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Development Missing in Metastasis Mediates Directional Sensing During Guided Cell Migration Studies on Cell Migration in Hydra Single Cancer Cell Migration Mechanisms in Micromolded 3D Collagenmicrostracks The Cytoskeleton in T Cell Migration and Activation Modelling Cell Migration in 3D Micro-environments Role of Cell Protrusions During Cell Migration in Vivo Tracking Stem Cell Migration in Pathologically Challenged Hearts Using GFP Tagged Stem Cells Designing Tools for Quantitative, Single-cell Analysis of Mammalian Cell Migration Visualizing Cell Migration in Situ Effects of PTENB on Cell Migration in Gastrulating Zebrafish Embryos Collective Cell Migration in Embryogenesis as a Wetting Phenomenon Governed by Hydrodynamics of Active Liquids Characterization and Modulation of Precursor Cell Migration in Forebrain Slice Cultures Directing Cell Migration by Dynamic Control of Laminar Streams Neural Crest Cell Migration in Chicken and Mouse Embryos Experimental Studies of Primordial Germ Cell Migration in Xenopus Laevis

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Cell migration is a highly complex process which involves several compartments of the cell, including surface receptors, signalling elements and the cytoskeleton. It plays an essential role in embryogenesis, wound healing and inflammatory responses, and a dysregulation of cell movement can cause pathological states such as developmental defects, chronic inflammation, cancer invasion and metastasis. Covering extracellular regulatory signals and intracellular signal transduction pathways as well as the molecular mechanisms of migration in stem cells, leukocytes and tumor cells in the adult human organism, this book summarizes the current state of knowledge about cell migration. In the first part, the major aspects of different migratory cells in health and disease are covered, with special emphasis on T lymphocytes. The second part provides a comprehensive overview of the principal molecular mechanisms of migration such as adhesion receptors, cytoskeletal rearrangements and locomotor force generation, which, together, can be referred to as a cell's

'migrosome'.With contributions by eminent international scientists from different disciplines this book will serve as a valuable resource not only for researchers in cell biology, immunology and oncology, but also for clinicians who wish to learn more about the role of migratory processes in health and disease. Directed cell migration is essential in morphogenesis, regeneration and pathological conditions. Of particular interest is collective cell migration, in which groups of cells migrate in a coherent and coordinated manner while remaining in contact with one another. In vivo, migratory cells are exposed to a complex signalling milieu that directs their migration; however, how cells prioritize and translate these cues into directed migration is not fully understood. In vitro systems simplify the systematic study of the effect of guidance cues in cell migration by providing increased flexibility to manipulate these cues. This work describes novel in vitro tools and analytical metrics for the analysis of collective cell migration and utilizes them to probe the effects of combinations of guidance cues on cell migration. This includes an improved analytical methodology for the classical scratch wound assay in which individual cell migratory behaviour is characterised with high spatial and temporal resolution; a novel metric designed specifically for measuring cell-cell coordination during collective cell migration is also suggested. The tools described in this work were used to investigate the mechanism for propagation of guidance cues in epithelial cells. Migration guidance from topographical features was found to propagate to cells not directly exposed to them through mechanical interactions

between cells not mediated by cell-cell junctions or intracellular tension, but arising rather from volume exclusion. Additionally, the tools proposed were also used to characterise the effect of modifying the expression of the Planar Cell Polarity signalling protein Vangl1 on the collective migration of endothelial cells. Vangl1 expression was found to influence the migration of endothelial cells by modulating directedness in the scratch wound assay, but not in a variety of other migration assays, implying damage signals from the scratch were necessary for a Vangl1 migration phenotype. The work presented here is a first step to an improved experimental and analytical pipeline to understand the effect of combinations of guidance cues on directed collective cell migration. Interactions of cells with their chemical microenvironments are critical to many polarized processes, including differentiation, migration, and pathfinding. To investigate such cellular events, tools are required that can rapidly reshape the microscopic chemical landscapes presented to cultured cells. Existing chemical dosing technologies rely on use of pre-fabricated chemical gradients, thus offering static cell-reagent interactions. Such interactions are particularly limiting for studying migration and chemotaxis, during which cells undergo rapid changes in position, morphology, and intracellular signaling. This dissertation describes the use of laminar streams, containing cellular effector molecules, for precise delivery of effectors to selected subcellular regions. In this approach, cells are grown on an ultra-thin polymer membrane that serves as a barrier to an underlying reagent reservoir.

