forced him to become a eugenist. Experience equally seemed to suggest what should be done. Sterilization was, he thought, a suspect option — after all, civil liberties were central to American values. The way forward must lie in the institutional segregation of the unfit. Not only would that prevent defectives from breeding and create a supportive and humane environment for them, but it would provide a superb "human laboratory" (Goddard's standard phrase) for researching their mentalities and laying bare the pathology of the human psyche.

It would, as Zenderland persuasively argues, be misleading to cast Goddard simply as some sort of stock bigot. Doubtless he believed there was some kind of underclass, but he was remarkably free of racial and colour prejudice — what he mainly feared were poor whites. He is best seen primarily as a representative of an emergent cadre of experts, scientists and professional administrators, anxious to establish a place in the sun for themselves as the new priesthood serving a secularizing society, preaching the gospel not of laissez-faire capitalism but of informed social responsibility.

Zenderland does not pretend that her protagonist was a very profound or original thinker. Although a passionate champion of ubiquitous intelligence testing, Goddard never seems to have thought deeply about what precisely it was that was being measured. He was a doer, a technician, lucky enough to hold in his hands, in the Binet test, that device utterly appropriate to the needs of classification and control in a mass society. □

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Not black and white

Melanism: Evolution in Action
by Michael E. N. Majerus
Oxford University Press: 1998. 338 pp. £55, $105 (hbk), £23.95, $45 (pbk)

Jerry A. Coyne

From time to time, evolutionists re-examine a classic experimental study and find, to their horror, that it is flawed or downright wrong. We no longer use chromosomal polymorphism in *Drosophila pseudoobscura* to demonstrate heterozygous advantage, flower-colour variation in *Linanthus parryae* to illustrate random genetic drift, or the viceroy and monarch butterflies to exemplify Batesian mimicry. Until now, however, the prize horse in our stable of examples has been the evolution of 'industrial melanism' in the peppered moth, *Biston betularia*, presented by most teachers and textbooks as the paradigm of natural selection and evolution occurring within a human lifetime. The re-examination of this tale is the centrepiece of

Cautionary tale: the classic account of industrial melanism in the peppered moth now looks flawed.

Michael Majerus's book, *Melanism: Evolution in Action*. Depressingly, Majerus shows that this classic example is in bad shape, and, while not yet ready for the glue factory, needs serious attention.

According to the standard textbook litany, before the mid-nineteenth century, all *B. betularia* in England were white moths peppered with black spots, a form called *typica*. Between 1850 and 1920, *typica* was largely replaced by a pure black form (*carbonaria*) produced by a single dominant allele, the frequency of which rose to nearly 100% in some areas. After 1950, this trend reversed, making *carbonaria* rare and *typica* again common. These persistent and directional changes implied natural selection. In a series of studies, this conclusion was verified by several investigators, most prominently Bernard Kettlewell of Oxford.

According to these workers, the evolution of colour was caused by birds eating the moths most conspicuous on their normal resting site — tree trunks. The increase in black moths was attributed to pollution accompanying the rise of heavy industry. A combination of soot and acid rain darkened trees by first killing the lichens that festooned them and then blackening the naked trunks. The *typica* form, previously camouflaged on lichens, thus became conspicuous and heavily predated, while the less visible *carbonaria* enjoyed protection and increased in frequency. After the passage of the Clean Air Acts in the 1950s, trees regained their former appearance, reversing the selective advantage of the morphs. This conclusion was bolstered by a geographical correlation between pollution levels and morph frequencies (*carbonaria* was most common in industrial areas), and most prominently by Kettlewell's famous experiments which showed that, after releasing *typica* and *carbonaria* in both polluted and unpolluted woods, researchers recaptured many more of the cryptic than of the conspicuous form. The differential predation was supported by direct observation of birds eating moths placed on trees. Finally, Kettlewell demonstrated in the laboratory that each form had a behavioural preference to settle on backgrounds that matched its colour.

