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Large-scale violation of detailed balance in biological systems CHASE BROEDERSZ, Princeton University, CHRISTOPHER BATTLE, NIKTA FAKHRI, University of Goettingen , FRED MACKINTOSH, VU University Amsterdam, CHRISTOPHER SCHMIDT, University of Goettingen — Living systems are out of equilibrium. A fundamental manifestation of non-equilibrium dynamics in biological systems is the violation of detailed balance: at the microscopic level, enzymatic processes such as kinetic proofreading or molecular motor activity clearly violate detailed balance. We study how such non-equilibrium dynamics emerge at macroscopic scales in cellular assemblies. We measure the steady-state dynamics of two systems, beating flagella of *Chlamydomonas reinhardtii* and mechanosensitive primary cilia protruding from epithelial kidney cells. The flagellum exhibits clear non-equilibrium driving, whereas fluctuations in the primary cilium are difficult to differentiate from Brownian motion. We parameterize the shapes of the flagellum and primary cilium using a low-dimensional representation of their configuration phase space, and use the measured dynamics to infer the steady-state probability distributions and probability currents. For both the flagellum and the primary cilium we find significant, coherent circulating probability currents, demonstrating that these systems violate detailed balance at the mesoscopic scale.

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