All this glosses over a crucial assumption. In his derivation, Einstein simply assumed that successive collisions with the fluid molecules would be statistically independent in approximation. So in essence the position of the Brownian particle is a sum of independent random variables, and as in the theory of random errors that yields diffusive behaviour. But a truly microscopic analysis would have to treat the Brownian particle plus fluid as a dynamical system with very many degrees of freedom, governed by Newton's equations of motion, so deterministic dynamics must somehow account for the assumed statistical independence.

As early as 1918 Smoluchowski[4] had already identified the instabilities of mechanical motion as the main ingredient for the statistical independence of collisions. Today, an intricate mathematical theory has been developed in which such notions have a precise meaning. It turns out that Brownian statistics, such as the power spectrum found by Gaspard *et al.*, are a generic property[5] of dynamical systems with so-called hard chaos, in which the motion depends sensitively on initial conditions and there are no traces of quasiperiodic motion.

But, although microscopic chaos is sufficient to produce Brownian motion, it may not be necessary. The analysis of simplified models[6], such as a hard sphere immersed in an ideal gas and an impurity in a harmonic crystal, has shown that the motion may be Brownian even when the full dynamical system, particle plus fluid, is not chaotic. In these models it is largely the randomness of the initial conditions of the fluid molecules that leads to the erratic motion of the suspended particle.

Gaspard *et al.* show that the fluid in their experiment has chaotic dynamics after all. This points at an apparently general property of systems with many particles. From experience we know that fluids effectively maintain a well-defined local temperature and pressure. Of course, there can be turbulent motion, but even then a small fluid element is approximately in thermal equilibrium, and that is the basis of all of hydrodynamics. Also, external perturbations hardly change such a state of local equilibrium. If the motion of the fluid particles were quasiperiodic (governed by a finite number of frequencies) this stable macroscopic behaviour would be hard to explain.

Only chaotic mechanical motion generates enough intrinsic noise to ensure a robust average behaviour. Chaos is usually defined mathematically in terms of positive Lyapunov exponents, which characterize the exponential divergence of nearby trajectories in phase space (this exponential divergence is what makes these systems sensitive to initial conditions). For many-particle systems, the evidence points to a spectrum of Lyapunov exponents that scales with system size and has a positive part. Nevertheless, there can be pockets in phase space with quasiperiodic motion, where all Lyapunov exponents are zero, especially when forces are attractive. Presumably, such a mixed phase space will have little effect on the observed macroscopic features of fluids, because observable properties such as local temperature, velocity, and pressure are not sensitive to such fine dynamical details — but a great deal of effort is still required to understand, on the microscopic level, what degree of chaos in a mechanical many-particle system is needed in order to ensure the regular macroscopic behaviour we see around us. ☐

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Mimicry

Sheep in wolves' clothing

Graeme D. Ruxton

Avoiding being eaten is a vital activity for many animals. They can in part do so by looking like other, unpalatable species, and the study of this strategy (known as mimicry) has a long and distinguished pedigree — so long, in fact, that from the textbooks one might think that the topic was pretty much sewn up. In a paper in *Animal Behaviour*[1], however, MacDougall and Stamp Dawkins come up with a new angle. They argue that the ability of a predator to discriminate between types of prey has to be taken into account. The complications that introduces may well require revision of thinking on mimetic systems.

Aposematic coloration, where unpalatable, poisonous or dangerous animals adopt conspicuous markings, is a well-known phenomenon. The usual explanation is that predators learn to associate these markings with unpleasant experiences, and so are less likely to attack similarly marked individuals in future. This mechanism leads to selection pressure for similarity of markings between species, and hence mimicry; this can be seen in the many insects, some of them completely harmless, which have the yellow and black stripes characteristic of wasps. Traditionally mimicry is divided into two types: Müllerian, where two unpalatable species both benefit from sharing the mortality costs of predator learning; and Batesian, where a palatable species benefits from its resemblance to an unpalatable species, which in turn pays a cost because the palatable mimic degrades the quality of its aposematic signal.

There are two major objections to this story. First, it has been argued that true Müllerian mimicry can exist only in highly specialized and unrealistic circumstances[2], because there will always be a difference in palatability between two species and so the less palatable one will always be disadvantaged by the mimetic relationship.

Second, theory predicts that Müllerian mimics should be monomorphic, because the more similar-looking unpalatable individuals there are, the more there are to share the costs of attacks by naive predators. In contrast, the palatable Batesian mimics should be polymorphic; the reason is that the protection individuals of a given morph get from mimicking an unpalatable species decreases with the frequency of palatable mimics. It is strange, then, that several unpalatable (and so, by the definition

Figure 1 **Morphs and mimicry. The viceroy butterfly, *Limentis archippus,* occurs as two morphs and was once thought to be a polymorphic Batesian mimic. It turns out, however, that it is less palatable to its natural predators than the species that were assumed to be its models — the monarch (*Danaus plexippus,* left) for one morph and the queen (*Danaus gilippus*) for the other. In conventional theory, it is hard to explain cases of polymorphic Müllerian mimicry such as this. But the new ideas of MacDougall and Stamp Dawkins[1] may account for its occurrence.**

above, Müllerian) mimics are polymorphic[3] (Fig. 1).

