Figure 1 Approach of a population towards an optimum through selection of a series of random mutations, through a space of ten dimensions. The population begins at a point on the outer sphere, at a distance $d/2$ from the central optimum (where d is the diameter of the sphere). The first successful mutation has magnitude $r = 0.137d$, and takes the population 8.7% of the way to the optimum (first line, leading to the second sphere). The third successful mutation has the largest magnitude, $0.271d$; it is followed by smaller steps which, on average, follow a geometric series.

largest effect on fitness are most likely to be picked up by natural selection. Later, small changes do contribute, but they are not responsible for much of the improvement in fitness.

The prediction that the effects of the genes responsible for adaptation should follow an exponential distribution roughly applies to individual traits, as well as to the sum over all traits. Orr argues that studies⁷ of the quantitative trait loci (QTL), which distinguish close taxa, are consistent with this prediction. But it is not clear what would be predicted by other models of evolution, or whether these could be distinguished. Existing methods for detecting QTL are biased towards finding genes of spuriously large effect⁷. More convincing evidence for the importance of major genes comes from studies of 'candidate loci', which often contribute to divergence and standing variation^{8,9}. However, such examples hardly fit with Fisher's model, whereby mutations are drawn randomly from any of the many genes that might influence a trait.

Some functions may necessarily be composed of many minor changes. For example, the efficiency and accuracy of translation can be improved by using triplet codons that match the most abundant transfer RNAs. Each such change could have only a tiny effect on fitness¹⁰, so, for codon-usage bias, adaptation is based on minute variations. Nevertheless, such examples are hard to find and there are many limits to the success of weakly selected variants, beyond the low fixation probability identified by Kimura⁶ and Orr⁵. In a large, asexual population, a favourable allele can fix only if it confers an advantage that outweighs the loss in fitness owing to the deleterious alleles with which it arises⁴. Even with sexual reproduction, linkage reduces the effectiveness of natural selection, and can greatly reduce the fixation probability of a weakly favoured allele¹¹. Indeed, bias in codon usage is weaker in regions of reduced recombination in *Drosophila*¹².

Fisher's geometrical analogy is an extreme abstraction of organismic complexity. One problem is that it is hard to know what is meant by the number of dimensions, n . The morphology, development and behaviour of an organism can be described by an indefinite number of phenotypic dimensions that may all be influenced by many genes. The number of degrees of freedom, n , is presumably limited by the number of genetic loci ($\sim 10^5$ genes and $\sim 3 \times 10^9$ base pairs in man). However, once one thinks in terms of gene sequences rather than continuous traits, a different geometry is required. Although many sequences are possible (4^k with k bases), only a few ($\sim 3k$) can be reached by a single mutation. It may be possible to do an analysis similar to Orr's for this tightly restricted geometry¹³, although this might come to different conclusions. The issues raised by Orr's work are relevant to the optimization of any complex structure — be it computer software or a mechanical device. But the universal genetic code, together with simple mathematics of natural selection, may allow population genetics to provide a more general understanding of adaptation than is possible in other contexts. □

Nick Barton is in the Institute of Cell, Animal and Population Biology, King's Buildings, University of Edinburgh, Edinburgh EH9 3JT, UK.
e-mail: n.barton@ed.ac.uk

1. Darwin, C. *On the Origin of Species by Means of Natural Selection* (Murray, London, 1859).
2. Provine, W. *The Origins of Theoretical Population Genetics* (Univ. Chicago Press, 1971).
3. Orr, H. A. & Coyne, J. A. *Am. Nat.* **140**, 725–742 (1992).
4. Fisher, R. A. *The Genetical Theory of Natural Selection* (Oxford Univ. Press, 1930).
5. Orr, H. A. *Evolution* **52**, 935–949 (1998).
6. Kimura, M. *The Neutral Theory of Molecular Evolution* (Cambridge Univ. Press, 1983).
7. Lynch, M. & Walsh, J. B. *Genetics and Analysis of Quantitative Traits* (Sinauer, Sunderland, MA, 1998).
8. McKenzie, J. A. & Batterham, P. *Trends Ecol. Evol.* **9**, 166–170 (1994).
9. Long, A. D., Mullaney, S. L., Mackay, T. F. C. & Langley, C. H. *Genetics* **144**, 1497–1510 (1997).
10. Bulmer, M. *Genetics* **129**, 897–907 (1991).
11. Barton, N. H. *Genetics* **140**, 821–841 (1995).
12. Kliman, R. M. & Hey, J. *Genetics* **137**, 1049–1056 (1994).
13. Gillespie, J. H. *Evolution* **38**, 1116–1129 (1984).

Daedalus

Dead metallic silence

Noise, that curse of modern living, is spread in many ways. The racket of a diesel engine, for example, is greatly amplified by vibrating sheet-metal surfaces such as the rocker cover, the sump-case and the body panels of the vehicle housing it. Workplace machines, domestic gadgets, and even clattering pots and pans, also owe much of their characteristic noise to the undamped vibration of metal surfaces. If all our products could be made (say) of wood, life would be much more peaceful.

So Daedalus wants to load engineering metals with vibration-damping inclusions. Cast iron, for example, one of the quietest of metals, contains many tiny graphite inclusions which absorb vibration. Sadly, they also act as crack-initiating sites, and make it brittle. Daedalus recalls that polystyrene (which has rather a metallic ring itself) is damped by certain organo-metallic ring compounds. The organic ring in these molecules can rotate stepwise around the bond joining it to the metal. The polymer is strongly damped in the acoustic range of frequencies corresponding to the stepping rate of the ring.

So DREADCO chemists are synthesizing organic ring molecules capable of binding to iron and other engineering metals, and are using powder sintering to disperse the most likely candidates into bulk metals. Cunningly, they are seeking molecules that are the stablest combination of that set of atoms. Trapped in its metallic cage at the sintering temperature, such a molecule might well decompose; but it would re-form again when the metal cooled. The resulting metals will be acoustically dead yet still tough and ductile — single molecules are far too small to act as crack initiators.

When perfected, DREADCO's 'Dead Metal' range of alloys should sweep through society. The big noises, such as diesel engines, are the obvious targets. But Daedalus attributes much of the edginess of modern living to the quieter but ever-present background noise from central-heating systems, air-conditioning units, office equipment, refrigerators, cookers, washing machines and so on. The formless, ever-changing insistence of this endless accompaniment to life gets on our nerves in some very subtle way. He recalls the story of a housewife in a modern kitchen who, hearing a sudden change in its complex background racket, asked in bewilderment, "What's just stopped?" With Dead Metal, they will all stop.

David Jones