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ACTIVE GLASSES
The amorphous materials behind biophysics

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Assemblies of cells show rearrangements that are reminiscent of those found in amorphous solids. The tools of materials science can thus help to understand the role of mechanical stresses in aging and other biological processes.

Biological tissues, for the physicist, are disordered arrangements of particles, not unlike those found in amorphous solids or glasses, but endowed with mechanisms to convert energy into motion on the microscopic scale. These active mechanisms keep biological systems out of thermal equilibrium (and hence prevent them from decaying). Two recent papers in Nature Physics [1,2] have now established a close analogy between active glasses and the behaviour of amorphous materials under cyclic deformation. Exploring this analogy can help to port a large collection of results from the field of driven soft materials to biophysics.

Specific biology aspects aside, the physical consequences of combining mechanical interactions and active forces govern many aspects of living systems [3]. In tissues of epithelial cells, the individual cells are motile, but they show collective interactions that lead to their kinetic arrest. This phenomenon is often referred to as jamming, although studies exploring the analogies to the material world suggest that vitrification might be the more relevant term [4]. The observed similarities have sparked interest in model systems that combine features of kinetic arrest at high densities with activity on the particle level, and thus form active glasses.

Materials comprised of micrometre-sized entities are inherently soft, since their energy scales are such that mechanical moduli are weak. Soft materials are prone to strong non-linear response when externally driven, as seen in their rheological behaviour. External forces drive the system out of equilibrium, and thus, in a broader sense, driven soft materials should be comparable to active materials. This analogy did not go unnoticed in the soft-matter research community [5,6].

There is one difference, however. Rheology typically deals with well-controlled external forces that act in a prescribed direction. Active forces, on the other hand, act on the level of each particle, are randomly oriented, and change direction. Are the analogies then coincidental, or do they reveal something deeper? For thermal equilibrium, we know from statistical mechanics that, to some extent, details do not matter. Far from equilibrium, however, this is not the case anymore. To paraphrase the opening lines of Anna Karenina: all equilibrium systems are alike, yet each driven system is out of equilibrium in its own way.

Both Yagyik Goswami and collaborators [1] as well as Rishabh Sharma and collaborators [2] now argue that at the heart of the analogy between the rheology of amorphous materials and active materials lies in the fact that active forces are not persistent. They compared active model systems to glasses undergoing cyclic deformation. This opens a very interesting perspective: cyclic deformation can nudge the system into deeper potential energy minima, connected to the phenomenon of physical aging. Moreover, cyclically deformed amorphous systems 'learn': they can encode information of past deformation cycles in their microstructure such that it can later be read out [7].

By means of computer simulations of two different model systems, the researchers found that essentially the same happens in active systems. Instead of modelling cells, they purposefully reverted to particles with much simpler interactions, adding to each particle an active force that has a fixed strength but changes its direction after a certain persistence time. The key idea is that activity is controlled by two parameters, strength and persistence, and that these can be mapped onto the two parameters appearing in cyclic shear, namely amplitude and frequency (see Fig. 1).

Both papers establish this analogy between materials science and biology, and subsequently explore it further in different directions. Goswami and colleagues propose that boundary effects, known to be crucial in non-equilibrium materials, could play a role in epigenetic cell state transitions [1]. Sharma and colleagues focus on strain localization and a transition from ductile to brittle behavior, which is well known from amorphous metallic systems, and suggest an analogy in how biological tissues regulate their ductility by means of active forces [2]. Through the cyclic-shear connection, both studies give guidance on how to map parameters enabling to connect the physics of amorphous and active materials.

Where do we go from these analogies? Physics can offer the perspective of the generic, looking for common causes in the vast variety of biological phenomena. Cells changing their motility due to subtle changes in their interactions might hold a key to understanding the growth of certain tumors [8]. Diseased cells lose their ability to vitrify or show different fragility, a term describing how rapid changes in parameters change the motility, a notion borrowed from glass physics [9]. The findings now published in Nature Physics [1,2] suggest that certain biological aging phenomena might be connected to glass physics.

On a more speculative note, the cyclic-shear analogy could lead to novel protocols for encoding and reading memory, and making active materials learn [10]. In the reverse direction, studying active systems will help with better understanding non-equilibrium systems. It has already been noted that in complex materials featuring a yield stress, the mode of deformation (force-driven or deformation-rate-driven) can trigger different responses. Active forces are indeed more akin to forces and not deformations [1], and this might be an interesting hint towards universality (or at least, generality) classes of far-from-equilibrium systems.

So far these ideas rest on analogies with much simplified model systems studied in computer simulations. The full picture on tissue dynamics will of course eventually be a mix of the generic

– the stresses and mechanical effects governed by the physical balance laws of amorphous materials – and the specific – such as complex mechanisms regulating those physical forces by tailored biomolecular reactions. Yet, there might be a lot that we can already learn by mapping very different out-of-equilibrium systems onto each other, just as Goswami and colleagues and Sharma and colleagues have done.

