

variants cheat on their partners during the process of spore formation (Fig. 1).

In times of plenty, *Dictyostelium* live as individual amoebae in soil, preying on bacteria. But when food runs out and starvation is imminent, the previously independent amoebae form aggregates of as many as 100,000 cells². These aggregates go on to form motile slugs, which can move to fresh pastures. The slugs then construct fruiting bodies in which 80% of the cells form viable spores and the other 20% die in making a stalk. It is the death of the stalk cells, which seemingly sacrifice themselves for the common good, that makes *Dictyostelium* interesting to evolutionary biologists.

Strassmann, Zhu and Queller¹ show that some isolates of *Dictyostelium* have an advantage over others in chimaeras — mixtures of genetically different amoebae. These cheater isolates make a minimal contribution to the stalk population, leaving that onerous function to their partners. The authors made mixtures of isolates collected from the same area, let them form slugs, and then sampled regions fated to be spore (the rear of the slug) or stalk (the front). Using the polymerase chain reaction to amplify certain DNA sequence differences between two isolates, they could ask whether a strain was making its appropriate contribution to the stalk population. Often, but not always, the answer was 'no'. In one combination, a participant contributed almost no cells to the stalk. Life in the soil is not fair.

Several *Dictyostelium* variants, natural and laboratory-induced by mutagenesis, that achieve an advantage in chimaeras have been described^{3–6}. But all cheaters isolated from these variants had defective development without a partner (they would not have been noticed otherwise). Such strains would have been selected against in the wild, where single *Dictyostelium* spores are often dispersed to form clonal colonies — colonies in which all members have an identical genetic constitution.

By contrast, the isolates used in the experiments of Strassmann *et al.* developed normally without a partner. All also formed chimaeras with each other — that is, they aggregated, indicating that no incompatibility mechanisms had evolved among them. The authors suggest a view of *Dictyostelium* as a society of competing, genetically distinct individuals, which strike a balance between competition and cooperation depending on their relatedness, and so have much in common with insect societies. As Strassmann *et al.* point out, parasitism in insect societies is often based on stealing chemical signals. It is possible that the cheater mutants of *Dictyostelium* likewise send a signal to the other members of the aggregation that makes them form the stalk.

Evolutionary and developmental biologists will view these results differently. Evolu-

tionists will wonder why certain variants don't eliminate the others and become dominant. And if isolation is the way *Dictyostelium* avoids competition, how did the genetic diversity arise that is a prerequisite for the evolution of this elaborate fruiting behaviour? Is *Dictyostelium* evolution a story of constant warfare, of different strains angling for advantage and counter-advantage? Are there mechanisms that limit the invasion of one strain by another?

For comparison, there are other organisms that display similar behaviour. *Myxococcus xanthus*, for instance, develops into spores after a process of aggregation, and some mutant strains take advantage of others during fruiting⁷. Another example is *Botryllus schlosseri*, which is a relatively complex organism with elaborate feeding and circulatory systems. Individuals attach to seaweed and, when adjacent to each other, closely related individuals fuse, whereas more distantly related ones undergo an incompatibility reaction⁸. In some fusions, the germ cells of one variant invade the cytoplasm of a neighbouring variant and produce descendants at its expense.

As for developmental biologists, they have not yet succeeded in explaining how a properly proportioned *Dictyostelium* fruiting body forms. They can ask whether the approach used by Strassmann *et al.* will provide a way of identifying the signals that the developing

amoebae use to regulate their proportions and position. Certain mutagenesis schemes allow the affected genes to be recovered from cheater mutants^{6,9}. Only one such gene has been recovered so far and it dramatically affects the ratio of stalk cells to spore cells. It remains to be seen whether it proves to be the useful end of a string on which one can pull to haul in other genes that rule the elegant cell proportionality of the fruiting bodies. Given the molecular genetic and genomic opportunities offered by *Dictyostelium*, a combination of developmental and evolutionary approaches may be the most promising way to tackle these questions. ■

Richard H. Kessin is in the Department of Anatomy and Cell Biology, Columbia University, 630 West 168th Street, New York, New York 10032, USA.
e-mail: rhk2@columbia.edu

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Fundamental constants

Measuring big *G*

Terry Quinn

Newton's constant, *G*, which governs the strength of the gravitational attraction between two masses, is difficult to measure accurately. A new set of experiments aims to end 200 years of uncertainty.

