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AN ASSESSMENT OF THE SIGNIFICANCE OF THE PHYSIOLOGICAL CONTRIBUTIONS AFTER 1950

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I had the remarkable and valuable experience of working with McCulloch's group from 1950 to 1967, first in Chicago and then at M.I.T. During that time the physiologists who worked with McCulloch, J.Y. Lettvin and W. Pitts included Maturana, Chung, J. Brown and R. Gesteland. The impact of the work continues to be strongly felt both because of the ideas which were generated and because of techniques, and I will select what seem to me to be striking examples.

Techniques: *Data collection.* The 1950's saw the general use of microelectrodes of the glass fluid filled variety but it was quite apparent that these missed certain types of cell. It was discovered that metal electrodes whose tips were plated with platinum black revealed a whole new variety of small cells and fibres which had previously been unobservable. The work on the visual, olfactory and somatosensory systems depended on these new electrodes, and further developments continue to be made.

Data analysis: Until 1955 the analysis of slow waves, evoked potentials and compound action potentials in the central nervous system had been intuitive, often illogical and usually wrong. Taking field theory from physics and developing a practical method of source-sink analysis changed that. The use of that technique continues to expand, particularly now that computers can be used to replace the tedium of manual calculations.

Data Display: One of the many problems of the nervous system is that it generates too much information. The old laboratory became filled with miles of film or recording paper or tape and no one memory allowed a comparison of events. The dot or raster display produced an extraordinary compression of

significant data so that visual inspection immediately reveals significant changes and correlations. This method is now in such general use that its origin is almost forgotten.

The Results: Sensory modulation. McCulloch's 1955 paper which first used source-sink plots to follow nerve impulses, concluded that there was a type of inhibition that worked by blocking nerve impulses before they reached the synapses. The general phenomenon is now well established although discussion continues about the exact mechanism. The influence of this result led to consideration of the consequences of modulation of sensory input. For example the gate control theory of pain mechanisms clearly represents an extension of the ideas and results of that paper.

Vision: The papers on frog vision may well be the most important seminal work which has led to the present explosion of understanding of the visual system and therefore of sensory systems in general. I write this as an observer since I was not a member of the team which produced the work. Here was a complete break with the traditional past. Up to that time, the input to the brain was thought to be generated by a simple array from a mosaic of detectors each responding to a single type of change in a small area. Therefore sensory systems were tested with single isolated stimuli. The new work showed that the input was already able to analyze events in terms of sizes, shapes, movement and direction. All of this had previously been missed by the use of excessively simple stimuli but it set the stage for the new approach of presenting the organism with stimuli it was evolved to handle.