measurements of relative delays, such as time differences between ejections of electrons from two different energy levels of the investigated material.

Ossiander and colleagues overcame this limitation using a clever two-stage approach, which they demonstrated by examining photoemission from a clean tungsten surface using an attosecond streak camera. In the first stage of the approach, the authors deposited iodine molecules on the tungsten surface (Fig. 1a). They then applied an attosecond-duration extreme-ultraviolet light pulse to the material and measured the relative delay in photoemission from the tungsten surface and from the atoms in the iodine molecules. In the second stage, the authors applied the same light pulse to a gaseous mixture of small iodine-containing molecules and helium atoms, and measured the relative iodine–helium photoemission delay (Fig. 1b).

Helium atoms are the largest atoms for which streaking experiments can currently be modelled completely by *ab initio* quantum simulations[7]. The absolute photoemission delay for helium is therefore known. Ossiander *et al.* used this result in combination with their measured relative delays to determine absolute photoemission delays for the tungsten surface. Their approach opens the door to measurements of such delays in surface and gas-phase experiments for many other target materials.

However, two central assumptions must be made when using Ossiander and colleagues' technique. First, additional delays caused by interactions between the iodine atoms and the target material must be negligible or known. Second, the iodine atoms must be close enough to the material's surface that spatial variations in the streaking field have only a small effect on the photoemission measurements. In the authors' experiment, the validity of these assumptions was backed up by theory. A closer analysis of the general limits in resolution associated with the technique will be a challenging, but important, task for future work.

The idea of using molecules as a reference to calibrate photoemission timing has previously been applied to streaking experiments on dielectric (insulating) nanoparticles[8]. These experiments suggest that photoemission delays could be used to directly characterize the attosecond-scale collisional dynamics of electrons in dielectric materials. The approach of Ossiander *et al.* is therefore expected to further advance the diagnostic capabilities of photoemission-delay measurements.

Ossiander *et al.* report photoemission delays for several different energy levels of the investigated tungsten surface. Their results imply that electron ejection from the material is more complex than was anticipated from previous measurements of relative delays[3]. The observed absolute delays can be explained only by considering both transport and collisional effects of the electrons during their propagation through the material.

A promising future application of the technique is the characterization of more-complex electronic effects — such as correlation, dissipation and decoherence — using data on absolute photoemission delays. This would provide a key reference for theory. The authors' observation of an extremely short delay (a few attoseconds) from the outermost electron shell of the iodine atoms also highlights application potential for ultrafast switching in electronic devices that operate at extremely high (petahertz; 10^{15} Hz) frequencies. Ossiander and colleagues have therefore provided insights into the dynamics of photoemission that not only advance our understanding of nature but also open routes to new technology. ■

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BIOPHYSICS

Melting sculpts the embryo's body

Collections of cells in the tails of zebrafish embryos have now been found to transition between behaving as solids and fluids. This transition is responsible for the head–to–tail elongation of the embryo. SEE LETTER P.401

PIERRE-FRANÇOIS LENNE & VIKAS TRIVEDI

Understanding how different materials respond to force is central to the field of engineering. For instance, permanent application of force is required to deform a solid-like material, whereas a fluid-like material can be irreversibly deformed by transient forces. Over the past few decades, such concepts have also surfaced in biology. Much like inert materials such as foams and emulsions, collections of cells can switch from solid-like to fluid-like behaviours, depending on cell density and adherence. Processes that coordinate this tissue 'melting' with the application of forces have been shown to locally deform tissues while maintaining their global structure[1]. Mongera *et al.*[2] report on page 401 that the elongation of the head-to-tail axis in zebrafish embryos relies on spatially controlled tissue 'melting'.

