

laboratory experiments to realistic coastal conditions, reproduced in a state-of-the-art atmospheric smog chamber. They show that the photolysis of CH<sub>2</sub>I<sub>2</sub> at concentrations as low as 0.015 parts per billion by volume, well within levels often found in coastal environments, is a potent source of aerosol particles. Using a suite of instruments for characterizing the dynamics of particle formation and growth, and an aerosol mass spectrometer for determining chemical content as a function of particle size, they charted particle dynamics and confirmed that the particles formed in their chamber were predominantly composed of iodine oxides, the simplest of which may be OIO, HOI and I<sub>2</sub>O<sub>2</sub>. The authors' suggested reaction mechanism for the creation of these species, after the photochemical production of iodine from algal CH<sub>2</sub>I<sub>2</sub> emissions, is shown in their Fig. 2 on page 633.

To produce stable new particles in the clean, open-ocean marine atmosphere, concentrations of condensable vapour have to be high enough both to nucleate new nanometre-scale particles and to allow them to grow by agglomeration and vapour condensation to the stable 50–100-nm size range<sup>5</sup>. If there is too little condensable vapour, new particles don't form or they re-evaporate or agglomerate with pre-existing particles. O'Dowd *et al.*<sup>1</sup> describe modelling calculations which suggest that CH<sub>2</sub>I<sub>2</sub> concentrations over the open ocean might well be high enough for the resulting condensable iodine oxides to allow newly nucleated sulphuric acid particles to become large enough to survive. The authors propose that the resulting particles might be abundant enough to influence the Earth's radiative balance. At the least, their model suggests that iodine oxides produced from volatile organic iodide compounds such as CH<sub>2</sub>I<sub>2</sub> must be added to the list of precursors for secondary aerosol formation.

In retrospect, this might not be too surprising. In pioneering research off Hawaii<sup>14</sup> and Puerto Rico<sup>15</sup> in the 1970s, it was shown that iodine becomes concentrated in atmospherically processed sea-salt aerosol. In contrast, other halogens—chlorine and bromine—are depleted. These 30-year-old studies further showed that the iodine levels vary inversely with particle size, just as one would expect from a gas-phase condensable source of iodine oxide such as that described by O'Dowd *et al.*<sup>1</sup>

The obvious task that remains is to determine just how widespread this newly identified mechanism of particle growth is. To have a significant influence on climate, it would have to be effective over the oceans as a whole, not just in the coastal environment. The appropriate field-measurement tools and analytical models are already in hand. ■

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Developmental genetics

## Buffer zone

Massimo Pigliucci

Heat-shock proteins help to protect organisms from external stresses. The idea that they can also buffer against internal — genetic — variations has received support from studies of fruitflies and, now, of plants.

Living organisms are caught between a hammer and an anvil, evolutionarily speaking. On the one hand, they need to buffer the influences of genetic mutations and environmental stresses if they are to develop normally and maintain a coherent and functional form. On the other, stabilizing one's development too much may mean not being able to respond at all to changes in the environment and starting down the primrose path to extinction. On page 618 of this issue, Queitsch *et al.*<sup>1</sup> propose that, in plants, the balance between stability and the potential for change is made possible in part through a protein involved in 'heat-shock responses' in a wide variety of species, from plants to insects.

Heat-shock responses are a fundamental and widespread type of cellular defence against environmental stress. They have been studied for their effects on the fitness of organisms<sup>2</sup>; for their co-evolution with other cellular functions<sup>3</sup>; for their role in response to stresses not related to temperature<sup>4</sup>; and for the level of natural variation in the genes that encode the heat-shock proteins (Hsps)<sup>5</sup>, which mediate heat-shock responses. Notwithstanding the continuing debate<sup>6</sup> about the actual function of these proteins, it is now clear that they are a complex family of gene products that are involved in protecting other proteins. Some Hsps are expressed continuously in the organism, whereas others are triggered by several environmentally harsh conditions (not only increases in temperature).

Given the ubiquity of these proteins and their role in protecting organisms from environmental changes, it makes sense to ask a more subtle question: can they also help to protect against disruptive genetic variations? After all, the systems that allow organisms to develop from a fertilized egg to the adult form have been honed over millions of years of evolution, and it is likely that a mutation in any of the tens of thousands of genes involved would disrupt the entire process, just as a severe environmental stress does. This idea

is rooted in the 1940s, in Waddington's classic studies<sup>7,8</sup> of 'canalization' — the resistance of developing organisms to change when perturbed genetically or environmentally. More recently it has been suggested that, from the point of view of development, internal disturbances are simply another form of environmental change that needs to be properly 'canalized' to maintain a viable form (phenotype) tailored to specific functions<sup>9</sup>.

So can the Hsp proteins buffer genetic as well as environmental change? Rutherford and Lindquist<sup>10</sup> first tested the idea of a connection between Hsp activity and genetic variation by looking at a popular animal model of developmental genetics — the fruitfly *Drosophila melanogaster*. The results were stunning. When the authors disrupted Hsp90, by either mutating or inhibiting it, phenotypic variation in nearly every structure of adult *D. melanogaster* ensued, with the details depending on the genetic background of the insects used (that is, on which other specific genes were present in each individual). This led the authors to conclude that *D. melanogaster* accumulates hidden genetic variation, which is somehow kept by Hsp90 from affecting the phenotype. If the function of Hsp90 is partly compromised, the buffer breaks and we can see previously 'unavailable' phenotypic variants.

