REVIEW

Cell-cell adhesion interface: orthogonal and parallel forces from contraction, protrusion, and retraction [version 1; peer review: 2 approved]

Vivian W. Tang

Department of Cell and Developmental Biology, University of Illinois, Urbana-Champaign, IL, 61801, USA

V1 First published: 25 Sep 2018, 7(F1000 Faculty Rev):1544
<https://doi.org/10.12688/f1000research.15860.1>
Latest published: 25 Sep 2018, 7(F1000 Faculty Rev):1544
<https://doi.org/10.12688/f1000research.15860.1>

Abstract

The epithelial lateral membrane plays a central role in the integration of intercellular signals and, by doing so, is a principal determinant in the emerging properties of epithelial tissues. Mechanical force, when applied to the lateral cell-cell interface, can modulate the strength of adhesion and influence intercellular dynamics. Yet the relationship between mechanical force and epithelial cell behavior is complex and not completely understood. This commentary aims to provide an investigative look at the usage of cellular forces at the epithelial cell-cell adhesion interface.

Keywords

cell-cell, adhesion, force, actin, intercellular, lateral membrane, epithelial, contraction, protrusion, retraction

Open Peer Review

Approval Status

	1	2
version 1		
25 Sep 2018		

Faculty Reviews are review articles written by the prestigious Members of **Faculty Opinions**. The articles are commissioned and peer reviewed before publication to ensure that the final, published version is comprehensive and accessible. The reviewers who approved the final version are listed with their names and affiliations.

1. **Alex Mogilner**, New York University, New York, USA

2. **Alpha Yap**, The University of Queensland, Brisbane, Australia

Any comments on the article can be found at the end of the article.

Corresponding author: Vivian W. Tang (vtang@illinois.edu)

Author roles: Tang VW: Conceptualization, Funding Acquisition, Writing – Original Draft Preparation, Writing – Review & Editing

Competing interests: No competing interests were disclosed.

Grant information: The author is supported by the National Institute of Diabetes and Digestive and Kidney Diseases, the National Institutes of Health (R01 DK098398).

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Copyright: © 2018 Tang VW. This is an open access article distributed under the terms of the [Creative Commons Attribution License](#), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

How to cite this article: Tang VW. **Cell-cell adhesion interface: orthogonal and parallel forces from contraction, protrusion, and retraction [version 1; peer review: 2 approved]** F1000Research 2018, 7(F1000 Faculty Rev):1544
<https://doi.org/10.12688/f1000research.15860.1>

First published: 25 Sep 2018, 7(F1000 Faculty Rev):1544 <https://doi.org/10.12688/f1000research.15860.1>

Introduction

Mechanical force, which is neither genetically encoded nor biochemically tractable, is being recognized as a significant determinant in the behaviors and functions of cells and tissues¹⁻⁹. Whereas biochemical information is encoded in parameters such as post-translational modifications, biophysical information is encoded in parameters such as magnitude, frequency, and duration. Yet how these biophysical parameters of mechanical force contribute to the regulation of molecular and cellular events is not understood. Despite great efforts from biologists, physicists, and engineers to probe mechanical forces in living cells and tissues¹⁰⁻²², it remains tremendously difficult to measure the biophysical variables of mechanical forces inside cells. The purpose of this commentary is to explore, in the context of cell-cell interactions, the properties and usages of mechanical forces that can support cellular and molecular work²³⁻²⁶.

At the epithelial cell-cell adhesion interface, mechanical force is powered predominantly by actin dynamics and their associated molecular motors, including (a) protrusive force driven by actin polymerization and myosin activities^{24,27-35}; (b) retraction force contributed by cortical actin depolymerization, plasma membrane tension, retrograde actin flow, and myosin activities³⁶⁻⁴²; and (c) contraction force provided by actin dynamics and cross-linked actomyosin II activities⁴³⁻⁴⁸. This commentary will not discuss individual adhesion molecules and cytoskeletal regulators, which had been recently reviewed^{49,50}.

The three-dimensional epithelial cell

The epithelial cell forms distinct membrane domains by using two sets of adhesion molecules: one set for adhesion to extracellular matrix and another set for adhesion between cells. By having two sets of adhesion systems, an epithelial cell establishes structural and spatial organization with (a) a lateral membrane organized by cell-cell adhesions, (b) a basal membrane organized by cell-matrix adhesions, and (c) a free surface at the apical membrane. Through interactions with its environment and neighbors, the epithelial cell acquires emergent properties integral to the functions of epithelial tissues, such as coordinated multi-cellular junctional constriction and collective movement⁵¹⁻⁵⁹.

The three membrane domains of the epithelial cell contain actin nucleation factors, actin cross-linking proteins, and myosin II filaments that create distinct actomyosin II networks (Figure 1A)^{25,60-62}. The lateral membrane is further organized into apical, lateral, and basal intercellular interactions with distinct protein compositions, actin dynamics, and contractile properties⁶³. Mechanical forces generated at the apical, lateral, and basal actomyosin II cytoskeleton are transmitted to cell-cell contacts via linkage to adhesion proteins or the plasma membrane (Figure 1B).

Direction of forces

Unlike chemical signaling that is driven by random walks and does not have intrinsic directionality, mechanical force

Figure 1. Actin organization in a three-dimensional epithelial cell. (A) Actin arrangement on the apical, lateral, and basal membranes of the epithelial cell is illustrated at the mesoscopic cellular level. (B) Connectivity between cell-cell interface and the actin cytoskeleton is illustrated at the macroscopic multi-cellular level.

intrinsically has a direction that is important to guide biological processes^{64–68}. The directionality of the mechanical force is heavily influenced by the spatial organization of the actomyosin II cytoskeleton. Mechanical forces on the lateral adhesion

interface are frequently orthogonal or parallel to the cell boundary (Figure 2A, left panel). One exception to this generalization is at folded membranes (Figure 2A, right panel). When protrusions and retractions are formed on the lateral

Figure 2. Direction of forces at the lateral cell–cell adhesion interface. (A) Parallel and orthogonal forces are shown at the macroscopic multi-cellular (left panel) and mesoscopic cellular (right panel) scales. Cell–cell adhesions at the tip of a lateral membrane protrusion experience orthogonal force, whereas cell–cell adhesions at the trunk of the same membrane protrusion experience parallel force (right panel). (B) Forces in one, two, and three dimensions can be generated through spatial organization of actin dynamics and actomyosin activities. Orthogonal and parallel one-dimensional forces can be generated with actin filaments arranged orthogonal and parallel to the plasma membrane, respectively (upper panel). Orthogonal and parallel two- and three-dimensional forces can be generated with a cross-linked actin network to support processes on the lateral cell–cell adhesion interface (lower panel).

membrane, adhesion proteins are no longer in the same orientation as the cell–cell boundary. Consequently, the direction of force exerted on adhesion molecules would be dependent on their relative positions. Cell–cell adhesions formed at the tip of an intercellular membrane protrusion would experience orthogonal protrusion–retraction force, whereas cell–cell adhesions found at the trunk of an intercellular membrane protrusion would experience parallel drag force on the plane of the plasma membrane (Figure 2A, right panel).

