

out to be the source of most of the ions in Jupiter's magnetosphere.

Ground-based measurements provided further understanding of the torus. But it was spacecraft encounters with Io (Fig. 1) that provided the next surprises. Data from Voyager 1's 1979 encounter not only revealed intense emissions in the far-ultraviolet part of the spectrum, primarily due to sulphur and oxygen ions in several states of ionization, but also identified widespread volcanism and geyser activity on Io's surface. The source of the sulphur and oxygen ions was quickly shown to be sulphur dioxide; and, simultaneously, it was realized that the volcanic and geyser activity was due to intense internal heating of Io, a result of the tidal flexing by Jupiter. Studies of the Galileo Orbiter data have established that some of the volcanism occurs at unusually high temperatures.

But what was the origin of the sulphur and oxygen in the neutral atmospheric clouds and plasma torus? The ions in the torus are forced by Jupiter's magnetic field to rotate at nearly the same rate as the planet, and therefore bombard Io's atmosphere and surface at energies of hundreds of electron volts. This was identified as the source of the sulphur and oxygen — through a process called sputtering, ion bombardment of SO₂ on Io's surface releases atoms and molecules or ions into the atmosphere and neutral torus; the atoms and molecules are then dissociated and ionized by energetic electrons in the plasma torus. But the nature of the compound constituting the sodium source remained a puzzle. Theoretical modelling had shown that it is probably sodium chloride, and this is now confirmed by Lellouch *et al.*¹, who report its detection in vapour form.

This part of the story begins two years ago with Küppers and Schneider's identification of chlorine ions in the plasma torus⁴. Their observation in the near infrared was quickly confirmed in the far ultraviolet⁵. On the theoretical side, Fegley and Zolotov⁶ extended their earlier predictions of the gases and vapours that would be expected to be emitted by volcanic magmas on Io. To their assumed magma composition, taken to occur at high temperatures (1,000–2,000 K), they added sodium, potassium and chlorine in cosmic abundances. This chemical model produced copious NaCl vapour (along with sodium atoms, potassium chloride, SO₂ and other sulphur compounds).

Using the 30-m IRAM (Institut de Radio-Astronomie Millimétrique) radio telescope, sited near Granada in Spain, Lellouch *et al.* have now identified two spectroscopic lines of NaCl vapour, at wavelengths of 1.3 mm and 2.1 mm, in Io's atmosphere. They also detect three lines of SO₂ and provide a tentative detection of KCl. The NaCl occurs only in patches in the atmosphere, consistent with there being just a few volcanic sources. An alternative, but much less likely, explanation

is that the NaCl stems from evaporation or sputtering from material condensed on SO₂ snowdrifts on Io's surface. Earlier observations of SO₂ with the same telescope show that SO₂ is also distributed patchily, and for this more volatile molecule both sources — volcanism and sputtering — are plausible.

The amount of Na and Cl in the torus, in various forms, has been calculated to be only some 2% of the total composition. The NaCl supply rate found by Lellouch *et al.* is too large to be consistent with this figure, but their estimate includes some uncertain parameters and the agreement appears to be satisfactory. Thus, 28 years after Brown's discovery of sodium at Io, we may be

close to understanding how it reaches the atmosphere and torus. ■

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Molecular evolution

Duplication, duplication

Axel Meyer

Duplicated genes are common in genomes, perhaps because they provide redundancy: if one copy is inactivated, the other can still work. A new study quantifies the effects of deleting 'singletons' and duplicated genes in yeast.

In fairy tales, things frequently come in twos: there are, for instance, two witches ruling over different parts of the land of Oz, two ugly sisters vying for the attention of Cinderella's prince, and so on and so on. And the phenomenon of duplication is not restricted to stories. In eukaryotes (loosely speaking, those organisms, such as humans, whose DNA is packaged into cell nuclei), genomes seem to be far from optimally designed, in that most stretches of DNA sequence do not code for proteins, and even those small portions that do are often duplicated. Why do organisms tolerate such apparent wastage? Gu and colleagues¹ tackle this question on page 63 of this issue, looking specifically at the effects of duplicated genes on the 'fitness' of individuals.

