

BIOGRAPHICAL SKETCH

NAME Michael Levin		POSITION TITLE	
eRA COMMONS USER NAME LEVIN MICHAEL (ORCID 0000-0001-7292-8084)		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	Post-doctoral research	1996-2000	Molecular embryology

A. Personal Statement

My original background was in computer science, which motivated my interest in biophysical mechanisms of information processing during regulative morphogenesis. My group's long-term mission is to produce 1) constructivist understanding of pattern formation mechanisms that encompasses both physical and information-level control mechanisms, and 2) biomedical interventions that utilize changes in bioelectrical properties of key cell groups to induce complete *in situ* regeneration of limbs, eyes, and other organs for applications targeting birth defects, injuries, and cancer.

In recent years, my lab has: identified several novel very early mechanisms in left-right patterning, discovered a new role for pre-nervous serotonin as a morphogen, revealed a highly conserved chiral cytoskeletal structure that, together with four ion channels and pumps, amplifies cell chirality into true left-right asymmetry of the body, identified membrane voltage as a long-range environmental cue mediating the stem cell -> cancer cell transition *in vivo* and showed that control of resting potential can abrogate oncogenes' ability to induce tumorigenesis, uncovered an epigenetic voltage-based mechanism determining anterior-posterior polarity in planarian regeneration, developed a parallelized memory testing platform (machine vision system with environmental controls) to study the dynamics of memories in regenerating brains, created molecular protocols for manipulating ion flows to initiate the regeneration of complex appendages such as limbs and tails, and showed that modulation of resting potential in non-neural cells can reprogram tissues into entire organs such as eyes.

B. Positions**Employment and Appointments**

2016-present	Director, Allen Discovery Institute at Tufts
2010-present	Visiting Scholar, Wyss Institute at Harvard
2008-present	Professor , Biology Department, Tufts University, Medford (Vannevar Bush Chair) Director , Tufts Center of Regenerative and Developmental Biology
2008-present	Senior Research Investigator, Forsyth Institute, Boston
2008-2013	Associate Professor of Developmental Biology, Harvard University
2007-2008	Senior Member of Staff (equivalent to Full Professor), Forsyth Institute, Boston
2006-2009	Director, Forsyth Center for Regenerative and Developmental Biology
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

2014	Keynote speaker, Gordon Conference Research Symposium
2013	Distinguished Scholar Award , Tufts University
2013	Keynote speaker at NIH NCI's PS-OC National meeting
2013	Keynote speaker GSBSE conference
2012	Scientist of Vision Award , IFESS
2012	Keynote speaker, IFESS International conference, Canada
2012	Plenary speaker, 50 th Anniversary IBBME Symposium, Canada
2011	Vannevar Bush Endowed Chair appointment

2011	Keynote speaker, Gordon Conference Research Symposium
2007	Established Investigator Award from American Heart Association
2004	The work on the molecular basis of left-right asymmetry (Cell 1995) was chosen by the journal <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, paper on cognitive science and consciousness
1992-1995	NSF pre-doctoral fellowship for Ph.D. work
1990, 1991	Hughes Scholarships for research in developmental biophysics

