



Universiteit
Leiden
The Netherlands

Anisotropy in cell mechanics

Schakenraad, K.K.

Citation

Schakenraad, K. K. (2020, May 13). *Anisotropy in cell mechanics*. *Casimir PhD Series*. Retrieved from <https://hdl.handle.net/1887/87895>

Version: Publisher's Version

License: [Licence agreement concerning inclusion of doctoral thesis in the Institutional Repository of the University of Leiden](#)

Downloaded from: <https://hdl.handle.net/1887/87895>

Note: To cite this publication please use the final published version (if applicable).

Cover Page



Universiteit Leiden



The handle <http://hdl.handle.net/1887/87895> holds various files of this Leiden University dissertation.

Author: Schakenraad, K.K.

Title: Anisotropy in cell mechanics

Issue Date: 2020-05-13

Bibliography

- [1] J. D. Watson and F. H. C. Crick, 'Molecular Structure of Nucleic Acids: A Structure for Deoxyribose Nucleic Acid', *Nature* **171**, 737 (1953) (pp. 1, 2).
- [2] C. Monico, M. Capitanio, G. Belcastro, F. Vanzi and F. S. Pavone, 'Optical methods to study protein-DNA interactions in vitro and in living cells at the single-molecule level', *International journal of molecular sciences* **14**, 3961 (2013) (p. 1).
- [3] A. Ashkin, K. Schütze, J. M. Dziedzic, U. Euteneuer and M. Schliwa, 'Force generation of organelle transport measured in vivo by an infrared laser trap', *Nature* **348**, 346 (1990) (p. 1).
- [4] S. Smith, L. Finzi and C. Bustamante, 'Direct mechanical measurements of the elasticity of single DNA molecules by using magnetic beads', *Science* **258**, 1122 (1992) (p. 1).
- [5] E. Florin, V. Moy and H. Gaub, 'Adhesion forces between individual ligand-receptor pairs', *Science* **264**, 415 (1994) (p. 1).
- [6] K. Schakenraad, A. S. Biebricher, M. Sebrechts, B. ten Bonsel, E. J. G. Peterman, G. J. L. Wuite, I. Heller, C. Storm and P. van der Schoot, 'Hyperstretching DNA', *Nature Communications* **8**, 2197 (2017) (p. 1).
- [7] A. M. Turing, 'The chemical basis of morphogenesis', *Bulletin of Mathematical Biology* **52**, 153 (1990) (p. 1).
- [8] N. Bacaër, *A short history of mathematical population dynamics* (Springer Science & Business Media, 2011) (p. 1).
- [9] A. Anderson and K. Rejniak, *Single-cell-based models in biology and medicine* (Springer Science & Business Media, 2007) (pp. 1, 7, 72, 89).
- [10] A. G. Fletcher, M. Osterfield, R. E. Baker and S. Y. Shvartsman, 'Vertex models of epithelial morphogenesis', *Biophysical Journal* **106**, 2291 (2014) (p. 1).
- [11] R. Pfeifer, M. Lungarella and F. Iida, 'Self-organization, embodiment, and biologically inspired robotics', *Science* **318**, 1088 (2007) (p. 1).
- [12] H. Shin, S. Jo and A. G. Mikos, 'Biomimetic materials for tissue engineering', *Biomaterials* **24**, Synthesis of Biomimetic Polymers, 4353 (2003) (p. 1).

- [13] I. Prigogine, *Non-equilibrium statistical mechanics* (Courier Dover Publications, 2017) (p. 1).
- [14] S. Ramaswamy, 'Active matter', *Journal of Statistical Mechanics: Theory and Experiment* **2017**, 054002 (2017) (pp. 1, 73).
- [15] A. Cavagna and I. Giardina, 'Bird flocks as condensed matter', *Annual Review of Condensed Matter Physics* **5**, 183 (2014) (p. 2).
- [16] P. Cluzel, A. Lebrun, C. Heller, R. Lavery, J.-L. Viovy, D. Chatenay and F. Caron, 'DNA: an extensible molecule', *Science* **271**, 792 (1996) (p. 2).
- [17] S. B. Smith, Y. Cui and C. Bustamante, 'Overstretching B-DNA: the elastic response of individual double-stranded and single-stranded DNA molecules', *Science* **271**, 795 (1996) (p. 2).
- [18] J. F. Léger, G. Romano, A. Sarkar, J. Robert, L. Bourdieu, D. Chatenay and J. F. Marko, 'Structural transitions of a twisted and stretched DNA molecule', *Physical Review Letters* **83**, 1066 (1999) (p. 2).
- [19] J. F. Marko and E. D. Siggia, 'Stretching DNA', *Macromolecules* **28**, 8759 (1995) (p. 2).
- [20] M. M. Palm and R. M. H. Merks, 'Vascular networks due to dynamically arrested crystalline ordering of elongated cells', *Physical Review E* **87**, 012725 (2013) (pp. 2, 7).
- [21] S. E. Boas and R. M. H. Merks, 'Tip cell overtaking occurs as a side effect of sprouting in computational models of angiogenesis', *BMC systems biology* **9**, 86 (2015) (pp. 2, 7).
- [22] B. Guirao, S. U. Rigaud, F. Bosveld, A. Bailles, J. Lopez-Gay, S. Ishihara, K. Sugimura, F. Graner and Y. Bellaiche, 'Unified quantitative characterization of epithelial tissue development', *Elife* **4**, e08519 (2015) (pp. 2, 7).
- [23] B. K. A. Nelemans, M. Schmitz, H. Tahir, R. M. H. Merks and T. H. Smit, 'Mechanical strain can increase segment number in live chick embryos', *bioRxiv* (2018) 10.1101/211623 (pp. 2, 7).
- [24] L. Sui et al., 'Differential lateral and basal tension drive folding of drosophila wing discs through two distinct mechanisms', *Nature Communications* **9**, 4620 (2018) (p. 2).
- [25] T. Vicsek and A. Zafeiris, 'Collective motion', *Physics Reports* **517**, 71 (2012) (p. 2).
- [26] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen and O. Shochet, 'Novel type of phase transition in a system of self-driven particles', *Physical Review Letters* **75**, 1226 (1995) (p. 2).
- [27] J. Toner and Y. Tu, 'Long-range order in a two-dimensional dynamical XY model: how birds fly together', *Physical Review Letters* **75**, 4326 (1995) (p. 2).
- [28] A. J. Engler, S. Sen, H. L. Sweeney and D. E. Discher, 'Matrix elasticity directs stem cell lineage specification.', *Cell* **126**, 677 (2006) (pp. 2, 16, 34, 70).

-
- [29] B. Alberts, A. Johnson, J. Lewis, M. Raff, K. Roberts and P. Walter, *Molecular biology of the cell* (Garland Science, 2008) (pp. 3, 4, 9).
- [30] B. Trappmann et al., 'Extracellular-matrix tethering regulates stem-cell fate.', *Nature Materials* **11**, 642 (2012) (pp. 3, 16, 34, 70).
- [31] X. Wang, X. Hu, I. Dulinska-Molak, N. Kawazoe, Y. Yang and G. Chen, 'Discriminating the independent influence of cell adhesion and spreading area on stem cell fate determination using micropatterned surfaces', *Scientific Reports* **6**, 28708 (2016) (p. 3).
- [32] R. McBeath, D. M. Pirone, C. M. Nelson, K. Bhadriraju and C. S. Chen, 'Cell shape, cytoskeletal tension, and RhoA regulate stem cell lineage commitment', *Developmental Cell* **6**, 483 (2004) (pp. 3, 34).
- [33] K. A. Kilian, B. Bugarija, B. T. Lahn and M. Mrksich, 'Geometric cues for directing the differentiation of mesenchymal stem cells', *Proceedings of the National Academy of Sciences* **107**, 4872 (2010) (pp. 3, 34, 58).
- [34] N. Minc, D. Burgess and F. Chang, 'Influence of cell geometry on division-plane positioning', *Cell* **144**, 414 (2011) (pp. 3, 34).
- [35] M. Versaevel, T. Grevesse and S. Gabriele, 'Spatial coordination between cell and nuclear shape within micropatterned endothelial cells', *Nature Communications* **3**, 671 (2012) (pp. 3, 34).
- [36] C. S. Chen, M. Mrksich, S. Huang, G. M. Whitesides and D. E. Ingber, 'Geometric control of cell life and death', *Science* **276**, 1425 (1997) (pp. 3, 34).
- [37] N. Jain, K. V. Iyer, A. Kumar and G. V. Shivashankar, 'Cell geometric constraints induce modular gene-expression patterns via redistribution of HDAC3 regulated by actomyosin contractility', *Proceedings of the National Academy of Sciences* **110**, 11349 (2013) (pp. 3, 34).
- [38] S. van Helvert, C. Storm and P. Friedl, 'Mechanoreciprocity in cell migration', *Nature Cell Biology* **20**, 8 (2018) (p. 3).
- [39] O. V. Kim, R. I. Litvinov, J. W. Weisel and M. S. Alber, 'Structural basis for the nonlinear mechanics of fibrin networks under compression', *Biomaterials* **35**, 6739 (2014) (p. 3).
- [40] I. Pushkarsky et al., 'Elastomeric sensor surfaces for high-throughput single-cell force cytometry', *Nature Biomedical Engineering* **2**, 124 (2018) (pp. 3, 70).
- [41] S. Suresh, 'Biomechanics and biophysics of cancer cells', *Acta Materialia* **55**, 3989 (2007) (p. 3).
- [42] S. Kumar and V. M. Weaver, 'Mechanics, malignancy, and metastasis: the force journey of a tumor cell', *Cancer and Metastasis Reviews* **28**, 113 (2009) (p. 3).
- [43] Q. Tseng et al., 'A new micropatterning method of soft substrates reveals that different tumorigenic signals can promote or reduce cell contraction levels', *Lab Chip* **11**, 2231 (2011) (pp. 3, 58, 70, 81, 82, 86–88, 114, 115).

