

Mutation of *daf-2*, *age-1* or *pdk-1* results in the activation of *daf-16* and increased lifespan. Mutation of *daf-16* blocks this extension in lifespan.

Tissenbaum and Guarente find that, first, the life extension resulting from over-expression of *sir-2.1* is prevented by mutation of *daf-16*. This places *daf-16* downstream of *sir-2.1* in the insulin/IGF pathway. Second, the life-extending effects of over-expressing *sir-2.1* and mutating *daf-2* are not additive, again placing these genes in the same pathway. Further results confirm this. It seems that *sir-2.1* antagonizes the pathway: whereas *daf-2* acts to inhibit the downstream *daf-16* gene, and can no longer do so when mutated, *sir-2.1* works to activate *daf-16*, and can do so more strongly when over-expressed. The authors suggest that the silencing of genes upstream of *daf-16* by *sir-2.1* is involved in the response of the insulin/IGF pathway to caloric restriction.

Of course it remains to be shown that *sir-2.1* is involved in modifying chromatin in worms. Furthermore, a previous study involving *C. elegans* suggested that caloric restriction and insulin/IGF signalling are independent of each other<sup>14</sup>. Nonetheless, the idea of the regulation of animal longevity through changes in chromatin structure has appeal. In development, for example in pattern formation in *Drosophila*, changes in

chromatin structure have a major role. Perhaps that these latest findings<sup>1</sup> are telling us is that the passage through adulthood involves changes in gene regulation that are analogous to those occurring during development<sup>15</sup>, and are regulated through changes in chromatin structure. At the very least, it seems that some genetic determinants of longevity and ageing are conserved across animal groups — a fact that will encourage those studying ageing in model organisms. ■

David Gems is in the Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK.

e-mail: david.gems@ucl.ac.uk

1. Tissenbaum, H. A. & Guarente, L. *Nature* **410**, 227–230 (2001).
2. Guarente, L. & Kenyon, C. *Nature* **408**, 255–262 (2000).
3. Lin, Y.-J., Seroude, L. & Benzer, S. *Science* **282**, 943–946 (1998).
4. Brown-Borg, H. M., Borg, K. E., Meliska, C. J. & Bartke, A. *Nature* **384**, 33 (1996).
5. Coschigano, K., Clemmons, D., Bellush, L. & Kopchick, J. *Endocrinology* **141**, 2608–2613 (2000).
6. Martinez, D. E. *Exp. Gerontol.* **33**, 217–225 (1998).
7. Williams, G. C. *Evolution* **11**, 398–411 (1957).
8. Martin, G. M., Austad, S. N. & Johnson, T. E. *Nature Genet.* **13**, 25–34 (1996).
9. Sinclair, D. & Guarente, L. *Cell* **91**, 1033–1042 (1997).
10. Kaeberlein, M., McVey, M. & Guarente, L. *Genes Dev.* **13**, 2570–2580 (1999).
11. Jamet-Vierny, C., Begel, O. & Belcour, L. *Cell* **21**, 189–194 (1980).
12. Lin, S., Defossez, P. & Guarente, L. *Science* **289**, 2126–2128 (2000).
13. Apfeld, J. & Kenyon, C. *Nature* **402**, 804–809 (1999).
14. Lakowski, B. & Hekimi, S. *Proc. Natl Acad. Sci. USA* **95**, 13091–13096 (1998).
15. Gems, D. *J. Anat.* **197**, 521–528 (2000).



#### 100 YEARS AGO

Commander R. F. Scott, R. N., in naval charge of the British Antarctic Expedition, has stated to a representative of Reuter's Agency that the preparations for the British Antarctic Expedition are now practically complete. The *Discovery*, the expedition's ship, will be launched on March 23, and, after she has been handed over by the contractors, will come round to London, where her equipment and provisions will be put aboard. The *Discovery* has been built on whaler lines, only with greatly increased strength to withstand ice pressure. She is 171 feet long, and 34½ feet beam, and has 1500 tons displacement. She will have auxiliary steam, and is fitted with engines of the latest type. In her construction the lines of the *Fram*, though carefully studied, have not been adopted, as Nansen's ship would have been ill-adapted for the heavy seas the *Discovery* will have to encounter. The expedition will leave London in July or August, and will proceed to Melbourne, reaching there in November. From *Nature* 7 March 1901.