C. Selected peer-reviewed publications

Primary Papers

1. Levin, M., (1994), "A Julia set model of field-directed morphogenesis", **Computer Applications in the Biosciences**, 10(2): 85-103
2. Levin, M., and Ernst, Susan G., (1995), "AC magnetic field effects on early sea urchin development", **Bioelectromagnetics**, 16: 231-240
3. Levin, M., (1995), "Use of Genetic Algorithms to solve biomedical problems", **M.D. Computing**, 12(3): 193-198
4. Levin, M., (1995), "A genetic algorithm model of the evolution of communication", **BioSystems**, 36: 167-178
5. 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"]
6. Levin, M., D. Roberts, Holmes, and C. Tabin, (1996), "Laterality defects in conjoined twins", **Nature**, 385: 321-
7. Levin, M., and Susan G. Ernst, (1997), "DC magnetic field effects on early sea urchin development", **Bioelectromagnetics**, 18(3): 255-263
8. 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
9. Levin, M., (1998), "Follistatin mimics the endogenous streak inhibitory activity in early chick embryos", **International Journal of Developmental Biology**, 42: 553-559
10. Levin, M., and M. Mercola, (1998), "Gap junctions are involved in the early generation of left-right asymmetry", **Developmental Biology**, 203(1): 90-105
11. Levin, M., and M. Mercola, (1998), "Events upstream of asymmetrical Nodal expression: reconciling the chick and frog", **Developmental Genetics**, 23(3): 185-193
12. Levin, M., (1999), "Twinning and embryonic left-right asymmetry", **Laterality**, 4(3): 197-208
13. 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
14. 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
15. 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
16. 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
17. 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
18. 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
19. Bunney, T. D., De Boer, A. H., and M. Levin, (2003), "Fusicoccin signaling reveals 14-3-3 protein function as a novel step in left-right patterning during amphibian embryogenesis", **Development**, 130: 4847-4858

20. 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
21. 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
22. Fukumoto, T., and Levin, M., (2005), "Asymmetric expression of Syndecan-2 in early chick embryogenesis", **Mechanisms of Development Gene Expression Patterns**, 5: 525-528
23. 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
24. 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
25. 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
26. 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
27. 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
28. 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
29. 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
30. 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"]
31. 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
32. 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
33. Adams, D. S., and Levin, M., (2006), "Inverse drug screens: a rapid and inexpensive method for implicating molecular targets", **Genesis**, 44: 530-540
34. 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
35. 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]
36. 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
37. 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
38. 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
39. 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
40. 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]
41. 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
42. 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
43. Morokuma, J., Blackiston, D., Adams, D. S., Trimmer, B., Seebohm, G., and Levin, M., (2008), "Modulation of K⁺ channel confers a hyper-proliferative, invasive phenotype on embryonic stem cells", **PNAS**, 105(43): 16608-16613

44. 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
45. 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
46. 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
47. Oviedo, N. J., Morokuma, P., Walentek, et al., M. Levin, (2010), "Long-range neural and gap junction protein-mediated cues control polarity in planarian regeneration", **Developmental Biology**, 339:188-199 [Cover]
48. 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]
49. 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
50. Tseng, A-S., Beane, W. S., Lemire, J. M., Masi, A., and M. Levin, (2010), "Induction of vertebrate regeneration by a transient sodium current", **Journal of Neuroscience**, 30(39): 13192-13200 [cover]
51. Hechavarría, 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
52. 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
53. Blackiston, D., Adams, D. S., Lemire, J. M., Lobikin, M., and Levin, M., (2011), "Transmembrane potential of GlyCl-expressing instructor cells induces a neoplastic-like conversion of melanocytes via a serotonergic pathway", **Disease Models and Mechanisms**, 4: 67-85 [cover]
54. 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
55. 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)
56. Lange, C., Prenninger, S., Knuckles, P., Taylor V., Levin, M., and Calegari, F., (2011), "The H⁺ V-ATPase Maintains Neural Stem Cells in the Developing Mouse Cortex", **Stem Cells and Development**, 20(5): 1-8
57. 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
58. [Recommended by F1000, "Highly Cited" at BioMed Central]
59. Vandenberg, L. N., Pennarola, B. W., and Levin, M., (2011), "Low frequency vibrations disrupt left-right patterning in the *Xenopus* embryo", **PLoS One**, 6(8): e23306. doi:10.1371/journal.pone.0023306
60. 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
61. 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
62. 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
63. Vandenberg, L. N., and M. Levin, (2011), "Polarity proteins are required for left-right axis orientation and twin-twin instruction", **Genesis**, 50: 219-234
64. 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 [F1000 rating Exceptional]
65. Adams, D. S., and M. Levin, (2012), "General principles for measuring resting membrane potential and ion concentration using fluorescent bioelectricity reporters", **CSHL Protocols**, doi: 10.1101/pdb.top067710