Mechanical force applied in a directional manner could elicit different molecular and cellular events on the cell–cell adhesion interface^{65,66,69}. At the microscopic scale (Figure 2B, upper panel), actin dynamics can create one-dimensional (1D) protrusion and retraction forces orthogonal to the lateral membrane. Anti-parallel myosin II filaments on linear actin filaments can create 1D contraction force. Actin filaments arranged parallel

to the membrane would support force generation parallel to the cell–cell interface. Organization of branched actin networks using actin cross-linking proteins would create parallel and orthogonal forces to drive 2D and 3D events (Figure 2B, lower panel). Spatial and temporal control of forces in one, two, and three dimensions can support distinct force-dependent processes on the lateral membrane.

Pushing and pulling forces to drive kinetic processes

The kinetic energy produced by mechanical forces can be used to create movement, resulting in productive work such as pushing and pulling (Figure 3)^{41,70–76}.

Pulling forces can act on adhesions to unfold or disengage a protein by breaking intra-molecular or inter-molecular bonds, effectively changing the energy landscape of the cell–cell adhesion interface (Figure 3A)^{77–82}. Weaker interactions can be

Figure 3. Pushing and pulling to drive kinetic processes. (A) Pulling on adhesions and membrane can break intra-molecular and inter-molecular bonds, cause movement of adhesions on the membrane, and create undulations on the cell–cell adhesion interface. (B) Pushing parallel to the lateral membrane can disengage and disperse adhesions, resulting in mixing of the membrane components. Pushing orthogonal to the lateral membrane can increase cell–cell contact area and time to enhance adhesion engagement.

disrupted by weak forces but stronger interactions can resist weak forces and are selectively preserved. Thus, the input of different levels of kinetic energy would create different metastable states of the epithelial cell⁸³. For mobile and unanchored adhesions, pulling forces can result in sliding of the adhesion complex. Directional pushing can result in biased movement of the mobile fraction. Pulling orthogonally to the cell–cell interface can cause undulations of the lateral membrane, creating intercellular space and increasing the distance between apposing cell–cell adhesion molecules.

Pushing the lateral membrane can influence the distribution of protein complexes and membrane dynamics on the cell–cell adhesion interface (Figure 3B)^{70,75,84–89}. Pushing parallel to the membrane can disperse proteins and lipids, resulting in mixing of adhesion complexes and membrane components. By contrast, pushing orthogonal to the membrane can drive opposing cells together to increase contact time and area for adhesion engagement.

In summary, the spatial constraint created by organizing actin dynamics and actomyosin cytoskeleton can determine the magnitude, direction, and dimensionality of force. These biophysical properties of force are recognized by the 3D epithelial cells to drive different molecular and cellular events. Importantly, the orientation of the adhesion proteins on the plane of the plasma membrane determines the molecular outcome and ultimately the cellular effect of mechanical force on the cell–cell adhesion interface^{90–92}.

Pushing and pulling forces to drive thermodynamic processes

The energy supplied by mechanical forces can be stored as elastic energy to build up tension (a) on the plasma membrane (Figure 4A)^{93–96}, (b) on cell–cell adhesion molecules (Figure 4B)⁹⁷, and (c) within the actin cytoskeleton (Figure 4C)^{98–101}. At the mesoscopic level, tension can be coupled and integrated to facilitate processes on the lateral interface^{56,102,103}.

Actin dynamics and actomyosin activities can increase membrane tension by stretching the membrane (Figure 4A)^{104–106}. Tension generated on the plane of the membrane will decrease undulation^{107–109}, creating a taut region that supports lateral clustering of adhesion proteins^{103,110–112}. Orthogonal pulling force on the membrane can increase intercellular tension by stretching the extracellular domains of cell–cell adhesion proteins (Figure 4B)¹¹³.

Underneath the plasma membrane, tension can be generated in the cortical cytoskeleton (Figure 4C)^{114,115}. Pulling actin increases filament tension and decreases its susceptibility to severing by cofilin (Figure 4C, left panel)¹¹⁶ and results in changes in actin dynamics and filament stability^{117,118}. Altering filament length and actin stability would affect connectivity of the actomyosin network and force transmission^{119–122}. Pulling force on actin filaments could alter the spatial organization

of the entire actomyosin network, resulting in mesoscopic differences in compressibility, stability, and rigidity (Figure 4C, middle panel)^{123–127}.

Plasma membrane and cytoskeletal tension can be coupled to create an integrated membrane–adhesion–cytoskeleton ensemble with properties that are more complex than the sum of the individual components (Figure 4C, right panel)^{56,91,128–137}. Thus, the energy input by pushing and pulling forces to generate tension on the lateral membrane, adhesion proteins, and cortical actin cytoskeleton ultimately results in the emergence of new properties and organization at the cell–cell adhesion interface^{12,138–141}.

Magnitude of force

The reason to consider the magnitude of force is twofold. First, the magnitude of force dictates which process it can perform (Table 1, upper panel)^{27,40,78,142–148}. Whether the mechanical force is meant to create tension, unfold protein, cause movement, or mix components on the membrane would depend on the energy required for the specific process. The magnitude of force can have a differential effect on proteins; weak force will break weaker bonds and preserve stronger bonds, whereas strong force will break both weak and strong bonds. For example, unfolding alpha-catenin would require less force than detaching an E-cadherin homophilic bond. Thus, the magnitude of force, along with the intrinsic transition states of the cell–cell adhesion system, dictates the kinetic and thermodynamic pathways for epithelial processes such as adhesion remodeling and strengthening.

Second, the magnitude of force dictates which mechanism can supply the force (Table 1, lower panel)^{130,149–152}. Polymerization of a single actin filament supplies less force than a bundle of parallel actin filaments. To generate protrusion, a bundle of actin must polymerize in concert and work together¹⁵³. However, if force is needed only to push an adhesion protein closer to its binding partner on the membrane, a single actin filament may supply enough energy to promote biased diffusion. A myosin pulling on an actin filament produces less force than a bundle of myosin pulling on a bundle of parallel actin filaments. Anti-parallel myosin filaments pulling on parallel bundles of actin filaments produce less force than pulling on a cross-linked network of actin filaments. Thus, epithelial cells control the amount of force available by regulating the spatial distribution of actin dynamics and actomyosin II activities to dictate which molecular process is being executed at the lateral cell–cell adhesion interface¹⁵⁴.

