and offers a new method for testing the cerebellar learning hypothesis. However, available data from both behavioral and neuroimaging experiments suggest alternative explanations for the pattern of cerebellar activation. First, the inclusion of the distractor task during the initial acquisition phase may alter the neural landscape for learning. Previous imaging of the SRT task showed that learning-related changes under conditions of attentional distraction were associated with motor and parietal cortex, the two areas associated with learning in the current study (*9*, *10*) (see the figure). However, previous work also indicated that a different learning network is engaged when acquisition occurs without such distraction. This suggests that the cerebellum may be recruited only during the encoding of movement sequences when the distractor task is absent.

Second, learning in the SRT task, at least under low levels of practice, is fairly abstract and not linked to particular muscles or movements. Finger movement sequences learned during practice are largely preserved following transfer to a task where responses are made with arm movements or through vocalization (*11*). The cerebellum may not be designed for the development of abstract representations; rather, its contribution to motor control may be intimately linked to the coordination of patterns of specific muscle activities (*12*). For example, the repeated pairing of a tone and airpuff leads to a conditioned response of the muscles protecting the eye. Should that airpuff be redirected at a finger (or paw), one would not expect to see transfer in the form of flexion or extension of the finger.

The contrast between the SRT and eyeblink conditioning tasks underscores the difficulty in succinctly characterizing the part played by the cerebellum in motor learning (see the figure). In this regard, it is instructive to examine the computational requirements of the two tasks. It is possible that the cerebellum is essential for eyeblink conditioning because the animal not only learns to associate two contiguous events, but also must extract the temporal relationship between the tone and airpuff (*13*). This precise timing is what makes the conditioned response adaptive, protecting the eye from the adverse stimulus, with the cerebellum forming these temporal representations. It is unlikely that precise timing is essential for learning in the SRT task. At least during the initial stages, learning involves the formation of associations between a series of spatial locations, each presented and responded to as a chain of discrete events. The repeated finding that activity of the parietal cortex correlates with SRT learning is consistent with the hypothesis that such learning is primarily spatial.

Seidler *et al.* provide an instructive challenge to theorists and empiricists who have championed the cerebellum as the key instigator of motor learning. Just as important, their work reveals the murky waters we face when attempting to understand brain function in terms of general task descriptions such as "motor learning." Complex skills are supported by multiple representations, each of which can be the target of learning. Moreover, it is difficult to define the boundary between "motor" activity and neural activity that lies beyond the motor system. The ability of a World Cup soccer player to score requires not only coordination of the muscles to generate a powerful kick, but also identification and anticipation of the locations of the defenders. As is typical of many debates in science, we will need to move away from binary questions such as "Does the cerebellum contribute to motor learning?" toward more complex questions such as "How does the cerebellum contribute to motor learning?"

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PERSPECTIVES: OCEANOGRAPHY

Small Critters—Big Effects

André Morel and David Antoine

The tiny unicellular algae inhabiting the upper well-lit ocean, collectively called phytoplankton, are the prime producers and the first link in the marine food chain. Their capacity for synthesizing organic matter (their net primary productivity, NPP) is therefore of great interest, particularly for the purpose of managing fisheries in a sustainable manner (*1*, *2*).

The NPP is also important in the context of the biogeochemical cycling of carbon and other elements. Through the photosynthetic activity of phytoplankton, inorganic carbon is fixed, organic matter is formed, and particulate matter is created, resulting in a vertical flux of sinking materials in the sea. As CO_2 concentrations increase in the atmosphere, the NPP of phytoplankton and the mechanisms of oceanic carbon storage are receiving increasing attention (*3*).

A number of ingredients are needed to calculate NPP. The two most important factors are the biomass in a given part of the ocean, and the rate at which this biomass takes up carbon. Paradoxically, the best way to obtain these data is from space, at a distance some 10^{12} times the size of the organisms involved.

