

Ilya Levental, Ph.D.

CURRICULUM VITAE AND BIBLIOGRAPHY

August 2020

PRESENT TITLE: Associate Professor of Molecular Physiology and Biological Physics
University of Virginia

ADDRESS: Pinn Hall Rm 4011, 1340 Pefferson Park Ave, Charlottesville, VA 22908

CITIZENSHIP: USA

UNDERGRADUATE EDUCATION:

B.S. Chemical Engineering (2003) - Georgia Institute of Technology

GRADUATE EDUCATION:

Ph. D. Bioengineering (2008) - University of Pennsylvania (Advisor: Dr. Paul Janmey)

POSTGRADUATE TRAINING:

Postdoctoral Fellowship (2008-2012) - Max Planck Institute of Molecular Cell Biology and Genetics (Dresden, Germany) - Laboratory of Prof. Kai Simons

ACADEMIC APPOINTMENTS:

Associate Professor, 2020-present

Department of Molecular Physiology and Biological Physics, University of Virginia
Faculty, 2020 - present

Biomedical Sciences Graduate Program, University of Virginia

Associate Professor (with tenure), 2018-2020

Assistant Professor, 2012-2018

Department of Integrative Biology and Pharmacology, McGovern Medical School

Faculty member of Biochemistry and Cell Biology grad program, 2017 – 2020

Faculty member of Cell and Regulatory Biology grad program, 2012 – 2017

Graduate School of Biomedical Science

University of Texas Health Science Center at Houston

PROFESSIONAL ORGANIZATIONS:

Biophysical Society, 2012 – Present

American Society for Cell Biology, 2014 – Present

American Society for Biochemistry and Molecular Biology, 2012 – 2014

HONORS AND AWARDS:

2020 Dean's Excellence in Teaching Award (UTHealth Medical School)

2019 Biochemistry and Cell Biology Distinguished Faculty Award (Graduate School of Biomedical Sciences)

2018 Visiting Professor – Friedrich Alexander University (Erlangen, Germany)

2017 T.C. Hsu Endowed Faculty Research Award (Graduate School of Biomedical Sciences)

2016 Dean's Excellence in Teaching Award

2012-2016 New Scholar Recruitment Award - Cancer Prevention and Research Institute of Texas (CPRIT)
2008-2010 (*postdoc*) Humboldt Foundation Postdoctoral Fellowship (2008-2010)
2004-2006 (*graduate*) NIH Institute for Medicine and Engineering Cardiovascular Bioengineering Training Grant
1998-2003 (*undergraduate*) Jack Parker Scholarship; HOPE Scholarship; Undergraduate Research Scholarship; University President's Undergraduate Research Award; Dean's List

EDITORIAL SERVICE:

Biophysical Journal (Editorial Board)
Biochimica et Biophysica Acta (BBA) – Biomembranes (Editorial Board)
Chemistry and Physics of Lipids (Editorial Board)
ScienceMatters (Editorial Board)
Advances in Biomembranes and Lipid Self-Assembly (Editorial Board)

Ad hoc reviewer

PNAS (10x), *Nature* (2x), *Nature Chemical Biology*, *Biophysical Journal* (32x), *J Am Chem Soc* (3x), *BBA Biomembranes* (12x), *J Cell Biol* (4x), *Soft Matter* (10x), *Nature Communications* (7x), *eLife* (5x), *Nature Methods* (2x), *Science Advances* (2x), *Angewandte Chemie*, *Nature Reviews Drug Discovery*, *J Biol Chem*, *FASEB Journal*, *ACS Central Science*, *Biochemistry*, *Biomaterials* (2x), *Molecular Biology of the Cell* (3x), *J Phys Chem B* (2x), *J Phys Chem Letters* (2x), *Chemistry and Physics of Lipids* (2x), *PLOS one* (3x), *Trends in Cell Biol*, *J Lipid Res*, *J Royal Soc Interf*, *Royal Soc Open Sci*, *Molecular Biosystems*, *Cell Reports*, *Chem Rev*, *FEBS Letters*, *Langmuir* (2x), *J Proteomics*, *Scientific Reports*, *Neurochemistry International*, *JoVE*, *ChemBioChem*, *Advanced Materials*, *Nucleic Acid Research*, *J Molecular Biology*, *J Membrane Biology* (2x), *Oncotarget*, *Database*, *ReviewCommons*

SERVICE ON GRANT REVIEW PANELS, STUDY SECTIONS, COMMITTEES:

2019-present NIH study section Biochemistry and Biophysics of Membranes (permanent)
2020 Wellcome Trust
2020 Human Frontiers Science Program
2019 NSF *ad hoc* reviewer (Division of Molecular and Cell Biology)
2018 & 2015 NIH study section Biochemistry and Biophysics of Membranes (*ad hoc*)
2018 John S Dunn Foundation
2017 NSF panel on Lipid and Membrane Chemistry (Division of Chemistry)
2016 National Science Centre Poland
2014 NIH CSR Early Career Reviewer program
2014 Swiss National Science Foundation (*ad hoc* mail review)
2013 US Army (*ad hoc* mail review)
2013 Israeli Science Foundation (*ad hoc* mail review)

SERVICE ON UNIVERSITY COMMITTEES:

Medical School

2019-2020 Graduate Student Education Committee
2014-2020 Medical School Faculty Senate
2014-2020 Medical School Research Committee
2015 Collaborative Workshop organizer (Biology of Cellular Membranes)

