processing in distinct and often widely separated brain circuits (those responsible for vision, olfaction, somatic sensation, together with the amygdala and other centres involved in emotion), this unification of experiential components implies some sort of coordination between different brain areas. In their survey of various notions about consciousness, Crick and Koch observe that a common thread through all of the thinking about consciousness is the recognition of a need to bind together information from many separate parts of the brain.

In the paper Crick writes, "In biology, if seeking to understand function, it is usually a good idea to study structure". And thus he takes a fundamentally structural approach to consciousness: what brain regions, he asks, have properties that would suit them for the information gathering and analysis that is at the heart of the conscious experience? I know from conversations with Crick that he had a very strong hunch, one that bordered on a conviction, that the structure underlying consciousness is the claustrum.

What is the claustrum, and why pick on it as a key for understanding consciousness? The claustrum is a thin sheet of grey matter that resides parallel to and below part of the cortex (the cortex is the grey matter covering of the brain that carries out the computations involved in feeling, seeing, hearing, language and deciding what to do). The claustrum is present in all mammals, but it has been little studied and its function is not known. What is known, however, is that there are two-way connections between the claustrum and most, if not all, parts of the cortex as well as subcortical structures involved in emotion.

So the claustrum is not just a sort of shadow of the cortex, but rather a neural circuit with overlapping inputs from various cortical regions and outputs back to cortex. Because of its widespread connections, Crick and Koch liken the claustrum to the conductor of an orchestra, who is responsible for binding the performances by individual musicians into an integrated whole that can be much more than the sum of the parts. The neuroanatomical connections of the claustrum, then, just match with the 'conductor' required to bind together the various disparate components of the conscious experience represented in many different brain regions.

Crick told me that one of his main purposes in this paper was to encourage new studies of the claustrum, and had he lived longer, he would have liked to start a centre for investigating the claustrum, where neuroanatomical, electrophysiological and novel molecular biological approaches to the claustrum could be combined. Some of these ideas for studying the claustrum, like using molecular biological methods to specifically disrupt claustral function, are sketched in this paper.

Not everyone will buy the Crick and Koch idea that the claustrum is the seat of consciousness. For example, the fact that all mammals have a claustrum could be an argument against the proposal for those who cannot imagine consciousness without language and high-level symbolic reasoning. And I expect others will be sceptical on other grounds. Nevertheless, the proposal is an interesting and challenging one, from a scientific giant, and I believe every scientist will be fascinated to see how one of the greatest biologists attacked such a difficult problem. ■

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GRANULAR MATTER

A tale of tails

Martin van Hecke

Granular materials such as sand can either be jammed and rigid, or yield and flow. Puzzling changes in the forces between the grains deepen the mystery surrounding this basic, but poorly understood, transition.

Why does sand mimic a solid when we walk on it but emulate a fluid when it is in an hourglass? Why does salt flow only when its shaker is tipped far enough? These simple questions are without a clear answer, and have in recent years inspired investigations into what exactly happens when otherwise jammed[1] granular media lose rigidity and yield.

Two papers[2,3] in this issue suggest that the key to jamming and yielding are the networks formed by the contact forces between individual granular particles (Fig. 1a). On page 1075, Corwin, Jaeger and Nagel[2] report that jammed and yielded glass beads differ in the statistics of their force networks, and, on page 1079, Majmudar and Behringer[3] investigate the statistics and structure of force networks for jammed systems under compression or shear forces. The two experiments employ photoelastic materials (which rotate the polarization of light depending on stress, thus visualizing forces when viewed between polarizers) to obtain the grain–wall and grain–grain forces, respectively.

In Corwin and colleagues' experiment[2], a slowly rotating plunger exerted a constant, shearing force on glass beads filling a cylindrical container. The motion of the bottom layer of beads revealed that beads near the sides flowed past each other, whereas those near the centre remained jammed and rotated as a solid block. Corwin and colleagues measured the forces on a photoelastic bottom plate, and express the probability of a grain exerting a force of a certain magnitude in a distribution such as that in Fig. 1c. Their central finding is that a change in the 'tail' of this distribution (characterizing the particles carrying the largest forces) signals the point at which the system jams: jammed grains produce tails with an exponential fall-off, whereas yielded grains produce much steeper tails. Thus flowing grains avoid large forces more effectively than those that are jammed.

