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NUCLEAR PHYSICS AS NEW FRONTIER TO BIOLOGISTS AND BIOPHYSICISTS

Shobhit, Govt. P.G. College Hissar

Abstract: The nucleus is physically distinct from the cytoplasm in ways that suggest new ideas and approaches for interrogating the operation of this organelle. Chemical bond formation and breakage underlie the lives of cells, but the nonchemical aspects of cell nuclei present a new frontier to biologists and biophysicists. Here, we are discussing a new era of nuclear physics.

THE NUCLEUS BACK THEN

Classical (pre-1950) biophysics did not worry much about differences between nucleus and cytoplasm, mainly because the focus of physiology was on the latter compartment and in particular on actomyosin function. Francis Crick studied the viscosity of cytoplasm (Crick, 1950; Crick and Hughes, 1950), which is a still-intriguing issue. The nucleus sat in Crick's field of microscope observation as a sideshow, its DNA waiting quietly for his future attentions.

The nucleus was of necessity destroyed in early DNA studies, in which pus-filled bandages were the source and harsh extraction conditions were applied but subsequently, the organelle was isolated and studied. It soon became apparent that nuclei, both isolated and studied within intact cells, had physical properties different from the cytoplasm. For example, the nuclear envelope can display a membrane resting potential of about −15 mV. Electrical and related osmotic responses of isolated and in-cell nuclei when differentially responding to elevated extracellular Na^+, clearly indicate a basal osmotic strength different from cytoplasm. These studies illustrate the key fact that the nucleus is a distinct place not just in macromolecule populations but in basic physical properties.

THE MODERN AND POSTMODERN NUCLEUS

Electron microscopy of the 1950s presented the nucleus in high resolution, revealing that there are no internal membranes and that the chromatin, nucleolus, and other nuclear components are mixed together. This suggested that DNA replication, transcription, RNA processing, and other nuclear functions occurred via a wild melee of molecular interactions. Later this was refined by the realization that many DNA-acting (and some RNA-acting) proteins are confined to nucleic acid by nonspecific interactions that provide efficient kinetic pathways to search for specific targets. The notion followed that many nuclear functions may depend on the tethering of key factors to pre-existing entities.

The scheme of folding of the gigantic lengths of DNA (2 m in the human case) inside the interphase nucleus remains a deep puzzle. Even the question of the physiological relevance of the 30-nm fiber observed in biochemical studies remains open. In at least most differentiated somatic cell nuclei, individual interphase chromosomes lie in close opposition to one or more others, occupying distinct territories. Mapping of contacts by chromosome conformation capture has suggested a space-filling “fractal globule” folding scheme with intriguing functional consequences, most notably reduction of chromosome entanglements relative to the “null hypothesis” of random coil-like polymer organization.

Meanwhile, in the nuclear space not occupied by the genome, RNAs move by, or more precisely by anomalous subdiffusion arising from nuclear cul-de-sacs and short-lived contacts with chromatin. Here, in the interphase nucleoplasm between the chromosomes, various nuclear bodies are found and, in many cases, dynamically accrete and shed their parts. All this choreography is encased within the nuclear envelope and its underlying lamina. After years of being perceived as static, the nuclear lamina has recently become recognized as one of the most dynamic regions of the nucleus.

PHYSICAL BIOLOGY OF THE NUCLEUS