UTHealth Department of Integrative Biology and Pharmacology
2018-present IBP Faculty Search Committee

2015-2017 IBP seminar planning committee
2019-present Microscopy Core Advisory Committee

SERVICE ON GRADUATE SCHOOL COMMITTEES:

2018-present Co-Director of Biochemistry and Cell Biology (BCB) Graduate Program
2018-present Graduate School Executive Committee
2018-2019 Chair of Academic Standards Committee
2017-present Academic Standards Committee
2017-2018 BCB Program Examination Committee
2015-2016 CRB admissions committee
2014-2016 CRB recruitment committee

THESIS COMMITTEES:

2019-present PhD advisory committee for Joseph Barnes (Hu)
2019-present PhD advisory committee for Nabina Paudyal (Jayaraman)
2019-present PhD advisory committee for Ahmed Gad (Ahmed, Baylor)
2018-present PhD advisory committee for Celso Catumbela (Darkoh)
2018-present PhD advisory committee for Vinay Nair (Gorfe)
2018-present PhD advisory committee for Savannah West (Boehning)
2017-present PhD advisory committee for Ryan Durham (Jayaraman)
2017-2018 PhD advisory committee for Kristen Clemons (Venkatachalam)
2016-present PhD advisory committee external member for Swapnil Baral (Lyman, UDelaware)
2015-2019 PhD advisory committee for Jessica Jie Chen (Boehning)
2015-present PhD advisory committee for Barbara Diaz-Rohrer (mentor)
2015-2019 PhD advisory committee for Kimiya Memarzadeh (Bean)
2015-present PhD advisory committee for Jian Xiong (Zhu)

QUALIFYING EXAM COMMITTEES:

2018 Candidacy exam committee for Tristen Tellman
2018 Candidacy exam committee for Ryan Durham
2018 Candidacy exam committee for Ashabari Mukherjee
2018 Candidacy exam committee for Vinay Nair
2018 Candidacy exam committee for Walaa Kattan
2018 Candidacy exam committee for Nick Karagas
2015 Candidacy exam committee for Lingxiao Tan

SERVICE IN THE COMMUNITY:

2019-present Publications committee of Biophysical Society
2018 Chair of Biophysical Society Subgroup on Membrane Structure and Function
2016 Co-organizer of GCC Symposium on Membrane Biophysics
2016 Sponsor for Rice undergraduate (Skinkle) for independent research course
2017-present Presenting on “science as a tool” for area high schools
2015&2018 Lecturer for Rice Summer Science Academy for Texas AP Biology teachers
2014-present Faculty member of Training in Pharmacological Sciences Program
2014-present Faculty member of Houston Area Molecular Biophysics Program
2014 Examiner for thesis defense of Dr David Slachower (University of Pennsylvania)
2013 Sponsor for Rice undergraduate (Herrmann) for independent research course
2013 Presentation in GSBS on “Pathway to the Professoriat”

SPONSORSHIP OF CANDIDATES FOR POST-GRADUATE DEGREES:

2020-present Luis Real-Hernandez – BIMS / GSBS PhD student

- 2018-present Jessica Symons - GSBS PhD student (co-mentor)
- Houston Area Molecular Biophysics Training Grant (2019-2022)
 - American Legion Auxiliary Fellowship in Cancer Research (2019-2021)
 - Linda M. Wells GSBS Outreach Award (2020)
- 2014-2019 Barbara Diaz-Rohrer - GSBS PhD student
- Gordon Research Conference - Carl Storm Underrepresented Minority Fellowship (2019)
 - John J. Kopchick Fellowship
 - Antje Wuelfrath Gee and Harry Gee, Jr. Family Legacy Scholarship
 - Marine Biology Laboratory Physiology Course (2015)
 - minisymposium presentations at ASCB (2016 and 2019) and Biophysical Soc meetings
 - travel awards from ASCB each year from 2014-2018
 - travel awards from Biophysical Society 2017-2018
- 2015-2017 Eric Malmberg - GSBS Masters thesis

SPONSORSHIP OF POSTDOCTORAL FELLOWS:

- 2020-present Dr. Carolyn Shurer
- 2018-present Dr. Milka Doktorova
- Awarded F32 from NIGMS (2019-2022)
 - symposium presentation at Biophysical Society national meeting 2020
- 2018-present Dr. Ivan Castello-Serrano
- minisymposium presentation at ASCB national meeting 2019
- 2017-present Dr. Hong-Yin Wang
- symposium presentation at Biophysical Society national meeting 2020
- 2014-2019 Dr. Joseph Lorent (**Assistant Professor at Utrecht University**)
- minisymposium presentation at Biophysical Society national meeting 2017 and 2018
 - travel award from Biophysical Society 2018
 - UTH President's Research Award 2017
- 2014-2018 Dr. Xubo Lin (**Associate Professor at Beihang University**)
- travel award from Biophysical Society 2015
- 2013-2018 Dr. Lakshmi Ganesan (director of science communication at NCBS Bangalore)
- 2014-2017 Dr. Karolina Tulodziecka (Product Manager at Cellis Biotech)
- 2013-2014 Dr. Kevin Spring

SPONSORSHIP OF SUMMER RESEARCH STUDENTS AND UNDERGRADUATES:

- 2015-2019 Allison Skinkle (Rice U, currently PhD student UNC)
- first author publication in *Biophysical Journal*
 - co-author on 7 publications
 - travel awards to Biophysical Society and ASCB National Meetings
 - diversity supplement to R01
- 2017 Kristine McAndrews (MS1 Summer Researcher)
- 2015-2016 Gia Rivera-Longsworth (Rice University; current PhD student at Columbia U)
- 2013-2015 Emily Stockenbojer (Rice University)
- 2013-2014 Beatrice Herrmann (Rice University; current PhD student at U Penn)
- 2013 Alyce Chu (Rice University)

CURRENT TEACHING RESPONSIBILITIES:

- 2018-2020 Course director – Biochemistry and Cell Biology Workshop
2 semesters per year; 20 students per semester
Weekly seminars with student evaluations and discussion
- 2016-2020 Week director for GSBS Foundation Course
Teaching lectures and organizing 10-lecture week-long topic

2016-2018 Planning homeworks and class activities
 Course director - Signal Transduction Group seminar
 2 semesters per year; 2-6 students per semester
 Weekly seminars with student evaluations and discussion

2014-2020 Molecular Basis of Cell Signaling (~10 students)
 2 lectures (3 hours)

2014-2020 Medical Physiology
 3 lectures (1 hour each) and 2hr PBL session – Acid/base equilibrium
 Involved in planning new Medical School curriculum

2014-2015 GSBS bootcamp module presenter for incoming students

CURRENT GRANT SUPPORT:

PI: Ilya Levental, Ph.D.
 NIH / NIGMS (R35 GM134949)
 “Functional organization of mammalian membranes”
 \$2,300,000 (\$1,500,000 direct / \$338,000 annual) 2020-2025

PI: Ilya Levental, Ph.D.
 Human Frontiers Science Program (RGP0059/2019)
 “Regulation of membrane receptor function in the brain by lipid composition and dietary inputs”
 \$300,000 (all direct costs / \$100,000 annual) 2020-2023

PI: Ilya Levental, Ph.D.
 NIH / NIAID (R21 AI146880)
 “Compositional, biophysical, and functional consequences of membrane scrambling in immune cells”
 \$400,000 (\$275,000 direct costs / \$137,500 annual) 2020-2022

PI: Ilya Levental, Ph.D.
 NIH / NIGMS (R01 GM124072)
 “Structural bases and functional outputs of protein targeting to membrane domains”
 \$1,210,440 (\$786,000 direct costs / \$196,500 annual) 2017-2021

PI: Ilya Levental, Ph.D.
 Volkswagen Foundation (93 091)
 “Design principles of living membranes”
 375,000 EUR (~\$450,000 ; ~\$90,000 annual) 2017-2022

PI: Edward Lyman, Ph.D. (Levental co-Investigator)
 NIH / NIGMS (R01 GM120351-01A1)
 “Effects of lipidomic diversity on GPCR activity”
 \$2,000,000 (Levental portion = \$350,000 direct costs/ \$70,000 annual) 2017-2022

PAST GRANT SUPPORT:

PI: Ilya Levental, Ph.D.
 NIH / NIGMS (1R01GM114282)
 “Biochemical, biophysical, and functional differentiation of mesenchymal stem cell membranes”
 \$1,482,250 (\$962,500 direct costs / \$192,500 annual) 2015-2020
 Diversity supplement: \$132,000 (\$88,000 direct costs / \$44,000 annual) 2016-2018

PI: Ilya Levental, Ph.D.
Cancer Prevention and Research Institute of Texas (R1215)
“Membrane structure and function in oncogene addiction” 2012-2017
\$2,000,000 (\$1,900,000 direct costs / \$475,000 annual direct costs)

PI: Ilya Levental, Ph.D. (co-PI: Neal M Waxham)
UT BRAIN Seed Program (362640)
“Design principles of synapses: An integrated view of proteins and membranes”
\$100,000 direct costs 2015-2017

PI: Askar Akimzhanov Ph.D. (Levental co-Investigator)
NIH / NIGMS (GM115446)
“Dynamic protein palmitoylation in cell signaling”
\$140,000 (\$100,000 direct costs / \$20,000 annual) 2016-2020

PUBLICATIONS (h-index = 36 ; total citations ~7400 ; all stats from Google Scholar):

A. Refereed Original Articles in Journals

**denotes co-corresponding or co-first authors*

1. Heberle FA*, Doktorova M, Scott HL, Skinkle AD, Waxham MN*, Levental I*. Direct label-free imaging of nanodomains in biomimetic and biological membranes by cryogenic electron microscopy. *PNAS*. **2020**
selected for cover article
2. Lorent JH, Levental KR, Ganesan L, Rivera-Longsworth G, Sezgin E, Doktorova M, Lyman E, Levental I. Plasma membranes are asymmetric in lipid unsaturation, packing and protein shape. *Nature Chemical Biology*. **2020** 16(6):644-652

We defined the lipidomic asymmetry of mammalian plasma membranes and showed that the cytoplasmic leaflet was much more unsaturated than the inner. Computational modeling and biophysical experiments then showed that it is also less tightly packed and more diffusive than the outer leaflet, and that these properties affect membrane protein structure and trafficking.