By using a tightly-focused pulsed laser beam, micron-diameter pores can be ablated in the membrane upstream of desired subcellular dosing sites. Emerging through these pores are well-defined reagent streams, which dose the targeted regions. Multiple pores can be ablated to allow parallel delivery of effector molecules to an arbitrary number of targets. Importantly, both the directionality and the composition of the reagent streams can be changed on-the-fly under a second to present dynamically changing chemical signals to cells undergoing migration. These methods are applied to study the chemotactic responses of neutrophil precursor cells. The subcellular localization of the chemical signals emerging through pores is found to influence the morphological evolution of these motile cells as they polarize and migrate in response to rapidly altered effector gradients. Mammalian cell migration guides many important processes within the human body, from physiological activities such as embryonic development, immune cell trafficking, and wound healing to pathological conditions like cancer metastasis, multiple sclerosis, and rheumatoid arthritis. Cell migration is a highly complex, tightly regulated biological process that is dependent on the cellular microenvironment: composition, rigidity, and topography of the extracellular matrix, as well as chemical cues, can modulate migration by altering cell speed, direction, and persistence. Conventional techniques for studying cell migration in response to chemical cues (e.g., scratch, micropipette, and Transwell assays) are limited in their ability to 1) maintain a stable concentration gradient and 2) allow longitudinal, quantitative, single-

cell analyses of cell migration. The first limitation makes these techniques inappropriate for long-term studies of chemotaxis, which require a stable concentration gradient. The second limitation can cause data to be misinterpreted, as increases in proliferation (chemoproliferation) and speed (chemokinesis) in response to soluble cues can be misconstrued as directed migration (chemotaxis). To address these limitations, we developed a shear-free, microfluidic gradient generator to study cell migration. We used our microfluidic device to study the impact of soluble and insoluble cues on mammalian cell migration in two distinct applications: 1) chemotaxis of murine mast cells to kit ligand (KL) and 2) chemotaxis and chemokinesis of primary human myoblasts to basic fibroblast growth factor (bFGF). These applications are important for understanding the complex responses required for effective wound healing and muscle regeneration, respectively. In the first application, we found that KL caused a complex chemotactic response in mast cells, invoking chemoattraction at high concentrations and chemorepulsion at low concentrations. While the ability for a single cytokine to induce both attraction and repulsion is not unknown, this is the first reported observation of a bimodal chemotactic response mediated by a receptor tyrosine kinase (RTK). In the second application, we studied the impact of the underlying extracellular matrix (ECM) on the bFGF-stimulated responses (i.e., chemoproliferation, chemokinesis, and chemotaxis) of primary human myoblasts. We revealed that while the underlying ECM substrate did affect chemoproliferation, it did not have a significant effect on chemokinesis or chemotaxis.

