levels. Having started his assistant professorship at age 25, he remembers "a time when I looked younger than half of my students." Gallistel taught introductory psychology many times at Penn, and he remembers one term well: "I taught *all* of introductory psychology, which was almost 1,000 students. The university said it was the largest class ever taught in the Ivy League, but I don't know if that was true or not." Gallistel rose through the

Learning depends on what Gallistel calls a "read–write memory."

ranks at Penn, was promoted to full professor in 1976, and served as chair of the department of psychology from 1981 until 1984.

In 1989, Gallistel and his wife accepted offers from the University of California in Los Angeles and relocated to southern California. There, he continued his work on the electrical selfstimulation of the brain, focusing on psychophysics and neuroanatomy (8–10). In 2000, he and his wife moved back to the east coast, taking professorships at Rutgers in the Center for Cognitive Sciences.

The "Holy Grail" of Neuroscience

The driving force behind Gallistel's research on electrical self-stimulation of the brain was to explore the cellular and molecular basis of memory. The mystery surrounding memory, which he calls "one of the great 'Holy Grails' of neuroscience," is something that has long puzzled psychologists. To break the problem down into a smaller, testable area, he sought to understand the psychology of motivation and learning, which, he hoped, would help expose the underlying neurobiology of memory.

Gallistel's work on memory led to his next book, The Organization of Learning, which had a tremendous impact among psychologists (11). Gallistel describes this book as considerably more heretical than his previous work, because it challenged some commonly held beliefs about memory. "I essentially argued that the reason people weren't finding the neural basis of memory was because they were looking for the wrong thing," Gallistel said. The consensus at the time was that memory consists of changes in the synaptic connections between neurons (called associative bonds by psychologists and Hebbian synapses by neurobiologists); this belief is still widely held today. Gallistel contends that, instead of these associative bonds, learning depends on what he calls a "readwrite memory." This type of memory is functionally like the memory in a computer, in which values of variables are stored and retrieved when they are needed. Although popular, the book was not as influential as Gallistel would have hoped: "It didn't cause [psychologists] to abandon their commitment to the associative theory of learning," he said.

Still using learning and motivation as a means to pursue of the basis of memory, Gallistel has gradually shifted from a neuroanatomical to a genetic research approach. He and his team hope to elucidate the basis of memory by looking for a genetic component of memory malfunctions. Gallistel's laboratory is currently designing experiments in which mice must remember specific distances or time intervals. In one such experiment, called a water maze, animals are placed in a tank filled with opaque water. A platform is submerged just beneath the surface and is discovered by random swimming on the first trial. Because the platform remains in the same location, in repeated trials the animals learn to swim to the platform more directly. Gallistel and his team hope to use such experiments to identify animals with genetic malfunctions in their memory (12).

On the Learning Curve

One challenge facing Gallistel in his genetic malfunction work is that the study of animal learning has not been quantitatively oriented, a dilemma that poses problems in experiments that require screening the memories of many animals. Experiments generate large amounts of data to be processed by a computer. However, before a computer can analyze behavior, it must first be told what to look for and what to count. Gallistel and his team are writing algorithms for computer programs to extract quantitative properties from all of the stimulus and response events that transpire in testing apparatuses. Gallistel's laboratory envisions being able to assess hundreds of mice at once in computercontrolled tests and to thereby identify

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individual animals that remember incorrectly.

Accurately characterizing the learning curve in individual mice is an essential part of understanding the fundamental basis of learning. In his Inaugural Article (1), Gallistel and colleagues suggest that the concept of a gradual learning curve is inaccurate. The team has shown abrupt changes in behavior as an animal learns, which could mean that learning is not the gradual strengthening of associative bonds between synapses, as was previously thought. Gallistel's work has shown that the rate of learning can vary greatly from one subject to the next. Indeed, experimental data from experiments like the water maze suggest that learning spatial locations can occur after only a single experience. Therefore, Gallistel questions the validity of using

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group-average learning curves to characterize the learning process in individual subjects.

Gallistel has a firm idea of where to direct his future research. Having developed a means of assessing memory in mice, he knows that much work remains before genetic malfunctions in mice can be readily identified. "You've got to find some way of visualizing the behavior phenomena that you are recording in such detail and various ways of quantifying what's happening," he says. "And there just hasn't been much work done in that area." This is far from a simple problem: "There are thousands of reasons why an animal will fail to show you what it knows," he said. "You have to, somehow, devise tests that get around the problem."

Erik Stemmy, Science Writer

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