

visual field. They observe the same asymmetry in two, attentional demanding, detection and tracking (search) tasks. Given the absence of any profound difference in visual resolution between the upper and the lower visual field, the authors conclude that attentional resources are more finely deployed in the lower than in the upper field.

What is the likely site for this asymmetry? The lower visual field maps onto cortical areas above (superior to) the depth of the calcarine fissure in the back of the brain, while the upper visual field maps onto the expanse of cortex below (inferior to) this demarcation (see figure *a*). No gross anatomical asymmetries have been reported in either monkey or human upper and lower V1 or V2. So the new findings provide support for the idea, proposed by Crick and one of us (C. K.)³, that the neural correlate of awareness is not expressed in V1 neurons but must lie beyond. Whether or not this has anything to do with the fact that V1 has no direct projection to the frontal lobe, as originally surmised, remains completely open.

The first stage where substantial asymmetries in the upper and lower visual fields have been reported is in the third visual area. In the macaque, the areas anterior to the dorsal and ventral parts of V2 are so different from each other that they have been treated as distinct^{4,5} and termed V3 proper (the dorsal or superior part) and VP (ventral posterior area; see figure *b*). In particular, V3 receives a direct input from V1, whereas VP does not. These areas also differ functionally: the incidence of direction-selective cells in V3 is higher than it is in VP. For colour, the reverse is true. If there are similar differences in the equivalent areas in humans — as suggested by data from functional magnetic-resonance imaging⁶ — they would provide a convenient marker for evaluating the extent to which neurons in the V3/VP complex mediate the observed attentional asymmetries (see figure *b*).

The experiments of He and his colleagues also bear on the issue of the 'grain of visual awareness', that is, the visual resolution that is accessible to attention. The reader should try, for instance, to count heads in a crowd scene while fixating the centre of the image. Even accounting for the roughly inverse decline of visual acuity with retinal eccentricity, we have great difficulty with this task, possibly because neurons at higher stages that code for the

different elements of the image inhibit one another, leading to reduced firing rates and reduced performance.

A wonderful feature of science is that if there is a clearly defined problem then somebody will usually invent a method to address it. Thus, in the past two years, we have seen the introduction of several psychophysical methods that bypass visual awareness, yet still cause behavioural effects. Two recent examples are very fine gratings that cannot be perceived yet can still cause an orientation-dependent after-effect⁷, and induced blindsight in which subjects can 'guess' the location of a figure that remains hidden from awareness⁸ (although blindsight using dichoptic displays, so that each eye can be stimulated

separately, has proven to be very sensitive to the exact evaluation procedure; M. J. Morgan, J. A. Solomon and A. J. S. Mason, personal communication). Now we have the procedure described by He *et al.* It is possible that these techniques, combined with functional imaging⁹, will enable us to pin down the elusive neural correlate of consciousness. □

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OCEANOGRAPHY

Microbial ferrous wheel

David L. Kirchman

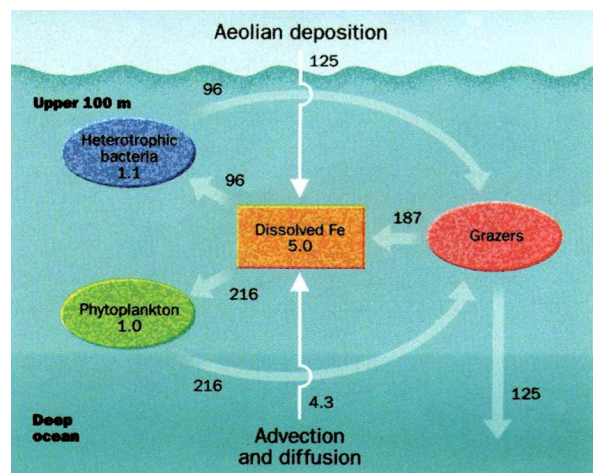
It has been nearly ten years since John Martin and colleagues suggested that iron limits primary production in some oceanic regimes, a hypothesis that turned oceanography upside down at the time. Since then we have come to know much about how iron regulates phytoplankton growth rates and how it interacts with other processes, especially grazing, to control the 'biological pump' — that is, the export of materials (most importantly carbon) to the deep ocean.