Although laminin promoted significantly faster migration speeds than fibronectin or collagen without bFGF stimulation, the addition of bFGF increased migration speed by equal amounts on all substrates, indicating an additive, not synergistic effect. In contrast to the robust chemokinesis observed, our studies revealed weak chemoattraction in myoblasts exposed to a bFGF gradient. Together, these data indicate that changes in the muscle ECM, which can occur as a result of aging or disease, may impact muscle regeneration by altering proliferation and migration. The ECM substrates used in the microfluidic studies described above are all naturally derived materials (e.g., laminin). Naturally derived biomaterials exhibit high batch-to-batch variation and material properties (e.g., stiffness and ligand density) cannot be independently tuned. To study the effects of substrate stiffness and topography on cell behavior, without altering the density of cell-adhesive ligands, we used an engineered extracellular matrix (eECM) comprised of elastin-like proteins (ELP) and cell-adhesive domains containing the RGD motif found in fibronectin. Soft lithography techniques were used to pattern the ELP substrates to create a grooved topography. We found that patterned substrates induced cell alignment and increased migration speed. Altering the ratio of ELP and crosslinker increased substrate stiffness and, consequently, resulted in faster cell migration rates. Myoblast migration is a key step in muscle regeneration, and culturing cells for 10 days on ELP substrates resulted in the formation of multi-nucleated myotubes that expressed [alpha]-actinin (a marker of mature muscle).

Many processes essential for human health are governed by a cell's ability to efficiently migrate within the body, making mammalian cell migration an essential topic for scientific investigation. We have developed two novel in vitro platforms that enable longitudinal, quantitative, single-cell analyses of mammalian cell migration in response to the microenvironment. These tools allowed us to deconstruct complex migratory behaviors in response to soluble (i.e, chemical) and insoluble (i.e., substrate composition, topography, and stiffness) cues that have important repercussions for wound healing and muscle regeneration. Understanding the mechanisms used to regulate mammalian cell migration holds the promise of new therapeutic approaches for disease treatments, cell transplantation therapies, and the development of artificial tissues. Viscoelasticity and Collective Cell Migration: An Interdisciplinary Perspective Across Levels of Organization focuses on the main viscoelastic parameters formulated based on multiscale constitutive modeling and how to measure these rheological parameters based on existent micro-devices such as micro-rheology and micro-elastography. The book sheds light on inter-relationships across viscoelasticity scales, an essential step for understanding various biomedical processes such as morphogenesis, wound healing and cancers invasion. Cumulative effects of structural changes at subcellular and cellular levels influence viscoelasticity at a supracellular level are also covered, providing valuable insights for biologists, physicists, engineers, students and researchers in the field of developmental biology. As this is a complex

multidisciplinary field, perspectives are included from experts in biology, biochemistry, biomedicine, biophysics and biorheology. Readers will gain a deeper understanding of the complex dynamics that represent challenges and the necessity for further development in the field. Discusses the biological/biochemical mechanisms of collective cell migration Covers the inter-relation between collective cell migration and viscoelasticity by proposing rheological parameters Contains critical consideration of various experimental techniques that are suitable to measure these parameters This volume covers various assays and techniques that have been developed to study and characterize the cell migration in vitro, ex vivo, and in vivo. The chapters in this book present readers with the latest protocols to observe, quantify, and control cell migration. Some of the topics explored in this book are: migration in confined environments, microfluidic devices, optogenetics, chemotaxis, electrotaxis, detection of migrasomes, migration of Q cells in Caenorhabditis elegans, of Drosophila macrophages, optogenetics of cell migration, intravital imaging. Written in the highly successful Methods in Molecular Biology series format, chapters include introductions to their respective topics, lists of the necessary materials and reagents, step-by-step, readily reproducible laboratory protocols, and tips on troubleshooting and avoiding known pitfalls. Cutting-edge and comprehensive, Cell Migration: Methods and Protocols is a valuable resource for anyone interested in learning more about this expanding field.

