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Cellular Sensing of Internal and External Conditions Across all Cell Types

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Description

The maintenance of the MP and the coupling of IMFs to membrane-bound chemical reactions are key components of cellular bioenergetics and physiology, as recognized in the chemi-osmotic theory of respiration. While the specific mechanisms of MP and IMF can be different across different membranes (e.g. mitochondrial versus plasma membrane in mammalian cells or the inner versus outer membranes in a bacterial cell), their generation always involves electro-static and electro-dynamic processes. IMFs can arise from selective transport or differential permeability to charged molecules, or can be generated through membrane-bound redox reactions of the respiratory chain. A key point to recognize is that IMF and MP are coupled to each other and further to cell volume and metabolism. The connection to volume arises from the distribution of ions and charged molecules (essential for the formation of MP), determining also the osmotic forces on cells. The connection to metabolism is achieved by four general mechanisms.

Biological Electrical Phenomena

Biological electrical phenomena were recognized by Luigi Galvani and his contemporaries in the eighteenth century through the study of animal muscles and the nervous system. These early studies have led to the development of major fields, especially neuroscience and cardiology. Outside of these fields, however, studies of bioelectricity, i.e. electrical and electrochemical processes in cellular systems, have remained fragmented. While it was discussed as early as the 1970s that bioelectricity may be fundamental to understanding various cellular behaviours, the electrical investigations of cells were only focused on cellular bioenergetics. The bioelectrical view of cells as a more general concept has remained confined to the fringes of biological research for five decades, during which molecular biology has made astonishing advancements in our understanding of cells and our ability to manipulate genes.

First, the steady-state concentrations of key metabolic redox and energy carrier pairs (NADH/NAD+ and ATP/ADP), which can determine metabolic pathway fluxes, can be altered by membrane-bound dehydrogenases and ATPases that can either use IMF to convert these pairs or use their conversions to sustain/generate it. Second, membrane transporters can couple the transport of metabolites, in particular organic acids and sugars, with the transport of ions, thereby linking this metabolically central process to IMF generation. Third, several ‘master’ compounds within central metabolism such as glutamate, which is involved in nitrogen assimilation and the synthesis of many other amino acids can also act as gating molecules to control the state of ion channels, thereby influencing IMFs via MP. Finally, the well-described excretions of metabolites and proteins from cells, as well as membrane-bound enzymatic processes, can influence the electrical and chemical potential of the cell microenvironment either directly or through redox reactions. In this context, it is worth noting that extracellular matrix polymers, such as collagen, chitin and cellulose, are shown to be piezoelectric.

We argue here that bioelectricity can lead to a fundamental understanding of single-cell behaviours, beyond its roles in the multicellular context. By cell behaviours, we refer to high-level processes such as proliferation, dormancy and differentiation that are underpinned by dynamic changes in gene expression programmes, metabolic flux switching and mechanical cell properties. Notably, these changes are ultimately linked to the integrated physio-chemical properties of the electrochemically active cell–microenvironment interface. This motivates a bioelectrical view of the cell, the development of which can lead to a predictive understanding of cell behaviour.

Electrochemical Nature of the Cells

The electrochemical nature of the cells and their microenvironments gives rise to a coupling between cell physiology and bioelectricity (i.e. MP and IMF). This bioelectrical conceptualization of the cell provides not only plausible explanations for many cell behaviours, but also a new framework to re-formulate much of the existing knowledge in cell physiology. To illustrate this point, we discuss here a few example cell behaviours in the bioelectrical contexts.

The nature of the bioelectricity metabolism coupling and its possible links to enabling different cell states are now being elucidated. In bacteria, it was recently shown that proliferating versus non-proliferating bacterial cells responds differently to electric fields. In addition, it has been shown that MP responses are different when bacterial cell metabolism or biosynthesis is perturbed by carbon starvation or antibiotic treatment, respectively. Other studies have also found that ionic fluxes can influence MP and physiological outputs such as the generation of metabolically dormant bacterial cells.

A coupling between bioelectricity and physiology is also evident in cellular sensing of internal and external conditions across all cell types. Osmoregulation of cell size can be achieved through both the production and consumption of key metabolites (e.g. glutamate) or through the alteration of ionic fluxes across the membrane. Both processes can alter MP. For example, in bacteria, osmotic changes result in a significant motility response, possibly through changes in IMF causing flagellar rotation.

Such a coupling between flagellar rotation and IMF has been characterized and recently been used to monitor changes in MP and cell metabolism through changes in flagellar rotation speeds.

Interestingly, the resulting findings from molecular studies highlight once again the importance of bioelectricity, and now there is a revival of a bioelectrical view of biological systems. Studies in diverse systems show that bioelectrical signals are at the heart of cell-cell communication in microorganisms, plants and animals. Bioelectricity can underpin efficient growth and antibiotic resistance in bacterial biofilms and organization, morphogenesis and regeneration in mammalian and plant tissues. These findings, together with the realization that externally applied electrical fields can modulate multicellular processes such as regeneration in plant and vertebrate tissue, have resulted in the recent proposition that multicellular organization, and development more broadly, can, and should, be studied as a bioelectrical paradigm.