#### 50 YEARS AGO

The annual report of the Chicago Natural History Museum for 1949 (pp. 140; Chicago: Chicago Natural History Museum, 1950; 1 dollar) gives some interesting facts concerning the activities of its Department of Public Relations. For an entire year, the Museum was brought to the notice of every person who looked up a telephone number in the "Red Book, Chicago Classified Telephone Directory"; for, through the courtesy of the publishers, the name of the Museum and a picture in colours of the exterior appeared on the front cover, while inside in a prominent page-one position was the story of the Museum. Considering the large number who consult a telephone directory in the course of a year, the cumulative effect of such publicity must be of a high order ... The museum continued to be represented each Saturday throughout the year by a series of stories on the "Children's Corner" radio programme. Special features, including television, were given on several of the broadcasting systems. Other publicity included the distribution of thousands of folders describing exhibits. Lecture courses for adults and children were advertised by posters displayed in railway stations and on suburban trains. Some of the methods adopted by the American museums may seem unusual; but all are worthy of consideration. From *Nature* 10 March 1951.

#### Condensed-matter physics

## First glimpse of the orbiton

Philip B. Allen and Vasili Perebeinos

Crystals are host to a variety of disturbances, which show up as waves or particles. Physicists think they may have seen a new type of disturbance called the orbiton.

On page 180 of this issue, Saitoh *et al.*<sup>1</sup> present evidence for the observation of a new particle in a solid. Although predicted to exist, this first sighting of the orbiton should allow it to join the list of 'particle excitations' found in solids, such as electrons, holes, phonons, magnons, excitons and plasmons. Working at low temperatures, the authors measured the frequency shift of the laser light scattered from a particularly perfect crystal of LaMnO<sub>3</sub>. This ceramic is the parent compound of a group of materials whose electrical properties switch under a magnetic field.

Modern condensed-matter theory asserts that a solid crystal is actually a gas of weakly interacting 'quasi-particles'. The prefix quasi is unnecessary. These particles are as real as the more familiar photons, electrons and protons. Particles in physics are generally connected with a property of the ground state known as 'broken symmetry'. In solids, the crystalline ground state is the lowest energy state.

Symmetry breaking is a common occurrence. For example, a pencil balanced on its tip has rotational symmetry — it looks the same from all sides — but when it falls it lands in one direction, breaking the symmetry. The fallen pencil also creates 'order' because it picks one direction in a previously unordered world. In physics, breaking symmetry and creating order go hand-in-hand. Perfect symmetry is an ideal vacuum with no order at all, but particles in such a vacuum are very dull. Fortunately, the real world is less symmetric, allowing more interesting particles to emerge.

In condensed-matter physics, symmetry breaking also leads to new particles. Consider a crystal of metallic iron. Each atom is surrounded by a lattice of neighbouring atoms with the symmetry of a cube. Left, right, up, down, front and back all look the same to the atom, until a compass needle reveals a magnetic field, pointing along one of the crystal axes. In simple terms, each iron atom has its

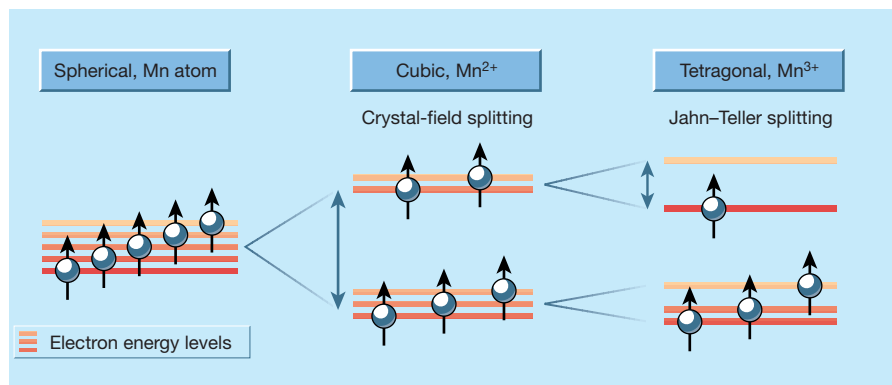


Figure 1 How electron energy levels are affected by their environment. Energy level diagrams for *d* orbital electrons (upward arrows indicate direction of spin) of a manganese (Mn) atom in free space (left, spherical environment), in a cubic environment (middle, such as divalent MnO), and in a tetragonal environment (right, such as trivalent LaMnO<sub>3</sub>). Saitoh *et al.*<sup>1</sup> now claim to have seen orbitons — a collective oscillation of partially occupied electron subshells — in a pure crystal of LaMnO<sub>3</sub>.

