1 Historical Introduction to Plant Electrophysiology

Rainer Stahlberg

It is hardly conceivable that reflex responses, memory and brain activity were once explained without consideration of the electrical activity in nerves and muscles. One must remember that electricity was only known then either as lightning or as the repelling/attracting charges that certain substances (such as amber, the Greek word for which is electron) accumulate when rubbed against wool or other textiles. Among the first people who thought about electrical phenomena and their possible biological consequences were de Sauvages (1706–1767), S. Hales (1677–1761), J.A. Nollet (1700–1770) and most importantly the prior Pierre Bertholon de St Lazare (1742–1791), who proposed to improve agriculture with a novel electroculture of crops (Bertholon 1783). This idea was repeatedly revived, e.g. by Lemstrom (1902), who attempted to demonstrate stimulating effects of natural electrostatic fields by growing plants outside and under Faraday cages. Effects of electrical fields on plants and animals continue to be a flourishing field of serious study and some controversy (see Chapter 11).

The birth of the larger field of experimental electrophysiology, however, is inseparably intertwined with the discovery of useable forms of electricity itself. The well-known common starting point was Luigi Galvani's discovery of "animal electricity" or his observing the contraction of isolated frog legs suspended between copper hooks and the iron grit of his balcony (Galvani 1791). Aside from stimulating dubious medical treatments such as "galvanism" and "mesmerism", this momentous event established electrophysiology as a major discipline of biology (Galvani's work was continued by the studies of A. Matteucci, E. Du Bois-Reymond and many others, see below) and stimulated A. Volta to develop the first practical batteries (the existence of batteries in ancient Egypt has been suggested, but cannot be reliably confirmed). These portable sources of electricity were called galvanic elements. Based on the different redox potentials of metals and non-metals, they provided reliable sources of various fixed voltages. This invention not only laid the foundations of electricity as a novel discipline of the physical sciences but also turned electricity into useable reality that would later serve as the basis for at least two industrial revolutions. Electrical currents, voltages, resistances and fields

University of Washington, POB 355325; Seattle, WA 98195, USA (e-mail: raista@u.washington.edu)

Plant Electrophysiology – Theory & Methods (ed. by Volkov)

could now be experimentally studied and applied to wires and wire networks as well as to animals and plants. The physical understanding of batteries itself also served well as a model to explain some fundamental phenomena of electrophysiology such as the stunning of prey by electrically hunting fishes from the new world (Du Bois-Reymond 1848). As reflected in this book, electrophysiology became to encompass not only the development of methods and instruments for the actual measurement of electrical signals but also the study of physiological effects deriving from electric and electromagnetic currents and fields.

It soon became clear that the role of the electric current in the contraction of frog legs was not to provide the energy for the movement, but to simulate a stimulus that existed naturally in the form of directionally transmitted electrical potentials. Frog legs had just been first and serendipitous current-recording devices to indicate the flow of electrical current in the moment they touched the iron grit of the balcony and their violent jerks were supposedly visible enough to scare Mrs. Galvani, the observant wife of the great scientist. In follow-up studies both Matteucci and Du Bois-Reymond then recognized that wounding of nerve strands generated the appearance of a large voltage difference (called wound potential) between the wounded (internal) and intact (external) site of nerves. This wound potential was the first, crude measurement of what later became known and understood as membrane or resting potential of nerve and other cells. Importantly, this potential could be measured and it was soon found that electrical or mechanical stimulation of the nerve reduced its size (in today's terms: these stimuli caused a depolarization). To describe the phenomenon, novel terms such as action potential (AP) and action current were created (Du Bois-Reymond 1848). After plasmolysis experiments in plant cells suggested that all living cells are surrounded by semi-permeable membranes (Pfeffer 1873, 1906, 1921), it did not take long until W. Nernst (1889) and J. Bernstein (1912) proposed an updated understanding of existing potentials and AP-mediated excitations on the basis of the existence and collapse of K^+ ion gradients across the plasma membrane. It was also recognized that nerves propagate such excitations instantly or with very high speed. In 1850, H. von Helmholtz succeeded in actually measuring this speed in the *Nervus ischiadicus* of frogs and Hermann (1868) developed the "Strömchen" theory to explain the speed and efficiency of AP propagation in nerves in analogy with a leaky wire cable. Until about 1930, this seemed to be all that was to know about nervous signals. However, clever experiments showed surprisingly that signaling between nerve cells through their dendritic connections does not occur by way of a continuation of the electrical action current but by the release of chemical signals diffusing through an intercellular cleft. Following the anatomical work of S. Ramon y Cajal, the biochemical studies of O. Loewi and the terminology of Sir Charles Sherrington, the phenomenon of synaptic transmission was recognized and this meant a gigantic step towards the understanding of nervous integration (Eccles 1964). With these events, the full range of modern electrophysiology