Queitsch, Sangster and Lindquist<sup>1</sup> have now expanded this research to another model of developmental genetics, the plant *Arabidopsis thaliana*<sup>11,12</sup>. These two species, *D. melanogaster* and *A. thaliana*, are of course very different in many ways. They have evolved separately over hundreds of millions of years. As one is a plant and the other an animal, they develop radically differently. And their breeding systems are not at all alike: fruit flies are obligatory 'out-crossers', meaning that they need a partner to produce offspring, whereas *A. thaliana* is mostly a 'selfer' — it fertilizes its own female gametes. Nonetheless, in *A. thaliana*, as in *D. melanogaster*, changes in Hsp90 release

previously hidden genetic variation, resulting in the production of novel phenotypes. These include altered leaf shapes, the accumulation of a purple pigment in hypocotyls (embryonic stems), and variations in hypocotyl length.

These latest findings<sup>1</sup> are also interesting for their differences from the previous results and for the potential follow-up that they make possible. For example, the range of phenotypes released by compromising Hsp90 function in *A. thaliana* seems less wide than the corresponding variation seen in *D. melanogaster* (in as much as it is possible to compare the phenotypes of insects and plants). This might be a result of the differences in developmental plasticity inherent to the two types of organism. Furthermore, by using sophisticated approaches to genetic analysis such as microarrays, it should be possible to further characterize the molecular basis of the phenotypic variation induced by blocking Hsp90 in *A. thaliana*.

More generally, there is no question about the importance of this sort of study for our understanding of the complex relationships between genes, environments and phenotypes. The mere ability to affect Hsp90 and possibly other similar proteins experimentally, thus producing an array of new phenotypes in a potentially wide range of organisms, provides evolutionary biologists with a powerful new research tool. It is less clear and more controversial whether these findings have long-term evolutionary implications, and the nature of the mechanisms that make the relationship between heat-shock proteins and hidden genetic variation possible is still unknown.

An obvious question is whether Hsp90 was actually selected to act as a 'capacitor' of morphological evolution, as it has been characterized by Rutherford and Lindquist<sup>10</sup>, or whether the storage of hidden genetic variation is instead a by-product of its normal physiological function. Although I would bet on the latter, only a phylogenetically informed comparative study, tracing the evolution of both the Hsp family itself and its phenotypic effects, will be able to shed light on this question.

Queitsch *et al.*<sup>1</sup> also suggest that, because of the breadth and strength of Hsp90's effects, it might have a large impact on evolutionary processes, and I am more inclined to agree on this point. But statements<sup>10</sup> to the effect that the conditional release of hidden genetic variation may have allowed the rapid diversification of forms (radiations) that are occasionally seen in the fossil record might be too premature a connection between developmental genetics and palaeontology. Then again, it is exactly this sort of connection that will be needed to enlarge modern evolutionary theory to include molecular and developmental genetics<sup>9</sup>. ■

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### Condensed-matter physics

## Indirect evidence

Andrew Millis

The ease with which electrons move through some metals depends on which direction they take. Watching electrons move along metal planes gives new insight, curiously, into how they move between them.

One of the fundamental issues in condensed-matter physics is conductivity, in other words how charge is transported through a material in response to an applied electric field. The essence of the conduction phenomenon in most materials is understood, thanks to work done from the 1930s to the 1950s by Bloch, Peierls and others. Over the past decade, however, the accepted wisdom has been challenged by measurements made on a wide range of 'strongly correlated metals', such as high-temperature copper-oxide superconductors, in which interactions between the conduction electrons dominate the physics.

On page 627 of this issue, T. Valla and colleagues (*Nature* 417, 627–630; 2002) use a pleasingly indirect method to obtain a new insight into the conductivity of strongly correlated metals. Their work concerns electrically anisotropic materials (high-temperature superconductors are again an example) in which current can flow more easily in some directions than in others. Such materials pose a particular challenge: the temperature dependence of the conductivity varies markedly depending on the direction of current flow. Above a certain temperature—typically in the range 50–200 K, depending on the material—one finds 'metallic' behaviour (that is, conductivity decreases as the temperature rises) for the highly conducting directions and 'insulating' behaviour (conductivity increases as the temperature rises) for the poorly conducting directions. At lower temperatures the temperature dependence is the same for both directions of current flow, although the magnitudes of the conductivities differ greatly.

The existence of different temperature dependences for different directions of current flow is difficult to understand within the conventional Bloch–Peierls picture, in which conductivity is expressed as the product of electron velocity and the 'transport

time' (roughly, the mean time between electron-scattering events, which significantly degrade the current). Electron velocity is generically anisotropic but not temperature dependent, whereas the scattering time is generically temperature dependent but is not expected to depend strongly on the direction of current flow. The difficulty has stimulated much creative theoretical work but no generally accepted solution has yet emerged, in part because conductivity results were the only data that theorists had to work with.

Valla *et al.* have performed a photoemission experiment that sheds new light on this phenomenon: they studied two different layered materials whose crystal structure forms planes along which current can easily flow but in which the conductivity between planes is much smaller. The photoemission measurements involve shooting a beam of high-energy photons at a solid, then measuring the energy and in-plane momentum of emitted electrons. It seems remarkable that an experiment in which electrons are violently ejected from a solid can tell us something about the motion of electrons inside that solid. It is even more remarkable that Valla *et al.* have extracted important information about the ability of electrons to move between planes by studying the dependence of the photoelectron spectrum on in-plane electron momentum: Polonius's phrase from *Hamlet*—"by indirection find directions out"—comes to mind.

To understand what Valla *et al.* have shown, it is helpful to recall the basic theory of conductivity in metals. The quantum-mechanical effect of wavefunction hybridization enables electrons to move from one atom in a solid to another. In most circumstances, the timescale associated with this hybridization is very short, so that one can think of electrons as moving ballistically through the crystal. Metallic conductivity is