Criticisms of this story have circulated in samizdat for several years, but Majerus summarizes them for the first time in print in an absorbing two-chapter critique (coincidentally, a similar analysis [Sargent *et al*., *Evol. Biol*. **30,** 299–322; 1998] has just appeared). Majerus notes that the most serious problem is that *B. betularia* probably does not rest on tree trunks — exactly two moths have been seen in such a position in more than 40 years of intensive search. The natural resting spots are, in fact, a mystery. This alone invalidates Kettlewell's release–recapture experiments, as moths were released by placing them directly onto tree trunks, where they are highly visible to bird predators. (Kettlewell also released his moths during the day, while they normally choose resting places at night.) The story is further eroded by noting that the resurgence of *typica* occurred well before lichens recolonized the polluted trees, and that a parallel increase and decrease of the melanic form also occurred in industrial areas of the United States, where there was no change in the abundance of the lichens that supposedly play such an important role.

Finally, the results of Kettlewell's behavioural experiments were not replicated in later studies: moths have no tendency to choose matching backgrounds. Majerus finds many other flaws in the work, but they are too numerous to list here. I unearthed additional problems when, embarrassed at having taught the standard *Biston* story for years, I read Kettlewell's papers for the first time.

Majerus concludes, reasonably, that all we can deduce from this story is that it is a case of rapid evolution, probably involving pollution and bird predation. I would, however, replace "probably" with "perhaps". *B. betularia* shows the footprint of natural selection, but we have not yet seen the feet. Majerus finds some solace in his analysis, claiming that the true story is likely to be more complex and therefore more interesting, but one senses that he is making a virtue of necessity. My own reaction resembles the dismay attending my discovery, at the age of six, that it was my father and not Santa who brought the presents on Christmas Eve.

Occupying a quarter of the book, the *Biston* analysis is necessary reading for all evolutionists, as are the introductory chapters on the nature of melanism, its distribution among animals, and its proposed causes. Majerus, however, designed his book for both professional and lay readers, and this causes some unevenness in the material. The *Biston* story is sandwiched between less compelling chapters, including long sections on the basic principles of genetics and evolution, which can be skipped by evolutionists. Other discussions, involving melanism in ladybirds and other Lepidoptera, as well as

the author's unpublished work on habitat selection, are full of technical details that will overwhelm the lay reader. Unfortunately, most of the work described is inconclusive; despite the widespread occurrence of melanism, its evolutionary significance is nearly always unknown.

What can one make of all this? Majerus concludes with the usual call for more research, but several lessons are already at hand. First, for the time being we must discard *Biston* as a well-understood example of natural selection in action, although it is clearly a case of evolution. There are many studies more appropriate for use in the classroom, including the classic work of Peter and Rosemary Grant on beak-size evolution in Galapagos finches. It is also worth pondering why there has been general and unquestioned acceptance of Kettlewell's work. Perhaps such powerful stories discourage close scrutiny. Moreover, in evolutionary biology there is little payoff in repeating other people's experiments, and, unlike molecular biology, our field is not self-correcting because few studies depend on the accuracy of earlier ones. Finally, teachers such as myself often neglect original papers in favour of shorter textbook summaries, which bleach the blemishes from complicated experiments.

It is clear that, as with most other work in evolutionary biology, understanding selection in *Biston* will require much more information about the animal's habits. Evolutionists may bridle at such a conclusion, because ecological data are very hard to gather. Nevertheless, there is no other way to unravel the forces changing a character. We must stop pretending that we understand the course of natural selection as soon as we have calculated the relative fitness of different traits. □

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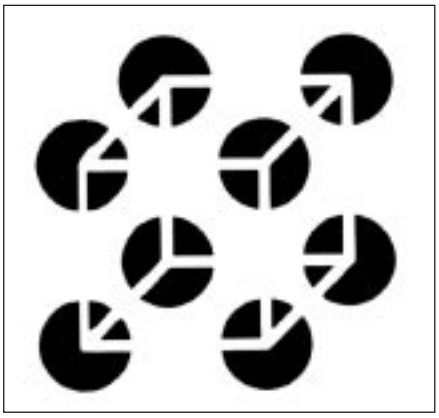
More than meets the eye

Visual Intelligence: How We Create What We See
by Donald D. Hoffman
Norton: 1998. 294 pp. $29.95, £21

John C. Marshall

It sometimes seems that a new visual area is discovered in the primate brain every week. The sheer amount of brain that has purportedly been colonized for vision makes one wonder how we can do anything other than see. It is likewise unclear whether this aggressive drive for *lebensraum* characterizes the biological evolution of the visual system or the cultural evolution of neuroscientists.