An important line of thinking about why duplicated genes might arise goes back 30 years to Susumo Ohno², who stated that "natural selection merely modified while redundancy created". Ohno reasoned that gene (and even genome) duplications are not a burden on the organism, but rather the raw material for evolutionary diversification — in other words, duplication allows new gene functions to evolve. One copy of a gene can carry out the original task while the duplicate becomes free to accumulate mutations, possibly developing new functions and allowing the big steps in evolution to occur. In today's era of wholesale genome sequencing, Ohno's hypothesis has gained many new adherents through the recognition that duplicate genes are abundant in most genomes and that significant portions of genomes are repeated. But, in general, the actual effects of 'singletons' and duplicated genes on evolutionary

fitness — that is, on roughly how well different individuals fare compared with others in terms of reproduction — have not been well studied at the whole-genome level.

On the other side of the coin, gene duplicates appear to have another important function: they can buffer the genome against environmental perturbations and mutations, because if one copy of the gene is somehow inactivated, another with the same or a similar function can be used instead. Such genetic redundancy is a headache for researchers trying to determine the role of a particular gene, because the standard technique of knocking out that gene in an organism might not have a noticeable effect, thanks to functional substitution by the duplicate. Gu *et al.*¹ shed new light on this issue.

The authors studied the budding yeast *Saccharomyces cerevisiae*, which has become the workhorse of the functional-genomics community³ since the publication of its genome sequence six years ago. In a previous high-throughput study⁴, nearly every one of the organism's 6,357 genes was knocked out, one at a time. The effects were then investigated under five different culture conditions, in which components of the culture medium that affect fermentation and respiration were varied. The fitness of each mutant yeast strain was measured by its ability to proliferate, relative to non-mutated strains.

Gu *et al.* have taken advantage of these data to determine the effects on fitness of duplicated and single-copy genes. Using a computational method, the authors started by searching for yeast genes that have a high degree of sequence similarity — that is, those that are alignable over at least 50% of their length. The

reasonable assumption behind this approach is that sequence similarity between two or more genes suggests that they are copies of an initially single gene. In this way, Gu *et al.* determined that about a quarter of all *S. cerevisiae* genes exist as duplicates. The degree of sequence similarity is presumed to provide some insight into when the genes were duplicated and how similar their functions are. Immediately after duplication, two genes will have identical sequences and functions. With time, their sequences and therefore, presumably, their functions will diverge more and more, or one copy will stop working completely (becoming a pseudogene).

Next, Gu *et al.* reanalysed the previously published data on *S. cerevisiae* fitness⁴ in light of their knowledge about the number of gene duplicates. They first show that knocking out singletons generally reduces fitness more severely than deleting one gene of a pair of duplicates. For instance, knocking out only 12.4% of genes that are part of a pair, compared to 29% of singletons, has a lethal effect — a significant difference. Moreover, knocking out 64.3% of genes that have a duplicate, but only 39.5% of singletons, has no or only a weak effect on fitness. Can these results be explained by functional compensation between duplicated genes (at least under these conditions)? If so, one might predict that deleting one duplicated gene of a pair would have a similar effect on fitness to deleting the other gene, but that deleting two randomly selected genes would have more pronounced differences in terms of fitness effects. This is exactly what Gu *et al.* find.

One would also predict that duplicated genes that are highly similar in sequence should be better at compensating for each other than duplicates whose sequences (and, presumably, functions) have diverged further. Gu *et al.* confirm this prediction, too. On average, however, even highly diverged duplicates still have weaker fitness effects when deleted than singletons, suggesting that some degree of functional compensation persists even here. The authors also looked at the effects of the level of expression of gene duplicates, using data from microarray experiments⁵. They found that negative fitness effects were more pronounced when a duplicated gene with a higher level of expression than its partner was deleted.