66. Adams, D. S., and M. Levin, (2012), "Measuring resting membrane potential using the fluorescent voltage reporters DiBAC4(3) and CC2-DMPE", **CSHL Protocols**, doi: 10.1101/pdb.prot067702 [cover]
67. Blackiston, D. J., and M. Levin, (2012), "Aversive training methods in *Xenopus laevis*: general principles", **CSHL Protocols**, doi: 10.1101/pdb.top068338
68. Beane, W. S., Tseng, A-S, Morokuma, J., and M. Levin, (2012), "Inhibition of planar cell polarity extends neural growth during regeneration, homeostasis, and development", **Stem Cells and Development**, 21(12): 2085-2094 [Most Read Article]
69. Chernet, B. T., Adams, D. S., and M. Levin, (2012), "Photoconversion for Tracking the Dynamics of Cell Movement in *Xenopus laevis* Embryos", **CSHL Protocols**, 10.1101/pdb.prot068502 [cover]
70. Chernet, B. T., and M. Levin, (2012), "A versatile protocol for mRNA electroporation of *Xenopus laevis* embryos", **CSHL Protocols**, doi: 10.1101/pdb.prot067694
71. Vandenberg, L., Adams, D. S., and M. Levin, (2012), "Normalized shape and location of perturbed craniofacial structures in the *Xenopus* tadpole reveal an innate ability to achieve correct morphology", **Developmental Dynamics**, 241: 863-878 [Highlighted]
72. Tseng, A-S., and M. Levin, (2012), "Transducing bioelectrical signals into epigenetic pathways during tadpole tail regeneration", **Anatomical Record**, 295:1541-1551
73. Lobikin, M., Wang, G., Xu, J-S, Hsieh, Y-W, Chuang, C-F, Lemire, J. M., and M. Levin, (2012), "Early, non-ciliary role for microtubule proteins in left-right patterning is conserved across kingdoms", **PNAS**, 109(31): 12586-12591
74. Vandenberg, L. N., Stevenson, C., and M. Levin, (2012), "Low frequency vibrations induce malformations in two aquatic species in a frequency-, waveform-, and direction-specific manner", **PLoS One**, 7(12): e51473. doi:10.1371/journal.pone.0051473
75. Pai, V. P., Vandenberg, L. N., Blackiston, D. J., and Levin, M., (2012), "Neurally-derived tissues in *Xenopus laevis* embryos exhibit a consistent bioelectrical left-right asymmetry", **Stem Cells International**, Vol. 2012, doi: 10.1155/2012/353491
76. Koustubhan, P., Kaplan, D., and Levin, M., (2012), "Humane anesthesia and pain management in amphibian limb surgery of *Rana pipiens*", **CSHL Protocols**, 2013(2): 149-55 [cover]
77. Lobikin, M., Chernet, B. T., Lobo, D., and Levin, M., (2012), "Resting potential, oncogene-induced tumorigenesis, and metastasis: the bioelectric basis of cancer *in vivo*", **Physical Biology**, 9: 065002 [cover]
78. Vandenberg, L. N., Morrie, R. D., Seebohm, G., Lemire, J. M., and Levin, M., (2013), "Rab GTPases are required for early orientation of the left-right axis in *Xenopus*", **Mechanisms of Development**, 130:254-271
79. Lobo, D., Malone, T. J., and Levin, M., (2013), "Towards a bioinformatics of patterning: a computational approach to understanding regulative morphogenesis", **Biology Open**, 2:156-169 [cover]
80. Beane, W. S., Morokuma, J., Lemire, J. M., and Levin, M., (2013), "Bioelectric signaling regulates head and organ size during planarian regeneration", **Development**, 140:313-322
81. Vandenberg, L. N., Lemire, J. M., and Levin, M. (2013), "Serotonin has early, cilia-independent roles in *Xenopus* left-right patterning", **Disease Models and Mechanisms**, 6: 261-268 [cover]
82. Lobo, D., Malone, T. J., and Levin, M. (2013), "Planform: an application and database of graph-encoded planarian regenerative experiments", **Bioinformatics**, 29(8): 1098-1100 [cover]
83. Blackiston, D. J., and Levin, M., (2013), "Ectopic eyes out side the head in *Xenopus* tadpoles provide sensory data for light-mediated learning", **Journal of Experimental Biology**, 216: 1031-1040
84. Adams, D. S., Tseng, A-S., and Levin, M., (2013), "Light-activation of the Archaerhodopsin H⁺ pump reverses age-dependent loss of vertebrate regeneration: sparking system-level controls *in vivo*", **Biology Open**, 2(3): 306-313
85. Chernet, B. T., and Levin, M., (2013), "Transmembrane voltage potential is an essential cellular parameter for the detection and control of tumor development", **Disease Models and Mechanisms**, 6: 595-607
86. Shomrat, T., and Levin, M., (2013), "An automated training paradigm reveals long-term memory in planaria and its persistence through head regeneration", **Journal of Experimental Biology**, 216: 3799-3810
87. Blackiston, D. J., and Levin, M., (2013), "Inversion of left-right asymmetry alters performance of *Xenopus* tadpoles in nonlateralized cognitive tasks", **Animal Behaviour**, 86: 459-466
88. Sundelacruz S., Li C., Choi Y.J., Levin M., and Kaplan D.L., (2013), "Bioelectric modulation of wound healing in a 3D *in vitro* model of tissue-engineered bone", **Biomaterials**, 34(28): 6695-705

