

BIOGRAPHICAL SKETCH**DO NOT EXCEED FOUR PAGES.**

NAME Michael Levin		POSITION TITLE	
eRA COMMONS USER NAME LEVIN_MICHAEL		Professor, Tufts University	
EDUCATION/TRAINING <i>(Begin with baccalaureate or other initial professional education, such as nursing, and include postdoctoral training.)</i>			
INSTITUTION AND LOCATION	DEGREE <i>(if applicable)</i>	YEAR(s)	FIELD OF STUDY
Tufts University, Medford, MA	dual B.S. degrees	1988-1992	Biology and Computer Science
Harvard University, Boston, MA	Ph.D.	1992-1996	Genetics
Harvard Medical School, Boston, MA	Post-doctoral research	1996-2000	Molecular embryology

A. Positions and Honors**Employment**

2010-present	Visiting Professor of Genetics, Harvard University (Wyss Institute)
2008-present	Professor, Biology department, Tufts University, Medford, and director of the Tufts Center of Regenerative and Developmental Biology
2008-present	Senior Research Investigator, Forsyth Institute, Boston
2007-2008	Senior Member of Staff (equivalent to Full Professor), Forsyth Institute, Boston
2006-2009	Director, Forsyth Center for Regenerative and Developmental Biology
2008-2009	Associate Professor, Dept. of Developmental Biology, Harvard School of Dental Medicine, Boston
2003-2006	Associate Member of staff (equivalent to Associate Professor), Forsyth Institute, Boston
2000-2003	Assistant Member of Staff (equivalent to Assistant Professor), Forsyth Institute, Boston
2000-2006	Assistant Professor, Harvard School of Dental Medicine, Boston
1996-2000	Research Fellow, Department of Cell Biology, Harvard Medical School, Boston

Awards and Honors

2011	Vannevar Bush Endowed Chair appointment
2007	Established Investigator Award from American Heart Association
2004	The work on the molecular basis of left-right asymmetry (<i>Cell</i> 1995) was chosen by <i>Nature</i> as a "Milestone in Developmental Biology in the last century"
2001	"Best Talk" award at the Juan March Foundation conference on Left Right Asymmetry in Madrid, Spain
2000	Junior Investigator Award, Society for Physical Regulation in Biology and Medicine
1997-2000	Helen Hay Whitney Foundation post-doctoral fellowship
1997	Alexander Imich Award - awarded for a paper on cognitive science and philosophy
1992-1995	NSF pre-doctoral fellowship for Ph.D. work
1990, 1991	Hughes Scholarships for research in developmental biophysics

B. Selected peer-reviewed publications [from 113 total; H-index = 29 as of 2011]Primary Papers

- Levin, M., "A Julia set model of field-directed morphogenesis", (1994), **Computer Applications in the Biosciences**, 10(2): 85-103
- Levin, M., and Ernst, Susan G., (1995), "AC magnetic field effects on early sea urchin development", **Bioelectromagnetics**, 16: 231-240
- Levin, M., (1995), "Use of Genetic Algorithms to solve biomedical problems", **M.D. Computing**, 12(3): 193-198
- Levin, M., (1995), "A genetic algorithm model of the evolution of communication", **BioSystems**, 36: 167-178
- Levin, M., R. L. Johnson, C. D. Stern, M. Kuehn, and C. Tabin, (1995), "A molecular pathway determining left-right asymmetry in chick embryogenesis", **Cell**, 82: 803-814 [Cover] [F1000 rating "Exceptional"]
- Levin, M., D. Roberts, Holmes, and C. Tabin, (1996), "Laterality defects in conjoined twins", **Nature**, 385: 321-