Surprisingly, the yielded force distributions are rate-independent (that is, they do not vary with flow speed), and can be characterized by describing the flowing beads as if they form an ordinary liquid (at a constant temperature). It is usually tacitly assumed that these slow, rate-independent granular flows are quasi-static, so that a snapshot of a flowing

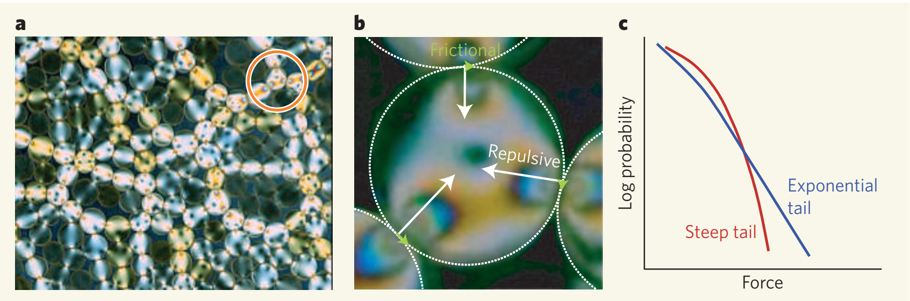

Figure 1 | Fluctuating forces. a, A force network, typical of granular media, revealed in a layer of photoelastic discs. The bright discs are experiencing the largest forces, and appear to align in 'force-chains'. **b,** An enlargement of the single particle indicated in (**a**) reveals a complex pattern of bright and dark bands, called fringes. From these, Majmudar and Behringer[3] measured the repulsive normal (white) and frictional tangential (green) contact forces inside force networks. **c,** Probability distributions for the contact forces in granular media. Corwin, Jaeger and Nagel[2] relate jammed systems to the blue curve, which has an exponential tail, and yielded systems to the red curve, which has a much steeper tail.

Box 1 Packing problems

When spherical grains in a container are shaken down, at the densest possible packing they fill a volume fraction of around 64%. This is 'random close packing' — a notoriously controversial concept[9], as regular periodic packings (similar to how oranges are packed in your grocery store) reach higher densities of 74%. Allowing small regular regions in disordered packings thus can increase the density beyond random close packing: 'random' and 'close' represent opposing trends[9]. (Incidentally, non-spherical grains, such as M&Ms, also pack more densely than 64%[11]). Even more elusive is random loose packing[10], which can be achieved by immersing spheres in a neutrally buoyant fluid and letting them settle gently, creating very fragile packings at volume fractions around 55%. Packing and jamming are related: soft, frictionless spheres jam, in the absence of shear, at a density precisely given by random close packing. Perhaps random loose packing might be defined, similarly, as the density where frictional spheres jam. **M.v.H.**

system cannot be distinguished from a stationary — jammed — state. Corwin and colleagues' experiment show that this assumption is incorrect — with the difference hidden in the force distributions.

What would happen if the rotating top disc of Corwin and colleagues' experiment were gradually stopped? The forces could simply freeze — but that would give yielded forces for jammed grains. The forces of the sheared grains could relax to a jammed distribution — but this would imply the breakdown of rate-independence. One solution to this conundrum could be the presence of additional characteristics such as packing density[4,5] or anisotropy[6] of the contact and force networks, which might differ between jammed and yielded grains. To uncover what goes on, we thus need to look inside granular media.

Majmudar and Behringer[3] have done just that, investigating a granular material consisting of a layer of discs made of photoelastic plastic. The discs exhibit characteristic fringe patterns that encode the contact forces in the system, and, through the analysis of the resulting images, the authors obtained the first quantitative determination of force networks (Fig. 1b). They illustrate the power of this method by comparing a strongly jammed, uniformly compressed system with a weakly jammed system under pure shear (compressed in one direction and expanded in the other). Even though both systems are jammed and therefore static, the force networks of the two systems are very different: the sheared system exhibits strong anisotropies[6], and 'force-chains' are much longer than is the case in a compressed system.

The tails of the force distributions established by Majmudar and Behringer[3] hold a surprise: they change from steep for compressed, strongly jammed systems to exponential for sheared, weakly jammed systems. The tails determined by Corwin and colleagues[2], in contrast, become steep only when the grains flow, and are exponential for all jammed cases — irrespective of whether the system has experienced a shear stress. The two experiments probe somewhat different aspects of the force network, but, even so, their results are not easily reconciled.

