slower way for a colony to protect itself; many weeks may elapse between the larval stage, when body size is determined, and the emergence of an adult. The production of new, large workers is costly as well as slow. Such costs include the energy differential needed to produce a large worker, and the losses the colony might suffer from enemy attack while it waits for more soldiers to develop. Benefits depend on how much better majors are than minors at defending the colony, and whether the presence of ants from another colony provides a reliable signal, with sufficient warning time, of future aggression.

Pheidole is a large and widespread genus, showing a remarkable diversity of behaviour. In many species, members of the major caste mill seeds or act as storage vessels for food, and do not carry out defensive duties[8]. Thus *P. pallidula* seems to be an unusual member of this evolutionarily labile genus. Rather than confirming that adaptive caste distributions are the rule, the new observations raise intriguing questions about this exceptional species. Is its ecology unusual among the *Pheidole*? Does a *P. pallidula* colony take many weeks to carry out an attack on another? Are the majors of this species more ferocious than those of other *Pheidole* species? Are the minors more timid? Passera and colleagues' result offers a new opportunity to investigate the evolutionary ecology of inducible defences. ☐

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NEUROBIOLOGY

The information superflyway

Rodney J. Douglas and Kevan A. C. Martin

It is a truth universally acknowledged that, to survive, living organisms are in need of accurate information about their world. This information is collected by a dazzling array of specialized receptors that transduce the stimulus energy, whether it be light, pressure, tension, heat, chemical or gravity, or whatever, into the internal signals of the nervous system.

Two papers published elsewhere in this issue[1,2] examine related aspects of this early processing in the visual system of blowflies. The neurons under scrutiny were the photoreceptors and the large monopolar cells (LMCs) in the compound eye, and two of the three classes of motion-sensitive neurons of the lobular plate, a further stage in the visual pathway. All are non-spiking neurons, so-called because they do not communicate with other neurons by nerve impulses, but instead transmit their messages across synapses as analogue signals coded in the form of graded voltages.

De Ruyter van Steveninck and Laughlin (page 642)[1] recorded the electrical activity of the photoreceptors in response to fluctuations in light intensity, and used Shannon's information theory to estimate that the rate of information capture was 1,000 bits s^{-1}. The LMCs are second-order neurons that receive convergent and thus redundant information from six photoreceptors. They achieve a capacity of 1,650 bits s^{-1}. These numbers are striking because they are much larger than the maximum rate of about 300 bits s^{-1} previously estimated for the third class of neurons in the lobular plate, which do communicate by nerve impulses[3].

One of the important ways in which the fly has to use this rich flood of information is to determine its motion relative to the world. In studying the neurons that are involved in this computation of motion, Haag and Borst (page 639)[2] discovered that transmission of visual signals along the dendrites of one subclass of motion-sensitive neurons in the lobular plate of the blowfly is enhanced by a fast sodium current that acts selectively to amplify incoming signals of high frequencies. Their experiments provide direct evidence for the importance of active mechanisms for the analogue processing of information that is carried out within all neurons.

These two papers, coming from different conceptual frameworks, illuminate a central question about the nature of the encoding of the world by a nervous system. What is the organism's strategy for balancing the need for extensive knowledge with the need for specific and immediate action? The tools of information theory used by de Ruyter van Steveninck and Laughlin were developed by Shannon and Weaver[4] for a very specific purpose, which was to calculate information transmission across a channel in a relatively well defined and simple physical system, such as a telephone network. In the case of the nervous system, the elements and processes, and their interactions, are often poorly understood. Consequently, information theoretic analyses of neural processing are confronted with substantial experimental difficulties, and must make bold, even extreme, simplifying assumptions. Among the most successful projects have been those that have addressed quite simple questions about the amount of information coded by spiking neurons.

From the time that Adrian[5] made the fundamental observation that the intensity of a stimulus is coded in the frequency of identical nerve impulses, it has been appreciated that the only data about the world to which the central nervous system has access are the absolute time of occurrence, or the time of occurrence of one impulse relative to other impulses. The critical question that information theorists have posed is this: what is the maximum amount of information that such a train of impulses could convey about the stimulus that it reflects? Notice that the question is posed in terms of the 'ideal observer', a platonic being who has the means to extract all the available information in the impulse train.

Bialek *et al.*[3] used optimization methods to construct the best 'ideal observer' for spiking neurons in the lobular plate of the blowfly and estimated that they could transmit information at a rate of about 300 bits s^{-1}. De Ruyter van Steveninck and Laughlin[1] have now used a related mathematical method to show that the rate of information transmission from photoreceptors to the next non-spiking neurons in the circuit is five times higher. Assuming that the 10^7 photoreceptors of the primate retina have equivalent performance, then the retinal receptors would seem to encode about a gigabyte per second — a data rate that would fill the hard disk of the latest personal computer in a second. Even for the few thousand photoreceptors of the compound eye of the fly, the potential information load is close to 0.5 megabytes per second.

This performance by non-spiking neurons is, of course, striking. But the reasons why the frequency-coding method used by spiking neurons is relatively slow and imprecise were pointed out by von Neumann almost 40 years ago[6]: non-spiking neurons can convey information in analogue form up to the frequency limits of their voltage fluctuations, whereas spiking neurons have to code the information by varying the interval between successive impulses, the interval being typically tens of milliseconds. Apparently, spiking neurons use about the least optimal means of coding.

However, the brain's higher visual centres are not television screens that receive a high-fidelity transmission of the visual image, which then has to be viewed and interpreted by some observer. Instead, as Barlow has emphasized[7], information from the photoreceptors appears to be processed in subsequent stages so as to use the fewest possible number of active neurons to achieve as complete a representation of the stimulus as is required for an appropriate behaviour. Such selective representations have the advantage of reducing considerably the volume of information that has to be propagated by a single neuron in a given time. Haag and Borst's experimental *tour de force* shows that some neurons use special mechanisms to transmit some of the information selected for the representation of motion.