Because photosynthesis results in simultaneous O_2 production and CO_2 uptake, the first estimates of oceanic primary production were based on local determinations of O_2 evolution or (after 1950) ^{14}C uptake, both of which can be measured during bottle incubations aboard ship. Such measurements give access to a rate (per unit of biomass); for estimates of NPP, they must be combined with the algal biomass distribution. Thanks to cruises carried out in various (but not all) parts of the ocean, the spatial distribution of phytoplankton, depicted by the chlorophyll concentration, has been progressively clarified. The extension of these unavoidably limited observations to the world ocean has, however, remained problematic. This is reflected in global estimates of NPP published from 1950 to 1980, which range from 20 to 126 Pg (1 Pg = 10^{15} g) of carbon fixed per year.

The situation changed dramatically in the 1980s, when ocean-color data obtained by the satellite-borne sensor CZCS (*4*) provided the first detailed chlorophyll concentration map of the entire ocean. Today, the spatial and temporal variability of algal biomass is documented on interannual scales with unprecedented accuracy with new sensors such as SeaWiFS, MODIS, and MERIS (*4*).

The phytoplankton biomass term can thus now be considered well constrained (*5*). But is the rate of carbon fixation (the incorporation of carbon into the biomass

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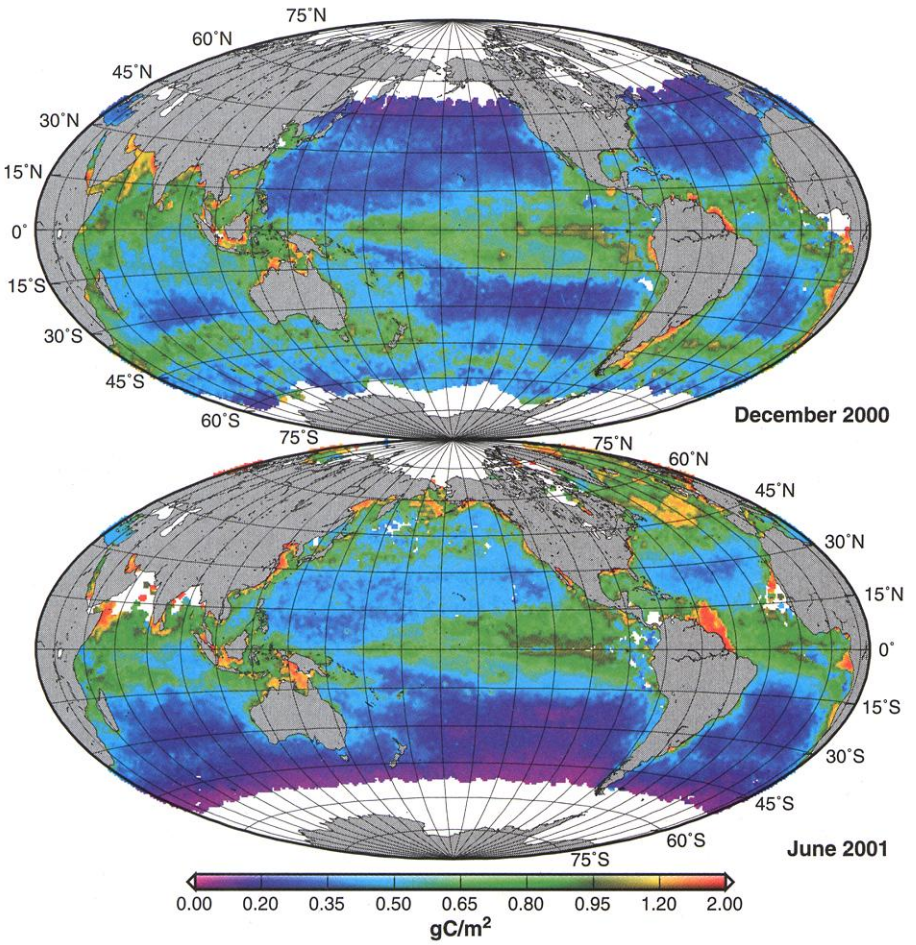

The end of spring in the sea. Average NPP, expressed on a per-day basis, computed [as in (*7*)] from SeaWiFS imagery for months that mark the end of spring in both hemispheres. Noteworthy features include the alternation of the vernal bloom (*24*), with high production in June in the North Atlantic and North Pacific, and in December along the belt corresponding to the subtropical convergence (40°S). The divergence along the equator induces an enhanced productivity, which was dramatically affected in the Pacific during the 1997–1998 El Niño/La Niña event, as recorded by SeaWiFS (*25*).

when organic molecules are built from dissolved CO_2) known and modeled with an equivalent accuracy?