- [44] C. M. Kraning-Rush, J. P. Califano and C. A. Reinhart-King, 'Cellular traction stresses increase with increasing metastatic potential', *PLOS ONE* **7**, 1 (2012) (pp. 3, 70).
- [45] V. Peschetola, V. M. Laurent, A. Duperray, R. Michel, D. Ambrosi, L. Preziosi and C. Verdier, 'Time-dependent traction force microscopy for cancer cells as a measure of invasiveness', *Cytoskeleton* **70**, 201 (2013) (pp. 3, 70).
- [46] S. Pellegrin and H. Mellor, 'Actin stress fibres.', *Journal of cell science* **120**, 3491 (2007) (pp. 4, 16, 17, 38, 71, 113).
- [47] K. Burridge and E. S. Wittchen, 'The tension mounts: Stress fibers as force-generating mechanotransducers', *The Journal of Cell Biology* **200**, 9 (2013) (pp. 4, 16, 17, 38, 71, 113).
- [48] U. S. Schwarz and S. A. Safran, 'Physics of adherent cells', *Reviews of Modern Physics* **85**, 1327 (2013) (pp. 4–6, 16, 34, 36, 37, 44, 57, 70, 71).
- [49] A. Chopra, E. Tabdanov, H. Patel, P. A. Janmey and J. Y. Kresh, 'Cardiac myocyte remodeling mediated by n-cadherin-dependent mechanosensing', *American Journal of Physiology-Heart and Circulatory Physiology* **300**, H1252 (2011) (pp. 4, 34).
- [50] A. J. Engler, M. A. Griffin, S. Sen, C. G. Bönnemann, H. L. Sweeney and D. E. Discher, 'Myotubes differentiate optimally on substrates with tissue-like stiffness', *The Journal of Cell Biology* **166**, 877 (2004) (pp. 4, 34).
- [51] T. Yeung et al., 'Effects of substrate stiffness on cell morphology, cytoskeletal structure, and adhesion', *Cell Motility* **60**, 24 (2005) (pp. 4, 7, 34, 45).
- [52] A. Zemel, F. Rehfeldt, A. E. X. Brown, D. E. Discher and S. A. Safran, 'Cell shape, spreading symmetry, and the polarization of stress-fibers in cells', *Journal of Physics: Condensed Matter* **22**, 194110 (2010) (pp. 4, 34, 35, 43, 57).
- [53] F. Grinnell, 'Fibroblast-collagen-matrix contraction: growth-factor signalling and mechanical loading', *Trends in Cell Biology* **10**, 362 (2000) (pp. 4, 7, 34, 45).
- [54] K. Burridge and M. Chrzanowska-Wodnicka, 'Focal Adhesions, Contractility, and Signaling', *Annual Review of Cell and Developmental Biology* **12**, 463 (1996) (pp. 4, 16, 36, 70).
- [55] H. Van Hoorn, R. Harkes, E. M. Spiesz, C. Storm, D. Van Noort, B. Ladoux and T. Schmidt, 'The nanoscale architecture of force-bearing focal adhesions', *Nano Letters* **14**, 4257 (2014) (pp. 5, 16, 20, 22, 34, 35, 50, 70, 113, 114).
- [56] J. L. Tan, J. Tien, D. M. Pirone, D. S. Gray, K. Bhadriraju and C. S. Chen, 'Cells lying on a bed of microneedles: an approach to isolate mechanical force.', *Proceedings of the National Academy of Sciences* **100**, 1484 (2003) (pp. 5, 16, 20, 34, 35, 43, 44, 50, 58, 70, 113–115).
- [57] L. Trichet, J. Le Dıgabel, R. J. Hawkins, S. R. K. Vedula, M. Gupta, C. Ribault, P. Hersen, R. Voituriez and B. Ladoux, 'Evidence of a large-scale mechanosensing mechanism for cellular adaptation to substrate stiffness',

-
- Proceedings of the National Academy of Sciences **109**, 6933 (2012) (pp. 5, 16, 20, 22, 34, 35, 50, 70, 113, 114).
- [58] M. Théry, ‘Micropatterning as a tool to decipher cell morphogenesis and functions’, *Journal of Cell Science* **123**, 4201 (2010) (pp. 5, 22, 40, 58, 70, 114).
- [59] M. Dembo and Y.-L. Wang, ‘Stresses at the cell-to-substrate interface during locomotion of fibroblasts’, *Biophysical Journal* **76**, 2307 (1999) (pp. 5, 70).
- [60] J. P. Butler, I. M. Tolić-Nørrelykke, B. Fabry and J. J. Fredberg, ‘Traction fields, moments, and strain energy that cells exert on their surroundings’, *American Journal of Physiology-Cell Physiology* **282**, C595 (2002) (pp. 5, 70).
- [61] B. Sabass, M. L. Gardel, C. M. Waterman and U. S. Schwarz, ‘High resolution traction force microscopy based on experimental and computational advances’, *Biophysical Journal* **94**, 207 (2008) (pp. 5, 70).
- [62] R. Bar-Ziv, T. Tlusty, E. Moses, S. A. Safran and A. Bershadsky, ‘Pearling in cells: a clue to understanding cell shape’, *Proceedings of the National Academy of Sciences* **96**, 10140 (1999) (pp. 6, 7, 16, 17, 34, 36, 38, 57, 71, 74, 75).
- [63] I. B. Bischofs, F. Klein, D. Lehnert, M. Bastmeyer and U. S. Schwarz, ‘Filamentous Network Mechanics and Active Contractility Determine Cell and Tissue Shape’, *Biophysical Journal* **95**, 3488 (2008) (pp. 6, 7, 16, 17, 20, 21, 34, 36–39, 57, 71–75, 113).
- [64] I. B. Bischofs, S. S. Schmidt and U. S. Schwarz, ‘Effect of Adhesion Geometry and Rigidity on Cellular Force Distributions’, *Physical Review Letters* **103**, 1 (2009) (pp. 6, 7, 16, 17, 21, 34, 36–38, 42, 57, 70–75, 113).
- [65] S. Banerjee and L. Gioni, ‘Polymorphism and bistability in adherent cells’, *Soft Matter* **9**, 5251 (2013) (pp. 6, 16, 36, 37, 42, 71).
- [66] L. Gioni, ‘Softly constrained films’, *Soft Matter* **9**, 8121 (2013) (pp. 6, 16, 36, 71).
- [67] L. Gioni, ‘Contour models of cellular adhesion’, in *Cell migrations: causes and functions*, edited by C. A. M. La Porta and S. Zapperi (Springer International Publishing, Cham, 2019), pp. 13–29 (pp. 6, 34, 36, 37, 57, 71).
- [68] S. Banerjee, R. Sknepnek and M. C. Marchetti, ‘Optimal shapes and stresses of adherent cells on patterned substrates’, *Soft Matter* **10**, 2424 (2014) (pp. 6, 7, 70, 71, 113).
- [69] P. J. Albert and U. S. Schwarz, ‘Dynamics of cell shape and forces on micropatterned substrates predicted by a Cellular Potts Model’, *Biophysical Journal* **106**, 2340 (2014) (pp. 6, 7, 58, 70, 72, 73, 75, 81, 82, 85, 86, 88–90, 114, 115).
- [70] M. F. Coughlin and D. Stamenović, ‘A prestressed cable network model of the adherent cell cytoskeleton’, *Biophysical Journal* **84**, 1328 (2003) (p. 7).
- [71] R. Paul, P. Heil, J. P. Spatz and U. S. Schwarz, ‘Propagation of mechanical stress through the actin cytoskeleton toward focal adhesions: model and experiment’, *Biophysical Journal* **94**, 1470 (2008) (p. 7).

