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After cell death: the molecular machinery of efferocytosis

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Cells constituting a multicellular organism die in a variety of ways throughout life, and most of them die via apoptosis under normal conditions. The occurrence of apoptosis is especially prevalent during development and in tissues with a high cellular turnover rate, such as the thymus and bone marrow. Interestingly, although the number of apoptotic cells produced daily is known to be innumerable in a healthy adult human body, apoptotic cells are rarely observed. This absence is due to the existence of a cellular process called efferocytosis that efficiently clears apoptotic cells. Studies over the past decades have focused on how phagocytes are able to remove apoptotic cells specifically, swiftly, and continuously, resulting in defined molecular and cellular events. In this review, we will discuss the current understanding of the clearance of apoptotic cells at the molecular level.

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INTRODUCTION

Apoptosis is an essential process that occurs in multicellular organisms to eliminate unwanted cells, such as superfluous cells produced during development, aged cells that have lost their function, cells that can develop into cancer, damaged cells, and cells infected with viruses or bacteria, throughout life¹. Through apoptosis, multicellular organisms can achieve developmental integrity, maintain tissue homeostasis, and protect themselves from the spread of infection². However, inducing cell death of unwanted cells alone cannot accomplish these tasks. The dead cells must eventually be removed, as they can induce inflammation themselves. Removal of apoptotic cells, known as efferocytosis, is the final step of apoptosis³. It is known that hundreds of billions of cells undergo apoptosis in a healthy human body daily. However, apoptotic cells are rarely observed, even in tissues with a high cellular turnover rate⁴. For example, although most developing thymocytes in the thymus undergo apoptosis, apoptotic thymocytes are seldom seen in the thymus because they are swiftly and continuously removed^{5,6}.

Efferocytosis is generally referred to as the phagocytosis of apoptotic cells because it involves the ingestion of extracellular substances⁷. Phagocytosis is the process of taking in extracellular particles larger than 0.5 µm in diameter by cells called phagocytes. In immunology, the term specifically refers to the ingestion and removal of bacteria and other pathogens within membrane-bound vesicles called phagosomes⁸. The common usage of the term phagocytosis for both pathogens and apoptotic cells may be confusing to individuals outside the field, as the immune response induced after phagocytosis of pathogens differs completely from the response after the engulfment of apoptotic cells. Pathogen phagocytosis often triggers proinflammatory responses, while engulfment of apoptotic cells generally induces anti-inflammatory responses or is immunologically silent^{9,10}. Therefore, to avoid confusion, the term efferocytosis, which means “taking to the grave” or “burying,” was proposed instead of phagocytosis of

apoptotic cells and is now used in the field³. Efferocytosis can be divided into four steps: recruitment of phagocytes to apoptotic cells, recognition of apoptotic cells by phagocytes, internalization of apoptotic cells into phagocytes, and degradation of apoptotic cells in phagocytes¹¹. In this review, we will discuss the molecular mechanisms underlying each of these steps in efferocytosis. In addition, calcium signaling holds considerable importance in a wide range of cellular processes, and efferocytosis is no different. In the later part of this review, our focus will be on calcium signaling during efferocytosis and elucidating its molecular-level influence on each individual step of efferocytosis, which has not been previously reviewed.

APOPTOTIC CELL GENERATION AND THE TYPE OF PHAGOCYTES

Our body is made up of ~37 billion cells, and it is estimated that ~300 billion cells undergo apoptosis every day to eliminate superfluous, aged, and damaged cells, which ultimately maintain homeostasis. This is an astonishing number, representing 1% of the cells that make up our body^{10,12,13}. Apoptosis occurs in various sites, especially in areas with a high cellular turnover rate, such as the thymus, bone marrow, mammary gland, and spleen. In the thymus, 95% of thymocytes undergo apoptosis during T-cell development, with only a small number of cells making it through key checkpoints⁶. In the bone marrow, a subset of excess immature B cells survives through a selection process during B cell development¹⁴. The mammary gland is also a site where apoptosis is actively occurring. After lactation, mammary epithelial cells undergo apoptosis^{15,16}. Aged cells in need of replacement also undergo apoptosis. For example, neutrophils, whose lifespan is approximately 24 h, undergo apoptosis after one day. There are ~3000 to 7000 neutrophils in 1 µl of blood, and therefore, at least 18 billion neutrophils undergo apoptosis in an adult body every day^{17,18}.