89. Sundelacruz S., Levin M., and Kaplan DL, (2013), "Depolarization alters phenotype, maintains plasticity of predifferentiated mesenchymal stem cells", **Tissue Engineering Part A**, 19(17-18): 1889-908
90. Rea, A. C., Vandenberg L. N., Ball R. E., Snouffer A. A., Hudson A. G., Zhu, Y., McLain D.E., Johnston L. L., Lauderdale J. D., Levin M., and Dore, T. M., (2013), "Light-activated serotonin for exploring its action in biological systems", **Cell Chemistry and Biology**, 20: 1536-1546
91. Chernet, B., and Levin, M., (2014), "Transmembrane voltage potential of somatic cells controls oncogene-mediated tumorigenesis at long-range", **Oncotarget**, 5(10): 3287-3306
92. Budnikova, M., Habig, J. W., Cornia, N., Levin. M., Lobo, D., and Andersen, T., (2014), "Design of a flexible component gathering algorithm for converting cell-based models to graph representations for use in evolutionary search", **BMC Bioinformatics**, 15: 178
93. Lobo, D., Feldman, E., Shah, M., Malone, T., and Levin, M., (2014), "A bioinformatics expert system linking functional data to anatomical outcomes in limb regeneration", **Regeneration**, 1(2): 37-56
94. Lan J. Y., Williams C., Levin M., and Black L.D. III, (2014), "Depolarization of Cellular Resting Membrane Potential Promotes Neonatal Cardiomyocyte Proliferation In Vitro", **Cellular and Molecular Bioengineering**, DOI: 10.1007/s12195-014-0346-7
95. Lobo, D., Feldman, E. B., Shah, M., Malone, T. J., and Levin, M., (2014), "Limbform: a functional ontology-based database of limb regeneration experiments", **Bioinformatics**, 30(24): 3598-3600
96. Adams, D.S., Lemire, J. M., Kramer, R. H., and Levin, M., (2014), "Optogenetics in developmental biology: using light to control ion flux-dependent signals in *Xenopus* embryos", **International Journal of Developmental Biology**, 58: 851-861
97. Vandenberg, L. N., Blackiston, D. J., Rea, A. C., Dore, T. M., and Levin, M., (2014), "Left-right patterning in *Xenopus* conjoined twin embryos requires serotonin signaling and gap junctions", **International Journal of Developmental Biology**, 58: 799-809
98. Jewhurst, K., Levin, M., and McLaughlin K. A., (2014), "Optogenetic control of apoptosis in targeted tissues of *Xenopus laevis* embryos", **Journal of Cell Death**, 7: 25-31
99. Ozkucur, N., Quinn, K. P., Pang, J. C., u, C., Georgakoudi, I., Miller, E., Levin, M., and Kaplan, D. L., (2015), "Membrane potential depolarization causes alterations in neuron arrangement and connectivity in cocultures", **Brain and Behavior**, 5(1): 24-38
100. Blackiston, D., Anderson, G. M., Rahman, N., Bieck, C., and Levin, M., (2015), "A novel method for inducing nerve growth via modulation of host resting potential". **Neurotherapeutics**, 12: 170-184
101. Bessonov, N., Levin, M., Morozova, N., Reinberg, N., Tosenberger, A., and Volpert, V., (2015), "On a model of pattern recognition based on cell memory", **PLoS One**, 10(2): e0118091
102. Chernet, B. T., Fields, C., and Levin, M., (2015), "Long-range gap junctional signaling controls oncogene-mediated tumorigenesis in *Xenopus laevis* embryos", **Frontiers in Physiology**, 5(519): 1-15
103. Pai, V., Lemire, J. M., Pare, J-F., Lin, G., Chen, Y., and Levin, M., (2015), "Endogenous gradients of resting potential instructively pattern embryonic neural tissue via Notch signaling and regulation of proliferation", **Journal of Neuroscience**, 35(10): 4366-4385
104. Friston, K., Levin, M., Sengupta B., and Pezzulo, G., (2015), "Knowing one's place - a free energy approach to pattern regulation", **Journal of the Royal Society Interface**, 12: 20141383
105. Lobo D., and Levin M., (2015), "Inferring regulatory networks from experimental morphological phenotypes: a computational method reverse-engineers planarian regeneration", **PLoS Computational Biology**, 11(6): e1004295 [>24,000 views]
106. Tosenberger, A., Bessonov, N., Levin, M., Reinberg, N., Volpert V., Morozova, N., (2015), "A Conceptual model of morphogenesis and regeneration", **Acta Biotheoretica**, 63(3): 283-294
107. Pai, V. P., Lemire J. M., Chen Y., Lin G., and Levin M., (2015), "Local and long-range endogenous resting potential gradients antagonistically regulate apoptosis and proliferation in the embryonic CNS", **International Journal of Developmental Biology**, 59: 327-340
108. Lobikin, M., Pare, J-F., Kaplan, D. L., and Levin, M., (2015), "Selective Depolarization Of Transmembrane Potential Alters Muscle Patterning and Muscle Cell Localization In Embryonic *Xenopus Laevis*", **International Journal of Developmental Biology**, 59:303-311 [cover]
109. Pai, V. P., Martyniuk, C. J., Echeverri, K., Sundelacruz, S., Kaplan, D. L., and Levin, M., (2015), Genome-wide analysis reveals conserved transcriptional responses downstream of resting potential change in *Xenopus* embryos, axolotl regeneration, and human mesenchymal cell differentiation,