- [72] P. Guthardt Torres, I. B. Bischofs and U. S. Schwarz, 'Contractile network models for adherent cells', *Physical Review E* **85**, 011913 (2012) (p. 7).
- [73] S. Banerjee and M. C. Marchetti, 'Controlling cell-matrix traction forces by extracellular geometry', *New Journal of Physics* **15**, 035015 (2013) (pp. 7, 70, 85, 113).
- [74] P. Kollmannsberger and B. Fabry, 'Linear and nonlinear rheology of living cells', *Annual Review of Materials Research* **41**, 75 (2011) (p. 7).
- [75] V. S. Deshpande, R. M. McMeeking and A. G. Evans, 'A bio-chemo-mechanical model for cell contractility', *Proceedings of the National Academy of Sciences* **103**, 14015 (2006) (pp. 7, 35, 43, 48, 57).
- [76] V. S. Deshpande, R. M. McMeeking and A. G. Evans, 'A model for the contractility of the cytoskeleton including the effects of stress-fibre formation and dissociation', *Proceedings of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* **463**, 787 (2007) (pp. 7, 35, 43, 48, 57).
- [77] A. Pathak, V. S. Deshpande, R. M. McMeeking and A. G. Evans, 'The simulation of stress fibre and focal adhesion development in cells on patterned substrates', *Journal of The Royal Society Interface* **5**, 507 (2008) (pp. 7, 35, 43, 57, 58, 76, 80, 81).
- [78] J. P. McGarry, J. Fu, M. T. Yang, C. S. Chen, R. M. McMeeking, A. G. Evans and V. S. Deshpande, 'Simulation of the contractile response of cells on an array of micro-posts', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **367**, 3477 (2009) (p. 7).
- [79] W. Ronan, V. S. Deshpande, R. M. McMeeking and J. P. McGarry, 'Cellular contractility and substrate elasticity: a numerical investigation of the actin cytoskeleton and cell adhesion', *Biomechanics and Modeling in Mechanobiology* **13**, 417 (2014) (pp. 7, 35, 43, 57).
- [80] F. Graner and J. A. Glazier, 'Simulation of biological cell sorting using a two-dimensional extended Potts model', *Physical Review Letters* **69**, 2013 (1992) (p. 7).
- [81] J. A. Glazier and F. Graner, 'Simulation of the differential adhesion driven rearrangement of biological cells', *Physical Review E* **47**, 2128 (1993) (pp. 7, 72).
- [82] A. Szabó and R. M. H. Merks, 'Cellular Potts modeling of tumor growth, tumor invasion, and tumor evolution', *Frontiers in oncology* **3**, 87 (2013) (p. 7).
- [83] B. Vianay, J. Käfer, E. Planus, M. Block, F. Graner and H. Guillou, 'Single cells spreading on a protein lattice adopt an energy minimizing shape', *Physical Review Letters* **105**, 128101 (2010) (pp. 7, 72).
- [84] P. J. Albert and U. S. Schwarz, 'Modeling cell shape and dynamics on micropatterns', *Cell Adhesion & Migration* **10**, 516 (2016) (pp. 7, 58, 72).
- [85] T. Vignaud, L. Blanchoin and M. Théry, 'Directed cytoskeleton self-organization', *Trends in Cell Biology* **22**, 671 (2012) (pp. 7, 34, 43, 45, 76).

-
- [86] B. Ladoux, R.-M. Mège and X. Trepât, ‘Front–rear polarization by mechanical cues: from single cells to tissues’, *Trends in Cell Biology* **26**, 420 (2016) (pp. 7, 34, 43, 45, 76).
- [87] N. T. Lam, T. J. Muldoon, K. P. Quinn, N. Rajaram and K. Balachandran, ‘Valve interstitial cell contractile strength and metabolic state are dependent on its shape’, *Integrative Biology* **8**, 1079 (2016) (pp. 7, 34, 43, 45, 50, 76, 79).
- [88] S. K. Gupta, Y. Li and M. Guo, ‘Anisotropic mechanics and dynamics of a living mammalian cytoplasm’, *Soft Matter* **15**, 190 (2019) (pp. 7, 34, 43, 45, 50, 76, 79).
- [89] P. Roca-Cusachs, J. Alcaraz, R. Sunyer, J. Samitier, R. Farré and D. Navajas, ‘Micropatterning of single endothelial cell shape reveals a tight coupling between nuclear volume in G1 and proliferation’, *Biophysical Journal* **94**, 4984 (2008) (pp. 7, 50, 70, 76, 79, 84, 85, 88, 113, 114).
- [90] K. Mandal, I. Wang, E. Vitiello, L. A. C. Orellana and M. Balland, ‘Cell dipole behaviour revealed by ECM sub-cellular geometry’, *Nature Communications* **5**, 5749 (2014) (pp. 7, 70, 84, 85, 88, 113, 114).
- [91] P.-G. De Gennes and J. Prost, *The physics of liquid crystals*, Vol. 83 (Oxford university press, 1993) (pp. 7, 8, 43, 44, 57, 76, 114).
- [92] G. Meier, E. Sackmann and J. G. Grabmaier, *Applications of liquid crystals* (Springer Science & Business Media, 2012) (p. 7).
- [93] D. Pauluth and K. Tarumi, ‘Advanced liquid crystals for television’, *Journal of Materials Chemistry* **14**, 1219 (2004) (p. 7).
- [94] L. Onsager, ‘The effects of shape on the interaction of colloidal particles’, *Annals of the New York Academy of Sciences* **51**, 627 (1949) (p. 7).
- [95] M. Nobili and G. Durand, ‘Disorientation-induced disordering at a nematic-liquid-crystal–solid interface’, *Physical Review A* **46**, R6174 (1992) (pp. 8, 45, 77).
- [96] M. Kleman and O. D. Lavrentovich, ‘Topological point defects in nematic liquid crystals’, *Philosophical Magazine* **86**, 4117 (2006) (pp. 8, 79).
- [97] T. Odijk, ‘Theory of lyotropic polymer liquid crystals’, *Macromolecules* **19**, 2313 (1986) (p. 8).
- [98] P. Prinsen and P. van der Schoot, ‘Shape and director-field transformation of tactoids’, *Physical Review E* **68**, 021701 (2003) (p. 8).
- [99] O. V. Manyuhina, K. B. Lawlor, M. C. Marchetti and M. J. Bowick, ‘Viral nematics in confined geometries’, *Soft Matter* **11**, 6099 (2015) (p. 8).
- [100] M. Leoni, O. V. Manyuhina, M. J. Bowick and M. C. Marchetti, ‘Defect driven shapes in nematic droplets: analogies with cell division’, *Soft Matter* **13**, 1257 (2017) (p. 8).
- [101] A. Doostmohammadi, J. Ignés-Mullol, J. M. Yeomans and F. Sagués, ‘Active nematics’, *Nature Communications* **9**, 3246 (2018) (p. 8).

- [102] T. J. Pedley and J. O. Kessler, 'Hydrodynamic Phenomena in Suspensions of Swimming Microorganisms', *Annual Review of Fluid Mechanics* **24**, 313 (1992) (pp. 8, 17, 37, 71, 73).
- [103] R. A. Simha and S. Ramaswamy, 'Hydrodynamic Fluctuations and Instabilities in Ordered Suspensions of Self-Propelled Particles', *Physical Review Letters* **89**, 058101 (2002) (pp. 8, 17, 37, 71, 73).
- [104] S. P. Thampi, R. Golestanian and J. M. Yeomans, 'Vorticity, defects and correlations in active turbulence', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **372**, 20130366 (2014) (p. 8).
- [105] L. Giomi, 'Geometry and topology of turbulence in active nematics', *Physical Review X* **5**, 031003 (2015) (p. 8).
- [106] L. Giomi, M. J. Bowick, P. Mishra, R. Sknepnek and M. Cristina Marchetti, 'Defect dynamics in active nematics', *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **372**, 20130365 (2014) (p. 8).
- [107] T. Sanchez, D. T. N. Chen, S. J. DeCamp, M. Heymann and Z. Dogic, 'Spontaneous motion in hierarchically assembled active matter', *Nature* **491**, 431 (2012) (p. 8).
- [108] V. Schaller and A. R. Bausch, 'Topological defects and density fluctuations in collectively moving systems', *Proceedings of the National Academy of Sciences* **110**, 4488 (2013) (p. 8).
- [109] Z. You, D. J. G. Pearce, A. Sengupta and L. Giomi, 'Geometry and mechanics of microdomains in growing bacterial colonies', *Physical Review X* **8**, 031065 (2018) (p. 8).
- [110] G. Duclos, S. Garcia, H. G. Yevick and P. Silberzan, 'Perfect nematic order in confined monolayers of spindle-shaped cells', *Soft Matter* **10**, 2346 (2014) (p. 8).
- [111] T. B. Saw et al., 'Topological defects in epithelia govern cell death and extrusion', *Nature* **544**, 212 (2017) (pp. 8, 58, 89).
- [112] A. Hall, 'Rho GTPases and the actin cytoskeleton', *Science* **279**, 509 (1998) (p. 8).
- [113] I. Dierking and S. Al-Zangana, 'Lyotropic liquid crystal phases from anisotropic nanomaterials', *Nanomaterials* **7**, 305 (2017) (p. 8).
- [114] W. R. Holmes and L. Edelstein-Keshet, 'A comparison of computational models for eukaryotic cell shape and motility', *PLOS Computational Biology* **8**, 1 (2012) (p. 9).
- [115] F. Ziebert and I. S. Aranson, 'Computational approaches to substrate-based cell motility', *Npj Computational Materials* **2**, 16019 (2016) (p. 9).
- [116] D. Selmecki, S. Mosler, P. H. Hagedorn, N. B. Larsen and H. Flyvbjerg, 'Cell motility as persistent random motion: theories from experiments', *Biophysical Journal* **89**, 912 (2005) (pp. 9, 97).