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Molecular Theories of Cell Life and Death Sungchul Ji, University of Medicine and Dentistry of New Jersey, 1991 Most of the chapters were written on the basis of lectures delivered at the International Colloquium on title held in Piscataway New Jersey May 1986 but some were solicited and submitted as late as mid 1989 The long delay in publication does not diminish the value here in fact some authors

Molecular Theory of the Living Cell Sungchul Ji, 2012-04-05 The book presents the first comprehensive molecular theory of the living cell ever published since the cell doctrine was formulated in 1838 1839 It introduces into cell biology over thirty key concepts principles and laws imported from physics chemistry computer science linguistics semiotics and philosophy The author formulates physically chemically and enzymologically realistic molecular mechanisms to account for basic living processes such as ligand receptor interactions enzymic catalysis force generating mechanisms in molecular motors chromatin remodelling and signal transduction Possible solutions to basic and practical problems facing contemporary biology and biomedical sciences have been suggested including pharmacotherapeutics and personalized medicine

National Library of Medicine Current Catalog National Library of Medicine (U.S.), 1992

Current Catalog National Library of Medicine (U.S.), 1993 First multi year cumulation covers six years 1965 70

Theoretical Information Studies: Information In The World Mark Burgin, Gordana Dodig-crnkovic, 2020-03-24 This is the first attempt to delineate the synthetic field of the theoretical study of information treating information as the basic phenomenon on the fundamental level of the world encompassing nature technology individuals and society The exploration of information is done within Info computational approaches to natural and social phenomena such as Bioinformatics Information Physics Informational Chemistry Computational Physics Cognitive and Social sciences with special emphasis on interdisciplinary crossdisciplinary and transdisciplinary knowledge The book presents results of collaboration across research fields within info computational and info structural frameworks in attempt to better theoretically and conceptually capture the phenomenon of information and its dynamics such as computation and communication as they appear on different levels of organization on different scales and in different contexts

Advances in Chemical Physics: Special Volume in Memory of Ilya Prigogine, Volume 135 Stuart A. Rice, 2007-04-10 This series provides the chemical physics field with a forum for critical authoritative evaluations of advances in every area of the discipline This stand alone special topics volume reports recent advances in electron transfer research with significant up to date chapters by internationally recognized researchers

Information And Complexity Mark Burgin, Cristian S Calude, 2016-11-28 The book is a collection of papers of experts in the fields of information and complexity Information is a basic structure of the world while complexity is a fundamental property of systems and processes There are intrinsic relations between information and complexity The research in information theory the theory of complexity and their interrelations is very active The book will expand knowledge on information complexity and their relations representing the

most recent and advanced studies and achievements in this area The goal of the book is to present the topic from different perspectives mathematical informational philosophical methodological etc *Unifying Themes in Complex Systems* Ali A. Minai, Yaneer Bar-Yam, 2007-08-06 In recent years scientists have applied the principles of complex systems science to increasingly diverse fields The results have been nothing short of remarkable their novel approaches have provided answers to long standing questions in biology ecology physics engineering computer science economics psychology and sociology The Third International Conference on Complex Systems attracted over 400 researchers from around the world The conference aimed to encourage cross fertilization between the many disciplines represented and to deepen our understanding of the properties common to all complex systems **Design and Information in Biology** J. A. Bryant, 2007 Highlighted with individual contributions from eminent specialists these multiauthored volumes combine authority inspiration and state of the art knowledge Both informative and inspiring they are designed to appeal to scientists and interested laypeople alike Volume 2 complements and extends the scope of the first with the biological viewpoint being stressed Following an introductory chapter on design as understood in biology the various aspects of the biological information revolution are addressed Areas discussed include molecular structure the genome development and neural networks A section on information theory provides a link with engineering and the scope is also broadened to include the implications of motion in nature and engineering *Physiological Basis of Aging and Geriatrics* Paola S. Timiras, 2007-08-16 Extensively revised and updated to reflect the current state of knowledge in the study of aging this Fourth Edition offers a complete profile of the aging process at all levels from molecules and cells to demography and evolution Written by international experts in current basic and clinical aging research this text includes aspects of individual comparative and differential aging and discussions of theories and mechanisms of aging This invaluable reference illustrates how bodily systems organs and functions are affected with aging describes how genetic and environmental factors influence age related changes and addresses some of the clinical consequences of these changes for health and longevity Well illustrated with numerous tables and graphs this book presents up to date information from internationally renowned experts in various bio medical fields [A Textbook of Biotechnology Vol-II](#) Rehana Khan, 2007 **Life. Death. Immortality.** Gennadiy Zhegunov, Denys Pogozhykh, 2023-04-29 What are life and death Is it possible to understand their essence and give clear definitions Countless books and articles have been devoted to trying to answer these intriguing questions However there are still no definite and generally accepted answers The intrigue remains And meanwhile human attempts to vanquish death and achieve immortality continue apace This book is an attempt to answer the eternal questions about life and death by analyzing synthesizing and rethinking the known facts that characterize life The material here should be of particular interest as it contains many hypotheses philosophical generalizations and well informed speculations What is most important for life matter energy or information How are individual lives and the phenomenon of life in general related What serves what does the genome serve the cell or does the

cell serve the genome What is the value of life and death Can we become immortal The inquisitive reader will find original answers to these and other exciting questions in the pages of this stimulating book