Conclusions

Mechanical force plays an important role at the cell–cell adhesion interface. How mechanical force regulates cellular and molecular processes depends on its encoded properties, including directionality and magnitude. Additional biophysical parameters such as frequency, duration, and waveform that are instructive signals for other biological regulatory systems

Figure 4. Pushing and pulling to create tension. (A) Stretching the membrane increases membrane tension at the mesoscopic lateral membrane level and can enhance intercellular interactions at the microscopic molecular level. (B) Pulling orthogonal to the membrane increases intercellular tension on the mesoscopic lateral membrane level and can enhance tension at cell–cell adhesion molecules at the microscopic molecular level. (C) Pulling actin filament alters actin dynamics and decreases cofilin severing at the microscopic molecular level (left panel). Changing the length distribution and organization of actin filaments alters cytoskeletal tension, ultimately affecting the compressibility and rigidity of cortical actin associated with the lateral membrane at the mesoscopic lateral membrane level (middle panel). Coupling membrane and cytoskeleton tension to adhesion proteins allows integration of intercellular, membrane, cytoskeletal forces on the lateral cell–cell adhesion interface (right panel).

Table 1. Magnitude of forces. (Upper) Different processes require different levels of force. **(Lower)** Different molecular mechanisms produce different levels of force.

Process	Force
Filopodium extension	< 3 pN
Unfolding vinculin binding site on α -catenin	5-10-15 pN
Unfolding intramolecular auto-inhibitory sites on ZO-1	5-20 pN
Detaching N-WASP from Arp2/3-F-actin complex	6-7 pN
Lamellipodia pushing force	10-20 pN
Breaking single E-cadherin-E-cadherin bond (without actin binding)	15-25 pN
Breaking single E-cadherin-E-cadherin bond	35-50 pN
Filopodium Retraction force (with actin and plasma membrane)	50-2000 pN
Machine	Force
Actin Polymerization	1 pN
Formin-driven Barbed-end Actin Polymerization	1-2 pN
Myosin I motor on actin	1-2 pN
Myosin VI motor on actin	2 pN
Myosin II single motor head on actin	1-6 pN
Myosin II minifilament on actin	20-50 pN
Myosin II minifilament on α -actinin-crosslinked actin bundle	100 pN
Myosin II minifilament on α -actinin-crosslinked actin network	1 micro N

such as calcium signaling and neuronal firing are also encoded in cellular mechanical forces, but their contribution to epithelial cell–cell interaction is currently unknown because of a lack of experimental data and approaches. However, if epithelial cells could encode and tune frequency, duration, and waveform in mechanical forces, it would greatly increase the parameter space, allowing epithelial cells to build complexity. Future development of techniques to measure cell-generated mechanical force will provide formal assessment of these biophysical variables in regulating epithelial cell–cell interactions and tissue behaviors.

Grant information

The author is supported by the National Institute of Diabetes and Digestive and Kidney Diseases, the National Institutes of Health (R01 DK098398).

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Acknowledgments

The author apologizes for not being able to cite all pertinent literature.

References

- Kim Y, Hazar M, Vijayraghavan DS, *et al.*: **Mechanochemical actuators of embryonic epithelial contractility.** *Proc Natl Acad Sci U S A.* 2014; **111**(40): 14366–71.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Jackson TR, Kim HY, Balakrishnan UL, *et al.*: **Spatiotemporally Controlled Mechanical Cues Drive Progenitor Mesenchymal-to-Epithelial Transition Enabling Proper Heart Formation and Function.** *Curr Biol.* 2017; **27**(9): 1326–35.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Acharya BR, Yap AS: **Pli Selon Pli: Mechanochemical Feedback and the Morphogenetic Role of Contractility at Cadherin Cell-Cell Junctions.** *Curr Top Dev Biol.* 2016; **117**: 631–46.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Dasbiswas K, Hannezo E, Gov NS: **Theory of Epithelial Cell Shape Transitions Induced by Mechanoactive Chemical Gradients.** *Biophys J.* 2018; **114**(4): 968–77.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Gross P, Kumar KV, Grill SW: **How Active Mechanics and Regulatory Biochemistry Combine to Form Patterns in Development.** *Annu Rev Biophys.* 2017; **46**: 337–56.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Petridou NI, Spiró Z, Heisenberg CP: **Multiscale force sensing in development.** *Nat Cell Biol.* 2017; **19**(6): 581–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Wickström SA, Niessen CM: **Cell adhesion and mechanics as drivers of tissue organization and differentiation: local cues for large scale organization.** *Curr Opin Cell Biol.* 2018; **54**: 89–97.
[PubMed Abstract](#) | [Publisher Full Text](#) | **F1000 Recommendation**
- Martino F, Perestrelo AR, Vinarský V, *et al.*: **Cellular Mechanotransduction: From Tension to Function.** *Front Physiol.* 2018; **9**: 824.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Yusko EC, Asbury CL: **Force is a signal that cells cannot ignore.** *Mol Biol Cell.*