This volume covers various assays and techniques that have been developed to study and characterize the cell migration in vitro, ex vivo, and in vivo. The chapters in this book present readers with the latest protocols to observe, quantify, and control cell migration. Some of the topics explored in this book are: migration in confined environments, microfluidic devices, optogenetics, chemotaxis, electrotaxis, detection of migrasomes, migration of Q cells in Caenorhabditis elegans, of Drosophila macrophages, optogenetics of cell migration, intravital imaging. Written in the highly successful Methods in Molecular Biology series format, chapters include introductions to their respective topics, lists of the necessary materials and reagents, step-by-step, readily reproducible laboratory protocols, and tips on troubleshooting and avoiding known pitfalls. Cutting edge and comprehensive, Cell Migration: Methods and Protocols is a valuable resource for anyone interested in learning more about this expanding field. One of the earliest steps of cancer metastasis is cellular migration through the surrounding collagenous stromal extracellular matrix (ECM) after dissemination from the primary tumor. The stroma through which cancer cells navigate is a complex network of fiber architectures. It is known that in vivo, some metastatic cancer cells migrate through pre-existing tracks within the collagenous ECM matrix. A subset of cells termed as "leader" cells create invasion paths (known as "microtracks") by degrading and remodeling the surrounding matrix using proteolytic enzymes. "Leader" cells first migrate through the stroma

leaving "tube-like" microtracks within the ECM of the stroma and other metastatic "follower" cells utilize these pre-existing microtracks as 'highways' to escape the primary tumor without any proteolytic activities. Despite numerous studies, the mechanisms modulating cancer cell migration through the stroma and particularly through these microtracks still remain unclear. In general, the process of cellular migration is governed by a balance between the molecular mechanisms regulating migration signaling and the physiological cues posed by the neighboring tumor microenvironment. However, much less is known about how the "follower" cancer cells migrate through these confined in vivo microtracks within the ECM. In this thesis, we utilized microfabrication technique to recreate in vitro collagen microtracks and recapitulate confined non-proteolytic metastatic cell migration to study the behavior of "follower" cells. Our results indicate that cell adhesion and polarization facilitate directional migration in in vitro collagen microtracks. Additionally, cellular focal adhesion dynamics and traction stresses dictate cell migration behavior in confined and partially confined spaces within the microtracks. Moreover, cell compliance and energy requirement impact cell migration choices in confined microtracks. These results help us to define how intracellular signals and extracellular microenvironments direct single cell migration in microtracks. Our findings could potentially lead to a targeted therapeutic approach to inhibit cell migration and ultimately cancer metastasis. While directed cellular migration facilitates the coordinated

movement of cells throughout development, in wound repair, and during an immune response, the precise mechanisms regulating such migration in vivo remain inadequately understood. Missing in Metastasis (MIM) is a defining member of the I-BAR subfamily of lipid binding, actin cytoskeletal regulators whose levels are altered in a number of cancers. Here I provide the first genetic evidence that I-BAR proteins regulate directed cell migration in vivo. MIM regulates the directional migration of several cell types responding to a number of different guidance cues. While regulating the directionality of migrating cells has been demonstrated in vitro, this role of an I-BAR protein in vivo was not previously observed. I demonstrate in these studies that Drosophila MIM (DMIM) is required for border cell migration, with loss of dmim function resulting in a lack of directional movement by the border cell cluster. In vivo endocytosis assays combined with genetic analyses demonstrate that the dmim product regulates directed cell movement by inhibiting endocytosis and antagonizing the activities of the endophilin/CD2AP/cortactin complex in these cells. These studies demonstrate that competition between BAR family members for pro-endocytic components underlies a directional sensing mechanism during guided cell migration. Cell Migration matches nearly all research areas in cell and developmental biology, genetics, and biomedicine. The field shows radical progress powered by the combination of new genomic tools, cell labeling techniques and the incorporation of new model systems. This is the first book to comprehensively cover cell migration from the

identification of molecular mechanisms to the understanding of certain pathological disorders and cancer development. Cell migration plays an important role during development and in many physiological and pathological processes, from wound healing to cancer. This edited volume presents a collection of contributions meant to illustrate the state of the art on this topic from an interdisciplinary perspective. Readers will find a detailed discussion of the properties of individual and collective cell migration, including the associated biochemical regulation and important biophysical and biomechanical aspects. The book includes information on the latest experimental techniques employed to study cell migration, from microfluidics to traction force microscopy, as well as the latest theoretical and computational models used to interpret the experimental data. Finally, the role of cell migration in cancer and in development is also reviewed. The contents of this work should appeal to students and researchers in biology and biophysics who want to get up to date on the latest interdisciplinary development in this broad field of research. The chapters are written in a self-contained form and can also be used as individual articles. Migration of cancer cells from the primary organ to distant sites is critical to the development of malignant metastasis. This is partly dependant on the various chemical factors present in the blood serum. Cell motility studies using conventional Boyden chamber assays require high volumes of reagents. The measurement provides only an end-point result and time-lapse study of the cell deformation and migration cannot be