The Structure of Evolutionary Theory Stephen Jay Gould, 2002-03-21 The world's most revered and eloquent interpreter of evolutionary ideas offers here a work of explanatory force unprecedented in our time a landmark publication both for its historical sweep and for its scientific vision With characteristic attention to detail Stephen Jay Gould first describes the content and discusses the history and origins of the three core commitments of classical Darwinism that natural selection works on organisms not genes or species that it is almost exclusively the mechanism of adaptive evolutionary change and that these changes are incremental not drastic Next he examines the three critiques that currently challenge this classic Darwinian edifice that selection operates on multiple levels from the gene to the group that evolution proceeds by a variety of mechanisms not just natural selection and that causes operating at broader scales including catastrophes have figured prominently in the course of evolution Then in a stunning tour de force that will likely stimulate discussion and debate for decades Gould proposes his own system for integrating these classical commitments and contemporary critiques into a new structure of evolutionary thought In 2001 the Library of Congress named Stephen Jay Gould one of America's eighty three Living Legends people who embody the quintessentially American ideal of individual creativity conviction dedication and exuberance Each of these qualities finds full expression in this peerless work the likes of which the scientific world has not seen and may not see again for well over a century

Life, Death, and Eternity Dr. Kawa Amin, 2024-05-16 Although uncertainty is an inherent part of life it is universally agreed that death as the end of an individual's current known life is inevitable Yet extensive research and careful analysis of scientific literature seems to show that our existence may continue beyond what we currently understand It is possible that we will transition through different stages adapting to new environments and circumstances Therefore the future holds the potential for exciting discoveries and a deeper understanding of what it means to be alive In an academic presentation consultant geriatrician Dr Kawa Amin delves into the fascinating realm of immortality and the attempts throughout history to overcome the inevitability of death While intertwining scientific evidence with philosophy faith and theology Dr Amin delivers a comprehensive qualitative analysis while meticulously considering several dimensions in relation to immortality and clarifying complex concepts such as resurrection life and death Life Death and Eternity combines scientific research with faith and philosophy to provide a deeper understanding of the concept of resurrection and the spiritual aspects of life and death

Processes of Believing: The Acquisition, Maintenance, and Change in Creditions Hans-Ferdinand Angel, Lluís Oviedo, Raymond F. Paloutzian, Anne L.C. Runehov, Rüdiger J. Seitz, 2017-04-13 This volume answers the question Why do we believe what we believe It examines current research on the concept of beliefs and the development in our understanding of the process of believing It takes into account empirical findings in the field of neuroscience regarding the processes that underlie beliefs and discusses the notion that beyond the interactive exploratory

analysis of sensory information from the complex outside world humans engage in an evaluative analysis by which they attribute personal meaning and relevance to the probabilistic representations of objects and events Beliefs exert a strong influence on behaviour decision making and identifying and solving problems Despite their importance beliefs have until recently not been at the centre of scientific interest In fact belief is an ill defined phenomenon From a transdisciplinary perspective the actual approaches to understanding belief seem incompatible as they attempt to highlight such different topics as belief religion belief spirituality belief faith belief knowledge belief attitude belief disbelief belief illusion and believing brain function This situation contradicts the idea that belief is close to pathological phenomena and that it should be eliminated from scientific discussions Rather believing is fundamental for understanding the many problems of every day life In fact the book shows that beliefs are relevant for politics international affairs economy law or religions also in modern societies This book presents the increasing scientific interest in beliefs and believing and reflects the change in focus from the content aspect of belief towards the fluid nature of believing