- 2014; **25**(23): 3717–25.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
10. Siedlik MJ, Varner VD, Nelson CM: **Pushing, pulling, and squeezing our way to understanding mechanotransduction.** *Methods*. 2016; **94**: 4–12.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  11. Haase K, Pelling AE: **Investigating cell mechanics with atomic force microscopy.** *J R Soc Interface*. 2015; **12**(104): 20140970.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  12. Harris AR, Daeden A, Charras GT: **Formation of adherens junctions leads to the emergence of a tissue-level tension in epithelial monolayers.** *J Cell Sci*. 2014; **127**(Pt 11): 2507–17.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  13. Collins C, Denisin AK, Pruitt BL, *et al.*: **Changes in E-cadherin rigidity sensing regulate cell adhesion.** *Proc Natl Acad Sci U S A*. 2017; **114**(29): E5835–E5844.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  14. Przybyla L, Lakins JN, Sunyer R, *et al.*: **Monitoring developmental force distributions in reconstituted embryonic epithelia.** *Methods*. 2016; **94**: 101–13.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  15. Stapleton SC, Chopra A, Chen CS: **Force measurement tools to explore cadherin mechanotransduction.** *Cell Commun Adhes*. 2014; **21**(3): 193–205.
[PubMed Abstract](#) | [Publisher Full Text](#)
  16. Campàs O, Mammoto T, Hasso S, *et al.*: **Quantifying cell-generated mechanical forces within living embryonic tissues.** *Nat Methods*. 2014; **11**(2): 183–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  17. Campàs O: **A toolbox to explore the mechanics of living embryonic tissues.** *Semin Cell Dev Biol*. 2016; **55**: 119–30.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  18. Serwane F, Mongera A, Rowghanian P, *et al.*: **In vivo quantification of spatially varying mechanical properties in developing tissues.** *Nat Methods*. 2017; **14**(2): 181–6.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  19. Rübsam M, Mertz AF, Kubo A, *et al.*: **E-cadherin integrates mechanotransduction and EGFR signaling to control junctional tissue polarization and tight junction positioning.** *Nat Commun*. 2017; **8**(1): 1250.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  20. Cartagena-Rivera AX, Van Itallie CM, Anderson JM, *et al.*: **Apical surface supracellular mechanical properties in polarized epithelium using noninvasive acoustic force spectroscopy.** *Nat Commun*. 2017; **8**(1): 1030.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  21. Freikamp A, Mehlich A, Klingner C, *et al.*: **Investigating piconewton forces in cells by FRET-based molecular force microscopy.** *J Struct Biol*. 2017; **197**(1): 37–42.
[PubMed Abstract](#) | [Publisher Full Text](#)
  22. Tang X, Tofangchi A, Anand SV, *et al.*: **A novel cell traction force microscopy to study multi-cellular system.** *PLoS Comput Biol*. 2014; **10**(6): e1003631.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  23. Bosch-Fortea M, Martín-Belmonte F: **Mechanosensitive adhesion complexes in epithelial architecture and cancer onset.** *Curr Opin Cell Biol*. 2018; **50**: 42–9.
[PubMed Abstract](#) | [Publisher Full Text](#)
  24. Malinova TS, Huveneers S: **Sensing of Cytoskeletal Forces by Asymmetric Adherens Junctions.** *Trends Cell Biol*. 2018; **28**(4): 328–41.
[PubMed Abstract](#) | [Publisher Full Text](#)
  25. Steinbacher T, Ebnet K: **The regulation of junctional actin dynamics by cell adhesion receptors.** *Histochem Cell Biol*. 2018; **150**(4): 341–350.
[PubMed Abstract](#) | [Publisher Full Text](#)
  26. Leckband DE, de Rooij J: **Cadherin adhesion and mechanotransduction.** *Annu Rev Cell Dev Biol*. 2014; **30**: 291–315.
[PubMed Abstract](#) | [Publisher Full Text](#)
  27. Sayyad WA, Amin L, Fabris P, *et al.*: **The role of myosin-II in force generation of DRG filopodia and lamellipodia.** *Sci Rep*. 2015; **5**: 7842.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  28. Prass M, Jacobson K, Mogilner A, *et al.*: **Direct measurement of the lamellipodial protrusive force in a migrating cell.** *J Cell Biol*. 2006; **174**(6): 767–72.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  29. **F** Footer MJ, Kerssemakers JW, Theriot JA, *et al.*: **Direct measurement of force generation by actin filament polymerization using an optical trap.** *Proc Natl Acad Sci U S A*. 2007; **104**(7): 2181–6.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  30. Krendel MF, Bonder EM: **Analysis of actin filament bundle dynamics during contact formation in live epithelial cells.** *Cell Motil Cytoskeleton*. 1999; **43**(4): 296–309.
[PubMed Abstract](#) | [Publisher Full Text](#)
  31. **F** Homem CCF, Peifer M: **Diaphanous regulates myosin and adherens junctions to control cell contractility and protrusive behavior during morphogenesis.** *Development*. 2008; **135**(6): 1005–18.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
  32. Campàs O, Mahadevan L, Joanny JF: **Actin network growth under load.** *Biophys J*. 2012; **102**(5): 1049–58.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  33. Zhu J, Mogilner A: **Mesoscopic model of actin-based propulsion.** *PLoS Comput Biol*. 2012; **8**(11): e1002764.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  34. Schaus TE, Borisy GG: **Performance of a population of independent filaments in lamellipodial protrusion.** *Biophys J*. 2008; **95**(3): 1393–411.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  35. Dimchev G, Steffen A, Kage F, *et al.*: **Efficiency of lamellipodia protrusion is determined by the extent of cytosolic actin assembly.** *Mol Biol Cell*. 2017; **28**(10): 1311–25.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  36. Reymann AC, Suarez C, Guérin C, *et al.*: **Turnover of branched actin filament networks by stochastic fragmentation with ADF/cofilin.** *Mol Biol Cell*. 2011; **22**(14): 2541–50.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  37. Leijnse N, Oddershede LB, Bendix PM: **Helical buckling of actin inside filopodia generates traction.** *Proc Natl Acad Sci U S A*. 2015; **112**(1): 136–41.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  38. Ryan GL, Holz D, Yamashiro S, *et al.*: **Cell protrusion and retraction driven by fluctuations in actin polymerization: A two-dimensional model.** *Cytoskeleton (Hoboken)*. 2017; **74**(12): 490–503.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  39. Peukes J, Betz T: **Direct measurement of the cortical tension during the growth of membrane blebs.** *Biophys J*. 2014; **107**(8): 1810–20.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  40. Bomschlögl T, Romero S, Vestergaard CL, *et al.*: **Filopodial retraction force is generated by cortical actin dynamics and controlled by reversible tethering at the tip.** *Proc Natl Acad Sci U S A*. 2013; **110**(47): 18928–33.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  41. Mège RM, Gavard J, Lambert M: **Regulation of cell-cell junctions by the cytoskeleton.** *Curr Opin Cell Biol*. 2006; **18**(5): 541–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
  42. Ashdown GW, Burn GL, Williamson DJ, *et al.*: **Live-Cell Super-resolution Reveals F-Actin and Plasma Membrane Dynamics at the T Cell Synapse.** *Biophys J*. 2017; **112**(8): 1703–13.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  43. Chew TG, Huang J, Palani S, *et al.*: **Actin turnover maintains actin filament homeostasis during cytokinetic ring contraction.** *J Cell Biol*. 2017; **216**(9): 2657–67.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  44. Bidone TC, Jung W, Maruri D, *et al.*: **Morphological Transformation and Force Generation of Active Cytoskeletal Networks.** *PLoS Comput Biol*. 2017; **13**(1): e1005277.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  45. Oelz D, Mogilner A: **Actomyosin contraction, aggregation and traveling waves in a treadmilling actin array.** *Physica D*. 2016; **318–319**: 70–83.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  46. Oelz DB, Rubinstein BY, Mogilner A: **A Combination of Actin Treadmilling and Cross-Linking Drives Contraction of Random Actomyosin Arrays.** *Biophys J*. 2015; **109**(9): 1818–29.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  47. Zimmermann D, Homa KE, Hocky GM, *et al.*: **Mechanoregulated inhibition of formin facilitates contractile actomyosin ring assembly.** *Nat Commun*. 2017; **8**(1): 703.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  48. Luxenburg C, Heller E, Pasolli HA, *et al.*: **Wdr1-mediated cell shape dynamics and cortical tension are essential for epidermal planar cell polarity.** *Nat Cell Biol*. 2015; **17**(5): 592–604.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  49. Charras G, Yap AS: **Tensile Forces and Mechanotransduction at Cell-Cell Junctions.** *Curr Biol*. 2018; **28**(8): R445–R457.
[PubMed Abstract](#) | [Publisher Full Text](#)
  50. Sluysmans S, Vasileva E, Spadaro D, *et al.*: **The role of apical cell-cell junctions and associated cytoskeleton in mechanotransduction.** *Biol Cell*. 2017; **109**(4): 139–61.
[PubMed Abstract](#) | [Publisher Full Text](#)
  51. Wyatt T, Baum B, Charras G: **A question of time: tissue adaptation to mechanical forces.** *Curr Opin Cell Biol*. 2016; **38**: 68–73.
[PubMed Abstract](#) | [Publisher Full Text](#)
  52. Khalilgharibi N, Fouchard J, Recho P, *et al.*: **The dynamic mechanical properties of cellularised aggregates.** *Curr Opin Cell Biol*. 2016; **42**: 113–20.
[PubMed Abstract](#) | [Publisher Full Text](#)
  53. **F** Tambe DT, Hardin CC, Angelini TE, *et al.*: **Collective cell guidance by cooperative intercellular forces.** *Nat Mater*. 2011; **10**(6): 469–75.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  54. Friedl P, Mayor R: **Tuning Collective Cell Migration by Cell-Cell Junction Regulation.** *Cold Spring Harb Perspect Biol*. 2017; **9**(4): pii: a029199.
[PubMed Abstract](#) | [Publisher Full Text](#)
  55. Danjo Y, Gipson IK: **Actin 'purse string' filaments are anchored by E-cadherin-mediated adherens junctions at the leading edge of the epithelial wound, providing coordinated cell movement.** *J Cell Sci*. 1998; **111**(Pt 22): 3323–32.
[PubMed Abstract](#)
  56. Duque J, Gorfinkel N: **Integration of actomyosin contractility with cell-cell adhesion during dorsal closure.** *Development*. 2016; **143**(24): 4676–86.
[PubMed Abstract](#) | [Publisher Full Text](#)
  57. Zulueta-Coarasa T, Fernandez-Gonzalez R: **Tension (re)builds: Biophysical mechanisms of embryonic wound repair.** *Mech Dev*. 2017; **144**(Pt A): 43–52.
[PubMed Abstract](#) | [Publisher Full Text](#)
  58. Begnaud S, Chen T, Delacour D, *et al.*: **Mechanics of epithelial tissues during**

