

Obituary

In memoriam Robert B. Barlow, Jr

July 31 1939 – December 24 2009

It is with great sadness that we mark the loss of Dr Robert (Bob) Barlow, a pioneering investigator into the neural basis of visual behavior. Bob had a passion for vision research that was vibrant and engaging. He would surely have remained scientifically active and productive for years to come, were it not for his passing at the young age of 70 after a year-long battle with leukemia.

Bob had a long and distinguished career as a vision scientist. He received a bachelorette degree in Physics from Bowdoin College in 1961 and a doctorate degree in Biophysics from Rockefeller University in 1967 under the tutelage of Dr H. Keffer Hartline, a Nobel Laureate. For his thesis work, Bob carefully mapped the spatial spread of inhibitory signals within the lateral eye of the horseshoe crab (*Limulus polyphemus*) using a stimulation system he developed for positioning a tiny optical fiber in direct contact with the cornea and delivering light to single retinal receptors. Bob discovered that the strength of inhibition between two receptors did not decrease monotonically with distance, as Hartline and others had assumed, but rather showed a maximum at intermediate distances of separation (Barlow, 1969). The experience was formative, as Bob went on to spend the next three decades investigating the inner workings of the *Limulus* visual system as a professor at Syracuse University and summer researcher at The Marine Biology Laboratory in Wood's Hole, MA, USA. His first major discovery as a principal investigator was that the physiological properties of the eye change dramatically when the retina is excised from the animal (Barlow and Kaplan, 1971). In a dish, retinal neurons are several log units less sensitive to light, and they are not spontaneously active in the dark. The loss of sensitivity indicated that the intact eye employs two receptor mechanisms to encode light intensity, just as vertebrate eyes do. The finding prompted a neurophysiological re-evaluation of *Limulus* response properties *in situ*, which Bob and his students carried out through the 1970s. It also cemented in his mind the need to study neural information processing in living behaving animals and inspired his neuroethological approach to vision research. The transition to *in vivo* experimentation led to his second major discovery, which is that the structure and function of the *Limulus* eye is modulated on a daily basis by efferent optic nerve signals from a circadian clock in the animal's brain (Barlow et al., 1977; Barlow et al., 1980). At night, input from the clock leads to compaction of the light-sensitive rhabdom of receptor cells and increased photon catch (at the cost of spatial acuity). Other effects of clock feedback at night, such as increased response gain, reduced receptor noise, and weakened lateral inhibition, and the cellular mechanisms underlying them were gradually resolved through the 1980s by Bob and his collaborators. During this period he also made a third major discovery, which is that the animal uses its lateral eyes for finding mates (Barlow et al., 1982). From then on, Bob moved his lab every summer from Syracuse to The Marine Biology Laboratory to observe the visual behavior of horseshoe crabs during their mating season. Through the 1990s he and his students trekked out to

mating beaches across Cape Cod day and night at high tide when the animals are active and recorded with overhead videocameras the animal's movements in the vicinity of objects of assorted size, shape and contrast. Surprisingly, Bob found that male crabs could see crab-like objects of widely different contrast almost equally well day and night despite the relatively simple design of their visual system (Powers et al., 1991). To understand how the animals accomplished this impressive feat, Bob put forth a computational model in the late 1990s that incorporated the wealth of knowledge about the lateral eye accumulated over the past century and fed the model movies recorded with a videocamera mounted above the eye of crabs moving in the ocean (Passaglia et al., 1997). The model showed that the spatiotemporal properties of the *Limulus* eye are tuned to detect moving objects resembling a potential mate and encodes them with characteristic patterns of activity across the ensemble of retinal receptors. The model still stands today as the largest and only neural network computer model that can accurately simulate the output of the retina of an animal behaving in its natural habitat. In the late 1990s Bob left Syracuse University to become the director of the Center for Vision Research and professor of ophthalmology, biochemistry and molecular biology at SUNY Upstate Medical University, where he remained for the rest of his career. Through the 2000s Bob embarked on a second scientific career, publishing several papers on the effects of metabolic stress from low blood glucose on the visual sensitivity of mice and its possible role in degenerative eye diseases.

Bob was also a gifted teacher and internationally recognized leader in the neuroscience community. He was featured in several radio and television programs in the US and abroad, such as the Discovery Channel and the BBC. He helped to establish the SUNY Eye Institute, direct the Doreen Grace Brain Center in Cape Cod, and served on the board of trustees of The Marine Biology Laboratory and the Association for Research in Vision and Ophthalmology and on National Advisory committees of the NIH. He will be missed by many.

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