-
- [117] L. Li, E. C. Cox and H. Flyvbjerg, ‘Dicty dynamics’: dictyostelium motility as persistent random motion’, *Physical Biology* **8**, 046006 (2011) (pp. 9, 98).
- [118] Y. Loosli, R. Luginbuehl and J. G. Snedeker, ‘Cytoskeleton reorganization of spreading cells on micro-patterned islands: a functional model’, *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **368**, 2629 (2010) (pp. 9, 89, 115).
- [119] T. Shemesh, A. D. Bershadsky and M. M. Kozlov, ‘Physical model for self-organization of actin cytoskeleton and adhesion complexes at the cell front’, *Biophysical Journal* **102**, 1746 (2012) (p. 9).
- [120] D. Shao, W.-J. Rappel and H. Levine, ‘Computational model for cell morphodynamics’, *Physical Review Letters* **105**, 108104 (2010) (p. 9).
- [121] F. Ziebert, S. Swaminathan and I. S. Aranson, ‘Model for self-polarization and motility of keratocyte fragments’, *Journal of The Royal Society Interface* **9**, 1084 (2012) (p. 9).
- [122] E. L. Barnhart, K.-C. Lee, K. Keren, A. Mogilner and J. A. Theriot, ‘An adhesion-dependent switch between mechanisms that determine motile cell shape’, *PLOS Biology* **9**, 1 (2011) (p. 9).
- [123] E. Tjhung, A. Tiribocchi, D. Marenduzzo and M. E. Cates, ‘A minimal physical model captures the shapes of crawling cells’, *Nature Communications* **6**, 5420 (2015) (p. 9).
- [124] A. F. M. Marée, V. A. Grieneisen and L. Edelstein-Keshet, ‘How cells integrate complex stimuli: the effect of feedback from phosphoinositides and cell shape on cell polarization and motility’, *PLOS Computational Biology* **8**, 1 (2012) (pp. 9, 58, 72, 89, 108, 115).
- [125] I. Niculescu, J. Textor and R. J. de Boer, ‘Crawling and gliding: a computational model for shape-driven cell migration’, *PLOS Computational Biology* **11**, 1 (2015) (pp. 9, 72, 89, 104, 108, 115–117).
- [126] H. C. Berg and D. A. Brown, ‘Chemotaxis in escherichia coli analysed by three-dimensional tracking’, *Nature* **239**, 500 (1972) (pp. 9, 107).
- [127] K. F. Swaney, C.-H. Huang and P. N. Devreotes, ‘Eukaryotic chemotaxis: a network of signaling pathways controls motility, directional sensing, and polarity’, *Annual Review of Biophysics* **39**, 265 (2010) (pp. 9, 96).
- [128] P. J. M. Van Haastert and P. N. Devreotes, ‘Chemotaxis: signalling the way forward’, *Nature Reviews Molecular Cell Biology* **5**, 626 (2004) (pp. 9, 96).
- [129] P. A. Iglesias and P. N. Devreotes, ‘Navigating through models of chemotaxis’, *Current Opinion in Cell Biology* **20**, 35 (2008) (p. 9).
- [130] T. Hillen and K. J. Painter, ‘A user’s guide to PDE models for chemotaxis’, *Journal of Mathematical Biology* **58**, 183 (2008) (p. 9).

- [131] J. B. McCarthy and L. T. Furcht, 'Laminin and fibronectin promote the haptotactic migration of B16 mouse melanoma cells in vitro.', *The Journal of Cell Biology* **98**, 1474 (1984) (pp. 9, 96).
- [132] C. M. Lo, H. B. Wang, M. Dembo and Y. L. Wang, 'Cell movement is guided by the rigidity of the substrate.', *Biophysical Journal* **79**, 144 (2000) (pp. 9, 16, 34, 70, 96).
- [133] D. G. Mallet and G. J. Pettet, 'A mathematical model of integrin-mediated haptotactic cell migration', *Bulletin of Mathematical Biology* **68**, 231 (2006) (p. 9).
- [134] G. Charras and E. Sahai, 'Physical influences of the extracellular environment on cell migration', *Nature Reviews Molecular Cell Biology* **15**, 813 (2014) (pp. 9, 96).
- [135] G. Yu, J. Feng, H. Man and H. Levine, 'Phenomenological modeling of durotaxis', *Physical Review E* **96**, 010402 (2017) (pp. 9, 101, 105, 107).
- [136] E. G. Rens and R. M. H. Merks, 'Cell Shape and Durotaxis Follow from Mechanical Cell-Substrate Reciprocity and Focal Adhesion Dynamics: A Unifying Mathematical Model', *arXiv:1906.08962* (2019) (pp. 9, 35, 43, 57, 58, 89, 115).
- [137] D. Caballero, J. Comelles, M. Piel, R. Voituriez and D. Riveline, 'Ratchetaxis: long-range directed cell migration by local cues', *Trends in Cell Biology* **25**, 815 (2015) (pp. 9, 96).
- [138] S. E. Kim et al., 'Cell migration according to shape of graphene oxide micropatterns', *Micromachines* **7**, 186 (2016) (pp. 9, 96).
- [139] E. L. Maout, S. L. Vecchio, A. Bhat and D. Riveline, 'Chapter 7 - Directing cell migration on flat substrates and in confinement with microfabrication and microfluidics', in *Microfluidics in cell biology part b: microfluidics in single cells*, Vol. 147, edited by M. Piel, D. Fletcher and J. Doh, *Methods in Cell Biology* (Academic Press, 2018), pp. 109–132 (pp. 9, 96).
- [140] J. Park, D.-H. Kim, H.-N. Kim, C. J. Wang, M. K. Kwak, E. Hur, K.-Y. Suh, S. S. An and A. Levchenko, 'Directed migration of cancer cells guided by the graded texture of the underlying matrix', *Nature Materials* **15**, 792 (2016) (pp. 9, 96).
- [141] J. Park, D.-H. Kim and A. Levchenko, 'Topotaxis: a new mechanism of directed cell migration in topographic ECM gradients', *Biophysical Journal* **114**, 1257 (2018) (pp. 9, 96).
- [142] C. Heo, C. Jeong, H. S. Im, J. U. Kim, J. Woo, J. Y. Lee, B. Park, M. Suh and T.-i. Kim, 'Cellular behavior controlled by bio-inspired and geometry-tunable nanohairs', *Nanoscale* **9**, 17743 (2017) (pp. 9, 96).
- [143] J. A. J. Wondergem, M. Mytiliniou, F. C. H. de Wit, T. G. A. Reuvers, D. Holcman and D. Heinrich, 'Chemotaxis and topotaxis add vectorially for amoeboid cell

-
- migration', *bioRxiv* (2019) 10.1101/735779 (pp. 9, 10, 89, 96, 98, 107, 108, 114, 116).
- [144] C. Bechinger, R. Di Leonardo, H. Löwen, C. Reichhardt, G. Volpe and G. Volpe, 'Active particles in complex and crowded environments', *Reviews of Modern Physics* **88**, 045006 (2016) (pp. 10, 97).
 - [145] A. Zöttl and H. Stark, 'Emergent behavior in active colloids', *Journal of Physics: Condensed Matter* **28**, 253001 (2016) (pp. 10, 97, 98).
 - [146] L. Angelani, A. Costanzo and R. Di Leonardo, 'Active ratchets', *Europhysics Letters* **96**, 68002 (2011) (pp. 10, 97).
 - [147] B.-q. Ai, Q.-y. Chen, Y.-f. He, F.-g. Li and W.-r. Zhong, 'Rectification and diffusion of self-propelled particles in a two-dimensional corrugated channel', *Physical Review E* **88**, 062129 (2013) (pp. 10, 97).
 - [148] B.-Q. Ai and J.-C. Wu, 'Transport of active ellipsoidal particles in ratchet potentials', *The Journal of Chemical Physics* **140**, 094103 (2014) (pp. 10, 97).
 - [149] M. S. Davies Wykes, X. Zhong, J. Tong, T. Adachi, Y. Liu, L. Ristroph, M. D. Ward, M. J. Shelley and J. Zhang, 'Guiding microscale swimmers using teardrop-shaped posts', *Soft Matter* **13**, 4681 (2017) (pp. 10, 97, 108, 115).
 - [150] J. Tong and M. Shelley, 'Directed migration of microscale swimmers by an array of shaped obstacles: modeling and shape optimization', *SIAM Journal on Applied Mathematics* **78**, 2370 (2018) (pp. 10, 97, 108, 115).
 - [151] P. K. Ghosh, V. R. Misko, F. Marchesoni and F. Nori, 'Self-propelled janus particles in a ratchet: numerical simulations', *Physical Review Letters* **110**, 268301 (2013) (pp. 10, 97).
 - [152] X. Ao, P. Ghosh, Y. Li, G. Schmid, P. Hänggi and F. Marchesoni, 'Active Brownian motion in a narrow channel', *The European Physical Journal Special Topics* **223**, 3227 (2014) (pp. 10, 97).
 - [153] E. Yariv and O. Schnitzer, 'Ratcheting of Brownian swimmers in periodically corrugated channels: a reduced fokker-planck approach', *Physical Review E* **90**, 032115 (2014) (pp. 10, 97).
 - [154] J. Katuri, D. Caballero, R. Voituriez, J. Samitier and S. Sanchez, 'Directed flow of micromotors through alignment interactions with micropatterned ratchets', *ACS Nano* **12**, 7282 (2018) (pp. 10, 97).
 - [155] M. N. Popescu, W. E. Uspal, C. Bechinger and P. Fischer, 'Chemotaxis of active janus nanoparticles', *Nano Letters* **18**, 5345 (2018) (pp. 10, 97).
 - [156] S. Saha, S. Ramaswamy and R. Golestanian, 'Pairing, waltzing and scattering of chemotactic active colloids', *New Journal of Physics* **21**, 063006 (2019) (pp. 10, 97).
 - [157] E. A. Novikova, M. Raab, D. E. Discher and C. Storm, 'Persistence-driven durotaxis: generic, directed motility in rigidity gradients', *Physical Review Letters* **118**, 078103 (2017) (pp. 10, 97, 101, 105, 107, 108).