- Levin, M., and Susan G. Ernst, (1997), "DC magnetic field effects on early sea urchin development", **Bioelectromagnetics**, 18(3): 255-263
- Levin, M., S. Pagan, D. Roberts, J. Cooke, M. Kuehn, and C. Tabin, (1997), "Left/Right patterning signals and the independent regulation of situs in the chick embryo", **Developmental Biology**, 189: 57-67
- Levin, M., (1998), "Follistatin mimics the endogenous streak inhibitory activity in early chick embryos", **International Journal of Developmental Biology**, 42: 553-559
- Levin, M., and M. Mercola, (1998), "Gap junctions are involved in the early generation of left-right asymmetry", **Developmental Biology**, 203(1): 90-105
- Levin, M., and M. Mercola, (1998), "Events upstream of asymmetrical Nodal expression: reconciling the chick and frog", **Developmental Genetics**, 23(3): 185-193
- Levin, M., (1999), "Twinning and embryonic left-right asymmetry", **Laterality**, 4(3): 197-208
- Zhu, L., M. J. Marvin, A. Gardiner, A. B. Lassar, M. Mercola, C. D. Stern, and M. Levin, (1999), "Cerberus regulates left/right asymmetry of the embryonic head and heart", **Current Biology**, 9(17): 931-938
- Levin, M., and M. Mercola, (1999), "Gap Junction-Mediated Transfer of Left-Right Patterning Signals in the Early Chick Blastoderm is Upstream of *Shh* Asymmetry", **Development**, 126: 4703-4714
- Levin, M., and M. Mercola, (2000), "Expression of Connexin30 in *Xenopus* embryos and its involvement in hatching gland function", **Developmental Dynamics**, 219(1): 96-101
- Levin, M., T. Thorlin, K. Robinson, T. Nogi, and M. Mercola, (2002), "Asymmetries in H⁺/K⁺-ATPase and cell membrane potentials comprise a very early step in left-right patterning", **Cell**, 111: 77-89
- Rutenberg, J., S. M. Cheng, and M. Levin, (2002), "Early embryonic expression of ion channels and pumps in chick and *Xenopus* embryogenesis", **Developmental Dynamics**, 225(4): 469-484
- Cheng, S. M., I. Chen, and M. Levin, (2002), "K_{atp} channel activity is required for hatching in *Xenopus*", **Developmental Dynamics**, 225(4): 588-591
- Bunney, T. D., De Boer, A. H., and M. Levin, (2003), "Fusicocin signaling reveals 14-3-3 protein function as a novel step in left-right patterning during amphibian embryogenesis", **Development**, 130: 4847-4858
- Levin, M., (2004), "A novel immunohistochemical method for evaluation of antibody specificity and detection of labile targets in biological tissue", **Journal of Biophysical and Biochemical Methods**, 58: 85-96
- Nogi, T., Yuan, Y., Sorocco, D., Perez-Tomas, R., and M. Levin, (2005), "Eye regeneration assay reveals an invariant functional left-right asymmetry in an early bilaterian, *D. japonica*", **Laterality**, 10(3): 193-205
- Fukumoto, T., and Levin, M., (2005), "Asymmetric expression of Syndecan-2 in early chick embryogenesis", **Mechanisms of Development Gene Expression Patterns**, 5: 525-528
- Fukumoto, T., Kema, I., and Levin, M., (2005), "Serotonin signaling is a very early step in patterning of the left-right axis in chick and frog embryos", **Current Biology**, 15: 794-803
- Qiu, D., Cheng, S.M., Wozniak, L., *et al.* and Levin, M., (2005), "Localization and loss-of-function implicate ciliary proteins in early, cytoplasmic LR asymmetry", **Developmental Dynamics**, 234: 176-189
- Shin, J-B., Adams, D., Paukert, M., Siba, M., Sidi, S., Levin, M., Gillespie, P. G., and Grunder, S., (2005), "*Xenopus* TRPN1 (NOMPC) localizes to microtubule-based cilia", **P.N.A.S.**, 102(35): 12572-12577
- Fukumoto, T., Blakely, R., and Levin, M., (2005), "Serotonin transporters are a conserved, early mechanism in left-right patterning", **Developmental Neuroscience**, 27(6): 349 - 363
- Nogi, T., and Levin, M., (2005), "Characterization of innexin gene expression and functional roles of gap-junctional communication in planarian regeneration", **Developmental Biology**, 287: 314 - 335
- Hibino, T., I. Yuichiro, Levin, M., and Nishino, A., (2006), "Ion flow regulates left-right asymmetry in sea urchin development", **Development, Genes and Evolution**, 216(5): 265-76
- Shimeld, S. M., and Levin, M., (2006), "Evidence for the regulation of left-right asymmetry in *Ciona intestinalis* by ion flux", **Developmental Dynamics**, 235(6): 1543-1553
- Adams D.S., Robinson K.R., Fukumoto T., Yuan S., Yelick P., Kuo L., McSweeney M., Levin M., (2006), "Early, H⁺-V-ATPase-dependent proton flux is necessary for consistent left-right patterning of non-mammalian vertebrates", **Development**, 133: 1657-1671 [F1000 rating "Exceptional"]
- Hicks, C., Sorocco, D., and Levin, M., (2006), "Automated analysis of behavior: a computer-controlled system for drug screening and the investigation of learning", **Journal of Neurobiology**, 66(9): 977-90
- Esser, A. T., Smith, K. C., Weaver, J. C., and Levin, M., (2006), "A mathematical model of morphogen electrophoresis through gap junctions", **Developmental Dynamics**, 235: 2144-2159