Regeneration, 3(1): 3-25

110. Lobikin, M., Lobo, D., Blackiston, D. J., Martyniuk, C. J., Tkachenko, E., and Levin, M., (2015), "Serotonergic regulation of melanocyte conversion: a bioelectrically regulated network for stochastic all-or-none hyperpigmentation", **Science Signaling**, 8(397): ra99
111. Pang, J., Ozkucur, N., Ren, M., Kaplan, D. L., Levin, M., and Miller, E. L., (2015), "An automatic neuron segmentation and neural network analysis method for phase contrast microscopy images", **Biomedical Optics Express**, 6(11) 4395-4416
112. Hammelman, J., Lobo, D., and Levin, M., (2016), "Artificial neural networks as models of robustness in development and regeneration: stability of memory during morphological remodeling", in Artificial Neural Network (ANN) Modelling, S. Shanmuganathan and S. Samarasinghe editors
113. Law, R., and Levin, M., (2015), "Bioelectric memory: modeling resting potential bistability in amphibian embryos and mammalian cells", **Theoretical Biology and Medical Modelling**, 12:22
114. Emmons-Bell, M., Durant, F., Hammelman, J., Bessonov, N., Volpert, V., Morokuma, J., Pinet, K., Adams, D. S., Pietak, A., Lobo, D., and Levin, M., (2015), "Gap junctional blockade stochastically induces different species-specific head anatomies in genetically wild-type *Girardia dorotocephala* flatworms", **International Journal of Molecular Sciences**, 16: 27865-27896 [cover]
115. Sundelacruz, S., Levin M., and Kaplan, D. L., (2015), "Comparison of the depolarization response of human mesenchymal stem cells from different donors", **Scientific Reports**, 5: 18279 (doi: 10.1038/srep18279)
116. Schatzberg, D., Lawton, M., Hadyniak S. E., Ross E. J., Carney T., Beane W. S., Levin, M., and Bradham, C. A., (2015), "H⁺/K⁺-ATPase activity is required for biomineralization in sea urchin embryos", **Developmental Biology**, 406(2): 259-270
117. Dimonte, A., Adamatzky, A., Erokhin, V., and Levin, M., (2016), "On chirality of slime mould", **BioSystems**, 140: 23-27
118. Whiting, J. G. H., Jones, J., Bull, L., Levin, M., and Adamatzky, A., (2016), "Towards a Physarum learning chip", **Scientific Reports**, 6:19948 (1-14)
119. McDowell, G. S., Lemire, J. M., Pare, J-F., Cammarata, G., Lowery, L. A., and Levin, M., (2016), "Conserved roles for cytoskeletal components in determining laterality", **Integrative Biology**, 8: 267-286
120. Chernet, B. T., Adams, D. S., Lobikin, M., and Levin, M., (2016), "Use of genetically encoded, light-gated ion translocators to control tumorigenesis", **Oncotarget**, 7(15): 19575-19588
121. Sullivan, K. G., and Levin, M., (2016), "Neurotransmitter signaling pathways required for normal development in *Xenopus laevis* embryos: a pharmacological survey screen", **Journal of Anatomy**, in press
122. Adams, D. S., Uzel S. G. M., Akagi J., Wlodkowic D., Andreeva V., Yelick, P. C., Devitt-Lee A., Pare J-F., and Levin, M., (2016), "Bioelectric signaling via potassium channels: a mechanism for craniofacial dysmorphogenesis in KCNJ2-associated Andersen-Tawil Syndrome", **Journal of Physiology**, in press
123. Davison A., McDowell G. S., Holden, J. M., Johnson H. F., Koutsovoulos G. D., Liu M. M., Hulpiau P., Van Roy F., Wade C. W., Banerjee R., Yang F., Chiba S., Davey J. W., Jackson, D. J., Levin M., and Blaxter, M. L., (2016), "Formin Is Associated with Left-Right Asymmetry in the Pond Snail and the Frog", **Current Biology**, 26(5): 654-60
124. Li, C., Levin, M., and Kaplan, D., (2016), "Bioelectric modulation of macrophage polarization", **Scientific Reports**, 6:21044, doi:10.1038/srep21044
125. Lobo, D., Hammelman, J., and Levin, M., (2016), "MoCha: molecular characterization of unknown pathways", **Journal of Computational Biology**, 23(4): 291-297
126. Rothman, G., Blackiston, D., and Levin, M., (2016), "Color and intensity discrimination in *Xenopus laevis* tadpoles", **Animal Cognition**, in press
127. Lobo, D., Morokuma, J., and Levin, M., (2016), "Computational discovery and in vivo validation of *hnf4* as a regulatory gene in planarian regeneration", **Bioinformatics** doi: 10.1093/bioinformatics/btw299

Peer-reviewed Hypotheses Papers, Reviews, and Book Chapters

1. Levin, M., (1993), "Current and potential applications of Bioelectromagnetics", **ISSEEM Journal**, 4(1): 77-87
2. Levin, M., (1997), "Left-Right Asymmetry in Embryonic Morphogenesis", **BioEssays**, 19(4): 287-296