- [158] C. Lozano and C. Bechinger, 'Diffusing wave paradox of phototactic particles in traveling light pulses', *Nature Communications* **10**, 2495 (2019) (pp. 10, 97).
- [159] K. S. Midwood, L. V. Williams and J. E. Schwarzbauer, 'Tissue repair and the dynamics of the extracellular matrix', *International Journal of Biochemistry and Cell Biology* **36**, 1031 (2004) (p. 16).
- [160] N. P. Barry and M. S. Bretscher, 'Dictyostelium amoebae and neutrophils can swim.', *Proceedings of the National Academy of Sciences* **107**, 11376 (2010) (p. 16).
- [161] H. Tanimoto and M. Sano, 'Dynamics of traction stress field during cell division', *Physical Review Letters* **109**, 1 (2012) (p. 16).
- [162] B. Geiger, J. P. Spatz and A. D. Bershadsky, 'Environmental sensing through focal adhesions', *Nature Reviews Molecular Cell Biology* **10**, 21 (2009) (p. 16).
- [163] D. E. Discher, P. Janmey and Y.-L. Wang, 'Tissue cells feel and respond to the stiffness of their substrate', *Science* **310**, 1139 (2005) (p. 16).
- [164] F. Jülicher, K. Kruse, J. Prost and J. F. Joanny, 'Active behavior of the Cytoskeleton', *Physics Reports* **449**, 3 (2007) (p. 16).
- [165] B. D. Hoffman, C. Grashoff and M. A. Schwartz, 'Dynamic molecular processes mediate cellular mechanotransduction.', *Nature* **475**, 316 (2011) (p. 16).
- [166] M. G. Mendez and P. A. Janmey, 'Transcription factor regulation by mechanical stress.', *The international journal of biochemistry & cell biology* **44**, 728 (2012) (p. 16).
- [167] Y. Sawada, M. Tamada, B. J. Dubin-Thaler, O. Cherniavskaya, R. Sakai, S. Tanaka and M. P. Sheetz, 'Force sensing by mechanical extension of the Src family kinase substrate p130Cas', *Cell* **127**, 1015 (2006) (pp. 16, 34, 70).
- [168] C. A. Reinhart-King, M. Dembo and D. A. Hammer, 'Cell-cell mechanical communication through compliant substrates', *Biophysical Journal* **95**, 6044 (2008) (pp. 16, 34).
- [169] R. D. Sochol, A. T. Higa, R. R. R. Janairo, S. Li and L. Lin, 'Unidirectional mechanical cellular stimuli via micropost array gradients', *Soft Matter* **7**, 4606 (2011) (pp. 16, 34, 70).
- [170] M. Ghibaudo, L. Trichet, J. Le Digabel, A. Richert, P. Hersen and B. Ladoux, 'Substrate topography induces a crossover from 2D to 3D behavior in fibroblast migration.', *Biophysical journal* **97**, 357 (2009) (pp. 16, 34).
- [171] D. A. Fletcher and R. D. Mullins, 'Cell mechanics and the cytoskeleton', *Nature* **463**, 485 (2010) (pp. 16, 34).
- [172] H. E. Balcioğlu, H. van Hoorn, D. M. Donato, T. Schmidt and E. H. J. Danen, 'The integrin expression profile modulates orientation and dynamics of force transmission at cell-matrix adhesions.', *Journal of Cell Science* **128**, 1316 (2015) (pp. 16, 22, 27).

-
- [173] E. H. J. Danen, P. Sonneveld, C. Brakebusch, R. Fässler and A. Sonnenberg, ‘The fibronectin-binding integrins $\alpha 5 \beta 1$ and $\alpha v \beta 3$ differentially modulate RhoA–GTP loading, organization of cell matrix adhesions, and fibronectin fibrillogenesis’, *The Journal of Cell Biology* **159**, 1071 (2002) (pp. 16, 17, 22, 34, 50, 113, 114).
 - [174] L. Giomi, N. Hawley-Weld and L. Mahadevan, ‘Swarming, swirling and stasis in sequestered bristle-bots’, *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences* **469**, 20120637 (2013) (p. 17).
 - [175] E. Kassianidou, C. A. Brand, U. S. Schwarz and S. Kumar, ‘Geometry and network connectivity govern the mechanics of stress fibers’, *Proceedings of the National Academy of Sciences* **114**, 2622 (2017) (p. 18).
 - [176] M. Théry, V. Racine, M. Piel, A. Pépin, A. Dimitrov, Y. Chen, J.-B. Sibarita and M. Bornens, ‘Anisotropy of cell adhesive microenvironment governs cell internal organization and orientation of polarity’, *Proceedings of the National Academy of Sciences* **103**, 19771 (2006) (pp. 22, 44, 45, 52, 57, 58, 76, 81, 89, 114, 115).
 - [177] Orientation], <http://bigwww.epfl.ch/demo/orientation>, 1999 (pp. 23, 25, 32, 63).
 - [178] T. Panciera, L. Azzolin, M. Cordenonsi and S. Piccolo, ‘Mechanobiology of yap and taz in physiology and disease’, *Nature Reviews Molecular Cell Biology* **18**, 758 (2017) (p. 34).
 - [179] S. Walcott and S. X. Sun, ‘A mechanical model of actin stress fiber formation and substrate elasticity sensing in adherent cells’, *Proceedings of the National Academy of Sciences* **107**, 7757 (2010) (pp. 35, 43, 57).
 - [180] A. Zemel, F. Rehfeldt, A. E. X. Brown, D. E. Discher and S. A. Safran, ‘Optimal matrix rigidity for stress-fibre polarization in stem cells’, *Nature Physics* **6**, 468 (2010) (pp. 35, 43, 57).
 - [181] N. Nisenholz, M. Botton and A. Zemel, ‘Early-time dynamics of actomyosin polarization in cells of confined shape in elastic matrices’, *Soft Matter* **10**, 2453 (2014) (pp. 35, 43, 57).
 - [182] M. Raab, J. Swift, P. D. P. Dingal, P. Shah, J.-W. Shin and D. E. Discher, ‘Crawling from soft to stiff matrix polarizes the cytoskeleton and phosphoregulates myosin-ii heavy chain’, *The Journal of Cell Biology* **199**, 669 (2012) (pp. 35, 43, 57).
 - [183] V. Schaller, C. Weber, C. Semmrich, E. Frey and A. R. Bausch, ‘Polar patterns of driven filaments’, *Nature* **467**, 73 (2010) (pp. 35, 43, 57).
 - [184] P. Kraikivski, R. Lipowsky and J. Kierfeld, ‘Enhanced ordering of interacting filaments by molecular motors’, *Physical Review Letters* **96**, 258103 (2006) (pp. 35, 43, 57).