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Competing interests

The author has no competing interests to declare.

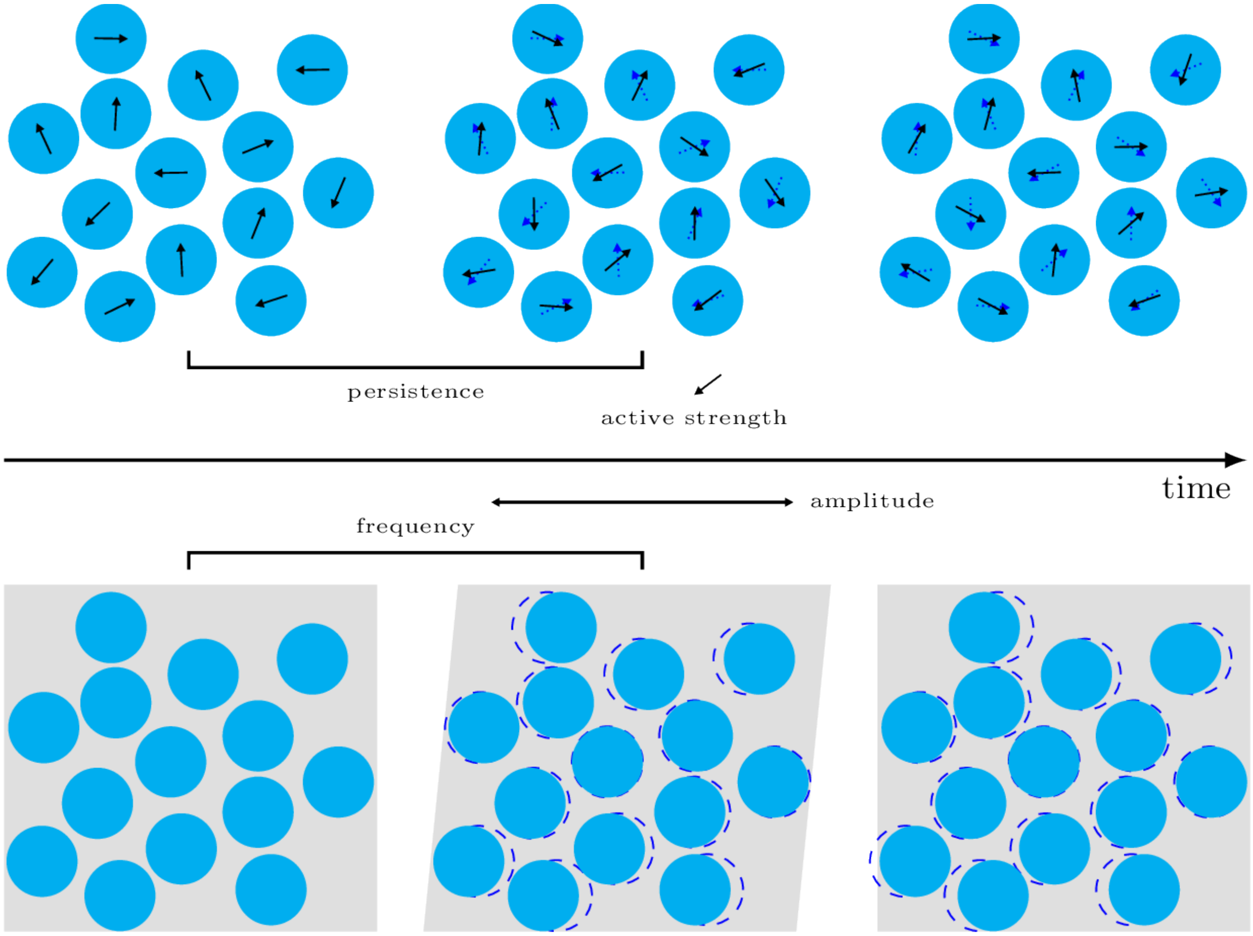

Fig.1~~:~~ **Active systems and soft materials under oscillatory shear.** Active particles (top) drive a living system out of equilibrium through self-propulsion forces characterized by an active strength (represented by little arrows in the particles) and a persistence time before reorienting. (Black arrows indicate the particles' instantaneous active strengths, blue dotted arrows their previous active strengths.) Many features of active glasses ~~(bottom)~~ might be understood, through analogies, by what we have learned from soft materials under cyclic shear (bottom), where amplitude and oscillation frequency are the corresponding parameters in the analogy paradigm. (Dashed circular outlines indicate the particles' previous positions.)