- Adams, D. S., and Levin, M., (2006), "Inverse drug screens: a rapid and inexpensive method for implicating molecular targets", **Genesis**, 44: 530-540
- Tseng, A-S., Adams, D. S., Qiu, D., Koustubhan, P., and Levin, M., (2007), "Apoptosis is required during early stages of tail regeneration in *Xenopus laevis*", **Developmental Biology**, 301: 62-69
- Adams, D. S., Masi, A., and Levin, M. (2007), "H⁺ Pump-dependent changes in membrane voltage are an early mechanism necessary and sufficient to induce tail regeneration", **Development**, 134: 1323-1335 [Cover]
- Oviedo, N. J., Levin, M., (2007), "Smed-inx11 is a Planarian Stem Cell Gap Junction Gene Required for Regeneration and Homeostasis", **Development**, 134: 3121-3131
- Oviedo, N. J., Nicolas, C. L., Adams, D. S., and Levin, M., (2008), "Live imaging of planarian membrane potential using DiBAC4(3)", **Cold Spring Harbor Protocols**, doi:10.1101/pdb.prot5055
- Oviedo, N. J., Nicolas, C. L., Adams, D. S., and Levin, M., (2008), "Gene knockdown in planarians using RNA interference", **Cold Spring Harbor Protocols**, doi:10.1101/pdb.prot5054
- Oviedo, N. J., Nicolas, C. L., Adams, D. S., and Levin, M., (2008), "Establishing and maintaining a colony of planarians", **Cold Spring Harbor Protocols**, doi:10.1101/pdb.prot5053
- Aw, S., Adams, D. S., Qiu, D., and Levin, M., (2008), "H,K-ATPase protein localization and Kir4.1 function reveal concordance of 3 axes during early determination of left-right asymmetry", **Mechanisms of Development**, 125: 353-372 [top-cited article for 2008-2010 at MOD]
- Morokuma, J., Blackiston, D., and Levin, M., (2008), "KCNQ1 and KCNE1 K⁺ channel components are involved in early LR patterning in *Xenopus* embryos", **Cellular Physiology and Biochem.**, 21: 345-360
- Oviedo, N. J., B. J. Pearson, M. Levin, and A. S. Alvarado, (2008), "Planarian PTEN homologs regulate stem cells and regeneration through TOR signaling", **Disease Models and Mechanisms**, 1: 131-143
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- Sundelacruz, S., M. Levin, and D. L. Kaplan, (2008), "Membrane potential controls adipogenic and osteogenic differentiation of mesenchymal stem cells", **PLoS One**, 3(11): e3737, 1-15
- Zhang, Y., and M. Levin, (2009), "Particle tracking model of electrophoretic morphogen movement reveals stochastic dynamics of embryonic gradient", **Developmental Dynamics**, 238(8): 1923-1935
- Zhang, Y., and M. Levin, (2009), "Left-right asymmetry in the chick embryo requires core planar cell polarity protein Vangl2", **Genesis**, 47(11): 719-728
- Oviedo, N. J., Morokuma, P. Walentek, et al., M. Levin, (2010), "Long-range neural and gap junction protein-mediated cues control polarity during planarian regeneration", **Developmental Biology**, 339:188-199 [Cover]
- Vandenberg, L. N., and M. Levin, (2010), "Consistent left-right asymmetry cannot be established by late organizers in *Xenopus* unless the late organizer is a conjoined twin", **Development**, 137(7):1095-105 [Cover]
- Aw, S., Koster, J., Pearson, W., Nicols, C., Shi, N. Q., Carneiro, K., and Levin, M., (2010), "The ATP-sensitive K⁺-channel (KATP) controls early left-right patterning in *Xenopus* and chick embryos", **Developmental Biology**, 346: 39-53
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- Hechavarria, D., Dewilde, A., Braunhut, S., Levin, M., and Kaplan, D. K., (2010), "BioDome regenerative sleeve for biochemical and biophysical stimulation of tissue regeneration", **Medical Engineering and Physics**, 32: 1065-1073
- Blackiston, D., Vandenberg, L. N., and Levin, M., (2010), "High-throughput *Xenopus laevis* immunohistochemistry using agarose sections", **Cold Spring Harbor Protocols**, doi:10.1101/pdb.prot5532
- Blackiston, D., Adams, D. S., Lemire, J. M., Lobikin, M., and Levin, M., (2011), "Transmembrane potential of GlyCI-expressing instructor cells induces a neoplastic-like conversion of melanocytes via a serotonergic pathway", **Disease Models and Mechanisms**, 4: 67-85 [cover]
- Beane, W. S., Morokuma, J., Adams, D. S., and Levin, M., (2011), "A chemical genetics approach reveals H,K-ATPase-mediated membrane voltage is required for planarian head regeneration", **Cell Chemistry and Biology**, 18: 77-89