- [185] S. Swaminathan, F. Ziebert, D. Karpeev and I. S. Aranson, 'Motor-mediated alignment of microtubules in semidilute mixtures', *Physical Review E* **79**, 036207 (2009) (pp. 35, 43, 57).
- [186] M. Soares e Silva, J. Alvarado, J. Nguyen, N. Georgoulia, B. M. Mulder and G. H. Koenderink, 'Self-organized patterns of actin filaments in cell-sized confinement', *Soft Matter* **7**, 10631 (2011) (pp. 35, 43, 45, 48, 50, 57).
- [187] J. Alvarado, B. M. Mulder and G. H. Koenderink, 'Alignment of nematic and bundled semiflexible polymers in cell-sized confinement', *Soft Matter* **10**, 2354 (2014) (pp. 35, 43, 45, 48, 50, 57).
- [188] S. Deshpande and T. Pfohl, 'Hierarchical self-assembly of actin in micro-confinements using microfluidics', *Biomicrofluidics* **6**, 034120 (2012) (pp. 35, 43, 57).
- [189] V. S. Deshpande, M. Mrksich, R. M. McMeeking and A. G. Evans, 'A bio-mechanical model for coupling cell contractility with focal adhesion formation', *Journal of the Mechanics and Physics of Solids* **56**, 1484 (2008) (pp. 35, 43, 57, 58, 89, 115).
- [190] A.-C. Reymann, J.-L. Martiel, T. Cambier, L. Blanchoin, R. Boujemaa-Paterski and M. Théry, 'Nucleation geometry governs ordered actin networks structures', *Nature Materials* **9**, 827 (2010) (pp. 35, 43, 57).
- [191] G. Letort, A. Z. Politi, H. Ennomani, M. Théry, F. Nedelec and L. Blanchoin, 'Geometrical and mechanical properties control actin filament organization', *PLOS Computational Biology* **11**, 1 (2015) (pp. 35, 43, 57).
- [192] A. P. Liu, D. L. Richmond, L. Maibaum, S. Pronk, P. L. Geissler and D. A. Fletcher, 'Membrane-induced bundling of actin filaments', *Nature Physics* **4**, 789 (2008) (pp. 35, 43, 57).
- [193] S. Thomopoulos, G. M. Fomovsky and J. W. Holmes, 'The development of structural and mechanical anisotropy in fibroblast populated collagen gels', *Journal of Biomechanical Engineering* **127**, 742 (2005) (p. 35).
- [194] W. Pomp, K. Schakenraad, H. E. Balcioğlu, H. van Hoorn, E. H. J. Danen, R. M. H. Merks, T. Schmidt and L. Giomi, 'Cytoskeletal anisotropy controls geometry and forces of adherent cells', *Physical Review Letters* **121**, 178101 (2018) (pp. 36, 37, 70, 71, 74, 75, 88).
- [195] A. D. Rape, W.-H. Guo and Y.-L. Wang, 'The regulation of traction force in relation to cell shape and focal adhesions', *Biomaterials* **32**, 2043 (2011) (pp. 42, 44, 58, 70, 85, 89, 115).
- [196] P. W. Oakes, S. Banerjee, M. C. Marchetti and M. L. Gardel, 'Geometry regulates traction stresses in adherent cells', *Biophysical Journal* **107**, 825 (2014) (pp. 42, 44, 50, 52, 58, 70, 76, 79, 80, 84, 85, 88, 89, 113–115).

-
- [197] J. Hanke, D. Probst, A. Zemel, U. S. Schwarz and S. Köster, 'Dynamics of force generation by spreading platelets', *Soft Matter* **14**, 6571 (2018) (pp. 42, 44, 58, 70, 89, 113, 115).
- [198] J. Fu, Y.-K. Wang, M. T. Yang, R. A. Desai, X. Yu, Z. Liu and C. S. Chen, 'Mechanical regulation of cell function with geometrically modulated elastomeric substrates.', *Nature Methods* **7**, 733 (2010) (pp. 43, 44, 58, 89, 114, 115).
- [199] G. L. Lin, D. M. Cohen, R. A. Desai, M. T. Breckenridge, L. Gao, M. J. Humphries and C. S. Chen, 'Activation of beta 1 but not beta 3 integrin increases cell traction forces', *FEBS Letters* **587**, 763 (2013) (pp. 43, 44, 58, 114, 115).
- [200] C. Roux, A. Duperray, V. M. Laurent, R. Michel, V. Peschetola, C. Verdier and J. Étienne, 'Prediction of traction forces of motile cells', *Interface Focus* **6**, 20160042 (2016) (pp. 43, 70, 89).
- [201] D. Riveline, E. Zamir, N. Q. Balaban, U. S. Schwarz, T. Ishizaki, S. Narumiya, Z. Kam, B. Geiger and A. D. Bershadsky, 'Focal contacts as mechanosensors: externally applied local mechanical force induces growth of focal contacts by an mDia1-dependent and ROCK-independent mechanism', *The Journal of Cell Biology* **153**, 1175 (2001) (pp. 43, 70, 89).
- [202] N. Q. Balaban et al., 'Force and focal adhesion assembly: a close relationship studied using elastic micropatterned substrates', *Nature Cell Biology* **3**, 466 (2001) (pp. 43, 70, 89).
- [203] B. Wehrle-Haller and B. A. Imhof, 'Actin, microtubules and focal adhesion dynamics during cell migration', *The International Journal of Biochemistry & Cell Biology* **35**, 39 (2003) (p. 44).
- [204] R. De, A. Zemel and S. A. Safran, 'Dynamics of cell orientation', *Nature Physics* **3**, 655 (2007) (p. 44).
- [205] A. Livne, E. Bouchbinder and B. Geiger, 'Cell reorientation under cyclic stretching', *Nature Communications* **5**, 3938 (2014) (p. 44).
- [206] J. Étienne, J. Fouchard, D. Mitrossilis, N. Bufi, P. Durand-Smet and A. Asnacios, 'Cells as liquid motors: mechanosensitivity emerges from collective dynamics of actomyosin cortex', *Proceedings of the National Academy of Sciences* **112**, 2740 (2015) (pp. 44, 58, 89, 114, 115).
- [207] P. W. Oakes, E. Wagner, C. A. Brand, D. Probst, M. Linke, U. S. Schwarz, M. Glotzer and M. L. Gardel, 'Optogenetic control of rhoa reveals zyxin-mediated elasticity of stress fibres', *Nature Communications* **8**, 15817 (2017) (pp. 44, 58, 89, 114, 115).
- [208] S. B. Khatau, C. M. Hale, P. J. Stewart-Hutchinson, M. S. Patel, C. L. Stewart, P. C. Searson, D. Hodzic and D. Wirtz, 'A perinuclear actin cap regulates nuclear shape', *Proceedings of the National Academy of Sciences* **106**, 19017 (2009) (p. 44).

- [209] K. Nagayama, Y. Yahiro and T. Matsumoto, 'Apical and basal stress fibers have different roles in mechanical regulation of the nucleus in smooth muscle cells cultured on a substrate', *Cellular and Molecular Bioengineering* **6**, 473 (2013) (p. 44).
- [210] M. Théry, A. Pépin, E. Dressaire, Y. Chen and M. Bornens, 'Cell distribution of stress fibres in response to the geometry of the adhesive environment', *Cell Motility* **63**, 341 (2006) (pp. 44, 45, 52, 57, 58, 76, 81, 87–89, 114, 115).
- [211] J. James, E. D. Goluch, H. Hu, C. Liu and M. Mrksich, 'Subcellular curvature at the perimeter of micropatterned cells influences lamellipodial distribution and cell polarity', *Cell Motility* **65**, 841 (2008) (pp. 44, 50, 52, 58, 76, 79, 81, 87–89, 114, 115).
- [212] J. Galanis, D. Harries, D. L. Sackett, W. Losert and R. Nossal, 'Spontaneous patterning of confined granular rods', *Physical Review Letters* **96**, 028002 (2006) (p. 48).
- [213] Y. H. Tee et al., 'Cellular chirality arising from the self-organization of the actin cytoskeleton', *Nature Cell Biology* **17**, 445 (2015) (pp. 49, 58, 80).
- [214] G. Duclos, C. Blanch-Mercader, V. Yashunsky, G. Salbreux, J.-F. Joanny, J. Prost and P. Silberzan, 'Spontaneous shear flow in confined cellular nematics', *Nature Physics* **14**, 728 (2018) (pp. 49, 58).
- [215] S. Jalal, S. Shi, V. Acharya, R. Y.-J. Huang, V. Viasnoff, A. D. Bershadsky and Y. H. Tee, 'Actin cytoskeleton self-organization in single epithelial cells and fibroblasts under isotropic confinement', *Journal of Cell Science* **132** (2019) (pp. 58, 80, 88).
- [216] F. J. Segerer, F. Thüroff, A. Piera Alberola, E. Frey and J. O. Rädler, 'Emergence and persistence of collective cell migration on small circular micropatterns', *Physical Review Letters* **114**, 228102 (2015) (pp. 58, 115).
- [217] M. Eastwood, V. C. Mudera, D. A. McGrouther and R. A. Brown, 'Effect of precise mechanical loading on fibroblast populated collagen lattices: morphological changes.', *Cell Motility and the Cytoskeleton* **40**, 13 (1998) (pp. 58, 89).
- [218] D. W. J. Van der Schaft, A. C. C. Van Spreeuwel, H. C. Van Assen and F. P. T. Baaijens, 'Mechanoregulation of Vascularization in Aligned Tissue-Engineered Muscle: A Role for Vascular Endothelial Growth Factor', *Tissue Engineering Part A* **17**, 2857 (2011) (pp. 58, 89).
- [219] O. Wartlick, P. Mumcu, F. Jülicher and M. Gonzalez-Gaitan, 'Understanding morphogenetic growth control - lessons from flies.', *Nature Reviews Molecular Cell Biology* **12**, 594 (2011) (pp. 58, 89).
- [220] R. F. M. Van Oers, E. G. Rens, D. J. LaValley, C. A. Reinhart-King and R. M. H. Merks, 'Mechanical Cell-Matrix Feedback Explains Pairwise and