Be that as it may, it is quite a relief to see



The "subjective" Necker cube: the black discs can be seen as behind the cube or as holes in front of it.

that Donald Hoffman's riveting introduction to *Visual Intelligence* contains very little about brains. Even when he describes how brain damage can cause loss of colour perception or of motion perception, Hoffman has his eye more on the functional ramifications of the loss than on the neuroanatomical underpinnings. For the most part, then, Hoffman adopts the classical approach of cognitive science and computer science: describe the rules according to which the visual system operates, and let somebody else worry about which neurons are where.

But what is vision? Here Hoffman quotes (and follows) the position originally expounded by David Marr: "Vision is a process that produces from images of the external world a description that is useful to the viewer and not cluttered with irrelevant information . . . ." And what in Hoffman's own terms is the fundamental problem of vision? That "the image at the eye has countless possible interpretations". And within which overall framework can the problem be solved? Hoffman sees a strong parallel between Noam Chomsky's arguments for rules of universal grammar and his own rules of universal vision. In both cases, the mature competence that quickly develops is grossly underdetermined by the fragmentary data presented to the senses.

Hoffman accordingly conjectures that "the innate rules of universal vision are part of the child's biology, and allow the child to acquire, through visual experiences that might vary from one culture to another, the rules of visual processing. The rules of visual processing, in turn, allow the visually competent child or adult to construct specific visual scenes by looking." Hoffman is happy to agree with James Gibson that retinal images, above all moving images, are "rich in information". They are just nowhere near rich enough to pick out our visual world from all the "countless possible visual worlds" that are compatible with such images.

Chapter two ("Inflating an artist's sketch") shows most clearly how Hoffman's strategy operates. The issue tackled is a fundamental puzzle in depth perception: "The image at the eye has two dimensions; therefore it has countless interpretations in three dimensions." Hoffman then solves (most of) the problem of how the visual system comes to the correct interpretation (most of the time) by conjecturing an ordered sequence of visual rules. These range from the simple "Always interpret a straight line in an image as a straight line in 3D" to the considerably less obvious "Interpret each concave point on a bound as a saddle point on a rim".

Hoffman leads the reader through the justification for these maxims by showing with line drawings and other two-dimensional patterns exactly how each rule serves to constrain the percept that we actually derive from the image. In other chapters, Hoffman deploys essentially the same strategy to show how the visual system recovers surfaces, shapes and their parts, colour, and the path of moving objects by "an intelligent process of active construction".

Hoffman's book has many virtues, of which sheer intellectual excitement is the foremost. *Visual Intelligence* has been aimed at the lay reader ("tourists", as Hoffman calls them) and is indeed sufficiently lucid to attract and hold such an audience without insulting their intelligence. Each of the many figures illustrates an argument. And, as so often happens in the theory of perception, Hoffman can show that artists often had an intuitive understanding of principles that the scientists later 'discovered'. From Brunelleschi to Picasso by way of Dürer, painters were using pictorial devices that are only now coming to be formally understood. Hoffman even manages to find palaeolithic cave drawings of bison that show the kinds of subjective contours studied to such great effect by Gaetano Kanizsa.

But this is no 'coffee table book', and I would be surprised if even the most experienced of visual scientists do not learn much from Hoffman's guidance. Even more rare in a book of 'popular science', Hoffman acknowledges the sources of ideas and findings that are not his own work, and gives a full and accurate list of references.

The scattered citations of earlier philosophical understanding (or misunderstanding) of vision include highly appropriate discussions of Berkeley, Locke and Malebranche, although to my considerable surprise Plato's cave has gone missing. If there is one image that sums up the thrust of Hoffman's work, surely it is that dungeon. The moral of *Visual Intelligence* is that we have spent so long in the cave that our brains can now derive what is really out there from the merest flickering of shadows on the wall. □

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