3. Levental KR*, Malmberg E, Fan YY, Chapkin RS, Ernst R, Levental I*. Homeostatic remodeling of mammalian membranes in response to dietary lipids is essential for cellular fitness. *Nature Communications*. **2020** 12;11(1):1339

We show that mammalian membranes are highly susceptible to external perturbations by dietary fatty acids. Compositional changes lead to biophysical disruptions, which the cell must compensate to retain viability.

4. Sezgin E, Carugo D, Levental I, Stride E, Eggeling C. Creating Supported Plasma Membrane Bilayers Using Acoustic Pressure. *Membranes*. **2020** 10(2):30
5. Skinkle A, Levental KR, Levental I. Cell-derived plasma membrane vesicles are permeable to hydrophilic macromolecules. *Biophysical Journal*. **2020** 24;118(6):1292-1300
6. Castello-Serrano I, Lorent JH, Ippolito R, Levental KR, Levental I. Myelin-associated MAL and PLP are unusual among multipass transmembrane proteins in preferring ordered membrane domains. *Journal of Physical Chemistry*. **2020** 24(28):5930-5939

7. Symons JL, Cho KJ, Chang JT, Du G, Waxham MN, Hancock JF, Levental I*, Levental KR*. Lipidomic atlas of mammalian cell membranes reveals hierarchical variation induced by culture conditions, subcellular membranes, and cell lineages. *Soft Matter* **2020**
8. Ballweg S, Sezgin E, Doktorova M, Covino R, Reinhard J, Wunnicke D, Hänel I, Levental I, Hummer G, Ernst R. Regulation of lipid saturation without sensing membrane fluidity. *Nature Communications*. **2020** 11(1):756.
9. Scott HL, Skinkle A, Kelley EG, Waxham MN, Levental I*, Heberle FA*. On the mechanism of bilayer separation by extrusion; or, why your large unilamellar vesicles are not really unilamellar. *Biophysical Journal*. **2019** 15;117(8):1381-1386
10. Madison MC, Landers CT, Gu BH, Chang CY, Tung HY, You R, Hong MJ, Baghaei N, Song LZ, Porter P, Putluri N, Salas R, Gilbert BE, Levental I, Campen MJ, Corry DB, Kheradmand F. Electronic cigarettes disrupt lung lipid homeostasis and innate immunity independent of nicotine. *J Clin Invest*. 2019 pii: 12853
11. Javanainen M, Enkavi G, Guixà-González R, Kulig W, Martinez-Seara H, Levental I, Vattulainen I. Reduced level of docosahexaenoic acid shifts GPCR neuroreceptors to less ordered membrane regions. *PLOS Computational Biology*. **2019** 15(5):e1007033
12. Lewis JD, Caldara AL, Zimmer SE, Stahley SN, Seybold A, Strong NL, Frangakis AS, Levental I, Wahl JK 3rd, Mattheyses AL, Sasaki T, Nakabayashi K, Hata K, Matsubara Y, Ishida-Yamamoto A, Amagai M, Kubo A, Kowalczyk AP. The desmosome is a mesoscale lipid raft-like membrane domain. *Molecular Biology of the Cell*. **2019** 30(12):1390-1405
13. J Jung, KJ Cho, A Naji, K Clemons, C Wong, M Villanueva, S Gregory, N Karagas, L Tan, H Liang, M Rousseau, K Tomasevich, A Sikora, Levental I, D van der Hoeven, Y Zhou, J Hancock, and Venkatachalam K. HRAS-driven cancer cells are vulnerable to TRPML1 inhibition. **2019** *EMBO Reports* 20(4). pii: e46685
14. McGraw C, Yang L, Levental I, Lyman E, Robinson AS. Membrane cholesterol depletion reduces downstream signaling activity of the adenosine A2A receptor. *BBA-Biomembranes*. **2019** 1861(4):760-767
15. Cornell CE, Skinkle AS, He S, Levental I, Levental KR, Keller SL. Tuning length-scales of small domains in cell-derived membranes and synthetic model membranes. *Biophys J*. **2018** Aug 21;115(4):690-701.
16. Lin X, Gorfe AA, Levental I. Protein Partitioning into Ordered Membrane Domains: Insights from Simulations. *Biophys J*. **2018** Apr 24;114(8):1936-1944.
17. Lorent JH, Diaz-Rohrer BB, Lin X, Spring K, Gorfe AA, Levental KR, Levental I. Structural determinants and functional consequences of protein affinity for membrane rafts. *Nature Communications* **2017**; 8(1):1219.
Highlighted in Nature Reviews Molecular Cell Biology
<https://doi.org/10.1038/s41580-020-00285-y>

Extensive experiments coupled to computational modeling defined the structural determinants of bitopic transmembrane protein partitioning to ordered membrane domains. We identified surface area, length and palmitoylation of transmembrane domains to be crucial factors and describe a general model to predict protein association with rafts. (93 citations)

18. Levental KR, Surma MA, Skinkle AD, Lorent JH, Zhou Y, Klose C, Chang JT, Hancock JF, Levental I. Polyunsaturated fatty acids direct differentiation of the membrane

phenotype in mesenchymal stem cells to potentiate osteogenesis. *Science Advances* **2017**; 3(11):eaao1193

Using lipidomics and biophysical characterization, we show that the plasma membranes of mesenchymal stem cells change during differentiation into osteoblasts and adipocytes. More importantly, we find that plasma membrane phenotypes can be manipulated by dietary lipids and can in turn affect cell physiology. (37 citations)