3. Levin, M., and N. Nascone, (1997), "Two models of initial Left-Right asymmetry determination", **Medical Hypotheses**, 49: 429-435
4. Levin, M., (1998), "Left-Right asymmetry in the chick embryo", **Seminars in Developmental Biology**, 9: 67-76
5. Levin, M., and M. Mercola, (1998), "The compulsion of chirality", **Genes & Development**, 12: 763-769
6. Mercola, M., and Levin, M. (2001), "Left-Right asymmetry determination in vertebrates", **Annual Review of Cell and Developmental Biology**, 17: 779-805
7. Levin, M., (2002), "Gap-junctional communication and embryonic development", **Journal of Membrane Biology**, 185 (3): 177-192
8. Levin, M., (2003), "Electromagnetic fields in morphogenesis", **Bioelectromagnetics**, 24: 295-315
9. Levin, M., (2003), "Motor protein control of ion flux is an early step in embryonic Left-Right asymmetry", **BioEssays**, 25(10): 1002-1010
10. 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.
11. Levin, M., (2004), "The embryonic origins of left-right asymmetry", **Critical Reviews in Oral Biology and Medicine**, 15(4): 197-206
12. 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]
13. 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
14. 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
15. 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
16. 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
17. Levin, M., Palmer, R., (2007), "Left-right patterning from the inside out", **BioEssays**, 29(3): 271-287
18. Levin, M., (2007), "Gap junctional communication in morphogenesis", **Progress in Biophysics and Molecular Biology**, 94 (1-2): 186-206
19. Levin, M., (2007), "Large-scale biophysics: ion flows & regeneration", **Trends in Cell Biology**, 17(6): 262-271
20. Oviedo, N., and Levin, M. (2007), "Gap junctions provide new links in Left-Right patterning", **Cell**, 129: 645-647
21. Ingber, D., and Levin, M. (2007), "What lies at the interface of regenerative medicine and developmental biology?", **Development**, 134: 2541-2547 [Cover]
22. 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
23. 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
24. Aw, S., and Levin, M., (2008), "What's Left in Asymmetry?", **Developmental Dynamics**, 237: 3453-3463
25. Oviedo, N., Nicolas, C. L., Adams, D. S., and Levin, M. (2008), "Planarians: a versatile and powerful model system for molecular studies of regeneration, adult stem cell regulation, aging, and behavior", in Emerging Model Organisms, Cold Spring Harbor Press
26. 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
27. Vandenberg, L. N., and Levin, M., (2008), "Perspectives and open problems in the early phases of left-right patterning", **Seminars in Cell and Developmental Biology**, 20: 456-463
28. Aw, S., and Levin, M., (2009), "Is LR asymmetry a form of planar cell polarity?", **Development**, 136: 355-366