Head-to-tail (anterior-to-posterior) axis elongation is a central event in the generation of the animal body plan, and involves large-scale tissue deformation. For example, the posterior tip of a zebrafish embryo doubles in length in about five hours[3]. During this time, cells at the tip — in a region called the mesoderm progenitor zone (MPZ) — differentiate, becoming presomitic mesoderm (PSM) cells as they are left behind when posterior elongation proceeds. Cells of the PSM form structures called somites that will give rise to the animal's vertebrae (Fig. 1).

There are several known modes of tissue elongation. Polarized rearrangement of neighbouring cells can cause elongation in one direction and narrowing along a perpendicular axis[4]. In addition, external boundaries and forces can mediate elongation — neighbouring tissues can constrain, pull[5,6] or compress[7,8] tissues, and differences in the volume and stiffness of the extracellular matrix around cells can also provide guidance[7,9]. But, with a few exceptions[10], we still do not know to what extent the material properties of cells as individuals and collectives control axis elongation *in vivo*, because it is technically challenging to simultaneously measure internal mechanical stresses and changing material properties within elongating tissues at cellular and supracellular scales.

Mongera *et al.* overcame this challenge by inserting magnetically responsive oil microdroplets between cells in the tails of zebrafish embryos undergoing elongation. They used changes in the shape of the microdroplets from spherical to ellipsoid to infer supracellular mechanical stresses, and so to map the spatial distribution of forces along the axis. First, the authors analysed the microdroplets in the absence of a magnetic field, which revealed a gradient of increasing force from the MPZ at the posterior tip of the embryo to the PSM. These supracellular stresses persisted for more than 30 minutes, on a par with the timescale over which PSM maturation leads to the formation of somites.

Second, the researchers applied a magnetic

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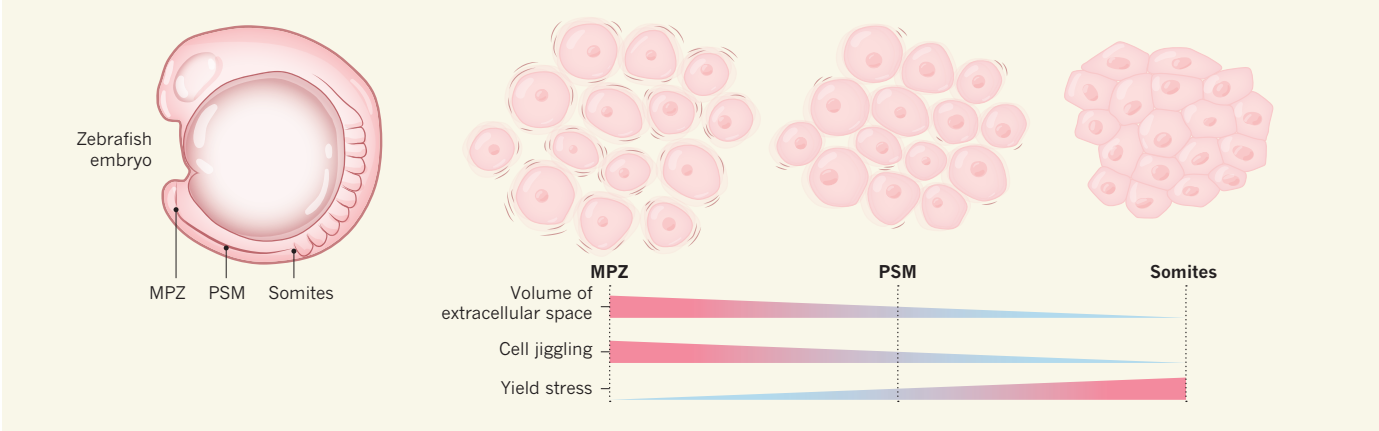