The mechanism of active dendritic amplification by sodium currents, discovered by Haag and Borst, provides a means for boosting transmission of the high-frequency components of the incoming motion signal. But the amplification is not simply linear. Because activation of the sodium currents is voltage dependent, the degree of amplification depends on the average dendritic depolarization. So the amplifier could possibly be switched on or off by the character of the input signal, or some control neuron. Moreover, the dynamics of the active process places limits on the fidelity of the signal transmission. Their results show that although the neuron can transmit the frequency of a sinusoidally modulated visual stimulus, the nonlinear amplification introduces significant distortions in the high-fidelity signal that is transmitted from the photoreceptors. These motion-sensitive neurons are not ideal observers.

Clearly, experimental work based on information theoretic analyses is a fertile area that could at least characterize the information loads faced by the nervous system and the transmission rates of this information along the processing paths. Such analyses may also lead to insights about how information is transformed into structural and functional properties of the neuronal circuits that represent an organism's knowledge of the world. As these two papers show, however, this is not an area for the faint-hearted. ☐

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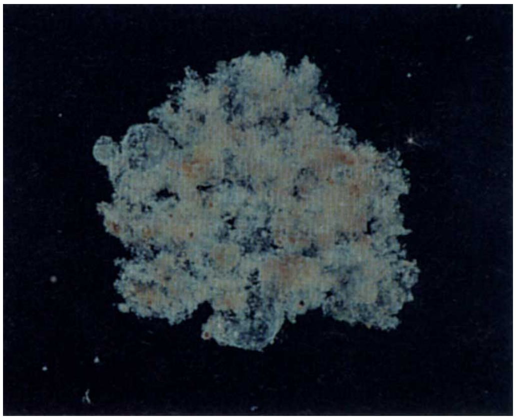
BIOLOGICAL OCEANOGRAPHY

Iron grip on export production

Alan Longhurst

SINGLE-CELLED microscopic plants living near the ocean surface take up carbon, and some of this carbon sinks out of surface waters and into the abyss below. This process, called 'export production', is an important link in the global carbon cycle and perhaps in climate change, but in many cases we do not understand what controls its rate. Two *Nature* papers give us part of the answer: over some of the ocean, the controlling factor is iron.


R. S. Lampitt

'Marine snow' particle (an aggregation of dead phytoplankton, zooplankton and faecal matter) about 5 mm across, collected from the seabed at a depth of 1,400 m on the northeastern Atlantic continental slope. The brown regions of the particle are rich in plant pigment, indicating that it sank quickly to the seabed before much degradation took place — one way that carbon can be carried away from the surface.

During the early evolution of plants the geochemical balance of our planet was thrown out of equilibrium as carbon dioxide was progressively removed from the primitive atmosphere by photosynthesis. Most of the carbon is sequestered in biogenic marine carbonates, and to a smaller extent in coal and shales. From this observation stems an urgent need to understand how marine plants, dominated by the single-celled phytoplankton of the open ocean, affect atmospheric CO_2 during natural climate changes. We may then hope to predict their response to even higher CO_2 levels than those already generated by forest clearance, cement production and fossil-fuel burning. The results of Coale *et al.*[1] (reported on page 621 of this issue) and Kumar *et al.*[2] bring us closer to an understanding of the limitation on phytoplankton growth, and on sinking of carbon to the sediments, in those large regions of the ocean where the classical limiting macronutrient nitrate (NO_3) remains in excess.

Both papers support the growing body of evidence for a critical lack of available iron in some of these HNLC (high nutrient, low chlorophyll) ocean areas. The observations of Kumar *et al.*[2] convincingly support the late John Martin's suggestion[3] that during the Last Glacial Maximum there were higher fluxes of iron-rich aeolian (wind-borne) dust than there are now, and that they induced increased plant growth and sedimentation of organic carbon in the Southern Ocean, at present an HNLC area having very low fluxes of aeolian dust. Martin suggested that this process contributed to the reduction of atmospheric carbon dioxide concentrations during the period. Kumar *et al.* examined marine sediments for three proxies (the ratios of protactinium-231 and beryllium-10 to thorium-230, as well as the burial rate of uranium precipitates produced *in situ*) of productivity and export production, and demonstrated that these ideas are substantially correct, though with some change of emphasis.

Increased export production was restricted to the subantarctic zone, and was associated with evidence for strongly enhanced transport of aeolian dust from Patagonia. Uranium burial rates indicate organic carbon export comparable to that observed in present-day coastal upwelling centres. They show that increased iron concentrations lead to increased export, and that the ceiling on this export — known from other modelling studies that assume there is enough iron to encourage production and all the nitrate is used up — is about 15 to 30 p.p.m. (parts per million) CO_2 drawdown, to be compared with around 80 p.p.m. drawdown observed for the glacial atmosphere.

Coale and colleagues address limitation by iron in a very different environment, today's equatorial Pacific Ocean near 140° W, where aeolian deposition at the sea surface is also low[4]. Earlier reports from their field studies[5] described how upwelling at the Equator maintains locally high levels of nitrate. Coale *et al.* now propose that iron from shallow hydrothermal sites in the western Pacific is entrained in the ribbon-like undercurrent which lies below the Equator, 200 m deep, 200 km wide and approaching 10,000 km long, and that upward mixing of iron and nitrate from the high-velocity core at 200 m supports a plankton bloom near the surface. However, the rates of supply of iron and nitrate are so unbalanced that only 20 per cent of the nitrate can be used by plants. This is consistent with the earlier report[5] that the iron–nitrate imbalance at the Equator causes suboptimal photosynthetic performance characteristic of