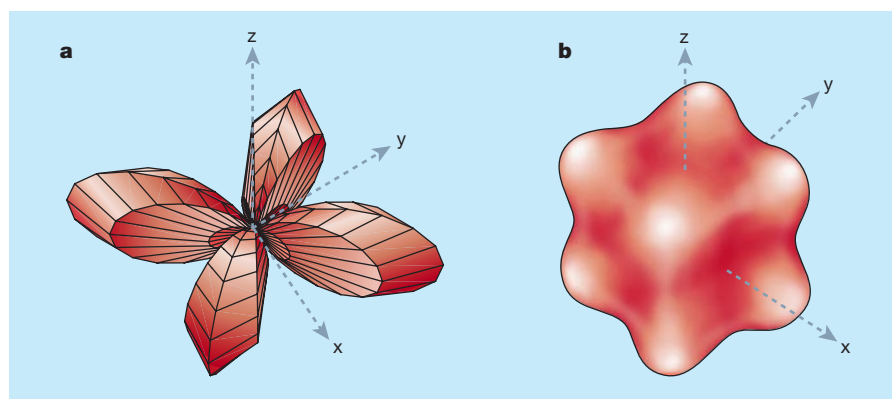


Figure 2 The shape of electron orbitals. a, The charge density of a single *d* orbital electron and b, the total charge density of a filled subshell with three *d* orbital electrons. The filled subshell has cubic symmetry. If both subshells were filled, the total charge density would look like a sphere, indistinguishable from the spherical symmetry of free space.

own ‘magnetic spin’. At temperatures above 770 °C, the spins turn rapidly and randomly; magnetism is not detected. But at lower temperatures, the spins spontaneously align, randomly choosing one of the six equivalent directions. As with the pencil, the rotational symmetry has been broken.

This symmetry breaking allows new disturbances in the solid, which physicists recognize as waves, or (with the wave–particle duality of quantum theory) as particles. For example, if the spin of one iron atom is turned away slightly from the overall direction of the magnetization, the neighbouring spins exert a restoring force. Rotational inertia prevents these spins from responding instantly, and wave propagation occurs when restoring forces encounter inertia. Therefore, spin disturbances propagate as spin waves, or particles called magnons.

But not all particles are straightforward to detect. Photons in light waves can be measured directly when they enter a photomultiplier tube. But magnons in iron can only be detected indirectly, by scattering a beam of photons or neutrons from the iron crystal. Inside the crystal a photon or neutron may interact with a magnon, causing

detectable changes in the properties of the scattered particles. This is how Saitoh *et al.*<sup>1</sup> set about looking for orbitons in LaMnO<sub>3</sub>.

The tetragonal crystal structure of the ceramic contains magnetic manganese ions (Mn<sup>3+</sup>). In addition to magnetic spins, which become ordered at –123 °C (ref. 2), the Mn<sup>3+</sup> ion has a partly filled electron shell, which provides a new way to break symmetry and create ‘orbital order’. Orbitals are the allowed energy states for electrons. When occupied by an electron, they are visualized as clouds of electron charge. Symmetry breaking in LaMnO<sub>3</sub> orbitals happens at about 475 °C. Below this temperature, LaMnO<sub>3</sub> has orbital order<sup>3</sup>, and orbital waves, or their corresponding orbitons, may exist.

To understand orbital order we need to review a little chemistry. Stable chemical species have filled electron shells. Only two electrons, one of each ‘spin orientation’, can be associated with each orbital, but each shell contains a set of orbitals. In atoms the shells are labelled 1s, 2s, 2p, 3s, 3p, 3d, 4s and so on. Argon, for example, is inert. It has 18 electrons filling the shells 1s through to 3p. The s shell has one orbital, which is spherically symmetric. The p shell contains three

orbitals. The filled p shell is spherically symmetric, but the individual p orbitals are elongated in three perpendicular directions (a bit like dumbbells).

The manganese atom, on the other hand, has seven electrons more than argon, and so has two electrons (of opposite spin) in a filled 4s shell and five electrons with the same spins in a half-filled 3d shell. Half filling is the next best thing to complete filling. Each individual d orbital is asymmetric, but when all the orbitals are occupied by one electron, the overall charge density is spherically symmetric. Figure 1 shows energy level diagrams for the five d orbitals of atomic manganese in different environments. In a cubic solid, the Mn<sup>2+</sup> ion (as in MnO) loses its two 4s electrons but keeps the half-filled 3d shell. Because spherical symmetry is broken by the cubic crystal lattice, the 3d shell is split into two subshells. Neither subshell alone has full spherical symmetry, but they still have cubic symmetry (Fig. 2).

