On small length-scales, the mechanics of soft materials may be dominated by their interfacial properties as opposed to their bulk properties. These effects are described by equilibrium models of elasto-capillarity and wetting. In these models, interfacial energies and bulk material properties are held constant. However, in biological materials, including living cells and tissues, these properties are not constant, but are ‘actively’ regulated and driven far from thermodynamic equilibrium. As a result, the constraints on work produced during the various physical behaviors of the cell are unknown. Here, by measurement of elasto-capillary effects during cell adhesion, growth and motion, we demonstrate that interfacial and bulk parameters violate equilibrium constraints and exhibit anomalous effects, which depend upon a distance from equilibrium. However, their anomalous properties are reciprocal, and thus in combination reliably define energetic constraints on the production of work arbitrarily far from equilibrium. These results provide basic principles that govern biological assembly and behavior.

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