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OBITUARY

Robert K. Josephson (1934–2016)

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Professor Robert K. Josephson died at his home in Laguna Beach, California, on 6 February 2016 following a 3 month fight with lymphoma. Over a career spanning more than half a century, and numerous venues world-wide, he became widely known and venerated as a mentor, teacher, colleague, physiologist and friend. His path to distinction began as an undergraduate at Tufts University (1952–1956). It was at Tufts that he was influenced by K. D. Roeder and became interested in pursuing graduate work in behavioral physiology. In the sixties and seventies there was considerable interest amongst researchers in a variety of invertebrate animals as many displayed rather stereotypical motor behaviors driven by neural pathways with few components, and neurons that were large and amenable to electrophysiological studies. The stated goal of many was to understand the complete behavior of an organism based on the underlying neuromuscular systems. Bullock and Horridge's (1965a,b) two-volume series, *The Structure and Function of the Nervous Systems of Invertebrates*, well attests to the thrust of research during that period. Not surprisingly, Bob went to Ted Bullock's laboratory at UCLA to pursue graduate studies (1956–1960).

Dissertation research in Bullock's laboratory set Bob on the first of two career pathways, both of which identify him as an innovative, creative and trend-setting leader in behavioral physiology. The first pathway was the behavioral physiology of 'simply' organized metazoan animals – namely of the Coelenterata (jellyfish, corals, hydroids); the second pathway was the physiology and design constraints of skeletal muscle. The two pathways overlap considerably over his research career.

Coelenterate 'behavioral physiology'

Early studies (late nineteenth, early twentieth century), notably by G. H. Parker, G. J. Romanes and C. F. A. Pantin, had established that cnidarians (hydroids, jellyfish, corals and ctenophores) are the earliest of the metazoan animals to possess neurons and that these neurons are organized into two-dimensional net-like structures that possess structural and physiological properties similar to those found in more recent animal forms. The essence of these earlier studies was featured in a recent contribution by Bob to the JEB Classics section (Josephson, 2004) highlighting work by Pantin (1935) on the properties of these nerve nets in the Actinozoa (corals) and, importantly their control of many behavioral observations. Notably, Bob realized that the seeming design simplicity of these nerve nets could be used to develop a digital computer model that might reliably be used to simulate naturally observed behaviors. A major component of Bob's dissertation work in Bullock's lab was pioneering in the application of digital computers to biological research and landed him a publication in the first volume of the

Journal of Theoretical Biology (Josephson et al., 1961; when computers were infants and housed in large rooms!). Bob went on to establish himself as a recognized leader and authority to this day in our understanding of conducting pathways underlying the behavior of the Cnidaria. In his usual display of humility, however, he recently acknowledged that the 'goal of understanding the complete behavior of even the simplest of organisms has been elusive'.

Physiology and design constraints of skeletal muscle

There are many characteristics and attributes one could use to describe Bob. Three appear consistently in nearly every discussion of Bob and clearly were instrumental in guiding his professional career. The first was his intense curiosity about everything – both the natural and physical world. The second was his keen desire to know and understand everything in the greatest detail. And the third was his insistence on accuracy and perfection. Two examples from the early 1970s serve to illustrate these qualities. Both occurred during summer research at the Marine Biological Laboratory at Woods Hole while Bob taught in the Invertebrate Zoology Course. The first example occurred when a student wanting to observe burrowing in marine worms came to Bob for suggestions. Together, they came up with a chamber consisting of two pieces of glass narrowly spaced together and filled with water and sand. After a day of testing, Bob inquired as to how the apparatus was working, only to find that it was difficult to observe the worms in the sand. After thinking about it, Bob remembered that he had read of a mineral

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(cryolite) that had the optical density of seawater. They ordered some, ground it into sand-like particles, and placed it in the chamber along with seawater and the worm. Voila! The worm was now perfectly visible as it burrowed in the cryolite! Bob later published a paper on cryolite as a medium for studying burrowing behavior (Josephson and Flessa, 1972).

The second example occurred as Bob was driving near Woods Hole with the window rolled down at dusk on a warm July evening. He suddenly pulled over and said, 'Do you hear that sound?'. Clearly, it was unavoidable – high pitched and continuous. Bob followed the sound and discovered that it was a male katydid stridulating in a bush. Bob went back the next evening armed with a guitar. He tracked down the audio signal and proceeded to pluck each string of the tuned guitar, until he had a signal match. This told him the frequency of the sound made by the stridulating katydid! Curiosity and the desire to know and understand led Bob to years of laboratory research on the structural properties and physiology of high-frequency sound producing muscles in katydids and subsequently cicadas – a diversion from his coelenterate work that generated a prolific and new pioneering research pathway in muscle physiology.

The crowning achievement of Bob's efforts in this direction brought to bear his technical expertise in computer electronics, his creative skills and his insistence on perfection. One cannot escape the observation that skeletal muscle has evolved as a successful effector of behavior across the Animal Kingdom. Its structural design is similar and recognizable wherever it occurs and yet it is malleable and accounts for widely differing physiologies and behaviors. The ultimate function of muscle is to shorten against a load and to do work – the work of movement. Bob found a way to measure the work done by skeletal muscles stimulated under normal, *in vivo* conditions (Josephson, 1985). A plot of the force generated as a function of length and phasic stimulation within a cycle of contraction creates a loop (the work loop), the area of which is the work performed by the muscle. The work loop method designed by Bob avoids the isometric or isotonic methods typically used to elucidate muscle properties and has shown us that muscles can play diverse roles in locomotion, not only to generate the work for propulsion but also serving to stabilize or even brake limbs. The technique has been reviewed as a JEB Classics article by Anna Ahn (2012).

The quality and magnitude of the legacy of Professor Robert Josephson leaves us in great awe and admiration of a career filled with a passion for life and a quizzical mind of enormous breadth and depth. His life-time effort includes 94 scholarly publications, 31 of which were single authored! It is especially appropriate to acknowledge that 43 of his publications were in the Journal of Experimental Biology; many were seminal and continue to be cited. If service is a measure of respect, his continuous service on the JEB Editorial Board from 1990 until his death deserves recognition.

Bob retired in 2005 after 34 years as Professor serving two departments at the University of California, Irvine – the Department of Neurobiology and Behavior and the Department of Ecology and Evolutionary Biology. His previous service was in the Department of Biology at Case Western University (1965–1970) and the Department of Zoology at the University of Minnesota (1962–1965). In addition to these academic homes, Bob and his family were summer residents in Woods Hole for nearly 60 years. He was first an instructor (1965–1969) then Director (1972–1974) of the Invertebrate Course at the Marine Biological Laboratory, and for more than 30 years was an investigative scientist. He continued to spend summers in Woods Hole up until his death. Bob is survived by his wife Trudy, a brother Paul, and three children (Beth, Sue and Eric) and seven grandchildren from his marriage to his first wife, Ginny.

The following poem written about Bob sums up his essence to those impacted by his love and support.

A gentle, gracious giant walked this earth
with mirth and girth
we were humbled and when we stumbled this giant
picked us up, made us pliant,
gave us direction through his vision, his example
to open our hearts, to wonder, to sample
the intrigue, the beauty, the wonderment of all that comes
to the table of life.

D. R. Stokes, 8 February 2016

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