but low physiological stress responses better or worse off than one displaying the reverse?

The second approach equates an animal's welfare with its subjective experiences[5,6]. Animals may grow, reproduce and appear to be healthy, yet still have poor welfare if they experience subjective suffering such as prolonged frustration from having little space in which to move. Here, largely, is the cause of public concern about animal welfare — if non-human animals were shown to lack conscious subjective experiences, that concern would almost certainly wane. For the scientist, the problem is that subjective states such as those that we call frustration, anxiety or pain are difficult to measure or cannot be measured at all.

Advocates of this approach have therefore developed methods based on the assumption that animals suffer if denied resources that they are strongly motivated to obtain, or exposed to stimuli that they will work hard to avoid[5]. Theories that emotions are important in motivating animal behaviour lend support to this assumption[7,8]. The methods involve finding out how much animals value resources by testing their preferences or, using techniques borrowed from human consumer economics, by measuring how high a price, in terms of time and energy, they will pay to access or avoid them[5,9]. These 'motivation'-based methods have limitations[5] — for example, sweet foods may be preferred in the short term but do not enhance health and welfare in the long term — but they circumvent the problem of integrating many different welfare indicators.

Most people in this field acknowledge that the 'welfare indicators' and 'motivation' methods complement each other[2,4,5]. Even so, the two approaches have largely been used in isolation — Mason and colleagues'[1] achievement is to have brought them together. The authors investigated whether the small wire-mesh cages used to house farmed mink cause frustration by preventing natural activities such as swimming or using several nest sites. Sixteen individually housed mink were each given access to seven cages containing resources such as an alternative nest site or a water pool. When made to work for access to the resources by pushing through weighted doors, mink worked hardest for the water pool. This conclusion was reached using four different calculations of how the mink valued each resource — a comprehensive analysis that sets new standards in animal welfare studies.

Following the assumption of the 'motivation' approach, these findings suggest that depriving mink of a water pool may result in suffering and poor welfare. Mason *et al.* tested this assumption by measuring changes in welfare indicators when the mink were prevented from visiting the pool for 24 hours. They observed a rise in urinary cortisol, an endocrine indicator of stress, that was not accompanied by an increase in activity and was indistinguishable from that seen when an essential resource, food, was removed for the same duration.

By using the 'motivation' and 'welfare' methodologies together, Mason *et al.* provide powerful evidence that the mink value the water pool highly and exhibit stress responses in its absence. So lack of a water pool may compromise the welfare of mink even if their growth and health are good. Answers to a number of remaining questions could strengthen this conclusion. The roles of expectation and experience of a resource in determining response to deprivation remain to be tackled. So too does the problem that resource valuation depends on what else is available (for instance, chewable objects might have been valued more highly if they were the only resource offered). Furthermore, deprivation of a valued resource may be stressful only in the short term, or if no adequate substitutes are available. For example, removing the highly valued alternative nest site did not induce a cortisol rise, perhaps because the animal's own nest was still accessible.

What of the wider implications? Captive animals are often denied resources or opportunities to behave in ways that, intuitively, would seem to be important to them. Confinement prevents domestic sows from building nests before they give birth; there is usually no dust-bathing substrate in cages for laying hens; and most laboratory rodents have limited opportunity to construct burrows or enclosed nests. Techniques such as those used by Mason *et al.* should allow us to go a good deal further than intuition in deciding whether these resources and opportunities are indeed highly valued by the animals, and whether their absence causes frustration and stress. If so, scientific argument for their provision will be strong and should form the basis for decisions to alter housing conditions, even though such decisions will inevitably be coloured by political, economic and practical considerations. ■

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1. Mason, G. J., Cooper, J. & Clarebrough, C. *Nature* **410,** 35–36 (2001).
2. Duncan, I. J. H. & Fraser, D. in *Animal Welfare* (eds Appleby, M. C. & Hughes, B. O.) 19–31 (CAB Int., Wallingford, Oxon, 1997).
3. McGlone, J. J. *J. Agric. Environ. Ethics* **6** (suppl. 2), 26–36 (1993).
4. Broom, D. M. & Johnson, K. G. *Stress and Animal Welfare* (Chapman & Hall, London, 1993).
5. Dawkins, M. S. *Behav. Brain. Sci.* **13**, 1–61 (1990).
6. Duncan, I. J. H. & Petherick, J. C. *J. Anim. Sci.* **69**, 5017–5022 (1991).
7. Cabanac, M. *J. Theor. Biol.* **155**, 173–200 (1992).
8. Rolls, E. T. *Behav. Brain. Sci.* **23**, 177–234 (2000).
9. Houston, A. I. *Anim. Behav.* **53**, 983–990 (1997).