Once the biomass is known, the assessment of the carbon-fixation rate and the calculation of NPP (for terrestrial as well as for aquatic vegetation) involves three main steps: determining the solar photosynthetic active radiation (PAR) available to the system; estimating the fraction of this radiation that is absorbed by the biomass; and applying a utilization efficiency that accounts for the quantum yield when radiant energy is used to build organic molecules from dissolved CO_2. Ideally, this calculation must be performed at each instant of the day, at each depth in the sea, and for each wavelength of the PAR. In other words, there exists an instantaneous, local, and spectral equation that expresses the net rate of production of biomass. This equation must be triply integrated (with respect to time, depth, and wavelength) to calculate the daily NPP in a given water column. Additional spatial and temporal integration then provides the NPP over a given domain and time period. Various simplifications of this analytical approach have been proposed (*6*), and precomputed lookup tables have been used to speed up the calculations (*7*).

On the basis of chlorophyll concentration maps from CZCS and SeaWiFS, recent computations according to the above scheme led to a global NPP of ~50 Pg of carbon per year (*8*, *9*). This figure is close to that of the terrestrial vegetation (*3*), despite the disproportionate sizes of their respective carbon pools (the terrestrial carbon pool is 500 times as large). A study still in progress (*9*), aimed at comparing the outputs of various models applied to the same global chlorophyll concentration fields derived from SeaWiFS data, has confirmed the above figure with a standard deviation of 25%, regardless of model complexity. It has also been shown that although the NPP fields are similar, notable divergences may occur in the amplitude of the gradients, especially in areas with extreme temperatures.

Given that the causes of variation in NPP are firstly the biomass and secondly the PAR availability, it is not surprising that geographical patterns and seasonal variations of productivity are similar in the various models. The simplifications used in some models and, perhaps more importantly, the various ways in which the photophysiological response of algae is parameterized, result in different outputs for the absolute NPP value and its zonal gradients.

Does the reasonable agreement between models mean that the answer is correct? Productivity measurements with in situ incubations are inevitably limited in space and time, and therefore, comparing a satellite global estimate with an equivalent field-derived value is an elusive goal. Astronomical and atmospheric parameters that determine the amount of incoming radiation are already modeled relatively accurately, as is the transfer of PAR through the water column, so model improvements can result mainly from a better parameterization of photophysiological processes (*10*–*11*). The in vitro determination of the photosynthesis versus irradiance response allows the derivation of needed parameters (*12*); they depend on physical, chemical, and ecological conditions and therefore may vary with the local conditions encountered in the various "biogeochemical provinces" (*13*). The complexity of the response of algal assemblages to environmental conditions (including circadian rhythms, adaptation to changing depth and irradiance, and ecological succession) is poorly represented in present models, because existing information is insufficient for reliable generalizations to be made.

Estimates of the fraction of NPP that can be exported to the interior of the ocean (and hence out of communication with the atmosphere over centennial time scales) are now obtained with ecosystem models embedded in general circulation models (GCMs) (*14*–*16*) or large-scale models accounting for observed nutrient fluxes (*17*). Although the chlorophyll distribution and total NPP produced by these simulations compare favorably with the satellite-derived information, this is not necessarily proof that the values are definitive. In effect, representations of algal physiology used in GCMs are similar to those used with color imagery to derive NPP. Assimilative models combining color information and satellite observations of sea surface height anomalies are promising (*18*), in particular to comprehensively resolve the mesoscale variability of the phytoplankton distribution, NPP, and the rate of carbon export.