- Blackiston, D., Shomrat, T., Nicolas, C. L., Granata, C., and Levin, M., (2011), "A second-generation device for automated training and quantitative behavior analyses of molecularly-tractable model organisms", **PLoS One**, 5(12): e14370 (p. 1-20)
- Lange, C., Prenninger, S., Knuckles, P., Taylor V., Levin, M., and Calegari, F., (2011), "The H⁺ Vacuolar ATPase Maintains Neural Stem Cells in the Developing Mouse Cortex", **Stem Cells and Development**, 20(5): 1-8
- Carneiro, K., et al., and M. Levin, (2011), "Histone deacetylase activity is necessary for left-right patterning during vertebrate development", **BMC Developmental Biology**, 11:29doi:10.1186/1471-213X-11-29 [*Recommended by F1000, "Highly Cited" at BioMed Central*]
- Vandenberg, L. N., B. W. Pennarola, and M. Levin, (2011), "Low frequency vibrations disrupt left-right patterning in the *Xenopus* embryo", **PLoS One**, 6(8): e23306
- Mondia, J. P., Adams, D. S., Orendorff, R. D., Levin, M., and Omenetto, F., (2011), "Patterned femtosecond-laser ablation of *Xenopus laevis* melanocytes for studies of cell migration, wound repair, and developmental processes", **Biomedical Optics Express**, 2(8): 2383-2391
- Mondia, J. P., Levin, M., Omenetto, F. G., Orendorff, R. D., Branch, M. R., and Adams, D. S., (2011), "Long-distance signals are required for morphogenesis of the regenerating *Xenopus* tadpole tail", **PLoS One**, 6(9): e24953. doi:10.1371/journal.pone.0024953
- Tseng, A.S., Carneiro, K., Lemire, J. M., and M. Levin, (2011), "HDAC activity is required during *Xenopus* tail regeneration", **PLoS One**, 6(10): e26382-. doi:10.1371/journal.pone.0026382
- Vandenberg, L. N., and M. Levin, (2011), "Polarity proteins are required for left-right axis orientation and twin-twin instruction", **Genesis**, in press
- Pai, V. P., Aw. S., Shomrat, T., Lemire, J. M., and M. Levin, (2012), "Transmembrane voltage potential controls embryonic eye patterning in *Xenopus laevis*", **Development**, 139: 313-323
- Adams, D. S., and M. Levin, (2012), "General principles for measuring resting membrane potential and ion concentration using fluorescent bioelectricity reporters", **CSHL Protocols**, in press
- Adams, D. S., and M. Levin, (2012), "Measuring resting membrane potential using the fluorescent voltage reporters DiBAC4(3) and CC2-DMPE", **CSHL Protocols**, in press
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Peer-reviewed Hypotheses Papers, Reviews, and Book Chapters

- Levin, M., "Current and potential applications of Bioelectromagnetics", (1993), **ISSEEM Journal**, 4(1): 77-87
- Levin, M., (1997), "Left-Right Asymmetry in Embryonic Morphogenesis", **BioEssays**, 19(4): 287-296
- Levin, M., and N. Nascone, (1997), "Two models of initial Left-Right asymmetry determination", **Medical Hypotheses**, 49: 429-435
- Levin, M., (1998), "Left-Right asymmetry in the chick embryo", **Seminars in Developmental Biology**, 9: 67-76
- Levin, M., and M. Mercola, (1998), "The compulsion of chirality", **Genes & Development**, 12: 763-769
- Mercola, M., and Levin, M. (2001), "Left-Right asymmetry determination in vertebrates", **Annual Review of Cell and Developmental Biology**, 17: 779-805
- Levin, M., (2002), "Gap-junctional communication and embryonic development", **Journal of Membrane Biology**, 185 (3): 177-192
- Levin, M., (2003), "Electromagnetic fields in morphogenesis", **Bioelectromagnetics**, 24: 295-315
- Levin, M., (2003), "Motor protein control of ion flux is an early step in embryonic Left-Right asymmetry", **BioEssays**, 25(10): 1002-1010
- Adams, D. S., and Levin, M. (2004). "Early patterning of the Left/Right axis" in Gastrulation: from Cells to Embryo (C. D. Stern, Ed.), pp. 403-417. Cold Spring Harbor, New York.
- Levin, M., (2004), "The embryonic origins of left-right asymmetry", **Critical Reviews in Oral Biology and Medicine**, 15(4): 197-206
- Levin, M., (2005), "Left-right asymmetry in embryonic development: a comprehensive review", **Mechanisms of Development**, 122(1): 3-25 [*one of the "10 Top Cited" articles in this journal for 2004-2005 period*]
- Levin, M., Lauder, J., and Buznikov, G., (2006), "Of minds and embryos: serotonin signaling as a pre-nervous morphogenetic mechanism", **Developmental Neuroscience**, 28:171-185