-
- Collective Endothelial Cell Behavior In Vitro', PLoS Computational Biology **10**, e1003774 (2014) (pp. 58, 73, 89).
- [221] P. Santos-Oliveira, A. Correia, T. Rodrigues, T. M. Ribeiro-Rodrigues, P. Matafome, J. C. Rodríguez-Manzaneque, R. Seica, H. Girão and R. D. M. Travasso, 'The Force at the Tip - Modelling Tension and Proliferation in Sprouting Angiogenesis', PLoS Computational Biology **11**, 1 (2015) (pp. 58, 89).
 - [222] D. S. Vijayraghavan and L. A. Davidson, 'Mechanics of neurulation: From classical to current perspectives on the physical mechanics that shape, fold, and form the neural tube', Birth Defects Research **109**, 153 (2017) (pp. 58, 89).
 - [223] D. L. Barton, S. Henkes, C. J. Weijer and R. Sknepnek, 'Active vertex model for cell-resolution description of epithelial tissue mechanics', PLoS Computational Biology **13**, 1 (2017) (pp. 58, 89).
 - [224] C. A. Reinhart-King, M. Dembo and D. A. Hammer, 'The dynamics and mechanics of endothelial cell spreading', Biophysical Journal **89**, 676 (2005) (p. 70).
 - [225] I. M. Tolić-Nørrelykke and N. Wang, 'Traction in smooth muscle cells varies with cell spreading', Journal of Biomechanics **38**, 1405 (2005) (p. 70).
 - [226] N. Wang, E. Ostuni, G. M. Whitesides and D. E. Ingber, 'Micropatterning tractional forces in living cells', Cell Motility **52**, 97 (2002) (p. 70).
 - [227] J. P. Califano and C. A. Reinhart-King, 'Substrate stiffness and cell area predict cellular traction stresses in single cells and cells in contact', Cellular and Molecular Bioengineering **3**, 68 (2010) (p. 70).
 - [228] C. A. Lemmon and L. H. Romer, 'A predictive model of cell traction forces based on cell geometry', Biophysical Journal **99**, L78 (2010) (pp. 70, 89).
 - [229] C. M. Edwards and U. S. Schwarz, 'Force localization in contracting cell layers', Physical Review Letters **107**, 128101 (2011) (pp. 70, 89).
 - [230] M.-C. Kim, D. M. Neal, R. D. Kamm and H. H. Asada, 'Dynamic modeling of cell migration and spreading behaviors on fibronectin coated planar substrates and micropatterned geometries', PLoS Computational Biology **9**, 1 (2013) (pp. 70, 89).
 - [231] B. L. Bangasser and D. J. Odde, 'Master equation-based analysis of a motor-clutch model for cell traction force', Cellular and Molecular Bioengineering **6**, 449 (2013) (p. 70).
 - [232] S. Lin, M. C. Lampi, C. A. Reinhart-King, G. Tsui, J. Wang, C. A. Nelson and L. Gu, 'Eigenstrain as a mechanical set-point of cells', Biomechanics and Modeling in Mechanobiology **17**, 951 (2018) (pp. 70, 113).
 - [233] P. W. Oakes, 'Balancing forces in migration', Current Opinion in Cell Biology **54**, 43 (2018) (p. 70).

- [234] D. Ben-Yaakov, R. Golkov, Y. Shokef and S. A. Safran, 'Response of adherent cells to mechanical perturbations of the surrounding matrix', *Soft Matter* **11**, 1412 (2015) (pp. 70, 84, 85, 88, 114).
- [235] R. Golkov and Y. Shokef, 'Elastic interactions between anisotropically contracting circular cells', *Physical Review E* **99**, 032418 (2019) (pp. 70, 84, 85, 88, 114).
- [236] M. Newman and G. Barkema, *Monte carlo methods in statistical physics* (Oxford University Press: New York, USA, 1999) (p. 72).
- [237] E. G. Rens and L. Edelstein-Keshet, 'From energy to cellular force in the Cellular Potts Model', *bioRxiv* (2019) 10.1101/601781 (p. 72).
- [238] N. J. Savill and P. Hogeweg, 'Modelling morphogenesis: from single cells to crawling slugs', *Journal of Theoretical Biology* **184**, 229 (1997) (p. 73).
- [239] K. Schakenraad, J. Ernst, W. Pomp, E. H. J. Danen, R. M. H. Merks, T. Schmidt and L. Giomi, 'Mechanical interplay between cell shape and actin cytoskeleton organization', *arXiv:1905.09805* (2019) (p. 75).
- [240] K. A. Kilian, B. Bugarija, B. T. Lahn and M. Mrksich, 'Geometric cues for directing the differentiation of mesenchymal stem cells', *Proceedings of the National Academy of Sciences* **107**, 4872 (2010) (pp. 81, 87, 88, 115).
- [241] C. Labouesse, A. B. Verkhovsky, J.-J. Meister, C. Gabella and B. Vianay, 'Cell shape dynamics reveal balance of elasticity and contractility in peripheral arcs', *Biophysical Journal* **108**, 2437 (2015) (p. 85).
- [242] S. Lee, E. Kassianidou and S. Kumar, 'Actomyosin stress fiber subtypes have unique viscoelastic properties and roles in tension generation', *Molecular Biology of the Cell* **29**, 1992 (2018) (pp. 89, 115).
- [243] E. Barnhart, K.-C. Lee, G. M. Allen, J. A. Theriot and A. Mogilner, 'Balance between cell-substrate adhesion and myosin contraction determines the frequency of motility initiation in fish keratocytes', *Proceedings of the National Academy of Sciences* **112**, 5045 (2015) (pp. 89, 115).
- [244] C. Abaurrea-Velasco, T. Auth and G. Gompfer, 'Vesicles with internal active filaments: self-organized propulsion controls shape, motility, and dynamical response', *New Journal of Physics* **21**, 123024 (2019) (pp. 89, 115).
- [245] P. J. Albert and U. S. Schwarz, 'Dynamics of cell ensembles on adhesive micropatterns: bridging the gap between single cell spreading and collective cell migration', *PLOS Computational Biology* **12**, 1 (2016) (p. 89).
- [246] K. Schakenraad, L. Ravazzano, N. Sarkar, J. A. J. Wondergem, R. M. H. Merks and L. Giomi, 'Topotaxis of active Brownian particles', *Physical Review E* **101**, 032602 (2020) (p. 89).
- [247] R. Magno, V. A. Grieneisen and A. F. Marée, 'The biophysical nature of cells: potential cell behaviours revealed by analytical and computational studies of cell surface mechanics', *BMC Biophysics* **8**, 8 (2015) (p. 89).

-
- [248] D.-H. Kim, K. Han, K. Gupta, K. W. Kwon, K.-Y. Suh and A. Levchenko, 'Mechanosensitivity of fibroblast cell shape and movement to anisotropic substratum topography gradients', *Biomaterials* **30**, 5433 (2009) (p. 96).
- [249] D. Arcizet, S. Capito, M. Gorelashvili, C. Leonhardt, M. Vollmer, S. Youssef, S. Rappl and D. Heinrich, 'Contact-controlled amoeboid motility induces dynamic cell trapping in 3d-microstructured surfaces', *Soft Matter* **8**, 1473 (2012) (p. 96).
- [250] X. Sun, M. K. Driscoll, C. Guven, S. Das, C. A. Parent, J. T. Fourkas and W. Losert, 'Asymmetric nanotopography biases cytoskeletal dynamics and promotes unidirectional cell guidance', *Proceedings of the National Academy of Sciences* **112**, 12557 (2015) (p. 96).
- [251] C. D. Paul, P. Mistriotis and K. Konstantopoulos, 'Cancer cell motility: lessons from migration in confined spaces', *Nature Reviews Cancer* **17**, 131 (2016) (pp. 96, 118).
- [252] N. D. Bade, T. Xu, R. D. Kamien, R. K. Assoian and K. J. Stebe, 'Gaussian curvature directs stress fiber orientation and cell migration', *Biophysical Journal* **114**, 1467 (2018) (p. 96).
- [253] L. Pieuchot et al., 'Curvotaxis directs cell migration through cell-scale curvature landscapes', *Nature Communications* **9**, 3995 (2018) (p. 96).
- [254] D.-H. Kim et al., 'Biomechanical interplay between anisotropic re-organization of cells and the surrounding matrix underlies transition to invasive cancer spread', *Scientific Reports* **8**, 14210 (2018) (p. 96).
- [255] B. Winkler, I. S. Aranson and F. Ziebert, 'Confinement and substrate topography control cell migration in a 3D computational model', *Communications Physics* **2**, 82 (2019) (p. 96).
- [256] R. Nossal, 'Mathematical theories of topotaxis', in *Biological growth and spread* (Springer, 1980), pp. 410–439 (p. 96).
- [257] D.-H. Kim, C.-H. Seo, K. Han, K. W. Kwon, A. Levchenko and K.-Y. Suh, 'Guided cell migration on microtextured substrates with variable local density and anisotropy', *Advanced Functional Materials* **19**, 1579 (2009) (p. 96).
- [258] D.-H. Kim, P. P. Provenzano, C. L. Smith and A. Levchenko, 'Matrix nanotopography as a regulator of cell function', *The Journal of Cell Biology* **197**, 351 (2012) (p. 96).
- [259] S. J. Ebbens and D. A. Gregory, 'Catalytic janus colloids: controlling trajectories of chemical microswimmers', *Accounts of Chemical Research* **51**, 1931 (2018) (p. 97).
- [260] G. Volpe, I. Buttinoni, D. Vogt, H.-J. Kümmerer and C. Bechinger, 'Microswimmers in patterned environments', *Soft Matter* **7**, 8810 (2011) (pp. 97, 98, 108, 115, 116).