Newton's gravitational constant, *G*, differs from all the other fundamental constants of physics in that there is no complete theory that links gravity to the other forces of nature. Hence there is no definitive relationship between *G* and the other fundamental constants. It also stands apart in that the accepted uncertainty of 0.15% for *G* is many orders of magnitude larger than for the other fundamental constants (as given in the 1998 CODATA report¹). It is astonishing that 200 years after the famous experiment of Henry Cavendish to 'weigh the Earth' we seem to have improved on his result by only a factor of ten. Now, in *Physical Review Letters*, Gundlach and Merkowitz² report a value for *G* with an uncertainty of about 0.001% — so is *G* finally becoming respectable?

The measurement of *G* is simple in theory: take two spherical masses *M*₁ and *M*₂ at a known distance *r* apart, and measure the

gravitational attractive force between them, $F = GM_1M_2/r^2$. The problem is that the gravitational attraction between any two laboratory-sized masses is simply too small to measure accurately. For example, if we take two 1-kg masses, 10 cm apart, the gravitational attraction between them is about 6×10^{-9} N. Put another way, if one of the masses is fixed, the acceleration of the other towards it is 6×10^{-9} m s⁻². Such an acceleration is infinitesimal compared with the local acceleration due to Earth's gravity, *g*, of 9.8 m s⁻².

From the time of Cavendish, the preferred method of measuring *G* has been the torsion balance, in which the restoring force of a twisted fibre balances the weak gravitational torque (twisting force) produced by the attraction between several test masses and a pendulum suspended at the end of the fibre (Fig. 1, overleaf). This method provides an excellent way of decoupling the gravitational



100 YEARS AGO

A few weeks ago the new anthropological collections in the American Museum of Natural History in New York were opened to the public, and these valuable collections now occupy five halls, and others are being provided. We learn from our contemporary, *Science*, that the accessions to the anthropological collections of the museum obtained during the last three years have largely been due to extended scientific research undertaken by the institution... an endeavour has been made to build up representative collections and to obtain, at the same time, the fullest and most detailed information in regard to specimens, so that each addition to the exhibit of the museum can be made thoroughly instructive and will represent a material contribution to science. There is no doubt this is the best way to build up a museum, and it is to be deplored that various museums of the British Islands do not follow the example so worthily set by this and other American museums. Our English method is rather to wait like a spider in its web in the hope that something will eventually be caught ... we are content with occasional specimens which usually have no history, or at most a very imperfect one, and for these we often have to pay a stiff profit to a dealer.

From *Nature* 20 December 1900.

50 YEARS AGO

For one of the staff — one of the “working staff” as Sir James Dewar used to call us — to be asked to give a Friday Evening Discourse is, I think, quite without precedent and I am very conscious of the honour the Managers have conferred on me in inviting me to give a talk about fifty years in the service of the Royal Institution. According to tradition, on one occasion many years ago, a Friday Evening lecturer had a sudden attack of stage fright at the last moment and, being unattended, fled. Fortunately, Faraday was present and stepped into the breach. So that there should be no recurrence of a similar catastrophe, every Friday evening someone waits outside with the lecturer to ensure that he enters this theatre as the clock strikes. For many years that has been one of my duties; but to-night the position has been reversed and I have been the guarded one. I can assure you I have every sympathy with Wheatstone, the one that ran away. *Ralph Cory, Librarian of the Institution.*

From *Nature* 23 December 1950.