performed. We have designed and evaluated a poly-dimethylsiloxane (PDMS) microfluidic device in order to study cell migration in the presence of gradients. Photolithography and soft lithography processes were used to fabricate the PDMS devices from the negative photoresist (SU-8) molds. The devices were then soft bonded to standard tissue culture plates. Conventional tissue culture techniques were employed and the cell culture environment was not compromised. Using our proposed designs, we can obtain cell number, location, migration rate and time taken for cells to migrate in response to chemoattractants. We propose two different methods to study cell migration in response to chemokine gradients. In the first method, the chemokines were continuously infused into the microfluidic system through a system of microchannels creating a sustainable gradient and migration of cells in this gradient environment was monitored. This device consists of three inlets and one outlet. The inlets were used to introduce chemokines along with culture media and cells in suspension. Time lapse video micrographs were used to determine concentration gradients and cell response in the gradients. The channels were designed to be 100 ıumı wide and 100 ıumı in height with two mixing stages leading into the outlet. The outlet was designed to be 900 ıumı wide and 100 ıumı in height. In the second method, the gradient was formed by diffusion over time in the microchannels after the chemoattractants were introduced. The device consists of two separate identical chambers that are interconnected by identical microchannels that are 10 ıumı high, 25 ıumı wide and 1 mm long. One

chamber contains cells whose migration characteristics are to be evaluated, while the other chamber contains media with chemoattractants towards which the response of the cells needs to be analyzed. Timelapse photography was used to determine the migration of cells in the microchannels and obtain information regarding migration rate, cell number and identify migration potential of various stimulants. Two such designs were tested. The first one had four reservoirs, two each for cell seeding and addition of chemoattractants. This reduced chemokine consumption compared to conventional assays however, we aimed to further reduce the volume of reagents required. The third design had only one reservoir each for cell seeding and addition of chemoattractants. Several cell lines were tested against various factors. Normal human epithelial prostate (HPV-7) cells were tested against growth factors. Similarly, prostate cancer (PC-3) cells, lung metastasized prostate cancer cells (PC-3-ML), breast cancer cells (MDA-MB-231), normal human mesangial (HMC) cells, kidney cancer (CaKi-2) cells were all tested against several antibodies and ionic chemicals. The migration rate, distance and cell numbers for each case were determined. Due to the ability of the microfluidic platform to mimic physiological dimensions and provide information regarding cell migration, we have called this platform as MiMiCTM standing for Microfluidic assay for Migration of Cells. This platform is cost effective and relies on very small volumes of reagents. It can maintain stable chemokine gradients in the channels, allow real-time quantitative study of cell migration and provide information about

cellular dynamics and help in biomechanical analysis. The results demonstrate the utility of this microfluidic device as a platform to study cancer cell migration and point to potential applications in the identification of specific chemokine agents and drugs targeting cell migration. It also has the potential to be a complementary technique to Prostate specific antigen (PSA), that is used in Prostate cancer diagnosis. The device also allows high throughput assays and real time observation. It is our understanding that these techniques have not all been incorporated in a single device until now. Cell migration is a key component of many biological processes including embryonic development, immune responses, wound healing, organ regeneration, and cancer cell metastasis, thus making it an exciting and crucial field of study. The aim of Cell Migration: Developmental Methods and Protocols, Second Edition is to bring together a wide range of these techniques from the more basic migration assays, which are still the foundation of many cell migration studies, to state-of-the-art techniques and recent technical advances. Divided into three convenient parts, the volume begins with a number of basic in vitro migration assays including measurements of wound healing, cell scattering, invasion, and chemotaxis, as well as more complex measurements of transendothelial migration, the use of microfluidic chambers, and imaging cell migration in 3D. It continues with procedures for the imaging and measurement of cell migration in vivo including protocols for the use of chick, drosophila, and zebrafish embryos, and methods to measure metastatic spread and angiogenesis in