- gap closure. *Curr Opin Cell Biol.* 2016; **42**: 52–62.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
59. Fadul J, Rosenblatt J: **The forces and fates of extruding cells.** *Curr Opin Cell Biol.* 2018; **54**: 66–71.
[PubMed Abstract](#) | [Publisher Full Text](#)
  60. Yano T, Kanoh H, Tamura A, *et al.*: **Apical cytoskeletons and junctional complexes as a combined system in epithelial cell sheets.** *Ann NY Acad Sci.* 2017; **1405**(1): 32–43.
[PubMed Abstract](#) | [Publisher Full Text](#)
  61. Arnold TR, Stephenson RE, Miller AL: **Rho GTPases and actomyosin: Partners in regulating epithelial cell-cell junction structure and function.** *Exp Cell Res.* 2017; **358**(1): 20–30.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  62. Grikscheit K, Grosse R: **Formins at the Junction.** *Trends Biochem Sci.* 2016; **41**(2): 148–59.
[PubMed Abstract](#) | [Publisher Full Text](#)
  63. **F** Tang V: **Cell-cell adhesion interface: rise of the lateral membrane [version 1; referees: 2 approved].** *F1000Res.* 2017; **6**(F1000 Faculty Rev): 276.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  64. Vahey MD, Fletcher DA: **The biology of boundary conditions: cellular reconstitution in one, two, and three dimensions.** *Curr Opin Cell Biol.* 2014; **26**: 60–8.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  65. Hadjivasiliou Z, Hunter GL, Baum B: **A new mechanism for spatial pattern formation via lateral and protrusion-mediated lateral signalling.** *J R Soc Interface.* 2016; **13**(124): pii: 20160484.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  66. Vasilopoulos G, Painter KJ: **Pattern formation in discrete cell tissues under long range filopodia-based direct cell to cell contact.** *Math Biosci.* 2016; **273**: 1–15.
[PubMed Abstract](#) | [Publisher Full Text](#)
  67. Ladoux B, Nelson WJ, Yan J, *et al.*: **The mechanotransduction machinery at work at adherens junctions.** *Integr Biol (Camb).* 2015; **7**(10): 1109–19.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  68. Mao Y, Baum B: **Tug of war—the influence of opposing physical forces on epithelial cell morphology.** *Dev Biol.* 2015; **401**(1): 92–102.
[PubMed Abstract](#) | [Publisher Full Text](#)
  69. Lappalainen P: **Actin-binding proteins: the long road to understanding the dynamic landscape of cellular actin networks.** *Mol Biol Cell.* 2016; **27**(16): 2519–22.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  70. Biswas KH, Hartman KL, Yu CH, *et al.*: **E-cadherin junction formation involves an active kinetic nucleation process.** *Proc Natl Acad Sci U S A.* 2015; **112**(35): 10932–7.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  71. Yang C, Hoelzle M, Disanza A, *et al.*: **Coordination of membrane and actin cytoskeleton dynamics during filopodia protrusion.** *PLoS One.* 2009; **4**(5): e5678.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  72. Pyrpassopoulos S, Feeser EA, Mazerik JN, *et al.*: **Membrane-bound myo1c powers asymmetric motility of actin filaments.** *Curr Biol.* 2012; **22**(18): 1688–92.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  73. Ricca BL, Venugopalan G, Fletcher DA: **To pull or be pulled: parsing the multiple modes of mechanotransduction.** *Curr Opin Cell Biol.* 2013; **25**(5): 558–64.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  74. Vogel SK, Greiss F, Khmelinskaja A, *et al.*: **Control of lipid domain organization by a biomimetic contractile actomyosin cortex.** *eLife.* 2017; **6**: pii: e24350.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  75. **F** Efimova N, Svitkina TM: **Branched actin networks push against each other at adherens junctions to maintain cell-cell adhesion.** *J Cell Biol.* 2018; **217**(5): 1827–45.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  76. Carlsson AE: **Membrane bending by actin polymerization.** *Curr Opin Cell Biol.* 2018; **50**: 1–7.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  77. Mykuliak VV, Haining AWM, von Essen M, *et al.*: **Mechanical unfolding reveals stable 3-helix intermediates in talin and α -catenin.** *PLoS Comput Biol.* 2018; **14**(4): e1006126.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  78. **F** Yao M, Qiu W, Liu R, *et al.*: **Force-dependent conformational switch of α -catenin controls vinculin binding.** *Nat Commun.* 2014; **5**: 4525.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
  79. Manibog K, Yen CF, Sivasankar S: **Measuring Force-Induced Dissociation Kinetics of Protein Complexes Using Single-Molecule Atomic Force Microscopy.** *Meth Enzymol.* 2017; **582**: 297–320.
[PubMed Abstract](#) | [Publisher Full Text](#)
  80. **F** Rakshit S, Zhang Y, Manibog K, *et al.*: **Ideal, catch, and slip bonds in cadherin adhesion.** *Proc Natl Acad Sci U S A.* 2012; **109**(46): 18815–20.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  81. Nunes-Alves A, Arantes GM: **Mechanical Unfolding of Macromolecules Coupled to Bond Dissociation.** *J Chem Theory Comput.* 2018; **14**(1): 282–90.
[PubMed Abstract](#) | [Publisher Full Text](#)
  82. Seifert C, Gräter F: **Protein mechanics: How force regulates molecular function.** *Biochim Biophys Acta.* 2013; **1830**(10): 4762–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
  83. Agosti A, Ambrosi D, Turzi S: **Strain energy storage and dissipation rate in active cell mechanics.** *Phys Rev E.* 2018; **97**(5–1): 052410.