19. Cornell CE, McCarthy NLC, Levental KR, Levental I, Brooks NJ, Keller SL. n-Alcohol Length Governs Shift in Lo-Ld Mixing Temperatures in Synthetic and Cell-Derived Membranes. *Biophys J* **2017**; pii: S0006-3495(17)30757-9.
20. Burns M, Wisser K, Wu J, Levental I, Veatch SL. Miscibility transition temperature scales with growth temperature in a zebrafish cell line. *Biophys J* **2017**; pii: S0006-3495(17)30505-2.
21. Rissanen S, Grzybek M, Orlowski A, Rog T, Cramariuc O, Levental I, Eggeling C, Sezgin E, Vattulainen I. Phase partitioning of GM1 and its bodipy-labeled analog determine their different binding to Cholera toxin. *Front Physiol* **2017**; 8:252.
22. He J, Zhang F, Tay LW, Boroda S, Nian W, Levental KR, Levental I, Harris TE, Chang JT, Du G. Lipin-1 regulation of phospholipid synthesis maintains endoplasmic reticulum homeostasis and is critical for triple-negative breast cancer cell survival. *FASEB J* **2017**; pii: fj.201601353R.
23. Ganesan L, Shieh P, Bertozzi CR, Levental I. Click-Chemistry Based High Throughput Screening Platform for Modulators of Ras Palmitoylation. *Sci Rep* **2017**; 7:41147.
24. Lin X, Lorent JH, Skinkle AD, Levental KR, Waxham MN, Gorfe AA*, Levental I*. Domain stability in biomimetic membranes driven by lipid polyunsaturation. *J Phys Chem B* **2016**; 120(46):11930-11941.
25. Lin X, Zhang S, Ding H, Levental I*, Gorfe AA*. The aliphatic chain of cholesterol modulates bilayer interleaflet coupling and domain registration. *FEBS Lett* **2016**; 590(19):3368-3374.
26. Tulodziecka K, Diaz-Rohrer BB, Farley MM, Chan RB, Di Paolo G, Levental KR, Waxham MN*, Levental I*. Remodeling of the postsynaptic plasma membrane during neural development. *Molecular Biology of the Cell* **2016**; 7;27(22):3480-3489.

The first study to show how the lipidomes of synaptic membranes evolve during development. We showed that neurons likely recruit raft domains to the post-synaptic plasma membranes and hypothesized how these domains are recruited and the physiological purpose thereof. (47 citations)

27. Levental KR, Lorent JH, Lin X, Skinkle AD, Surma MA, Stockenbojer EA, Gorfe AA, Levental I. Polyunsaturated lipids regulate membrane domain stability by tuning membrane order. *Biophys J* **2016**;110(8):1800-10

We show that dietary lipids are powerful manipulators of the biochemical and biophysical phenotypes of mammalian membranes. Further, we reveal that mammalian cells sense such perturbations and respond by orchestrated membrane remodeling. (93 citations)

28. Tisza MJ, Zhao W, Fuentes JS, Prijic S, Chen X, Levental I*, Chang JT*. Motility and stem cell properties induced by EMT require destabilization of lipid rafts. *Oncotarget* **2016**; doi: 10.18632/oncotarget.9928
29. Wolfe AR, Debeb BG, Lacerda L, Larson R, Bambhroliya A, Huang X, Bertucci F, Finetti P, Birnbaum D, Van Laere S, Diagaradjan P, Ruffell B, Trenton NJ, Chu K, Hittelman W, Diehl M, Levental I, Ueno NT, Woodward WA. Simvastatin prevents triple-negative breast cancer metastasis in pre-clinical models through regulation of FOXO3a. *Breast Cancer Res Treat* **2015**;154(3):495-508
30. Sezgin E, Gutmann T, Buhl T, Dirx R, Grzybek M, Coskun Ü, Solimena M, Simons K, Levental I*, Schwille P*. Adaptive lipid packing and bioactivity in membrane domains. *PLOS One* **2015**; 10(4):e0123930
top 10% cited papers in PLOSone in 2013 ; 63 citations
31. Beck-García K, Beck-García E, Bohler S, Zorzín C, Sezgin E, Levental I, Alarcón B, Schamel WW. Nanoclusters of the resting T cell antigen receptor (TCR) localize to non-raft domains. *Biochim Biophys Acta* **2015**; 1853(4): 802-9
32. Ihida-Stansbury K, Ames J, Chokshi M, Aiad N, Sanyal S, Kawabata KC, Levental I, Sundararaghavan HG, Burdick JA, Janmey P, Miyazono K, Wells RG, Jones PL. Role played by Prx1-dependent extracellular matrix properties in vascular smooth muscle development in embryonic lungs. *Pulm Circ* **2015**; 5(2): 382-7
33. Diaz-Aguilar B, Levental K, Simons K, Levental I. Membrane raft association is a determinant of plasma membrane localization. *Proc Natl Acad Sci USA (PNAS)* **2014**; 111(23):8500-5.
selected for cover article ; 125 citations
- We showed that raft affinity is necessary and sufficient for plasma membrane localization of a set of transmembrane proteins. This work revealed a raft-dependent trafficking pathway for protein recycling from the endosomal system.*
34. Schwarzer R, Levental I, Gramatica A, Scolari S, Buschmann V, Veit M, Herrmann A. The cholesterol-binding motif of the HIV-1 glycoprotein gp41 regulates lateral sorting and oligomerization. *Cell Microbiol* **2014**; 16(10):1565-81.
35. Zhou Y, Maxwell KN, Sezgin E, Lu M, Hong L, Hancock JH, Dial EJ, Lichtenberger LM, Levental I. Bile acids modulate signaling by functional perturbation of plasma membrane domains. *J Biol Chem* **2013**; 288(50):35660-70
selected for cover article
36. Sezgin E, Chwastek G, Aydogan G, Levental I, Simons K, Schwille P. Photoconversion of bodipy-labeled lipid analogues. *ChemBiochem* **2013**; 14(6):695-8.
37. Sezgin E, Levental I, Schwarzmann G, Mueller V, Belov VN, Eggeling C, Coskun U, Simons K, Schwille P. Partitioning, diffusion, and ligand binding of raft lipid analogs in model and cellular plasma membranes. *Biochim Biophys Acta* **2012**;1818(7):1777-84.
most cited papers in BBA-Biomembranes in 2012 ; 264 citations
38. Sezgin E, Kaiser HJ, Baumgart T, Schwille P, Simons K, Levental I. Elucidating membrane structure and protein behavior using Giant Plasma Membrane Vesicles. *Nature Protocols* **2012**; 7(6):1042-51