Figure 1 | A gradient of mechanical behaviour sculpts zebrafish. Zebrafish embryos undergo a period of rapid elongation at their tails, during which cells originally in a mesodermal progenitor zone (MPZ) at the tip of the embryo become presomitic mesoderm (PSM) cells, and then form structures called somites that will give rise to vertebrae. Mongera *et al.*[2] have shown that cells in the MPZ behave in a fluid-like manner, and become progressively more solid-like as they mature into PSM and somites. Changes in three physical factors govern this transition: decreases in the volume of extracellular space around cells; decreases in the rate at which cells 'jiggle', changing their contacts with neighbours; and increases in yield stress (the amount of stress needed to permanently deform the tissue). The gradients in yield stress and in the volume of extracellular space are controlled by the cell-adhesion protein N-cadherin (not shown), the concentration of which is similar in the MPZ and PSM.

field to the microdroplets to distend them, causing deformation of the tissue around them, and then investigated whether the droplets returned to their original spherical shape. This experiment revealed the amount of stress needed to permanently deform the tissue (a property called yield stress), which provides information about the material properties of the cells. Mongera *et al.* showed that yield stress also increases in a posterior-to-anterior direction, indicating that the MPZ is more fluid-like, and the PSM solid-like.

These measurements hint at the possibility of fluid-to solid 'jamming' — a concept well established to describe the transition of foam-like systems from wet to dry states[11]. In foams, jamming depends on mechanical stresses, density and temperature[11-13]. Mongera and colleagues hypothesized that equivalent parameters might govern the ability of the MPZ to 'unjam' and behave in a fluid-like way. They therefore investigated, in addition to mechanical stresses, the volume of extracellular space between cells, and fluctuations in the contacts between cells (known as cell jiggling, a property often interpreted as the effective temperature) in their embryos.

This is a remarkable technical achievement, because measurements of all three parameters have not previously been made in the same system, even in inert soft materials. The experiments demonstrated that, whereas mechanical supracellular stresses decreased towards the MPZ, the volume of extracellular spaces increased, as did the extent of cell jiggling (Fig. 1). Of these factors, the researchers found that jiggling had the dominant role in keeping the MPZ unjammed. Their measurements of cell-scale mechanical stress (made by analysing small deformities in the ellipsoid nature of the microdroplets in the absence of a magnetic field) revealed that these stresses last only about one minute and show no spatial bias along the anterior–posterior axis. However, because the yield stress is lower in the MPZ than in the PSM, cell-scale stress fluctuations are sufficient to drive cell jiggling in the MPZ and thereby tissue melting — by contrast, they fail to do so in the PSM.

Together, Mongera and colleagues' data fit with typical scenarios for a jamming transition[1], in which the volume between interacting objects, here cells, is key to whether the objects behave as a fluid or a solid. In a final set of experiments, the authors show that the gradients in yield stress and in the volume of extracellular space are controlled by the cell-adhesion protein N-cadherin (although the concentration of the protein is not itself graded). The molecular mechanisms underpinning cell jiggling remain to be clarified, but the authors' work, in agreement with previous reports on 2D multicellular systems[13,14], show that the mechanics of cell–cell contacts — of adhesion in particular — have a prominent role in the jamming transition. Fluid-to-solid transitions are likely to occur in other animals, both in embryos and in adult organisms, but we expect that the molecules that control them might differ from those that modulate axis elongation in zebrafish.

"Fluid-to-solid transitions are likely to occur in other animals, both in embryos and in adult organisms."

It will be interesting to determine how the parameters that control this transition in living materials relate to and differ from those at play in inert materials. In inert materials, the timescale over which material properties change is usually much larger than the timescale of typical deformations. By contrast, the mechanical properties of living matter can vary simultaneously with changes in the shape of tissues, and can, in turn, lead to further shape changes. This creates a strong coupling between the overall material properties of the tissue, its shape changes as a result of cellular movements, and the force field generated and experienced by the constituent cells. We therefore expect living materials to provide us with a rich phenomenology, distinct from that of inert materials.

Axis elongation is widespread in development, and it will be important to look for hallmarks of similar transitions in other systems. It will be fascinating to learn more about how living systems obey the laws of physics using cellular and molecular strategies. ■

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