29. Levin, M., (2009), "Bioelectric mechanisms in regeneration: unique aspects and future perspectives", **Seminars in Cell and Developmental Biology**, 20: 543-556
30. 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
31. 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]
32. 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]
33. 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
34. 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
35. Levin, M., (2012), "Molecular bioelectricity in developmental biology: new tools and recent discoveries", **BioEssays**, 34(3): 205-217 [cover]
36. Levin, M., and Stevenson, C., (2012), "Regulation of cell behavior and tissue patterning by bioelectrical signals: challenges and opportunities for biomedical engineering", **Annual Reviews in Biomedical Engineering**, 14: 295-323
37. Lobo, D., Beane, W., and Levin, M., (2012), "Modeling planarian regeneration: a primer for reverse-engineering the worm", **PLoS Computational Biology**, 8(4): e1002481. [cover]
38. Levin, M., (2012), "Morphogenetic fields in embryogenesis, regeneration, and cancer: non-local control of complex patterning", **BioSystems**, 109: 243-261 [most downloaded article]
39. Tseng, A-S., and Levin, M., (2013), "Cracking the bioelectric code: probing endogenous ionic controls of pattern formation", **Communicative and Integrative Biology**, 6(1): 1-8 [cover]
40. Adams, D. S., and Levin, M., (2013), "Endogenous Voltage Gradients as Mediators of Cell-Cell Communication: Strategies for Investigating Bioelectrical Signals During Pattern Formation", **Cell and Tissue Research**, 352:95-122 [cover]
41. Vandenberg, L. N., and Levin, M., (2013), "A unified model for left-right asymmetry? Comparison and synthesis of molecular models of laterality", **Developmental Biology**, 379: 1-15 [cover]
42. Levin, M., (2013), "Reprogramming cells and tissue patterning via bioelectrical pathways: molecular mechanisms and biomedical opportunities", **WIREs Systems Biology and Medicine**, 5(6): 657-676 [Top Ten Most Cited Article in 2014]
43. Vandenberg, Laura N., Joan M. Lemire, and Levin, M., (2013), "It's never too early to get it right", **Communicative and Integrative Biology**, 6(6): e27155
44. Lobo, D., Solano, M., Bubenik, G. A., and Levin M., (2014), "A linear-encoding model explains the variability of the target morphology in regeneration", **Journal of the Royal Society Interface**, 11: 20130918 [F1000Prime recommended]
45. Lobikin, M., and Levin, M., (2014), "Endogenous bioelectric cues as morphogenetic signals in vivo", chapter 15 in **Fields of the Cell**, edited by D. Fels and M. Cifra, p. 283-302
46. Pai, V., and Levin, M., (2014), "Bioelectric Controls of Stem Cell Function", in **Stem Cells**, edited by F. Calegari and C. Waskow, CRC Press, Chapter 5, p. 106-145