Now consider the Mn<sup>3+</sup> ion in the environment of LaMnO<sub>3</sub>. The 3d shell now has only four electrons (Fig. 1). At high temperatures the Mn<sup>3+</sup> ion has cubic symmetry: the lower subshell is filled and the upper subshell is half-filled. To reduce its energy, this ion would prefer a lower symmetry in which the upper subshell splits in two. So below 475 °C, LaMnO<sub>3</sub> stretches along one axis of the crystal to become tetragonal. The occupied d orbital electrons now have a tetragonal shape, and the crystal has orbital order (also called cooperative Jahn–Teller order).

In LaMnO<sub>3</sub>, the tetragonal shape of the occupied 3d orbital in the upper subshell can be deformed. There is a restoring force discouraging such deformation, and inertia to slow the process. Therefore, orbital wave propagation is expected — a collective oscillation of partially occupied electron subshells. This is the orbiton particle that Saitoh *et al.*<sup>1</sup> claim to have seen.

In the experiment, Saitoh and colleagues picked out a component of the scattered laser light whose frequency shift corresponds, they believe, to excitation of an orbiton. With increasing temperature, this component weakens and completely disappears above 475 °C, the temperature at which cubic symmetry is restored and orbital order is lost. Their identification of the orbiton rests on a theoretical calculation that agrees nicely with the low-temperature data. But the case is not airtight. For simplicity, the theory<sup>4</sup> omits the coupling of orbitons to phonons (vibrations of the crystal lattice)<sup>5,6</sup>. It needs to be shown that good agreement remains when this effect is included, both at low and at room temperature.

Orbitons should play a role in the thermal properties of orbitally ordered solids such as LaMnO<sub>3</sub>, so they could be looked for in measurements of heat capacity and heat transport in crystals. Their effect on magnon

and phonon spectra should also be calculated and measured. One might expect orbitons to occur in other orbitally ordered materials, such as high-temperature superconductors. Indeed, the partially empty *d* orbital shell of Cu<sup>2+</sup> in copper oxide superconductors can have orbital excitations. Over a decade ago, these excitations were used by Weber<sup>7</sup> in a theory of the superconducting coupling between electrons that allows them to flow without resistance. Perhaps he should revive his theory now that the orbiton's existence is more established. ■

Philip B. Allen and Vasili Perebeinos are in the Department of Physics and Astronomy, State University of New York, Stony Brook, New York 11794-3800, USA.

e-mail: allen@felix.physics.sunysb.edu

1. Saitoh, E. *et al.* *Nature* **410**, 180–183 (2001).
2. Moussa, F. *et al.* *Phys. Rev. B* **54**, 15149–15155 (1996).
3. Murakami, Y. *et al.* *Phys. Rev. Lett.* **81**, 582–585 (1998).
4. Okamoto, S., Ishihara, S. & Maekawa, S. *Phys. Rev. B* **61**, 14647–14655 (2000).
5. Hotta T., Malvezzi, A. L. & Dagotto, E. *Phys. Rev. B* **62**, 9432–9452 (2000).
6. Allen, P. B. & Perebeinos, V. V. *Phys. Rev. Lett.* **83**, 4828–4831 (1999).
7. Weber, W. Z. *Phys. B* **70**, 323–329 (1988).

Evolutionary biology

## What's in a baboon's behind?

R. I. M. Dunbar

It is often thought that sexual 'ornaments', such as the swellings that adorn ovulating female baboons, are signalling something about fertility — but what? Long-term studies of wild baboons provide an answer.

The Victorians were so embarrassed by the large swellings that occasionally adorn the bottoms of some primate species — notably baboons and chimpanzees — that many zoos insisted that females in this condition be kept out of public view. The swellings, which occur in about 10% of all primate species, can be so large and grotesque that females cannot sit comfortably. Less squeamish primatologists of subsequent eras remained puzzled by this all but unique phenomenon. The fact that swellings coincide with ovulation made it obvious that females must be signalling something about their fertility, but exactly what remained elusive. On page 204 of this issue<sup>1</sup>, Domb and Pagel show that females are in fact signalling their own genetic quality.

Sexual swellings are found only among Old World monkeys and apes. Detailed analyses of the distribution of swellings indicate that they have evolved independently in three quite separate lineages. Typically they are associated with the evolution of social groups containing several males and several females, where mating is promiscuous and females have greater choice in mating partners<sup>2–5</sup>. Swellings are seen, for example, in chimpanzees, whose mating system is close to a sexual free-for-all. But — as readers have no doubt noticed — they do not occur in the chimpanzees' closest relatives (our own species), whose mating system is typically, though by no means exclusively, focused on monogamous couples.