Selected for cover article ; 302 citations

39. Levental I, Grzybek M, Simons K. Raft domains of various properties and compositions in plasma membrane vesicles. *Proc Nat Acad Sci USA (PNAS)* **2011**; 108(28):11411-6.

188 citations

40. Levental I, Lingwood D, Grzybek M, Coskun U, Simons K. Palmitoylation regulates raft affinity for the majority of integral raft proteins. *Proc Nat Acad Sci USA (PNAS)* **2010**; 107(51): 22050-4.

Highlighted in Faculty of 1000 ; 411 citations

41. Kaiser HJ, Surma M, Mayer F, Levental I, Grzybek M, Klemm RW, Da Cruz S, Meisinger C, Mueller V, Simons K, Lingwood D. Molecular convergence of bacterial and eukaryotic surface order. *J Biol Chem* **2011**; 286: 40631-40637.

42. Thaa B, Levental I, Herrmann A, Veit M. Intrinsic membrane association of the cytoplasmic tail of influenza virus M2 protein and lateral membrane sorting regulated by cholesterol binding and palmitoylation. *Biochem J* **2011**; 437(3):389-97.

43. Levental I*, Levental KR*, Klein EA, Assoian R, Miller RT, Wells RG, Janmey PA. A simple indentation device for measuring micrometer-scale tissue stiffness. *J Phys - Cond Matt* **2010**, 22(19).

44. Kaiser HJ, Lingwood D, Levental I, Sampaio JL, Kalvodova L, Rajendran L, Simons K. Order of lipid phases in model and plasma membranes. *Proc Nat Acad Sci USA (PNAS)* **2009**; 106(39): 16645-50.

45. Christian DA, Tian A, Ellenbroek WG, Levental I, Rajagopal K, Janmey PA, Liu AJ, Baumgart T, Discher DE. Spotted vesicles, striped micelles and Janus assemblies induced by ligand binding. *Nature Materials* **2009**; 8: 843-9.

46. Miller WJ, Levental I, Scarsella D, Haydon PG, Janmey PA, Meaney D. Mechanically induced reactive gliosis causes ATP-mediated alterations in astrocyte stiffness. *J Neurotrauma* **2009**; 26(5): 789-97.

47. Klein EA, Yin L, Kothapalli D, Castagnino P, Byfield FJ, Xu T, Levental I, Hawthorne E, Janmey PA, Assoian RK. Cell cycle control by physiological matrix elasticity and in vivo tissue stiffening. *Curr Biol* **2009**; 19(18): 1511-18.

48. Byfield F, Wen Q, Levental I, Nordstrom K, Arratia P, Miller RT, Janmey PA. Absence of filamin A prevents cells from responding to stiffness gradients on gels coated with collagen but not fibronectin. *Biophys J* **2009**; 96(12): 5095-102.

Selected for Faculty of 1000

49. Levental I, Byfield FJ, Chowdhury P, Gai F, Baumgart T, Janmey PA. Cholesterol-dependent phase separation in cell derived giant plasma membrane vesicles. *Biochem J* **2009**; 424(2):163-7.

Accelerated Publication; highlighted in same issue ; 137 citations

50. Levental I*, Christian DA*, Madara JJ, Discher DE, Janmey PA. Calcium-dependent lateral organization in phosphatidylinositol (4,5) bisphosphate (PIP₂)- and cholesterol-containing monolayers. *Biochemistry* **2009**; 48(34): 8241-8.

51. Levental I, Cebers A, Janmey PA. Combined electrostatics and hydrogen bonding determine PIP₂ intermolecular interactions. *J Am Chem Soc* **2008**; 130(28):9025-30.

52. Levental I, Janmey PA, Cebers A. Electrostatic contribution to the surface pressure of charged monolayers containing polyphosphoinositides. *Biophys J* **2008**; 95(3):1199-205.

53. Heinrich M*, Levental I*, Janmey PA, Baumgart T. Critical exponents for line tension and dipole density difference from lipid monolayer domain boundary fluctuations. *J Phys Chem B* **2008**; 112(27): 8063-8.