Condensed matter

Memories of paste

David A. Weitz

Pastes are not the simple materials they appear to be. It seems they have a 'memory': after a force has been applied, they recover and move back in the opposite direction.

Pastes are familiar materials we use every day, for example, when we brush our teeth. They are prototypic 'soft' materials[1]: they behave as a solid until a sufficiently large load or stress is applied, at which point they flow like a fluid. So a squeeze is all that is required to put toothpaste on a brush. But the way pastes and similar soft solids behave remains poorly understood, partly because it is difficult to perform reproducible experiments on these materials — their properties seem to change with time and depend strongly on their history. As they discuss in *Physical Review Letters*, however, Cloitre, Borrega and Leibler[2] have developed new experimental techniques and show that the way a paste recovers from an applied stress is remarkably like the behaviour of glasses and gels[3,4].

Pastes typically consist of a suspension of small particles in a background fluid. These particles are crowded, or jammed together like grains of sand on a beach, forming a disordered, glassy or amorphous structure, and giving pastes their solid-like character. This jamming together gives pastes some of their most unusual properties. The particles exert large forces on their neighbours, but in solid pastes the material, and hence each individual particle, is stationary, so the net sum of the forces on each particle must be zero. Because of the high degree of disorder inherent in any paste, some of these local force balances will be precarious. A very small change, perhaps induced by a fluctuation in temperature, can disrupt the balance, causing a relaxation in the structure that can ripple through a large volume because of the close proximity of the particles and the requirement that all local forces have to be balanced.

After relaxation from such a small disturbance, the new state is likely to be more stable and disruptions will be less probable.

A slightly greater disruption is required to cause further relaxation. This results in the paste 'ageing' — it relaxes more slowly as the waiting time increases or as the sample gets 'older'. The relaxation continues to slow as time goes by, so the ageing process never comes to a complete stop. The time that a relaxation takes to occur typically depends on the paste's age, and can be plotted onto a logarithmic curve, known as a master curve.

In the pastes studied by Cloitre *et al.*[2], the particles are microgels, which are small chunks of gel swollen by a solvent. At low concentrations, these microgels are not jammed together, and their properties are determined by the solvent. But as their number is increased, the microgel particles begin to squeeze on each other, creating the paste-like behaviour.

Rather than study the structure of the pastes directly, Cloitre *et al.* instead look at their rheological, or mechanical, properties, which determine both flow and structure. Because the relaxation in the solid paste depends on its age, the authors set up an initial state as a reference point from which to determine the age of the sample. They do this by applying a very large shear stress which 'melts' the sample, changing the paste to a fluid-like state. The ageing begins when the stress is removed and the paste becomes a solid again. Cloitre *et al.* then probe the mechanical properties of the paste by using very small stresses that are just enough to elicit a measurable response.

The authors make a remarkable observation: although the sample was completely fluidized by the large shear stress, it developed a 'memory' of the direction in which the stress was applied, and the solid-like paste slowly 'pulled back' on itself in the opposite direction, eventually passing beyond its initial position. This 'recovery' follows the logarithmic master curve that typifies the ageing behaviour. The memory effect is robust. The direction in which the small additional stress is applied does not matter: the long-time strain recovery is always in the opposite direction.

Similar ageing effects are observed in measurements of long-term 'creep'; here a stress that is just enough to make the sample flow is applied some time after the sample is melted. The flow or creep does not begin immediately, but instead requires some onset time, which again depends on the waiting time. Similar effects are observed in the ageing of glasses, and Cloitre *et al.* use an analysis akin to that used in the description of glassy polymers: like the paste samples of Cloitre *et al.*, such glasses display ageing, and the relaxation data can again be scaled onto a single master curve.

