

such as dislocations, and the X-ray scattering from such defects is greater than the scattering from bonding electrons. But using an electron microscope it is possible to image the crystal, select a perfect region between crystal defects, and form a diffraction pattern from this perfect region. Zuo *et al.*¹ use an electron beam focused to nanometre dimensions to find a region of the crystal where the perfect-crystal theory of diffraction applies. They also filtered the electrons transmitted by the specimen to remove inelastically scattered electrons and ease comparison with theory. Using these methods, very accurate charge-density maps can be made which reveal the shape of the electron bonds.

In metal oxides, the metal ions interact mainly with the oxygen atoms. But in many copper- and silver-oxide compounds the metal ions are found in close-packed crystal structures, leading to predictions of short-range metal-metal bonding. Such bonding would be covalent, and therefore require non-spherical orbitals, unlike the usual ionic bonding, which involves electrostatic interactions between spherical ions. The non-spherical charge density observed by Zuo *et al.* around Cu atoms in Cu₂O reveals unusual *d*-orbital holes (where the *d*_{z²} orbital is unoccupied) and provides strong evidence for Cu-Cu bonding.

How does this work relate to high-temperature superconductivity? We now know that in the simple oxide Cu₂O there are *d*-orbital holes located on the Cu atoms. We also know that in the copper-oxide super-

conductors, which have CuO₂ (rather than Cu₂O) conducting planes, the charge carriers in the normal state are holes and in the superconducting state are hole pairs. In the CuO₂ superconductors, the available evidence suggests that the holes are on oxygen sites rather than on copper sites^{3,4}, whereas the work of Zuo *et al.* shows that for Cu₂O the holes are on copper sites. It would be of great interest to extend this approach to measuring charge densities to the more complex CuO₂ superconductors. Such an experiment should give us the following information about high-temperature superconductors: first, whether the holes are on copper or oxygen sites; second, how many holes there are per CuO₂ unit in the conduction planes and how many holes are elsewhere in the structure. Finally, we would like to know whether the distribution of holes in the conduction planes is actually periodic, as is usually assumed, or if there is an irregular two-phase charge density of holes as recently proposed⁵. Zuo *et al.*¹ have provided us with a tool to answer all these questions. ■

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Ecology

Bite the mother, fight the daughter

Erkki Haukioja

Induced defences — which emerge or develop to full strength when activated by the presence of an enemy — are widespread in sedentary or slowly moving prey¹. Such induced resistance, as opposed to constitutive resistance (which is present all the time), is profitable when defences are metabolically expensive, and when attack is unpredictable but recurrent². Induced defensive traits are diverse. Water fleas, for example, form long, helmet-shaped spines on their necks, making it difficult for predators to handle them. Plants, on the other hand, can produce high levels of toxic compounds in their leaves. Much of the literature on induced plant defences contains reports of predators having a bad time of it if they try to target a plant that has already been attacked. However, these observations do not exclude the possibility that the poor quality of previously damaged plants is a fortuitous by-product of recovery from

attack, not a sign of increased defence.

This is not the case for the organisms described by Agrawal *et al.*³ on page 60 of this issue. These authors have used radish plants (*Raphanus raphanistrum*) and water fleas (*Daphnia cucullata*) to provide the best evidence yet that predator-activated responses



Figure 1 Radish plant under attack by the butterfly larva *Pieris rapae*. The plant's defence response includes the production of bitter-tasting, toxic compounds, and the development of hairy trichomes.

help the victims to survive an attack⁴. Not only that, but they show that these defences can be transmitted from an organism to its offspring. Induced defence is known to be a form of genotypic plasticity — that is, the ability of a given gene sequence (genotype) to produce various traits (phenotypes) depending on environmental conditions. But it has never previously been reported to extend across generations.

To be ready when needed, induced traits must develop quickly in the presence of a predator. This might be a real problem. Fortunately, it can be overcome if the target organism receives cues of the predator before the actual attack, or if the first attack is unlikely to be lethal. Although plant defences may be induced simply because herbivores are chewing the foliage, many organisms have sophisticated early-warning systems. Some plants, for example, switch on their defence mechanisms as soon as they detect volatile chemicals released by damaged plants close by⁵. Some of these volatiles also directly lure predators to attack plant-eating insects or mites⁶. But the first encounter with a predator is likely to be fatal for young water fleas, so they develop long neck spines in response to chemical cues emitted from their invertebrate predators. In the field, this causes water fleas to develop spiny, defensive helmets when living in a pond also inhabited by predators.

Agrawal and co-workers³ now report that in both wild radish, which is a cruciferous plant (its petals are arranged in a cross shape), and the water flea, the risks of a young individual's first encounter with predators can be reduced by the experiences of their parents. In the case of the wild radish, the authors allowed butterfly larvae (*Pieris rapae*; Fig. 1) to attack the leaves in a controlled manner. The radish plants responded by a ten-fold increase in the concentration of glucosinolate, and they also developed more numerous hairy trichomes on their leaves. Glucosinolates are bitter-tasting, toxic compounds that reduce insect feeding; hairy trichomes on leaves have a similar effect. The authors then exposed seedlings produced by these plants to further larval predation. They found that the offspring of damaged mothers provided less suitable diets for larvae than seedlings from undamaged, control plants.