Although much has been learned, a report by Tortell *et al.*, which appears on page 330 of this issue¹, illustrates how far we have to go. In experiments carried out in the subarctic Pacific, Tortell *et al.* found large amounts of iron in heterotrophic bacteria and high uptake rates, spokes of a 'microbial ferrous wheel' (as coined by Farooq Azam, although 'ferric wheel' would, chemically, be more correct). It was in the subarctic Pacific that Martin and Fitzwater² first demonstrated iron limitation, which explained in part why phytoplankton growth is not more luxuriant here despite abundant plant nutrients.

Oceanographers did not have to trouble with heterotrophic bacteria in thinking about iron limitation, but cyanobacteria have been very much part of the iron story. These photosynthetic microbes, which are functionally akin to eukaryotic phytoplankton, can contribute much to primary production in the open ocean. Heterotrophic bacteria, in contrast, live on dis-

solved organic matter released by many processes and are the first component of the microbial loop which can mineralize a large fraction of primary production. Oceanographers knew about the microbial loop, but not the microbial ferrous wheel.

Of course, it is not news that heterotrophic bacteria contain iron. These microbes have a few of the same iron-



An iron budget for the subarctic Pacific. Rates are in $\text{nmol Fe m}^{-2} \text{ d}^{-1}$ and standing stocks in $\mu\text{mol Fe m}^{-2}$, all taken from the paper by Tortell *et al.*¹. Grazing rates were assumed to balance iron uptake rates. Regeneration and export rates of iron were assumed to follow analogous rates of the nitrogen cycle (the *f* ratio) for this region³. Brand¹⁰ summarized rates of aeolian deposition and inputs from the deep ocean.

bearing components found in phytoplankton, most notably nitrate reductase, the enzyme required for nitrate use. The largest ferric lode in heterotrophic bacteria, however, is in the electron transport chain of oxidative phosphorylation, which a bacterium uses to obtain energy during oxidation of organic carbon to CO_2 . Identifying why a microbe needs iron is easy; the hard part is to estimate quantitatively

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the amount of cellular iron, or as oceanographers like to express it, the Fe:C ratio. This ratio is critical in understanding how iron affects carbon cycling, the biological pump and the role of oceanic biota in global climate.

The Fe:C ratios found by Tortell *et al.* will be a surprise to many. In iron-deficient cultures and in the subarctic Pacific, Fe:C ratios in heterotrophic bacteria are twice those in eukaryotic phytoplankton, a difference that is not predictable even after reviewing the biochemistry of aerobic heterotrophy and photosynthesis. Cell size probably has something to do with the difference, as does the energetic cost of heterotrophic bacteria living in organic-poor waters such as the open oceans (more on this later). Further work on Fe:C ratios in cyanobacteria and in heterotrophic eukaryotic protozoa may help sort out whether being a prokaryote or a heterotroph is more decisive in determining the high iron content of heterotrophic bacteria.

Although it is unclear why Fe:C ratios in bacteria and phytoplankton differ, the data clearly indicate that in the subarctic Pacific the heterotrophic bacterial assemblage contains more iron than either eukaryotic phytoplankton or cyanobacterial communities. That observation may not surprise microbial ecologists familiar with work showing that the standing stocks of bacteria and phytoplankton are roughly equal in the open oceans³. In spite of their known ecological importance, however, bacteria have been completely ignored in discussions of how iron controls phytoplankton growth; the main battle has been over the role of grazing by zooplankton.

Tortell *et al.* now decisively add bacteria to the fray. What may be more important than the amount of iron is the rate at which heterotrophic bacteria take it up. These rates are much more difficult to come by, but fortunately several different methods turn up roughly the same answer. The take-home message is that heterotrophic bacteria account for 20–45 per cent of total iron uptake in the subarctic Pacific, suggesting that bacteria are competing with phytoplankton for this potentially limiting micronutrient.

As well as having a higher surface-area-to-volume ratio, bacteria can excrete ligands (siderophores) in order to complex and ultimately assimilate dissolved iron, an uptake mechanism unknown to eukaryotic phytoplankton. It may be more than coincidental that the binding constants of these bacterial siderophores are similar to those of dissolved iron complexes in seawater⁴.