54. Solon J*, Levental I*, Sengupta K, Georges PC, Janmey PA. Fibroblast adaptation and stiffness matching to soft elastic substrates. *Biophys J* **2007**; 93:4453-61.

886 citations

55. Levental I, Georges PC, Janmey PA. Soft biological materials and their impact on cell function. *Soft Matter* **2007**; 3: 299-306.

753 citations

56. Tandon R, Levental I, Huang C, Byfield FJ, Ziembicki J, Schelling JR, Bruggeman LA, Sedor JR, Janmey PA, Miller RT. HIV infection changes glomerular podocyte cytoskeletal composition and results in distinct cellular mechanical properties. *Am J Physiol – Renal Physiol* **2007**; 292(2):F701-10.

B. Invited articles (reviews, editorials)

1. Levental I. Lipid rafts come of age. *Nature Reviews Molecular Cell Biology*. **2020** 21(8):420.

2. Levental I, Wang HY. Membrane domains beyond the reach of microscopy. *Journal of Lipid Research*. **2020** 61(5):592-594

3. Levental I, Heberle FA. Lipid rafts: controversies resolved, mysteries remain. *Trends in Cell Biology*. **2020** 30(5):341-353

4. Ernst R, Ballweg S, Levental I. Cellular mechanisms of physicochemical membrane homeostasis. *Current Opinion in Cell Biology*. **2018** 53:44-51.

5. Sezgin E, Levental I, Mayor J, Eggeling C. The mystery of membrane organization: composition, regulation and physiological relevance of lipid rafts. *Nature Reviews Molecular Cell Biology* **2017**; 18(6):361-374. doi: 10.1038/nrm.2017.16.

636 citations

6. Plasma gelsolin: indicator of inflammation and potential as a diagnostic tool and therapeutic target. Piktel E, Levental I, Durnaś B, Janmey PA, Bucki R. *Int J Mol Sci*. 2018 Aug 25;19(9). pii: E2516. doi: 10.3390/ijms19092516.

7. Levental I, Veatch SL. The continuing mystery of lipid rafts. *Journal of Molecular Biology*. 2016

176 citations

8. Piktel E, Niemirowicz K, Wnorowska U, Watek M, Wollny T, Gluszek K, Gozdz S, Levental I, Robert Bucki. The role of cathelicidin LL-37 in cancer development. *Arch Immunol Ther Exp*. 2016;64(1):33-46

9. Lorent JH, Levental I. Structural determinants of protein partitioning into ordered membrane domains and lipid rafts. *Chem Phys Lipids* 2015 192, 23-32

10. Ganesan L, Levental I. Pharmacological inhibition of protein lipidation. *J Mem Biol* **2015** 248 (6), 929-941

11. Diaz-Aguilar B, Levental K, Levental I. Rafting through traffic. *BBA – Biomembranes*. **2015** Aug 15;1838(12):3003-3013

12. Levental I, Grzybek M, Simons K. Greasing their way: protein partitioning to membrane rafts. *Biochemistry* **2010**; 49(30): 6305–16.

5th most downloaded article in Biochemistry in 2010 ; 350 citations

13. Lingwood D, Kaiser HJ, Levental I, Simons K. Lipid rafts as functional heterogeneity in cell membranes. *Biochem Soc Trans* **2009**; 37:955-60.

14. Bucki R, Levental I, Kulakowska A, Janmey PA. Plasma gelsolin: function, prognostic value and potential therapeutic use. *Curr Prot Pept Sci* **2008**; 9(6):541-51.

15. Bucki R, Levental I, Janmey PA. Antibacterial peptides: A bright future or a false hope. *Anti-infective agents in chemical medicine* **2007**; 6(3):175-84

16. Georges PC, Levental I, de Jesus W, Miller RT, Janmey PA. Effect of substrate stiffness on the structure and function of cells. *Biophys Rev Lett* **2006**; 1(2).

C. Book chapters

1. Lorent JH, **Levental I**. Preparation and properties of Giant Plasma Membrane Vesicles and GUVs from natural membranes. *The Giant Vesicle Book* **2019**
2. Levental KR, **Levental I**. Giant plasma membrane vesicles: models for understanding membrane organization. *Curr Top Membr* **2015**; 75:25-57.
3. Levental KR, **Levental I**. Isolation of giant plasma membrane vesicles for evaluation of plasma membrane structure and protein partitioning. *Methods Mol Biol* **2015**; 1232:65-77.

INVITED LECTURES (*invited talks at international meetings):

2020

**Biophysical Society Annual Meeting – Platform Presentation in Membrane Structure and Function Subgroup*

Weill Cornell Medical School - Department of Physiology and Biophysics

University of Virginia - Department of Molecular Physiology and Biological Physics

National Institute of Health – NIHCD Affinity Group on Physical Biology and Medicine

Carnegie Mellon University – Dept of Physics (virtual seminar during COVID)

Swiss Federal Institute of Technology Lausanne (EPFL) (virtual seminar during COVID)

Membrane Biophysics Webinar <https://www.youtube.com/watch?v=eeNXEoeAQgl> (1000 views)

Postponed due to COVID19

*FASEB Summer Research Conference on Phospholipids

*Cellular communication systems and their regulation (Les Treilles, France)

*61th International Conference on the Bioscience of Lipids (ICBL) (Utrecht, The Netherlands)