A similar thing happened when Agrawal *et al.* exposed water fleas (Fig. 2) to chemical cues called kairomones from two invertebrate predators — the water fleas developed long helmets. Furthermore, the offspring of kairomone-treated mothers produced longer helmets than offspring from control mothers, irrespective of the environment in which the offspring were raised. The authors saw the same effect in successive broods produced later by the kairomone-treated mothers in clean water. This result confirms that

the development of long helmets in the embryonic stages resulted from maternal effects, and did not need to be directly induced by kairomones. However, offspring produced by the kairomone-treated mothers in clean water had shorter helmets than offspring raised in water that contained the chemical. This indicates that a recurrent induction is needed for a maximum-strength defensive response.

At first glance, the observation that certain traits are carried over to the next generation looks like an example of Lamarckian inheritance. This theory, proposed by the nineteenth-century botanist and zoologist Jean-Baptiste Pierre Antoine de Lamarck, holds that organisms can pass on to their offspring traits that they have acquired during their lifetime. Lamarck's theory is surely wrong if it is interpreted as meaning, say, that mice with cut tails would have offspring with no tails, or that people with trained muscles would produce muscly babies. But if the parent's environment affects how the genetic code in the offspring is translated, then certain acquired traits can be delivered to the offspring.

Accordingly, the most parsimonious explanation of Agrawal and colleagues' findings is that the genes that were switched on in the parent to generate the defensive response are also switched on in the offspring. The internal milieu of the radish seeds was indeed different between induced and control mothers, the induced mothers containing higher concentrations of glucosinolate. But this does not need to be the decisive

switch — several alternative mechanisms, passed on from either the mother or the father, can lead to the inheritance of environmentally affected traits⁷. Because the genetic code inscribed in the chromosomes does not change, however, the inter-generational carry-over effect is presumably reversible.

Nonetheless, the demonstration that chemically mediated defensive traits can be carried over between generations in two totally unrelated species hints that such phenomena might be widespread. Interest is growing in the idea that certain environmental effects can be inherited in many types of organism, from bacteria to plants, insects and mammals⁷. Although it is not yet clear to what extent these inter-generational responses are adaptive (that is, tailored to equip an organism for a particular situation), they have been reported in cases when parents and offspring meet similar environmental challenges. For example, parental crowding alters the physiology, behaviour, coloration and structures of the offspring in some species of locust⁸ and lepidopteran⁹. This helps them to manage at high or low

population densities — situations that often occur over several successive generations. Such observations indicate that if we do not take into account the environmental fates of the parents of experimental organisms, we may find unexplained variance in the results of ecological experiments. This is particularly true for research on induced defences, and Agrawal and colleagues' study indicates that ecologists have much to do to uncover sources of variation, such as how dynamic or long-lasting the effects of induced defences can be. ■

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Random fluctuations

Unsolved problems of noise

Peter V. E. McClintock

Random noise, and its effect on physical systems, has always been an interdisciplinary subject. Using the study of fluctuations as a unifying theme can lead to interesting scientific conferences, such as the recent *UPoN'99* meeting in Adelaide, Australia*.

Over the years, noise has attracted some of the best scientists: in 1828 the botanist Robert Brown¹ discovered the random fluctuations of tiny particles in a fluid, which remained a mystery until Einstein's epoch-making paper² on Brownian motion in 1905. But it was not until later that the ubiquitous presence of noise began to be appreciated. A milestone was Johnson's 1927 paper³ in which he identified noise in electrical circuits as being of thermal origin. In the middle of the twentieth century, noise seemed merely a nuisance — to be eliminated or minimized wherever possible. It spoiled radio reception and musical recordings, and limited the precision of physical measurements. Later, it was found to wash out the fine structure of beautiful fractal patterns generated by nonlinear systems.

But noise is much more than just a nuisance. By the 1970s it became apparent that noise can play a creative role too. One of the

first examples was the observation of noise-induced transitions⁴, whereby the state of a nonlinear system can be utterly changed by the introduction of noise above a critical intensity. Another was stochastic resonance, in which a weak periodic signal in a nonlinear system can be amplified by added noise. Stochastic resonance was introduced^{5,6} to try to explain the Earth's ice-age cycle, but it is now recognized to be far more common, occurring for example in lasers, electronic circuits and sensory neurons. Yet another creative effect of noise is seen in Brownian ratchets⁷ where a net current of particles can be driven by noise, providing that there is an appropriate asymmetry in the system: this particular phenomenon may underlie the transport of macromolecules within biological cells. And, of course, it is noise in the sense of thermal fluctuations that drives chemical reactions, including those responsible for life itself.

The negative aspects of noise are still with us and, given its Janus-like character, how is noise to be perceived, pursued and investigated? A proper appreciation of noise must involve studies of both the mechanisms that produce it, for example in semiconductor devices, and the effect that it has on systems subject to it. Both these aspects were well represented at *UPoN'99*.

Of the several kinds of Brownian ratchet



Figure 2 Mother knows best. Agrawal *et al.*³ have shown that defence responses induced in response to predators in female water fleas (pictured carrying eggs) can be passed on to their offspring.