Yielding by shear is the main mechanism by which grains are made to flow. Indeed, Osbourne Reynolds suggested more than 100 years ago a relation between packing density and yielding: flowing grains dilate[4]. These new experiments[2,3] illustrate that force networks also play a crucial role by signalling stresses, jamming and yielding — in other words, the state of the granular system. The precise connection between packing geometry, force networks and jamming, however, is still a puzzle[7].

Recently, theoretical progress has been made by considering simplified systems without friction or shear such as packings of deformable, frictionless particles. One of the most exciting findings is that the jamming–yielding transition in this system, which occurs when the confining pressure is lowered to zero, has many properties of a phase transition such as that which occurs between the solid and liquid states of matter. Near the critical point at which the transition occurs, the number of contacts reaches the minimal value allowed by mechanical stability, and the packing fraction approaches random close packing[5] (Box 1): jamming, packing geometry and critical phenomena are thus connected. But what happens for systems that yield under shear? How do force networks fit into this picture? Are these ideas relevant to jamming and yielding of realistic frictional granular media?

Studies relating jamming to the packing geometry for compressed frictional systems may start to bridge the gap between theory and experiment. The packing-densities of frictional granular media under low pressure span a wide range from random close packing to random loose packing[5,8–10] (see Box 1). In the experiments conducted by Majmudar and Behringer[3], frictional forces are small ('weakly mobilized'). But does this remain true for lower packing densities? Does random loose packing correspond to a maximal mobilization of friction[8]? Do frictional grains approach a critical point at random loose packing similar to frictionless grains at random close packing[5,8]?

Simple questions of the behaviour of sand and salt lead to deep riddles and complex physics. Granular scientists, armed with marbles and plastic discs, are finding that some of these are now yielding to scrutiny. ■

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1. Liu, A. J. & Nagel, S. R. *Nature* **396,** 21–22 (1998).
2. Corwin, E. I., Jaeger, H. M. & Nagel, S. R. *Nature* **435,** 1075–1078 (2005).
3. Majmudar, T. S. & Behringer, R. P. *Nature* **435,** 1079–1082 (2005).
4. Reynolds, O. *Phil. Mag.* **20,** 467–481 (1885).
5. O'Hern, C. S., Silbert, L. E., Liu, A. J. & Nagel, S. R. *Phys. Rev. E* **68,** 011306 (2003).
6. Snoeijer J. H., Vlugt, T. J. H., van Hecke, M. & van Saarloos, W. *Phys. Rev. Lett.* **92,** 054302 (2004).
7. Daniels, K. E. & Behringer, R. P. *Phys. Rev. Lett.* **94,** 168001 (2005).
8. Makse, H. A., Johnson, D. L. & Schwartz, L. M. *Phys. Rev. Lett.* **84,** 4160–4163 (2000).
9. Torto, S., Truskett, T. M. & Debenedetti, P. G. *Phys. Rev. Lett.* **84,** 2064–2067 (2000).
10. Onoda, G. Y. & Liniger, E. G. *Phys. Rev. Lett.* **64,** 2727–2730 (1990).
11. Donev, A. *et al. Science* **303,** 990–993 (2004).

NEUROSCIENCE

An intrusive chaperone

Anders S. Kristensen and Stephen F. Traynelis

Stargazin is best known for helping to ferry receptor proteins to the surface of neurons. The discovery that it has an unexpected additional role has widespread implications for the way that neurons talk to each other.

Cognition relies on the fast transmission of excitatory signals between neurons. To achieve this, neurotransmitters such as glutamate are released from one neuron into the synapse (the junction between neurons) where they are picked up by receptors on the opposing 'postsynaptic' cell. Glutamate receptors called AMPARs form ion channels embedded in the cell membrane that, upon binding of glutamate, open rapidly to allow cations to flood into the neuron — converting the chemical signal from the neurotransmitter into an electrical pulse. In this issue, Tomita *et al.* (page 1052)[1] show that an accessory protein that helps to shuttle AMPARs into the membrane does double-duty to amplify the effectiveness with which glutamate opens the channel. AMPARs are among the most intensively studied of the neurotransmitter ion channels, so this discovery of an 'overlooked' accessory subunit is quite a surprise.

Tomita *et al.*[1] describe a functional analysis of the membrane-spanning protein Stargazin, which until recently was known only as a