Five explanations for the evolution of sexual swellings have been offered<sup>4,6</sup>. First, females want to attract males to join their groups, so as to provide the females and their young with an effective defence against predators. Second, females are in effect try-

ing to provoke males into competing among themselves for opportunities to mate, thereby enabling the females to mate with the 'best' males in the group (a form of indirect female choice). Third, females are encouraging promiscuous mating so as to confuse paternity. This would mean that the risk of killing their own offspring deters males from infanticide — a problem that is particularly serious for primates because they have long intervals between births<sup>7</sup>. Fourth, given that the timing of ovulation is itself unpredictable, females want to persuade individual males to stay with them. This would assure the males of paternity, and provide the females with a bodyguard so as to reduce the levels of harassment that they would otherwise suffer in multimale groups (this is the 'hired-gun' hypothesis). And fifth, swelling size is an indicator of a female's genetic quality, enabling her to attract the best males to mate with her and so maximize the genetic quality of her offspring<sup>8</sup>.

One of the problems that evolutionary biologists have encountered in trying to test these hypotheses is that they often make similar predictions. As a result, comparative data drawn from across the primate species are often compatible with several hypotheses; indeed, there is evidence to support all five hypotheses<sup>4</sup>. In such cases, to choose between competing theories we need to explore the mechanisms involved in more detail, rather than just look at the superficial phenomenon.

Domb and Pagel<sup>1</sup> provide the first uncontroversial mechanistic evidence that the size of sexual swellings is correlated with a male's willingness to compete for individual ovulating females, and with indices of a female's own fitness. The authors were able to reach this conclusion only because they used long-

term demographic data from the baboon population that (together with Jane Goodall's more famous chimpanzees) inhabits the Gombe National Park, Tanzania. Both the chimp and the baboon populations have been under continuous study for more than 30 years.

Domb and Pagel show that the females with the largest swellings had attained sexual maturity earlier (and so had longer reproductive lifespans) than those with smaller swellings. The females with larger swellings also produced more offspring, as well as more surviving offspring, over their lifetime. Males competed more heavily, and incurred more injuries from fighting, for females with larger swellings. As males are willing to do this, it follows that they must be using swelling size as an index of a female's heritable reproductive quality. These findings thus explain why there are such consistent differences between females in the size and quality of their swellings. But it may not explain why sexual swellings evolved in the first place — it is possible that females have exploited for this new purpose a signal that first evolved for one of the other reasons.

Evolutionary biologists have been much exercised of late as to whether such signals of quality have to be honest, by which they mean costly to produce. Although there is some evidence to suggest that this need not always be so, most theoretical models of signal evolution agree that when cues are cheap to produce they are too susceptible to cheating, and so are evolutionarily unstable. Herein, perhaps, lies the weak link in Domb and Pagel's argument — they are able to provide only circumstantial evidence that swellings are costly for females to produce. Their evidence is that female body weight increases by 14 to 25% when swellings are at their maximum size. It is unlikely that the swellings are in themselves energetically expensive, because they are produced simply by the selective retention of extracellular water. But it is possible that they make females less fleet — and thus at greater risk of being caught by a predator — and that carrying the added weight increases the energetic costs of travel. If either of these could be demonstrated, the case would be satisfyingly closed. ■

R. I. M. Dunbar is in the Population and Evolutionary Biology Division, School of Biological Sciences, Nicholson Building, University of Liverpool, Liverpool L69 3GS, UK.  
e-mail: rimd@liv.ac.uk

1. Domb, L. G. & Pagel, M. *Nature* **410**, 204–206 (2001).
2. Hrdy, S. B. & Nicholson, N. in *Primate Societies* (eds Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T.) 370–384 (Chicago Univ. Press, 1987).
3. Sillén-Tullberg, B. & Møller, A. P. *Am. Nat.* **141**, 1–25 (1993).
4. Nunn, C. L. *Anim. Behav.* **58**, 229–246 (1999).
5. Dixson, A. F. *Primate Sexuality* (Oxford Univ. Press, 1998).
6. Manson, J. H. *Curr. Anthropol.* **38**, 353–374 (1997).
7. van Schaik, C. P. & Kappeler, P. M. *Proc. R. Soc. Lond. B* **264**, 1687–1694 (1997).
8. Pagel, M. *Anim. Behav.* **47**, 1333–1341 (1994).