Workshop on "Lipid Asymmetry in Natural and Synthetic Systems" (Oak Ridge National Lab)

University of Toledo

University of Utah - Membrane Trafficking Symposium

2019

University of Chicago - Department of Biochemistry and Molecular Biology

**Biomembrane Days 2019 workshop (Berlin, Germany)*

**EMBO workshop on Lipid Function in Health and Disease (Dresden, Germany)*

Cambridge University (Cambridge, UK) - Department of Biochemistry

**Gordon Research Conference on Membrane Biology*

**Gordon Research Conference on Molecular and Cellular Biology of Lipids*

**FASEB Summer Research Conference on Protein Lipidation*

**Biological Membranes and Membrane Proteins Symposium (Santa Fe, NM)*

Marie Curie Institute – Faculty of Chemical Biology (Paris, France)

*16th International Membrane Research Forum (Okinawa, Japan)

*Annual Meeting of the American Chemical Society

**Gordon Research Conference on Physical Sciences of Cancer*

20th annual Berkeley Statistical Mechanics Meeting (UC Berkeley, CA)

2018

Oxford University (Oxford, UK) – Human Immunology Unit

*EU Consortium Summer School on Lipids in Microbiology (Madrid, Spain)

**CECAM International workshop on "Biological Membranes" (Helsinki, Finland)*

Friedrich Alexander University – Department of Biology (Erlangen, Germany)
qBio workshop

University of Tennessee Knoxville - Department of Cell Biology
University of California Berkeley - Department of Bioengineering
Akron University (Akron, OH) - Department of Chemistry
Cornell University - Department of Bioengineering

*Gordon Research Conference on *Sphingolipids*
*Annual Meeting of the American Chemical Society

2017

University of Colorado (Boulder) - Department of Chemistry & Biochemistry
*Workshop on Inhomogeneous Membranes - Oak Ridge National Lab
**New Horizons in Membrane Transport and Communication* (Frankfurt, Germany)
*Biological Membranes and Membrane Proteins Symposium (Santa Fe, NM)
Baylor University – Current Topics in Computational Biology
Volkswagen Foundation (Hannover, Germany)
Emory University - Department of Cell Biology

2016

McGovern Medical School at UTHealth - Breakthrough Symposium
Max Planck Institute for Cell Biology and Genetics (Dresden, Germany)
University of Erlangen-Nuremberg (Erlangen, Germany) – Department of Computational Biology
**Biomembrane Days workshop* (Berlin, Germany)
University of Groningen (Groningen, Holland) – Molecular Dynamics & Chemical Biology
*CECAM Workshop on “*Biomembranes: consequences of complexity*” (Helsinki, Finland)
*FASEB Summer Research Conference on *Membrane Biophysics*
Lehigh University – Department of Chemistry
Rice University – Center for Theoretical Biological Physics
*Biophysical Society Annual Meeting – **full symposium presentation**
*Gordon Research Conference on *Phosphorylation and G-protein signaling networks*
Texas Tech University - Department of Cell Physiology and Molecular Biophysics

2015

University of Virginia - Molecular Physiology and Biophysics
University of Washington – Department of Chemistry
*American Society for Cell Biology Annual Meeting – **minisymposium presentation**
Delaware University Symposium on “*Membrane Proteins*”
*Heraeus Seminar “*Advanced Microscopy of Membrane Biophysics*” (Bad Honnef, Germany)
*Princeton University workshop on “*Intracellular Phase Transitions*”
*TSC Workshop “*Mechanistic Studies in Membrane Biophysics: Experiments and Theory*”
*Biophysical Society – **minisymposium presentation**
proposed and chaired minisymposium

2014

*American Society for Cell Biology
Cornell University - Department of Biophysics
University of Michigan – Department of Biophysics
University of Pennsylvania – Biochemistry and Biophysics
*Oakridge Workshop on Biomembrane Research
Baylor University – Computational and Integrative Biomedical Research Center
University of Texas Health Science Center – Biochemistry and Molecular Biology

University of Texas Health Science Center – Institute of Molecular Medicine

2013

Texas A&M Department of Nutrition and Food Science

Rice University – Theoretical and Computational Biology Retreat

*FASEB Summer Research Conference on “Lipid Modifications and Membrane Domains”

Max Planck Institute of Cell Biology and Genetics

Goethe University of Frankfurt – Institute of Biochemistry

University of Texas Health Science Center – Center for Membrane Biology

*American Society of Biochemistry and Molecular Biology Annual Meeting

University of Pennsylvania – Institute for Medicine and Engineering

2010-2012

University of Texas Health Science Center at Houston Medical School Retreat

Rice University Department of Bioengineering

Max Planck Institute of Biophysical Chemistry in Goettingen, Germany

University of California Santa Barbara – Department of Biochemistry

University of Texas in Austin – Molecular Cell and Developmental Biology

Washington University in St. Louis – Cell Biology and Physiology

University of Texas Southwestern Medical Center – Physiology and Biochemistry

University of Texas Health Science Center at Houston – Integrative Biology and Pharmacology

*FASEB Summer Research Conference

Symposium and workshop on membrane structure, Yeditepe University, Istanbul

Humboldt University, Berlin

National Biomedical Engineering Society Conference (BMES)

Center for Genomic Regulation, Barcelona

Weizmann Institute, Lipid raft and membranes workshop