mice, then concludes with a vital section on emerging techniques in the cell migration field including the use of TIRF, FRAP, and FRET microscopy. Written in the highly successful Methods in Molecular BiologyTM series format, chapters include introductions to their respective topics, lists of the necessary materials and reagents, step-by-step, readily reproducible laboratory protocols, and notes from the experts on troubleshooting and avoiding known pitfalls. Comprehensive and up-to-date, Cell Migration: Developmental Methods and Protocols, Second Edition provides a comprehensive catalogue of techniques for the study of cell migration that can be used as a useful reference source for any researcher who wishes to explore this significant area of cell biology. The migration of stem cells has been found to be critical during early development for the organization of the embryonic body as well as during adult life with tissue homeostasis and regeneration of organ function. Due to the low frequency of these cells in vivo, problems in identifying and prospectively purifying tissue specific stem cells near homogeneity, and, most importantly, a lack of adequate technologies and protocols to study stem cell migration in vivo, this vital research has been quite difficult until recently. In Stem Cell Migration: Methods and Protocols, experts in the field compile and highlight the standard and novel techniques that allow the studying of the migration of stem cells in one succinct manual. Including protocols on germ, neuronal, and hematopoietic stem cells, during development and adulthood with a clear emphasis on in vivo technologies, the volume also extends its coverage to in vitro approaches

toward several developmentally-conserved signaling pathways. Written in the highly successful Methods in Molecular BiologyTM series format, chapters include introductions to their respective topics, lists of the necessary materials and reagents, step-by-step, readily reproducible laboratory protocols, and tips on troubleshooting and avoiding known pitfalls. Practical and convenient, Stem Cell Migration: Methods and Protocols provides key, state-of the art information on experimental techniques for studying stem cell migration both at a cellular and molecular level in development, regeneration, and disease. During development, cells are generated at specific locations within the embryo and then migrate into their destinations. At their destinations, they assemble together through cell adhesions, eventually leading to the formation of tissues and organs. In some cases, orchestration of cell adhesion and migration produces the global movement of cell groups, called collective cell migration, which is also required for the development of basic tissue structures such as spheres, clusters, and vesicles in the morphogenetic processes of development. Therefore, individual regulation and orchestration of cell adhesion and migration are quite important for appropriate tissue/organ formation during development. However, how cell adhesion and migration are regulated, and orchestrated during development? How cell adhesion and migration affects tissue formation during development? To answer these questions, we assembled several review and research articles in this eBook. By assembling these articles, we could explore the presence of core

regulatory mechanisms and deepen the current understanding of cell adhesion and migration during the development of multicellular organisms. This book covers multi-scale biomechanics for oncology, ranging from cells and tissues to whole organ. Topics covered include, but not limited to, biomaterials in mechano-oncology, non-invasive imaging techniques, mechanical models of cell migration, cancer cell mechanics, and platelet-based drug delivery for cancer applications. This is an ideal book for graduate students, biomedical engineers, and researchers in the field of mechanobiology and oncology. This book also: Describes how mechanical properties of cancer cells, the extracellular matrix, tumor microenvironment and immuno-editing, and fluid flow dynamics contribute to tumor progression and the metastatic process Provides the latest research on non-invasive imaging, including traction force microscopy and brillouin confocal microscopy Includes insight into NCIs' role in supporting biomechanics in oncology research Details how biomaterials in mechano-oncology can be used as a means to tune materials to study cancer

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