This Week’s Citation Classic

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To the Memory of
W. Alden Spencer, MD
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"My pleasure in having our article selected as a 'Citation Classic' is clouded by the tragic and untimely death of my colleague, W. Alden Spencer. I can imagine no scientific tribute that would have pleased Spencer more than to know that our initial paper on habituation has been identified as one that has 'left its mark on the progress of the whole of science.'

"Under the circumstances, a brief personal commentary is in order. Spencer and I became very close friends when we were undergraduates together at Reed College. We then followed somewhat different career lines--Alden obtained an MD and postdoctoral research in neurophysiology, and I obtained a PhD in physiological psychology and postdoctoral research in neurophysiology. We later joined forces as faculty members at the University of Oregon Medical School, Alden in psychiatry and I in psychiatry and medical psychology. Our collaborative effort extended over a period of several years in the 1960s.

"Our plan was to utilize simplified neuronal systems as models of phenomena of behavioral plasticity. We selected the hindlimb flexion reflex of acute spinal cat as a model. An elementary but important form of behavioral plasticity, habituation, is very prominent in this preparation. Slow rates of cutaneous stimulation (e.g., 1/sec. to 1/5 secs.) produce a pronounced decrease in flexion reflex amplitude that requires a period of many minutes to recover--a form of learning not to respond. There were perhaps three major contributions of our work:

"First, characterization of the process of habituation. This is a general definitional issue. There was lack of agreement on the properties and definitions of behavioral habituation and the literature was often contradictory. We surveyed the behavioral literature in detail and identified some nine consistent parametric features relating to stimulus and training variables that characterized habituation. These properties have come to be accepted in the field as the detailed definition of habituation.

"Second, use of simplified neuronal systems as models of behavioral plasticity. This is an epistemological issue. How does one decide that response change or plasticity in a given simplified neuronal system is a good model of the general behavioral process? We were able to show, using the criteria noted above, that our spinal model system was in fact a good model of the process of habituation.

"Third, analysis of neuronal mechanisms of habituation. In simplified systems, it is possible to use 'strong inference'--to eliminate possible mechanisms. We ruled out decrement at sensory input, motor output, and the motor neurons themselves. The process was located in interneurons. We suggested that the mechanism involved synaptic depression occurring presynaptically at (interneuron) axon terminals. More recent studies from several laboratories using monosynaptic models of habituation have consistently supported this general mechanism."