- Adams, D., and Levin, M., (2006), "Strategies and techniques for investigation of biophysical signals in patterning", in Analysis of Growth Factor Signaling in Embryos, M. Whitman and A. K. Sater eds., pp. 177-214, Methods in Signal Transduction Series, CRC Press
- Levin, M., (2006), "Is the early Left-Right axis like a plant, a kidney, or a neuron? The integration of physiological signals in Left-Right asymmetry", **Birth Defects Research (Part C)**, 78: 191-223
- Koustubhan, P., Sorocco, D., and Levin, M., (2007), "Establishing and maintaining a *Xenopus laevis* colony for research laboratories", in Source Book of Models for Biomedical Research, M. Conn ed., Humana Press
- Levin, M., Palmer, R., (2007), "Left-right patterning from the inside out", **BioEssays**, 29(3): 271-287
- Levin, M., (2007), "Gap junctional communication in morphogenesis", **Progress in Biophysics and Molecular Biology**, 94 (1-2): 186-206
- Levin, M., (2007), "Large-scale biophysics: ion flows & regeneration", **Trends in Cell Biology**, 17(6): 262-271
- Oviedo, N., and Levin, M. (2007), "Gap junctions provide new links in Left-Right patterning", **Cell**, 129: 645-647
- Ingber, D., and Levin, M. (2007), "What lies at the interface of regenerative medicine and developmental biology?", **Development**, 134: 2541-2547 [Cover]
- Oviedo, N., and Levin, M., (2008), "Planarian regeneration model drug effects & mechanisms", in Planaria: A Model for Drug Action and Abuse, Raffa RB & Rawls SM (eds), RG Landes Co.: Austin, pp. 95-104
- Nicolas, C.L., Abramson, C.I., and Levin, M. (2008), "Analysis of behavior in the planarian model", in Planaria: A Model for Drug Action and Abuse, Raffa RB & Rawls SM (eds), RG Landes Co.: Austin, pp. 83-94
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- Tseng, A-S., and Levin, M., (2008), "Tail regeneration in *Xenopus laevis* as a model for understanding tissue repair", **Critical Reviews in Oral Biology and Medicine**, 87(9): 806-816
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- Levin, M., (2009), Bioelectric mechanisms in regeneration: unique aspects and future perspectives, **Seminars in Cell and Developmental Biology**, 20: 543-556
- Sundelacruz, S., Levin M., Kaplan, D. L., (2009), "Role of membrane potential in the regulation of cell proliferation and differentiation", **Stem Cell Reviews**, 5(3): 231-46
- Blackiston, D. J., K. McLaughlin, and Levin, M., (2009), "Bioelectric controls of cell proliferation: ion channels, membrane voltage, and the cell cycle", **Cell Cycle**, 8(21): 3527-3536 [Cover]
- Vandenberg, L. N., and Levin, M., (2010), "Far from solved: a perspective on what we know about early mechanisms of left-right asymmetry", **Developmental Dynamics**, 239: 3131-3146 [Cover]
- Levin, M., (2011), Endogenous Bioelectric Signals as Morphogenetic Controls of Development, Regeneration, and Neoplasm", in The Physiology of Bioelectricity in Development, Tissue Regeneration, and Cancer, C. Pullar ed., CRC Press
- Levin, M., (2011), "The wisdom of the body: future techniques and approaches to morphogenetic fields in regenerative medicine, developmental biology, and cancer", **Regenerative Medicine**, 6(6): 667-673
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Professional Society Memberships: BEMS, ASCB, SDB, SPRB, SfN;

Editorial Boards: *JSE*, *Laterality*