American Medicine, 1906 *Symbiosis: Cellular, Molecular, Medical and Evolutionary Aspects* Malgorzata Kloc, 2020-12-02 This volume presents a comprehensive overview of the latest developments in symbiosis research It covers molecular organellar cellular immunologic genetic and evolutionary aspects of symbiotic interactions in humans and other model systems The book also highlights new approaches to interdisciplinary research and therapeutic applications Symbiosis refers to any mutually beneficial interaction between different organisms The symbiotic origin of cellular organelles and the exchange of genetic material between hosts and their bacterial and viral symbionts have helped shaped the current diversity of life Recently symbiosis has gained a new level of recognition due to the realization that all organisms function as a holobiome and that any kind of interference with the hosts influences their symbionts and vice versa and can have profound consequences for the survival of both For example in humans the microbiome i e the entirety of all the microorganisms living in association with the intestines oral cavity urogenital system and skin is partially inherited during pregnancy and influences the maturation and functioning of the human immune system protects against pathogens and regulates metabolism Symbionts also regulate cancer development wound healing tissue regeneration and stem cell function The medical applications of this new realization are vast and largely uncharted The composition and robustness of human symbionts could make them a valuable diagnostic tool for predicting impending diseases and the manipulation of symbionts could yield new strategies for the treatment of incurable diseases

In the Sanctuary Albert Van der Naillen, 1895 *Apoptosis* Sidartha Ray, 1997-07 **Molecular Cytology V2** Jean Brachet, 2012-12-02 *Molecular Cytology Volume 2 Cell Interactions* deals with the morphology and biochemistry of the cell with emphasis on the more dynamic aspects of cytology It looks at gene transfer in somatic cells nucleocytoplasmic interactions in oocytes and eggs and cell differentiation transformation malignancy aging and death Organized into four chapters this volume begins with a discussion of nucleocytoplasmic interactions in somatic cells and unicellular organisms

The next chapter examines the experimental interventions at early stages in the egg cytoplasm with reference to *Xenopus* oocytes as well as oogenesis the structure and composition of the cytoplasm and the nucleus fertilization of sea urchin eggs and the nuclear determinants of early embryogenic development Additionally a chapter explains the mechanisms underlying cell senescence arrest of cell growth and cell death the mechanisms of cell differentiation as the normal outcome of embryonic development the morphological and biochemical changes that occur in cells when they become senescent and the metastasis of cancer cells The book concludes with a chapter that presents a few general ideas about biochemical cytology This book is a valuable reference for cell biologists biochemists cytologists advanced students research workers and laypersons interested in learning the fundamentals of descriptive cytology biochemistry embryology genetics and molecular biology

The Top Books of the Year Molecular Theories Of Cell Life Death The year 2023 has witnessed a remarkable surge in literary brilliance, with numerous compelling novels enthralling the hearts of readers worldwide. Lets delve into the realm of top-selling books, exploring the fascinating narratives that have charmed audiences this year. The Must-Read : Colleen Hoover "It Ends with Us" This heartfelt tale of love, loss, and resilience has captivated readers with its raw and emotional exploration of domestic abuse. Hoover masterfully weaves a story of hope and healing, reminding us that even in the darkest of times, the human spirit can succeed. Uncover the Best : Taylor Jenkins Reids "The Seven Husbands of Evelyn Hugo" This spellbinding historical fiction novel unravels the life of Evelyn Hugo, a Hollywood icon who defies expectations and societal norms to pursue her dreams. Reids captivating storytelling and compelling characters transport readers to a bygone era, immersing them in a world of glamour, ambition, and self-discovery. Discover the Magic : Delia Owens "Where the Crawdads Sing" This captivating coming-of-age story follows Kya Clark, a young woman who grows up alone in the marshes of North Carolina. Owens crafts a tale of resilience, survival, and the transformative power of nature, captivating readers with its evocative prose and mesmerizing setting. These popular novels represent just a fraction of the literary treasures that have emerged in 2023. Whether you seek tales of romance, adventure, or personal growth, the world of literature offers an abundance of engaging stories waiting to be discovered. The novel begins with Richard Papen, a bright but troubled young man, arriving at Hampden College. Richard is immediately drawn to the group of students who call themselves the Classics Club. The club is led by Henry Winter, a brilliant and charismatic young man. Henry is obsessed with Greek mythology and philosophy, and he quickly draws Richard into his world. The other members of the Classics Club are equally as fascinating. Bunny Corcoran is a wealthy and spoiled young man who is always looking for a good time. Charles Tavis is a quiet and reserved young man who is deeply in love with Henry. Camilla Macaulay is a beautiful and intelligent young woman who is drawn to the power and danger of the Classics Club. The students are all deeply in love with Morrow, and they are willing to do anything to please him. Morrow is a complex and mysterious figure, and he seems to be manipulating the students for his own purposes. As the students become more involved with Morrow, they begin to commit increasingly dangerous acts. The Secret History is a brilliant and gripping novel that will keep you speculating until the very end. The novel is a warning tale about the dangers of obsession and the power of evil.

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