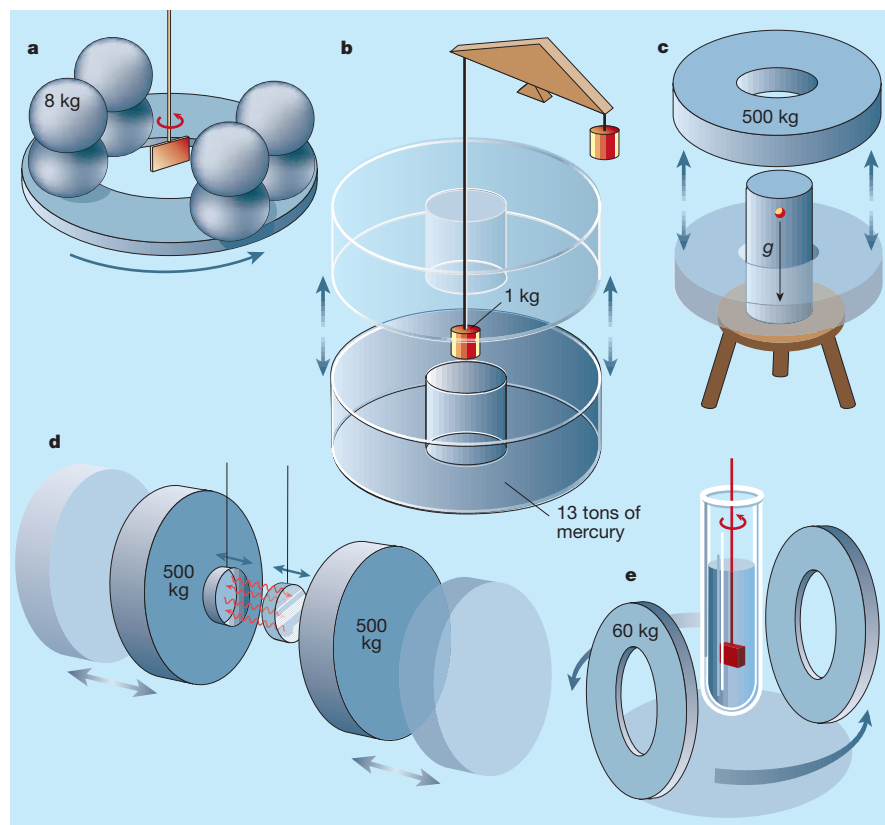


Figure 1 Updating Cavendish in measuring G . a, Gundlach and Merkowitz² have set a new standard for measuring G with a torsion-balance experiment in which eight spheres on a rotating disc turn to follow a thin plate suspended on a fibre, driven by the gravitational torque from the spheres. There are other ways to measure G , for example: b, an experiment in which a beam balance is used to measure the weight of a 1-kg mass on the pan of the balance when 13 tons of mercury are displaced from above to below it; c, an experiment in which laser interferometry is used to measure the change in downward acceleration of a falling body when a 500-kg mass is displaced from above to below it; d, an experiment using the gravitational attraction of large 500-kg masses to displace small masses hanging from a pair of pendulums that act as optical or microwave cavities; and e, a cryogenic torsion balance in liquid helium in which doughnut-shaped masses (at room temperature) turn around a thin plate suspended from the cold fibre.

attraction from the effects of g . However, whether G is measured using a torsion balance or any other device, it is necessary to construct test masses whose dimensions and density are known with sufficient accuracy. If spherical or cylindrical masses are used that have perfect geometry, the effects of density variation can be eliminated by random changes in orientation. But this does not work if the geometry is not perfect and, in any case, becomes more difficult with larger masses.

In the absence of any advances in physics linking gravity to the rest of science, there have been no really new methods of measuring G since the time of Cavendish. Despite a flurry of excitement over the ‘fifth force’ in the 1980s, or apparently strange gravitational effects acting on spinning rotors reported in the 1990s, Newton continues to reign supreme in laboratory gravitation. Nevertheless, measurements of G hold great interest for both cosmology and particle physics; in the latter case it has been suggested that the compact dimensions predicted by ‘superstring theory’ might show up in the behav-

iour of G at small (< 1 mm) distances³.

The current interest in measuring G was stimulated by the publication⁴ in 1996 of a value for G that differed by 0.6% from the accepted value given in the previous 1986 CODATA report. To take account of this, the 1998 CODATA report recommends a value for G of $6.673 \times 10^{-11} \text{ m}^3 \text{ kg}^{-1} \text{ s}^{-2}$ with an uncertainty of 0.15%, some ten times worse than in 1986. Whereas the other fundamental constants were more accurately known in 1998 than in 1986, the uncertainty in G increased dramatically. The G community appeared to be going backwards rather than forwards.

Since 1998, several groups around the world have set about measuring G , using a range of different methods. At a symposium held in London in 1998 to celebrate the bicentenary of Cavendish’s experiment, reports of eight experiments then under way were presented⁵, some of which are shown in Fig. 1. The target uncertainty for these experiments is between 0.01% and 0.001%. Mostly preliminary results have been published so

far, but all, including the new result of Gundlach and Merkowitz², are in rough agreement and do not support the controversial 1996 value. This is good news because the different techniques have different sources of error, reducing the likelihood of systematic errors affecting the final result.

But not all the improvements in accuracy have resulted from new techniques — there have also been similar advances in torsion balance experiments^{6–9}. Gundlach and Merkowitz's result is based on a torsion-balance method that has several advantages over previous experiments. The design eliminates much of the uncertainty resulting from the distribution of the pendulum mass suspended from the torsion fibre (Fig. 1a). If this suspended mass is a thin flat plate, corrections due to the shape, the total mass and the mass distribution of the plate cancel out in the analysis. Using a set of eight spherical test masses, almost all effects resulting from the suspended mass become negligible.

Gundlach and Merkowitz measure the angular acceleration of their suspended mass by rotating the whole system on a turntable. This has the advantage that the torsion wire is never twisted, so the measurement of G is independent of anelasticity in the fibre properties¹⁰. The rotation also averages out the effects of local gravity gradients. The result has an uncertainty of 0.001%, well below anything claimed before. But their value for G is 0.024% above the original 1986 CODATA value. Is it right?