What causes this ageing behaviour and the memory effect? The microscopic origin is unclear — local forces may be involved, but why they lead to a memory and a strain in the negative direction is not clear. Nevertheless, the great appeal of these simple pictures for ageing is that, even without complete understanding, it is still possible to scale the data onto universal curves using the age of the sample as a scaling parameter. The question that must now be addressed is how much impact this scaling behaviour, the ageing and the highly unusual rheology have. Are they fascinating peculiarities of this system, depending on the microscopic nature of the microgels? Or are they symptomatic of more general behaviour that will be observed in other materials? If the latter, this may have implications for manufacturing and processing of soft materials in industrial applications. ■

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1. Sollich, P., Lequeux, F., Hébraud, P. & Cates, M. E. *Phys. Rev. Lett.* **78,** 2020–2023 (1997).
2. Cloitre, M., Borrega, R. & Leibler, L. *Phys. Rev. Lett.* **85,** 4819–4822 (2000).
3. Bonn, D., Tanaka, H., Wegdam, G., Kellay, H. & Meunier, J. *Europhys. Lett.* **45,** 52–57 (1998).
4. Cipelletti, L., Manley, S., Ball, R. C. & Weitz, D. A. *Phys. Rev. Lett.* **84,** 2275–2278 (2000).

Apoptosis

Baiting death inhibitors

Donald W. Nicholson

Enzymes called caspases that start the process of programmed cell death can be dangerous if activated at the wrong time. A feat of self-restraint keeps one such caspase under control.

Most of the cell death that takes place in mammals occurs by apoptosis — the result of a dedicated biochemical pathway. At the heart of this pathway lies a family of protein-cleaving enzymes, the caspases, which normally lie dormant in healthy cells and become activated in response to diverse stimuli when cell death

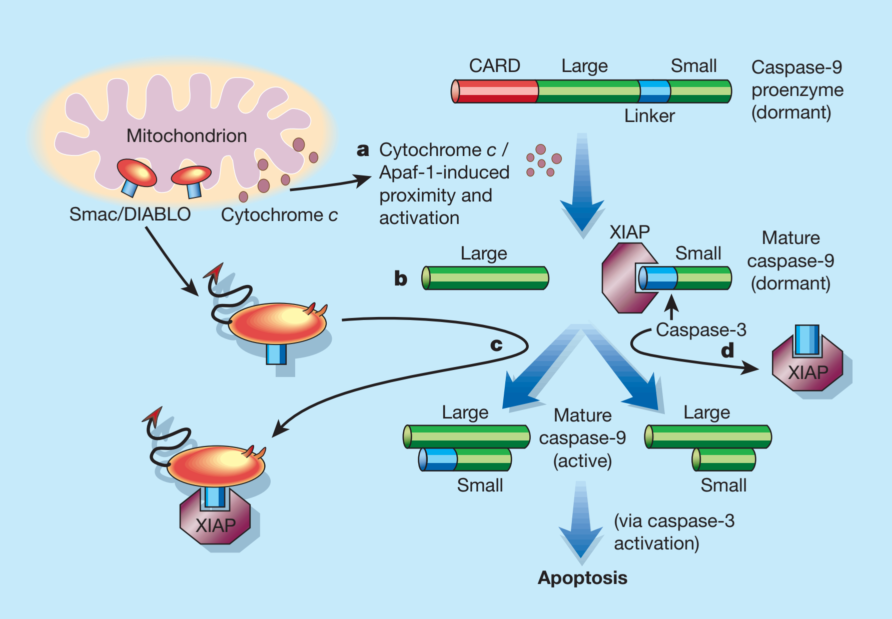

Figure 1 **The branch of the programmed-cell-death (apoptosis) pathway that includes caspase-9 and its regulators.** a, **In response to death stimuli (not shown), a molecule called Apaf-1, together with cytochrome *c*, which is released from mitochondria, induces the aggregation and processing of caspase-9 proenzymes. The processing includes the removal of the 'CARD' domain, and separation of the large subunit from the linker peptide that connects it to the small subunit. This exposes the linker peptide.** b, **As shown by Srinivasula *et al.*[2], one end of the linker peptide mimics the XIAP-binding peptide of Smac/DIABLO, allowing XIAP — an inhibitor of apoptosis — to bind to mature caspase-9. This keeps caspase-9 in a catalytically dormant state.** c, d, **This suppression of caspase-9 might be counteracted by two mechanisms — competition for XIAP by the apoptosis-promoting protein Smac/DIABLO** (c), **or caspase-3-mediated removal of the XIAP-binding peptide from caspase-9** (d).