

## In Memory of Leslie G. Ungerleider

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Received: 5 January 2021 / Accepted: 12 January 2021

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Dr. Leslie Ungerleider, who together with Mortimer Mishkin established the model of “two functionally dissociated cortical visual pathways in the primate brain” [1], passed away on December 11, 2020. Ungerleider’s model of two visual pathways is one of the most profound and influential theories in contemporary neuroscience. In addition, Leslie’s impact on the Chinese cognitive neuroscience community [2] is so strong that we feel moved to write this essay to memorize her, our beloved colleague and mentor. We hope her scientific heritage will continue to inspire us and give impetus to our scientific efforts to develop cognitive neuroscience in China.

Leslie was an elected member of the National Academy of Sciences (2000), the American Academy of Arts and Sciences (2000), and the Institute of Medicine of the

National Academy of Sciences (2001), a rare triple-play in science. Leslie won nearly every honor in the field of cognitive neuroscience and psychological science, including the Women in Neuroscience Lifetime Achievement Award (2001), the George A. Miller Award (2005), the William James Fellow Award (2010), the Grawemeyer Award (2012), the Andrew Carnegie Prize (2013), and the Glass Brain Award (2020).

Leslie grew up in New York City. She earned her bachelor’s degree at the State University of New York at Binghamton. Then she got her doctorate with Edgar Coons at New York University, where Leslie published her first paper, which was in *Science* [3]. In 1972, she became a Postdoc at Stanford University and began her research in non-human primates. In 1975, she moved to the National Institute of Mental Health and worked with Mortimer Mishkin in the Laboratory of Neuropsychology. In 1995, she established her own laboratory, the Laboratory for Brain and Cognition, where she remained for the rest of her career. In 2008, Leslie became an NIH Distinguished Investigator.

Leslie was an immensely influential functional anatomist. She conducted a series of investigations studying the cortical and subcortical projections of visual areas (e.g., V4, MT, TEO, and IT) in the macaque [4–19]. Moreover, her studies based on behavioral assessments of selective brain lesions in macaques made outstanding achievements in relating neuroanatomy to behavior [20–36]. Most notably, her research with Mortimer led to one of her best-known discoveries: two cortical visual systems in primates—a ventral pathway projecting from the striate cortex into the temporal cortex, specializing in object recognition (the “what” stream), and a dorsal pathway projecting from the striate cortex into the parietal cortex, specializing in visuospatial perception (the “where”

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stream) [1]. This pivotal work continues to be one of the most impactful and influential concepts in visual neuroscience and has guided numerous subsequent studies in non-human primates as well as in humans. Later in her career, Leslie and her colleagues have expanded the two-visual pathway model. They proposed that the ventral visual pathway is a recurrent network that provides visual information to at least six distinct cortical and subcortical areas, each mediating different forms of learning and memory [37]. Recently, Leslie and her colleagues proposed that there is a third visual pathway on the lateral brain surface specializing in higher sociocognitive functions based on dynamic social cues (e.g., moving faces and bodies) [38]. Together, these studies have provided us a broader, systems-level picture of the primate visual system.

Leslie was also an enormously talented experimental physiologist and cognitive neuroscientist. Over years, she made a significant cumulative contribution to understanding the neural mechanisms underlying cognitive processes, including perception, memory, attention, emotion, and decision-making, especially in the visual modality (for reviews, see [39–44]).

Throughout her entire career, Leslie was a pioneer in combining cutting-edge technologies with classical approaches. She was keenly aware of the importance of neuroimaging techniques (e.g., positron emission tomography and magnetic resonance imaging [fMRI]) for understanding the structure-function relationships of brain regions at the macroscopic level [45, 46]. By combining fMRI with effective connectivity analysis, Leslie and her colleagues systematically revealed the neural mechanisms of attention [47–50]. In recent years, Leslie combined fMRI with anatomical tracing techniques, interventional physiology, pharmacological manipulation, and electrophysiological recording to investigate the brain in a comprehensive way. By this multidisciplinary approach, Leslie and her colleagues greatly expanded our knowledge of the functional architecture and properties of visual cortices [51–58]. Moreover, her parallel fMRI studies conducted in humans and non-human primates tested the generality of this knowledge across species [59–61].

Leslie was a warm colleague and mentor for many Chinese scholars and students. She visited China multiple times. In April 2004, Leslie was invited to give a keynote speech at the 3rd International Symposium on Cognitive Neuroscience in Hong Kong. A few months later, invited by Lin Chen, Leslie visited Beijing in October and gave a talk entitled “How the Brain Pays Attention”. In June 2012, Leslie visited Beijing for the second time and gave a talk entitled “Functional Architecture of Face Processing in the Primate Brain” at the Organization for Human Brain Mapping Annual Meeting. Over the years, Leslie had built up an international network of collaborators including

many researchers from China. Leslie also mentored a steady stream of young Chinese researchers, many of whom have come back to China as independent scientists. As shown below, they will eternally cherish the memory of Leslie, their beloved mentor and colleague.

“Leslie was a wonderful scientist and mentor. I learned from her how to think and work more critically. She taught me that solid work is the only thing that eventually matters. Leslie knew the difficulties that young scientists might meet, especially women scientists. So, she always tried her best to help us. Because she was there, I felt supported and found the courage to face difficulties and move forward. Everything I learned from her made me continue my career in science. She will always be there, in our memories, in our knowledge, and the skills that we learned from her.”—Ning Liu (Institute of Biophysics, Chinese Academy of Sciences), a Postdoc with Leslie.

“As a scientist, Leslie’s groundbreaking work on the ‘two cortical visual systems’ has revolutionized the way we think about the functional architecture of the brain and has been immensely influential on generations of brain scientists. As a mentor, Leslie was very patient, warm, generous, inspired, and supportive—she always tried her best to help us in many aspects. Knowing her support was there and always available if I ever needed it was so important to me to set up my own lab and continue my career in science. As a leader, Leslie was straightforward but compassionate. Everyone was cared for deeply and equally by her excellent leadership. Leslie is a giant of cognitive neuroscience, vision science, and psychology and will live on in our memories and textbooks.”—Xilin Zhang (School of Psychology, South China Normal University), a Postdoc with Leslie.

“As a giant in the field of neuroscience, Leslie’s many research studies have not only profoundly influenced researchers in the fields of neuroscience, psychology, vision, and brain science, but have also inspired researchers in the new fields of computer science and artificial intelligence. As a wonderful mentor, she was always there, giving young researchers, including Chinese scholars like me, generous support and help. It is because of her encouragement and support that I have enough confidence and courage to face all the challenges of pursuing my science career.”—Hui Zhang (School of Medicine and Engineering, Beihang University), a Postdoc with Leslie.

“Leslie is one of most respected scientists I have ever met. I still remember the days when we listened to her insightful comments on papers and studies in lab meetings. She profoundly influenced many of us young investigators on how to think about the world in a scientific way. I also remember the wonderful moments when I discussed our studies with her. She was always warm, kind, and supportive to everybody in the lab. Leslie’s excellent work

is a milestone in cognitive neuroscience, and her encouragement inspires me to continue pursuits in this field”—Jiongjong Yang (School of Psychological and Cognitive Sciences, Peking University), a visiting fellow with Alex Martin in the joint Lab of Brain and Cognition with Leslie.

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