[PubMed Abstract](#) | [Publisher Full Text](#)
  84. Breslin JW, Zhang XE, Worthyake RA, *et al.*: **Involvement of local lamellipodia in endothelial barrier function.** *PLoS One.* 2015; **10**(2): e0117970.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  85. Petersen EN, Chung HW, Nayeibosadri A, *et al.*: **Kinetic disruption of lipid rafts is a mechanosensor for phospholipase D.** *Nat Commun.* 2016; **7**: 13873.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  86. Gauvin TJ, Young LE, Higgs HN: **The formin FMNL3 assembles plasma membrane protrusions that participate in cell-cell adhesion.** *Mol Biol Cell.* 2015; **26**(3): 467–77.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  87. **F** Köster DV, Husain K, Iljazi E, *et al.*: **Actomyosin dynamics drive local membrane component organization in an *in vitro* active composite layer.** *Proc Natl Acad Sci U S A.* 2016; **113**(12): E1645–54.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  88. Lemièrre J, Valentino F, Campillo C, *et al.*: **How cellular membrane properties are affected by the actin cytoskeleton.** *Biochimie.* 2016; **130**: 33–40.
[PubMed Abstract](#) | [Publisher Full Text](#)
  89. Mesarec L, Gózdź W, Kralj S, *et al.*: **On the role of external force of actin filaments in the formation of tubular protrusions of closed membrane shapes with anisotropic membrane components.** *Eur Biophys J.* 2017; **46**(8): 705–18.
[PubMed Abstract](#) | [Publisher Full Text](#)
  90. Letort G, Politi AZ, Ennomani H, *et al.*: **Geometrical and mechanical properties control actin filament organization.** *PLoS Comput Biol.* 2015; **11**(5): e1004245.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  91. **F** Dmitrieff S, Nédélec F: **Amplification of actin polymerization forces.** *J Cell Biol.* 2016; **212**(7): 763–6.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  92. Boujmaa-Paterski R, Galland R, Suarez C, *et al.*: **Directed actin assembly and motility.** *Methods Enzymol.* 2014; **540**: 283–300.
[PubMed Abstract](#) | [Publisher Full Text](#)
  93. Pontes B, Monzo P, Gauthier NC: **Membrane tension: A challenging but universal physical parameter in cell biology.** *Semin Cell Dev Biol.* 2017; **71**: 30–41.
[PubMed Abstract](#) | [Publisher Full Text](#)
  94. **F** Pontes B, Monzo P, Gole L, *et al.*: **Membrane tension controls adhesion positioning at the leading edge of cells.** *J Cell Biol.* 2017; **216**(9): 2959–77.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  95. Diz-Muñoz A, Fletcher DA, Weiner OD: **Use the force: membrane tension as an organizer of cell shape and motility.** *Trends Cell Biol.* 2013; **23**(2): 47–53.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  96. Anishkin A, Loukin SH, Teng J, *et al.*: **Feeling the hidden mechanical forces in lipid bilayer is an original sense.** *Proc Natl Acad Sci U S A.* 2014; **111**(22): 7898–905.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  97. Priya R, Yap AS: **Active tension: the role of cadherin adhesion and signaling in generating junctional contractility.** *Curr Top Dev Biol.* 2015; **112**: 65–102.
[PubMed Abstract](#) | [Publisher Full Text](#)
  98. Ma R, Berro J: **Structural organization and energy storage in crosslinked actin assemblies.** *PLoS Comput Biol.* 2018; **14**(5): e1006150.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  99. Mak M, Zaman MH, Kamm RD, *et al.*: **Interplay of active processes modulates tension and drives phase transition in self-renewing, motor-driven cytoskeletal networks.** *Nat Commun.* 2016; **7**: 10323.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  100. Romet-Lemonne G, Jégou A: **Mechanotransduction down to individual actin filaments.** *Eur J Cell Biol.* 2013; **92**(10–11): 333–8.
[PubMed Abstract](#) | [Publisher Full Text](#)
  101. Jégou A, Romet-Lemonne G: **Single Filaments to Reveal the Multiple Flavors of Actin.** *Biophys J.* 2016; **110**(10): 2138–46.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  102. Sadhu RK, Chatterjee S: **Actin filaments growing against an elastic membrane: Effect of membrane tension.** *Phys Rev E.* 2018; **97**(3–1): 032408.
[PubMed Abstract](#) | [Publisher Full Text](#)
  103. Johannes L, Pezeshkian W, Ipsen JH, *et al.*: **Clustering on Membranes: Fluctuations and More.** *Trends Cell Biol.* 2018; **28**(5): 405–15.
[PubMed Abstract](#) | [Publisher Full Text](#)
  104. **F** Lieber AD, Yehudai-Resheff S, Barnhart EL, *et al.*: **Membrane tension in rapidly moving cells is determined by cytoskeletal forces.** *Curr Biol.* 2013; **23**(15): 1409–17.
[PubMed Abstract](#) | [Publisher Full Text](#) | [F1000 Recommendation](#)
  105. **F** Chugh P, Clark AG, Smith MB, *et al.*: **Actin cortex architecture regulates cell surface tension.** *Nat Cell Biol.* 2017; **19**(6): 689–97.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)
  106. Venit T, Kalendová A, Petr M, *et al.*: **Nuclear myosin I regulates cell membrane tension.** *Sci Rep.* 2016; **6**: 30864.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
  107. **F** Smith AS, Nowak RB, Zhou S, *et al.*: **Myosin IIA interacts with the spectrin-actin membrane skeleton to control red blood cell membrane curvature and deformability.** *Proc Natl Acad Sci U S A.* 2018; **115**(19): E4377–E4385.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | [F1000 Recommendation](#)