The only way we can generate confidence in a result is by having several independent measurements made using different experimental techniques. Agreement has yet to be achieved at the 0.01% level, let alone 0.001%. Although we do not yet have a theoretical prediction for G against which to test the results, a reliable and accurate experimental value is important for testing future theories. The G community awaits with great interest the final results of the other measurements in progress. In the meantime, the result of Gundlach and Merkowitz sets a new standard for all G experiments to match. ■

Terry Quinn is at the Bureau International des Poids et Mesures, Pavillon de Breteuil, F-92312 Sèvres, France.

e-mail: tquinn@bipm.org

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Neurobiology

Moving forward by looking away

Larry Snyder

In one model of the brain, a central processing region is sandwiched between separate input and output areas. But studies of humans, and now monkeys, hint that this model may be too simplistic.

A conventional approach to studying the brain is to determine whether a particular signal or region is mainly sensory or motor in nature, reflecting what comes into the brain or what flows out, respectively. In this view, the input region (the sensory cortex) processes sensory signals to generate several neuronal representations of the information. Next, a central processor, found outside the sensory cortex, uses information about the goals of the task in hand to select the most appropriate sensory representation for directing motor output. This selection is the key step in the 'sensorimotor transformation'. But in another model, task-specific information influences the processing of incoming signals from an early stage. Pure sensory signals are rare, and the sensorimotor transformation is distributed throughout the brain. This view has begun to take hold among researchers who study the human brain¹. But convincing evidence is still needed. On page 971 of this issue, Zhang and Barash² provide just such evidence from studies of monkeys.

The task of moving one's eyes to a visual target involves a clear sensory input (from the target) and motor output (the eye movement), so it seems ideal for studying sensorimotor transformations. But experiments based on eye movements are often handicapped by a difficulty in distinguishing neuronal representations of what we see and what we plan to do. Imagine being inspired by the sight of a travel poster and deciding to visit London. Before you choose how and when to travel, your plan is best represented by the image on the poster — the poster is both the stimulus that evokes your plan, and an early representation of the plan itself.

A similar confusion occurs when studying directed eye movements. A simple way to introduce a distinction between representations of visual stimuli and plans to move the eyes to those stimuli is to study both prosaccades, which are eye movements towards a visual target, and antisaccades, eye movements away from the target³. The colour of a 'fixation spot' tells the subject whether to move their eyes towards or away from the target. This combination allows the researcher to determine whether neuronal activity is more closely related to the stimulus or the movement goal, and therefore where task-specific processing begins.

The lateral intraparietal area (LIP) in the posterior parietal cortex of monkey brains is likely to participate in, or even initiate,

sensorimotor transformations during saccades⁴. Neurons in this region link sensory and motor areas. Individual neurons are activated when a behaviourally relevant stimulus appears within the cell's receptive field. LIP neurons also fire shortly before an eye movement to a remembered or visible target in the receptive field.

Last year, Gottlieb and Goldberg⁵ recorded the activity of single neurons in the LIP while monkeys performed prosaccades and antisaccades. They found that most of the sampled neurons represented the location of the visual target. Few represented the direction of the eye movement; when they did, they fired quite late, around the time of the movement.

Zhang and Barash² have now repeated Gottlieb and Goldberg's experiment with a slight change, and obtained very different results. Rather than having the monkeys move their eyes as soon as they saw a target, Zhang and Barash trained the animals to delay their movements. In this way, signals time-locked to the sensory stimulus could be more easily distinguished from signals related to the motor response. Neuronal activity began hundreds of milliseconds before the signal to make the saccade and well after the sensory stimulus, reflecting the direction of the movement, not the location of the target. So, the sensorimotor transformation occurs in the LIP long after the stimulus appears but well before the eye movement begins.

Zhang and Barash also report evidence of an earlier sensorimotor transformation in the LIP. During both prosaccade and antisaccade trials, many LIP neurons become active shortly after a stimulus falls inside their receptive field. The authors show that a subset of these cells also becomes active soon after a stimulus appears outside their receptive field that will direct an antisaccade so that the stimulus falls into the field (Fig. 4b, page 973). Zhang and Barash refer to this as 'paradoxical activity'. These neurons show activity that is time-locked to the onset of the visual stimulus, suggesting that they are driven directly by visual inputs. But they also respond to a stimulus outside the receptive field on an antisaccade trial, consistent with an input that codes the end of the planned movement rather than the target's location. This activity probably represents the start of the sensorimotor transformation for an antisaccade.

But this transformation is incomplete on at least two counts. First, these neurons often fire when a stimulus outside their receptive