All of this suggests that gene duplication provides a means of preserving function; even when two copies of a gene have diverged widely, they can still substitute for each other functionally to some degree. This, together with the fact that many genes and gene networks are similar in evolutionarily diverse species, hints that maybe Ohno was wrong after all. Are duplicated genes the stuff of developmental stability and of conservation of function rather than evolutionary innovation? If so, how did the diversity of life around us appear?

The answer may lie in part with such factors as the evolution of novel gene-regulatory sequences, the generation of alternative protein products from a single gene, and the recruitment of duplicated genes into diverse functions and into many different networks of interactions. The importance of these mechanisms in relation to gene and genome duplication remains unclear. But gene duplication is an important phenomenon to understand. The discovery of many duplicated genes and parts of genomes has been an unexpected but interesting by-product of genome-sequencing projects. And recent comparative genomic analyses found a duplication rate of about 1% per gene per million years^{6,7}, which is quite high on evolutionary timescales.

We are only now beginning to comprehend just how malleable genomes are, and also how resilient they are in the face of so much genetic perturbation; for instance, rearrangements and duplications of chromosomal segments are also commonplace^{8,9}. Gu *et al.*¹ have provided the first estimate (23–59%) of the contribution of duplicated genes to genetic robustness. This may be one

reason why duplicated genes do not diverge to produce pseudogenes, or 'die', as quickly or as often as had been predicted on the basis of population-genetics theory¹⁰. I would guess that the existence of multiple gene functions and their recruitment into novel gene networks provide another explanation. But more needs to be learned about the evolution of gene networks, through comparisons of complete genome sequences and through further functional-genomic analyses, before this question can be answered. ■

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Condensed-matter physics

Two bodies are better than one

Bernard Barbara

Single-molecule magnets can change their spin states through quantum tunnelling. A more complete picture of the interactions occurring in a system of such magnets must include two-body transitions.

To avoid the complexity of the macroscopic world and get at the fundamental mechanisms of nature, physicists prefer to study ensembles of simple, identical objects, such as quantum dots or single molecules. In time, these objects may become the elementary parts that are assembled into functionalized devices: as Richard Feynman said, physical laws do not imply any limitation on our ability to construct and assemble objects at the atomic scale.

Although single atoms can be handled relatively easily, manipulation of the quantum properties of spin systems must be achieved if the potential of quantum-spin devices is to be realized. As well as having applications in 'spintronics', spin manipulation is a bridge to understanding a basic problem in quantum mechanics — how the quantum properties of spins are affected by their environment¹.

Another step towards understanding a quantum spin in its environment has been taken by Wernsdorfer *et al.*² with their study of single-molecule magnets (SMMs), published in *Physical Review Letters*. SMMs carry a well-defined spin, S , and can be arranged in model systems so as to minimize the

magnetic interactions between them³. Spin reversal can then occur through the quantum process of tunnelling^{4,5}.

Typically, SMMs have a large uniaxial magnetic anisotropy — that is, the directions of their spins are oriented either one way or the other (usually represented as '+' and '−'). In their study, Wernsdorfer *et al.*² used an SMM with the chemical formula $\text{Mn}_4\text{O}_3(\text{OSiMe}_3)(\text{OAc})_3(\text{dbm})_3$ — known simply as Mn_4 — that, in its ground state, has spin $S = 9/2$. In a magnetic field, the energy levels associated with the different spin states of the SMM suffer 'Zeeman splitting' (Fig. 1a): the spin states split into positive and negative values, and the energy of the $-9/2$ state becomes higher than that of the $+9/2$ state, and similarly for the other spin states available to the SMM ($\pm 7/2$, $\pm 5/2$, $\pm 3/2$ and $\pm 1/2$, a total of $(2S + 1)$ energy states).

At low temperature, where thermal fluctuations are negligible, an SMM can reverse its spin (from a positive to a negative value, or vice versa) by tunnelling through the energy barrier between the potential wells of two spin states^{4,5}. For the conservation of energy to hold, the energy levels associated with each state must coincide. This tunnelling