

one is on a strict diet, so that one wants to extract  $W$  calories of free energy from the system, plus or minus  $\epsilon$ .

Åberg supplies us with a clever recipe for doing exactly this. First, identify a set of low-energy states with net probability  $<\epsilon$ , and change the energies of these states alone to a very high value. As the total probability of finding the system in these states is  $<\epsilon$ , with high probability,  $>(1-\epsilon)$ , this step takes no work. Now thermalize the system at  $T$ , then gradually change the energies back to their original level, keeping the system in contact with the thermal reservoir. As long as this restoration is sufficiently gradual, the amount of work extracted from the system is almost deterministic, and Åberg shows that this work is the maximum amount that can be extracted in this way.

In their quantum-mechanical treatment, Horodecki and Oppenheim derive the same limit to certain work extraction. In the quantum case, however, decoherence

adds an extra source of microscopic irreversibility: as in the case of the quantum version of Maxwell's demon<sup>7,8</sup>, when the environment 'measures' a quantum system, the probabilistic nature of the outcome increases entropy.

These studies limiting 'almost certain' work extraction, together with related works<sup>3–6</sup> represent the latest additions to the cookbook of microscopic statistical mechanics. Starting from Einstein's theory of dissipation in Brownian motion<sup>9</sup>, moving through the fluctuation-dissipation theorem<sup>10</sup> and culminating recently with the Jarzynski equality and Cooke theorem<sup>11</sup>, investigations of the role of fluctuations in thermal systems at the microscopic scale have proved a touchstone for revealing deep truths about nature.

The fundamentally statistical origins of thermodynamics imply that chance is necessarily part of any thermodynamic endeavour, including the extraction of

work. Nonetheless, the simple relationship between the degree of certainty required in extraction and the amount of work that can be extracted is surprising — and delectable, even though the calories are limited. □

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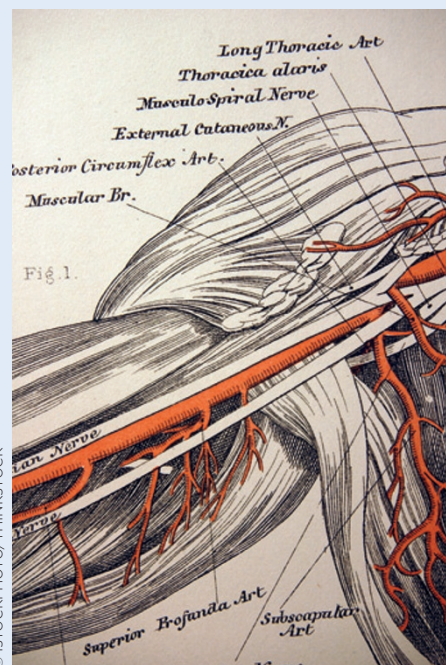
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## BIOPHYSICS

# Critical contraction

It takes a matter of milliseconds for muscles to flex actively in response to a stimulus. But they are capable of responding passively on even shorter timescales — contracting and extending, seemingly without consuming any energy. This behaviour can be attributed to the unfolding of proteins linking the muscle fibres. Just how this is achieved, however, has proved difficult to pin down. As they report in *Physical Review Letters*, Matthieu Caruel and colleagues have determined that this strange passive response is related to cooperativity between the cross-linking proteins and leads to intriguing material properties, including a negative stiffness in equilibrium and a tailored response to different loading conditions (*Phys. Rev. Lett.* **110**, 248103; 2013).

Collective behaviour in biological systems is often associated with a breaking of detailed balance. But as the coordination of proteins linking muscle fibres can be detected during very rapid responses to applied force, Caruel *et al.* reasoned that the problem can be treated in equilibrium, without taking activity into account. They invoked a well-studied model, showing that the equilibrium response of muscle material involves highly synchronized behaviour at the



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microscale, which explains its ability to flex passively.

The tell-tale cooperative behaviour was revealed under isotonic loading, in which the muscle length is allowed to vary. The physiological case, for which the length is fixed, is known as isometric loading, and

induces a disordered state characterized by randomly distributed cross-linkers. The behavioural difference between these two types of loading has been detected in experiments, but the origin of the disparity has so far proved elusive. Caruel *et al.* cite the non-equivalence of their equilibrium ensembles as the reason behind this difference — noting that stiffness can be negative under isometric conditions, whereas it is necessarily positive for isotonic loading.

Using their model to fit experimental data, the authors determined that the system lies close to a critical point. The associated diverging correlation length and macroscopic fluctuations are consistent with observations of muscles under stall-force conditions. Caruel *et al.* argue that marginal stability of the critical state allows the muscle material to amplify interactions, ensuring strong feedback and robustness to perturbation — and offering a way to rapidly switch between synchronized and desynchronized modes of operation. The generality of their formulation suggests that passive collective behaviour may be a property common to many cross-linked biological networks.

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