108. Simon C, Caorsi V, Campillo C, *et al.*: **Interplay between membrane tension and the actin cytoskeleton determines shape changes.** *Phys Biol.* 2018; **15**(6): 065004.
[PubMed Abstract](#) | [Publisher Full Text](#)
109. Biswas A, Alex A, Sinha B: **Mapping Cell Membrane Fluctuations Reveals Their Active Regulation and Transient Heterogeneities.** *Biophys J.* 2017; **113**(8): 1768–81.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
110. Delanoë-Ayari H, Al Kurdi R, Vallade M, *et al.*: **Membrane and acto-myosin tension promote clustering of adhesion proteins.** *Proc Natl Acad Sci U S A.* 2004; **101**(8): 2229–34.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
111. Pontani LL, Jorjadze I, Bruijic J: **Cis and Trans Cooperativity of E-Cadherin Mediates Adhesion in Biomimetic Lipid Droplets.** *Biophys J.* 2016; **110**(2): 391–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
112. Strale PO, Duchesne L, Peyret G, *et al.*: **The formation of ordered nanoclusters controls cadherin anchoring to actin and cell-cell contact fluidity.** *J Cell Biol.* 2015; **210**(2): 333–46.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
113. **F** Kannan N, Tang VW: **Myosin-1c promotes E-cadherin tension and force-dependent recruitment of α -actinin to the epithelial cell junction.** *J Cell Sci.* 2018; **131**(12): pii: jcs211334.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
114. Weirich KL, Banerjee S, Dasbiswas K, *et al.*: **Liquid behavior of cross-linked actin bundles.** *Proc Natl Acad Sci U S A.* 2017; **114**(9): 2131–6.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
115. Carvalho K, Lemièrre J, Faqir F, *et al.*: **Actin polymerization or myosin contraction: two ways to build up cortical tension for symmetry breaking.** *Philos Trans R Soc Lond B Biol Sci.* 2013; **368**(1629): 20130005.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
116. **F** Hayakawa K, Tatsumi H, Sokabe M: **Actin filaments function as a tension sensor by tension-dependent binding of cofilin to the filament.** *J Cell Biol.* 2011; **195**(5): 721–7.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
117. **F** Yamashiro S, Tanaka S, McMillen LM, *et al.*: **Myosin-dependent actin stabilization as revealed by single-molecule imaging of actin turnover.** *Mol Biol Cell.* 2018; **29**(16): 1941–7.
[PubMed Abstract](#) | [Publisher Full Text](#) | **F1000 Recommendation**
118. De La Cruz EM, Gardel ML: **Actin Mechanics and Fragmentation.** *J Biol Chem.* 2015; **290**(28): 17137–44.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
119. **F** Reymann AC, Boujemaa-Paterski R, Martiel JL, *et al.*: **Actin network architecture can determine myosin motor activity.** *Science.* 2012; **336**(6086): 1310–4.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
120. **F** Ennomani H, Letort G, Guérin C, *et al.*: **Architecture and Connectivity Govern Actin Network Contractility.** *Curr Biol.* 2016; **26**(5): 616–26.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
121. Vasquez CG, Martin AC: **Force transmission in epithelial tissues.** *Dev Dyn.* 2016; **245**(3): 361–71.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
122. McFadden WM, McCall PM, Gardel ML, *et al.*: **Filament turnover tunes both force generation and dissipation to control long-range flows in a model actomyosin cortex.** *PLoS Comput Biol.* 2017; **13**(12): e1005811.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
123. Rottner K, Kage F: **Actin Networks: Adapting to Load through Geometry.** *Curr Biol.* 2017; **27**(23): R1274–R1277.
[PubMed Abstract](#) | [Publisher Full Text](#)
124. Kobb AB, Zulueta-Coarasa T, Fernandez-Gonzalez R: **Tension regulates myosin dynamics during *Drosophila* embryonic wound repair.** *J Cell Sci.* 2017; **130**(4): 689–96.
[PubMed Abstract](#) | [Publisher Full Text](#)
125. Yap AS, Duszyc K, Viasnoff V: **Mechanosensing and Mechanotransduction at Cell-Cell Junctions.** *Cold Spring Harb Perspect Biol.* 2018; **10**(8): pii: a028761.
[PubMed Abstract](#) | [Publisher Full Text](#)
126. Wu SK, Budnar S, Yap AS, *et al.*: **Pulsatile contractility of actomyosin networks organizes the cellular cortex at lateral cadherin junctions.** *Eur J Cell Biol.* 2014; **93**(10–12): 396–404.
[PubMed Abstract](#) | [Publisher Full Text](#)
127. Dasanayake NL, Carlsson AE: **Stress generation by myosin minifilaments in actin bundles.** *Phys Biol.* 2013; **10**(3): 36006.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
128. Haase K, Pelling AE: **Resiliency of the plasma membrane and actin cortex to large-scale deformation.** *Cytoskeleton (Hoboken).* 2013; **70**(9): 494–514.
[PubMed Abstract](#) | [Publisher Full Text](#)
129. Tsai FC, Koenderink GH: **Shape control of lipid bilayer membranes by confined actin bundles.** *Soft Matter.* 2015; **11**(45): 8834–47.
[PubMed Abstract](#) | [Publisher Full Text](#)
130. Pyrpassopoulos S, Arpağ G, Feeser EA, *et al.*: **Force Generation by Membrane-Associated Myosin-I.** *Sci Rep.* 2016; **6**: 25524.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
131. Pontes B, Ayala Y, Fonseca AC, *et al.*: **Membrane elastic properties and cell function.** *PLoS One.* 2013; **8**(7): e67708.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
132. Pontes B, Viana NB, Salgado LT, *et al.*: **Cell cytoskeleton and tether extraction.** *Biophys J.* 2011; **101**(1): 43–52.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
133. Trichet L, Campàs O, Sykes C, *et al.*: **VASP governs actin dynamics by modulating filament anchoring.** *Biophys J.* 2007; **92**(3): 1081–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
134. Simunovic M, Voth GA: **Membrane tension controls the assembly of curvature-generating proteins.** *Nat Commun.* 2015; **6**: 7219.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