The theory proposed by MacDougall and Stamp Dawkins[1] offers a resolution to both problems. The authors accept that the less palatable species will generally be disadvantaged by its resemblance to the more palatable one (what we could term a misidentification cost). But they suggest that there can be a hitherto unconsidered advantage to mimicry which benefits both parties, and which may outweigh the misidentification costs paid by the less palatable species: mimicry reduces the risk to individuals from both species of being misidentified by the predator as belonging to a third and even more palatable prey species (that is, it can provide a misidentification benefit). Predators often have a wide diet, so they have to differentiate between a large number of categories of prey appearance and associate a palatability score with each category. Because of cognitive limitations of the predator, the more categories there are, the more mistakes will be made.

MacDougall and Stamp Dawkins propose that mimicry reduces the number of categories, and therefore may reduce the frequency of mistakes where unpalatable species are misidentified as palatable. Thus, they claim, Müllerian mimicry, where both species benefit from their similarity, is possible in realistic circumstances. Further, the resemblance between two unpalatable species could be either Müllerian or Batesian, depending on the relative strengths of the misidentification costs and benefits, which could explain the existence of unpalatable but polymorphic mimics.

The conceptual leap here is that the mimetic relationship between two species cannot be understood without proper consideration of their shared predator. Whether the relationship is Müllerian or Batesian will depend on the discrimination abilities of the predator, and also on the properties of alternative prey. The relationship could be different for different predators, or for the same predator at different times or in different places.

All this is theory, however, and experiments on learning and cognition in predatory species will be needed[4]. This work is likely to be best achieved initially in the laboratory, but several predictions are ready for testing in the field. For example, the new theory has it that polymorphic but unpalatable mimics do not benefit strongly from mimicry that produces a reduction in predator misclassification errors. This could arise because the common predators of these species feed on only a few species or have highly developed discriminatory powers. Field investigation of the foraging behaviour of these predators could be fruitful.

There is also scope for taking theory further. Misidentification is costly to the predator, so we should not, as in the past, consider the predator's abilities as fixed and then ask how these abilities influence the evolution and maintenance of mimicry in prey species. Rather we should ask how prey mimicry and predator discrimination co-evolve and co-exist. Because it now appears that the operation of both Müllerian and Batesian mimicry require mistakes by the predator, the results of this enquiry should be both subtle and illuminating. ☐

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Synaptic plasticity

Down with novelty

Richard G. M. Morris

"Too many new ideas around here," I tease my colleagues, when unfinished but much-loved experiments are dropped in favour of pursuing something else dreamed up the night before. "But you always say that the best experiments start in the pub," they intone, "...and it's different from the same old stuff we've been doing for years." Duly defeated, I frown my way back to the office wondering whether the new is always destined to drive out the old. An intriguing observation on synaptic plasticity, reported by Xu *et al.*[1] on page 891 of this issue, suggests that this old aphorism may indeed have some physiological basis. They have investigated what happens when animals in which long-term potentiation (LTP) has recently been induced are transferred from a familiar environment, where electrical recordings from the brain have hitherto been made, into a new one. And they find that LTP disappears rapidly as animals explore a new place and, presumably, encode new information.

LTP is widely held as a model of the activity-dependent synaptic plasticity that may underlie the automatic encoding of new information[2,3]. One area of interest is the mechanisms of plasticity that are responsible for decreasing the efficacy of synaptic transmission. Such decreases could occur immediately after LTP is induced, in a phenomenon called depotentiation. Or, they could occur from a baseline at which synaptic efficacy has already stabilized, as in long-term depression.

Attempts have been made to identify patterns and frequencies of stimulation that lead to these decreases. Long trains of low-frequency stimulation[4] or pairs of pulses[5] are effective *in vitro* and sometimes[6] (although not always) *in vivo*[7,8]. Stimulation at 5 Hz is particularly effective in triggering depotentiation within a short time after induction of LTP, and this may involve the destabilization of synaptic interactions mediated by integrin receptors[9].

Xu *et al.*[1] investigated whether behavioural manipulations, rather than artificial trains of electrical stimulation, could have similar effects. They first recorded the brain activity of rats in a small — but well-lit — Perspex box with which the animals were familiar. The rats were then transferred to a box with different lighting conditions and fresh wood shavings on its floor. An important two-pathway control established (although it is unclear how many of these experiments were conducted) that exposure to a new environment could depotentiate recently induced LTP, without disturbing an independent but non-potentiated pathway.

These results rule out the potential contribution of artefacts (such as changes in brain temperature of the exploring rats), and reveal that the underlying mechanism shows input specificity. Merely handling the animal shortly after induction of LTP did not cause depotentiation, suggesting that it may be necessary for the rat to explore the new place. However, exploration alone is insufficient, because synapses at which LTP had been induced the day before could not be depotentiated, even though the rats explored the new place just as much as the old one. Stress is also unlikely to be important, because the new environment was deliberately made non-stressful, and the rats showed neither behavioural nor hormonal indices of stress. The emerging picture is that non-stressful exploration of a new place can cause recent synaptic potentiation to be reset, without affecting synapses at which LTP has already stabilized.

A puzzle about Xu and colleagues' findings is the apparently immediate effect of exposure to the new environment. Given the relatively long trains of stimulation that are needed to induce depotentiation in physiological studies, one might have expected a more gradual time course to exploration-induced depotentiation than the apparently sudden decrease to near baseline within a few minutes. It is also slightly puzzling that the peak of the electroencephalographic activity at 6–8-Hz that accompanied exploratory movements did not seem to occur until after the depotentiation had already been triggered.