- [261] Y. Fily, A. Baskaran and M. F. Hagan, 'Dynamics of self-propelled particles under strong confinement', *Soft Matter* **10**, 5609 (2014) (pp. 97, 98).
- [262] Y. Fily, A. Baskaran and M. F. Hagan, 'Dynamics and density distribution of strongly confined noninteracting nonaligning self-propelled particles in a nonconvex boundary', *Physical Review E* **91**, 012125 (2015) (pp. 97, 98).
- [263] M. Khatami, K. Wolff, O. Pohl, M. R. Ejtehadi and H. Stark, 'Active Brownian particles and run-and-tumble particles separate inside a maze', *Scientific Reports* **6**, 37670 (2016) (pp. 97, 108, 115).
- [264] P. Galajda, J. Keymer, P. Chaikin and R. Austin, 'A wall of funnels concentrates swimming bacteria', *Journal of Bacteriology* **189**, 8704 (2007) (p. 97).
- [265] L. Angelani and R. Di Leonardo, 'Geometrically biased random walks in bacteria-driven micro-shuttles', *New Journal of Physics* **12**, 113017 (2010) (p. 97).
- [266] S. A. Mallory, C. Valeriani and A. Cacciuto, 'Curvature-induced activation of a passive tracer in an active bath', *Physical Review E* **90**, 032309 (2014) (p. 97).
- [267] L. Angelani, R. Di Leonardo and G. Ruocco, 'Self-starting micromotors in a bacterial bath', *Physical Review Letters* **102**, 048104 (2009) (p. 97).
- [268] S. Pattanayak, R. Das, M. Kumar and S. Mishra, 'Enhanced dynamics of active Brownian particles in periodic obstacle arrays and corrugated channels', *The European Physical Journal E* **42**, 62 (2019) (pp. 97, 98, 103).
- [269] C. Reichhardt and C. J. Olson Reichhardt, 'Active matter transport and jamming on disordered landscapes', *Physical Review E* **90**, 012701 (2014) (p. 97).
- [270] M. Zeitz, K. Wolff and H. Stark, 'Active Brownian particles moving in a random Lorentz gas', *The European Physical Journal E* **40**, 23 (2017) (pp. 97, 98, 102–104, 108).
- [271] A. Morin, D. Lopes Cardozo, V. Chikkadi and D. Bartolo, 'Diffusion, subdiffusion, and localization of active colloids in random post lattices', *Physical Review E* **96**, 042611 (2017) (pp. 97, 108, 115).
- [272] O. Chepizhko and T. Franosch, 'Ideal circle microswimmers in crowded media', *Soft Matter* **15**, 452 (2019) (p. 97).
- [273] G. Volpe and G. Volpe, 'The topography of the environment alters the optimal search strategy for active particles', *Proceedings of the National Academy of Sciences* **114**, 11350 (2017) (pp. 97, 108, 115).
- [274] H. Takagi, M. J. Sato, T. Yanagida and M. Ueda, 'Functional analysis of spontaneous cell movement under different physiological conditions', *PLOS ONE* **3**, 1 (2008) (p. 98).
- [275] P. Denissenko, V. Kantsler, D. J. Smith and J. Kirkman-Brown, 'Human spermatozoa migration in microchannels reveals boundary-following navigation', *Proceedings of the National Academy of Sciences* **109**, 8007 (2012) (p. 98).

-
- [276] V. Kantsler, J. Dunkel, M. Polin and R. E. Goldstein, 'Ciliary contact interactions dominate surface scattering of swimming eukaryotes', *Proceedings of the National Academy of Sciences* **110**, 1187 (2013) (p. 98).
 - [277] C. R. Doering, X. Mao and L. M. Sander, 'Random walker models for durotaxis', *Physical Biology* **15**, 066009 (2018) (pp. 101, 105, 107).
 - [278] T. Chinnasamy, J. L. Kingsley, F. Inci, P. J. Turek, M. P. Rosen, B. Behr, E. Tüzel and U. Demirci, 'Guidance and self-sorting of active swimmers: 3D periodic arrays increase persistence length of human sperm selecting for the fittest', *Advanced Science* **5**, 1700531 (2018) (p. 103).
 - [279] A. Pototsky and H. Stark, 'Active Brownian particles in two-dimensional traps', *Europhysics Letters* **98**, 50004 (2012) (p. 106).
 - [280] M. Hennes, K. Wolff and H. Stark, 'Self-induced polar order of active Brownian particles in a harmonic trap', *Physical Review Letters* **112**, 238104 (2014) (p. 106).
 - [281] A. P. Solon, M. E. Cates and J. Tailleur, 'Active brownian particles and run-and-tumble particles: a comparative study', *The European Physical Journal Special Topics* **224**, 1231 (2015) (p. 106).
 - [282] O. Dauchot and V. Démery, 'Dynamics of a self-propelled particle in a harmonic trap', *Physical Review Letters* **122**, 068002 (2019) (p. 106).
 - [283] I. Berdakin, Y. Jeyaram, V. V. Moshchalkov, L. Venken, S. Dierckx, S. J. Vanderleyden, A. V. Silhanek, C. A. Condat and V. I. Marconi, 'Influence of swimming strategy on microorganism separation by asymmetric obstacles', *Physical Review E* **87**, 052702 (2013) (pp. 108, 115).
 - [284] M. Mijalkov and G. Volpe, 'Sorting of chiral microswimmers', *Soft Matter* **9**, 6376 (2013) (pp. 108, 115).
 - [285] T. Bertrand, Y. Zhao, O. Bénichou, J. Tailleur and R. Voituriez, 'Optimized diffusion of run-and-tumble particles in crowded environments', *Physical Review Letters* **120**, 198103 (2018) (pp. 108, 115).
 - [286] O. Chepizhko and F. Peruani, 'Diffusion, subdiffusion, and trapping of active particles in heterogeneous media', *Physical Review Letters* **111**, 160604 (2013) (pp. 108, 115).
 - [287] D. Takagi, J. Palacci, A. B. Braunschweig, M. J. Shelley and J. Zhang, 'Hydrodynamic capture of microswimmers into sphere-bound orbits', *Soft Matter* **10**, 1784 (2014) (pp. 108, 115).
 - [288] T. Jakuszeit, O. A. Croze and S. Bell, 'Diffusion of active particles in a complex environment: role of surface scattering', *Physical Review E* **99**, 012610 (2019) (pp. 108, 115).
 - [289] T. Bretschneider, H. G. Othmer and C. J. Weijer, 'Progress and perspectives in signal transduction, actin dynamics, and movement at the cell and tissue level: lessons from dictyostelium', *Interface Focus* **6**, 20160047 (2016) (pp. 108, 118).

- [290] E. Sahai, 'Illuminating the metastatic process', *Nature Reviews Cancer* **7**, 737 (2007) (pp. 108, 118).
- [291] P. Friedl and S. Alexander, 'Cancer invasion and the microenvironment: plasticity and reciprocity', *Cell* **147**, 992 (2011) (pp. 108, 118).
- [292] P. Friedl, S. Borgmann and E.-B. Bröcker, 'Amoeboid leukocyte crawling through extracellular matrix: lessons from the dictyostelium paradigm of cell movement', *Journal of Leukocyte Biology* **70**, 491 (2001) (pp. 108, 118).
- [293] L. Van Steijn, J. A. J. Wondergem, K. Schakenraad, D. Heinrich and R. M. H. Merks, 'Modeling topotaxis with the Cellular Potts Model', in preparation (pp. 116, 117).
- [294] C. M. de Korne et al., 'Regulation of plasmodium sporozoite motility by formulation components', *Malaria Journal* **18**, 155 (2019) (p. 118).
- [295] B. M. F. Winkel et al., 'Quantification of wild-type and radiation attenuated plasmodium falciparum sporozoite motility in human skin', *Scientific Reports* **9**, 13436 (2019) (p. 118).