135. McConnell RE, Tyska MJ: **Leveraging the membrane - cytoskeleton interface with myosin-1.** *Trends Cell Biol.* 2010; **20**(7): 418–26.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
136. Kaya M, Tani Y, Washio T, *et al.*: **Coordinated force generation of skeletal myosins in myofilaments through motor coupling.** *Nat Commun.* 2017; **8**: 16036.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
137. Bendix PM, Koenderink GH, Cuvelier D, *et al.*: **A quantitative analysis of contractility in active cytoskeletal protein networks.** *Biophys J.* 2008; **94**(8): 3126–36.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
138. Dumont S, Prakash M: **Emergent mechanics of biological structures.** *Mol Biol Cell.* 2014; **25**(22): 3461–5.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
139. **F** Lecuit T, Yap AS: **E-cadherin junctions as active mechanical integrators in tissue dynamics.** *Nat Cell Biol.* 2015; **17**(5): 533–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | **F1000 Recommendation**
140. **F** Liu Z, Tan JL, Cohen DM, *et al.*: **Mechanical tugging force regulates the size of cell-cell junctions.** *Proc Natl Acad Sci U S A.* 2010; **107**(22): 9944–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
141. Leerberg JM, Gomez GA, Verma S, *et al.*: **Tension-sensitive actin assembly supports contractility at the epithelial zonula adherens.** *Curr Biol.* 2014; **24**(15): 1689–99.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
142. Cojoc D, Difato F, Ferrari E, *et al.*: **Properties of the force exerted by filopodia and lamellipodia and the involvement of cytoskeletal components.** *PLoS One.* 2007; **2**(10): e1072.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
143. Shahapure R, Difato F, Laio A, *et al.*: **Force generation in lamellipodia is a probabilistic process with fast growth and retraction events.** *Biophys J.* 2010; **98**(6): 979–88.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
144. **F** Spadaro D, Le S, Laroche T, *et al.*: **Tension-Dependent Stretching Activates ZO-1 to Control the Junctional Localization of Its Interactors.** *Curr Biol.* 2017; **27**(24): 3783–3795.e8.
[PubMed Abstract](#) | [Publisher Full Text](#) | **F1000 Recommendation**
145. Fujiwara I, Suetsugu S, Uemura S, *et al.*: **Visualization and force measurement of branching by Arp2/3 complex and N-WASP in actin filament.** *Biochem Biophys Res Commun.* 2002; **293**(5): 1550–5.
[PubMed Abstract](#) | [Publisher Full Text](#)
146. Bajpai S, Feng Y, Wirtz D, *et al.*: **β -Catenin serves as a clutch between low and high intercellular E-cadherin bond strengths.** *Biophys J.* 2013; **105**(10): 2289–300.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
147. Bajpai S, Feng Y, Krishnamurthy R, *et al.*: **Loss of alpha-catenin decreases the strength of single E-cadherin bonds between human cancer cells.** *J Biol Chem.* 2009; **284**(27): 18252–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
148. Yao M, Goult BT, Chen H, *et al.*: **Mechanical activation of vinculin binding to talin locks talin in an unfolded conformation.** *Sci Rep.* 2014; **4**: 4610.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
149. **F** Kovar DR, Pollard TD: **Insertional assembly of actin filament barbed ends in association with formins produces piconewton forces.** *Proc Natl Acad Sci U S A.* 2004; **101**(41): 14725–30.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#) | **F1000 Recommendation**
150. Stadler RV, White LA, Hu K, *et al.*: **Direct measurement of cortical force generation and polarization in a living parasite.** *Mol Biol Cell.* 2017; **28**(14): 1912–23.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
151. Chuan P, Spudich JA, Dunn AR: **Robust mechanosensing and tension generation by myosin VI.** *J Mol Biol.* 2011; **405**(1): 105–12.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
152. Koenderink GH, Dogic Z, Nakamura F, *et al.*: **An active biopolymer network controlled by molecular motors.** *Proc Natl Acad Sci U S A.* 2009; **106**(36): 15192–7.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
153. Démoulin D, Carlier MF, Bibette J, *et al.*: **Power transduction of actin filaments ratcheting *in vitro* against a load.** *Proc Natl Acad Sci U S A.* 2014; **111**(50): 17845–50.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
154. Fritzsche M, Li D, Colin-York H, *et al.*: **Self-organizing actin patterns shape membrane architecture but not cell mechanics.** *Nat Commun.* 2017; **8**: 14347.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)

Open Peer Review

Current Peer Review Status:

Editorial Note on the Review Process

Faculty Reviews are review articles written by the prestigious Members of **Faculty Opinions**. The articles are commissioned and peer reviewed before publication to ensure that the final, published version is comprehensive and accessible. The reviewers who approved the final version are listed with their names and affiliations.

The reviewers who approved this article are:

Version 1

1. Alpha Yap

Division of Cell Biology and Molecular Medicine, Institute for Molecular Bioscience, The University of Queensland, Brisbane, QLD, Australia

Competing Interests: No competing interests were disclosed.

2. Alex Mogilner

Courant Institute and Department of Biology, New York University, New York, NY, USA

Competing Interests: No competing interests were disclosed.

The benefits of publishing with F1000Research:

- Your article is published within days, with no editorial bias
- You can publish traditional articles, null/negative results, case reports, data notes and more
- The peer review process is transparent and collaborative
- Your article is indexed in PubMed after passing peer review
- Dedicated customer support at every stage

For pre-submission enquiries, contact research@f1000.com

F1000Research