47. Chernet, B. T., and Levin M., (2014), "Endogenous voltage potentials and the microenvironment: bioelectric signals that reveal, induce, and normalize cancer", **Journal of Clinical and Experimental Oncology**, S1: doi:10.4172/2324-9110.S1-002
48. Levin, M., (2014), "Endogenous bioelectrical networks store non-genetic patterning information during development and regeneration", **Journal of Physiology**, 592(11): 2295-2305
49. Hernandez-Diaz S., and Levin, M., (2014), "Alteration of bioelectrically-controlled processes in the embryo: a teratogenic mechanism for anticonvulsants", **Reproductive Toxicology**, 47: 111-114
50. Mustard, J., and Levin, M., (2014), "Bioelectrical mechanisms for programming growth and form: taming physiological networks for soft body robotics", **Soft Robotics**, 1(3): 169-191
51. Zhu, F., Skommer, J., Huang, Y., Akagi, J., Adams, D. S., Levin, M., Hall, C. J., Crosier, P. S., and Wlodkowic, D., (2014), "Fishing on chips: up-and-coming technological advances in analysis of zebrafish and *Xenopus* embryos", **Cytometry A**, 85A: 921-932

52. Levin, M., (2014), Molecular bioelectricity: how endogenous voltage potentials control cell behavior and instruct pattern regulation in vivo”, **Molecular Biology of the Cell**, 25: 3835-3850
53. Pezzulo, G., and Levin, M., (2015), “Re-membling the body: applications of computational neuroscience to the top-down control of regeneration of limbs and other complex organs”, **Integrative Biology**, 7: 1487-1517 [cover]
54. Blackiston, D. J., Shomrat, T., and Levin, M., (2015), "The Stability of Memories During Brain Remodeling: a Perspective", **Communicative and Integrative Biology**, 8(5): e1073424
55. Bessonov, N., Levin, M., Morozova, N., Reinberg, N., Tosenberger, A., Volpert, V., (2015), “Target morphology and cell memory: a model of regenerative pattern formation”, **Neural Regeneration Research**, 10(12): 1901-1905
56. Lobo, D., and Levin, M., (2016), "Computing a worm: reverse-engineering planarian regeneration", Advances in Unconventional Computing, Andrew Adamatzky ed., Springer, in press
57. Edelstein, L., Fuxe, K., Levin, M., Popescu, B., and Smythies, J., (2016), "Telocytes in their context with other intercellular communication agents”, Seminars in Cell and Developmental Biology, in press
58. Blackiston, D. J., and Levin, M., (2016), “Reversals of Bodies, Brains, and Behavior: quantitative analysis of laterality and its disturbance in model species”, in Lateralized Brain Functions, edited by Dr. Wolfgang Walz
59. Durant, F., Lobo, D., Hammelman, J., and Levin, M., (2016), “Physiological controls of large-scale patterning in planarian regeneration: a molecular and computational perspective on growth and form”, **Regeneration**, 3(2): 78-102

D. Editorial Boards: *JSE, Laterality, Regeneration*