Completing the microbial ferrous wheel is iron regeneration, the input of iron back to the dissolved pool by grazing and viral lysis. Like the nitrogen cycle, iron regeneration supports much primary production in many parts of the world's oceans⁵ (see figure). Unlike nitrogen and other plant nutrients, the form of released

iron may differ greatly depending on the prey (bacteria or phytoplankton) and the mode of regeneration (viral lysis or grazing by protists and multicellular organisms). The end result is that this microbial ferrous wheel — the uptake, storage and ultimate release of iron from heterotrophic bacteria — may greatly affect iron availability and thus primary production in waters such as the subarctic Pacific.

Might heterotrophic bacteria be limited by iron like some phytoplankton? A recent report⁶ says so, but most microbial ecologists think that bacterial growth rates are limited by organic carbon in open oceans. Tortell *et al.* suggest a more subtle limitation, involving both carbon and iron deficiency. They observed that the growth efficiency of several bacterial strains was lower under iron limitation, probably because of deleterious effects on the iron-rich electron-transport system. If so, to maintain growth rates bacteria would require more organic material as iron concentrations decrease. As a result, bacterioplankton could exhibit both carbon and iron deficiencies. The potential effect of iron on the bacterial growth efficiency is quite important; this efficiency indicates whether carbon flows through bacteria either to CO₂ or to higher trophic levels via bacteriovores.

A model that incorporates both grazing and iron limitation for understanding what controls primary production is really not much more complicated than the iron-ruled ocean first proposed by Martin and colleagues. A microbial ferrous wheel, however, complicates our simple models, and we will need further work before we see how everything meshes together. An important opportunity may be part of the Southern Ocean programme of the US Joint Global Ocean Flux Study, which went to sea a few weeks ago. The story of iron limitation began in the subarctic Pacific and an epiphany was realized with work in the equatorial Pacific⁷, but its climax may be in the Southern Ocean. All three areas have relatively low phytoplankton growth in spite of high concentrations of major plant nutrients. But it is the vast Southern Ocean that matters most for the biological pump and its role in global climate⁸. □

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Astromagnetics

How did the first stars form? The accepted theory is that a large volume of very dilute hydrogen gas slowly collapsed into stars by gravitational contraction. But such masses would warm up as they grew denser, generating pressure which would oppose the contraction. Only by radiating their heat away could the proto-stars contract further. Yet hydrogen is almost perfectly transparent, and therefore hardly radiates at all. Daedalus has been musing on the problem.

The early Universe, he says, had a magnetic field. One theory even claims that the fields of the stars are 'fossil' remnants of it, trapped and concentrated in the stars as they condensed. Now, materials with unpaired electrons are paramagnetic, and are attracted into a magnetic field. Interstellar hydrogen is an extreme case: it consists of single atoms with one electron each, so *all* its electrons are unpaired. Daedalus calculates that a field of 80 T could by itself pump cold monatomic hydrogen at one atom per cubic metre right up to the billions of atmospheres of a stellar interior. So in forming the first stars, he says, magnetism came to the aid of gravity.

Magnetic fields have tricks unknown to mere gravitational ones. They are always multipolar, for a start, and can be dragged around by moving magnetic material. The Sun heats its corona much hotter than its surface by exporting energy as hydromagnetic waves. Daedalus reckons the early stars did the same thing. The turbulence and spin of their contraction allowed them to radiate energy, not thermally, but magnetically.

These deductions have practical uses. One planned satellite will carry a huge neodymium–boron magnet, to look for anti-matter cosmic rays by their opposite deflection in its field. Daedalus expects it to concentrate interplanetary monatomic hydrogen as well. It could then form the basis of a deep-space rocket motor which would attract this gas as fuel. It would catalyse its conversion to dihydrogen — the most energetic chemical reaction known. The resulting hot exhaust would develop both thermal and magnetic thrust. Dihydrogen is diamagnetic, and would be repelled away from the motor.

Daedalus has even been dreaming of a satellite so intensely magnetized that it could hold an atmosphere of molecular oxygen, also a paramagnetic gas. It would thus form a tiny planet for astronauts to walk on, needing no space-suits but wearing iron-soled boots for adhesion. The oxygen atmosphere would even give them a faintly blue sky. Sadly, the field required exceeds the capacity of modern magnets.

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