Estimates of the magnitude of the global NPP may improve as better knowledge of algal physiology and ecology is incorporated into the computations. In contrast, the spatial and temporal evolution of the ocean productivity is already described with a tremendous wealth of detail. The synergistic use of modeling and data from various sensors (for ocean color, temperature, clouds, wind, surface height) is the recipe for future progress. An international strategy for the implementation of a global-scale, internally consistent, temporally uninterrupted set of such data is imperative (*19*).

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PERSPECTIVES: ORIGIN OF LIFE

Some Like It Hot, But Not the First Biomolecules

Jeffrey L. Bada and Antonio Lazcano

Ever since the pioneering work of Aleksandr Oparin and John Haldane nearly a century ago, the prebiotic soup theory has dominated thinking about how life emerged on Earth (*1*, *2*). According to the modern version of this theory, organic compounds accumulated in the primordial oceans and underwent polymerization, producing increasingly complex macromolecules that eventually evolved the ability to catalyze their own replication (see the figure). But is this really how life originated? And what were the conditions that favored its emergence?

Experimental support for the prebiotic soup theory was first provided in 1953 by Stanley Miller, who demonstrated that important biomolecules such as amino acids could be synthesized under simulated early-Earth conditions. The discovery of extraterrestrial amino acids in the Murchison meteorite in 1970 showed that reactions like those in Miller's experiment (involving ammonia, hydrogen cyanide, and aldehydes or ketones) occurred on meteorite parent bodies early in the history of the solar system.

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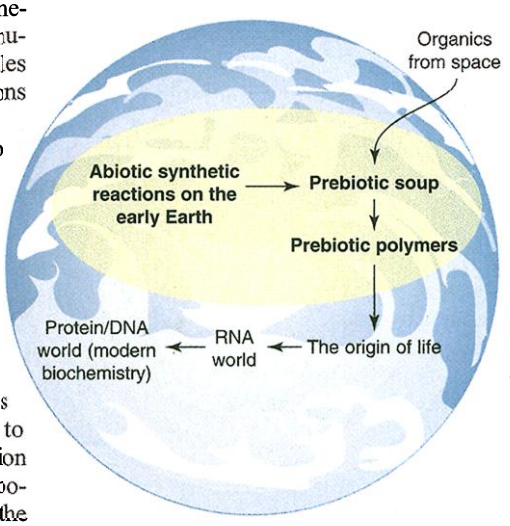
The inventory of organic compounds on the early Earth may thus have been derived from a number of sources: Earth-based syntheses, asteroid and comet impacts, and the accretion of meteorites and interplanetary dust particles. These abiotic, monomeric organic compounds would have accumulated in the early oceans, providing the raw material for subsequent reactions. Eventually these reactions would have led to life as we know it: membrane-enclosed systems of polymers such as nucleic acids and proteins, the core molecules involved in the central biological functions of replication and catalysis.

For monomers in the early oceans to undergo polymerization, a thermodynamically unfavorable process, concentration of the soup constituents, would have been required. Experimental evidence suggests that clays, metal cations, and imidazole derivatives, among others, may have catalyzed prebiotic reactions, including polymerization. Selective absorption of molecules onto mineral surfaces has been shown to promote concentration and polymerization of various activated monomers in the laboratory (*3*). Because absorption involves the formation of weak noncovalent bonds, mineral-based concentration would have been most efficient at low temperatures (*4*). Other processes such as evaporation of tidal lagoons and eutectic freezing of dilute aqueous solutions may also have assisted concentration. The latter process is particularly effective in the nonenzymatic synthesis of oligonucleotides (*5*).

As polymerized molecules became larger and more complex, some of them began to fold into configurations that could bind and interact with other molecules, expanding the list of primitive catalysts that could promote nonenzymatic reactions. Some of these catalytic reactions, especially those involving hydrogen-bond formation, may have assisted in making polymerization more efficient. As the variety of polymeric combinations increased, some polymers may have developed the ability to catalyze their own imperfect self-replication and that of their molecular



How did life emerge? Various steps thought to be involved in the origin of life on Earth. The shaded area represents the contribution from the metabolist theory to the overall scheme.

SOURCE: JEFFREY L. BADA, ILLUSTRATION: PRESTON MORRIGHAN/SCIENCE