region 1.5 mm in diameter (250- to 300-μm spacing between adjacent electrodes). Each probe could be independently adjusted with a precision of approximately 10 μm. The array weighed about 10 g and did not significantly restrict the free movement of the animal. Neural signals were buffered with two miniature, 25-channel integrated preamplifiers, then passed to a set of six, custom-built, eight-channel filter-amplifier modules. Action potentials were digitized at 33 kHz per channel and stored by seven synchronized 33-MHz 80486-based computers running customized data acquisition software. Rat head position and orientation were tracked at 20 Hz. Surgery was according to NIH guidelines. The animals were male Fischer 344 (F344) rats, 9 months of age.

13. For rats 1 and 2, the environment was a rectangular box 124 cm long by 62 cm wide by 62 cm high. The walls of the apparatus were covered with a variety of distinct visual and tactile cues. The apparatus was located within a curtained-off partition of the room containing the electrophysiological recording equipment. A slightly smaller apparatus was used for rat 3.
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TECHNICAL COMMENTS

Photochemistry in the Primitive Solar Nebula

In his recent article (*1*), J. Kasting refers to a paper by Prinn and Fegley [reference 21 in (*1*)] that discusses the blocking of solar ultraviolet (UV) light by dust in the primitive solar nebula and the effect this might have had on hydrodynamic escape. Although the reasoning used by Prinn and Fegley (*2*) is valid for most of the UV spectrum, it is not valid for the brightest UV feature—the HI 1216 Å line, which is known as the Lyman α line (Lyα).

In their currently accepted theory for the chemical evolution of the primitive solar nebula, Prinn and Fegley argue that photochemistry is unimportant and that thermochemistry controls the relative abundances of molecular species throughout the planet-forming region (*2*). They provide useful estimates of the chemical energy available to the solar nebula from several sources and establish that even the small photolysis rate resulting from starlight is more important than the photolysis rate from direct sunlight. For Lyα, however, this calculation does not include the contribution from backscattering of solar Lyα by hydrogen atoms in the interplanetary medium (IPM). The current brightness of the IPM in the vicinity of the Earth is about 400 Rayleighs (*3*) or, equivalently, about 4×10^8 photon cm^{-2} s^{-1} over the entire sky. For comparison, the direct Lyα flux from the sun is currently about 3 to 5×10^{11} photon cm^{-2} s^{-1} at the Earth (*4*). Although the direct flux is a more important source in the inner solar system, the IPM source falls off much more slowly (*3*) than the direct flux, so that the two sources are of comparable strength at the orbit of Neptune (*5*).

In the primitive solar nebula, the disk opacities were large enough that no direct solar Lyα could penetrate more than a few tenths of an astronomical unit from the protosun (*2*), even though the protosun, if comparable to a T-Tauri star, would be emitting up to 10^4 more Lyα photons than the current sun (*6*). However, because Lyα emissions are observed coming from T-Tauri stars, it seems plausible that the nondisk regions of the primitive solar nebula may have been relatively free of opacity. If so, then both sides of the nebular disk could have been bathed by a flux of up to 10^4 times more Lyα than is present in the IPM today. Furthermore, because the density of atomic hydrogen in the primitive IPM was probably much higher than it is today [the backscattering reflectivity of the IPM is currently only about a tenth of a percent or less (*7*)], there may have been an additional amplification factor in the early days of the solar system. At 10^4 times its current brightness, the IPM flux of Lyα available to the upper atmosphere of the Earth would have been about 10 times the current solar HI 1216 Å irradiation. So perhaps it is not necessary to assume that the solar nebula must have been dissipated before blowoff and isotopic fractionation could have occurred in the atmospheres of the terrestrial planets (*8*). The effects of IPM-backscattered Lyα are also pronounced for the outer regions of the primitive solar nebula. The photodissociation rates of, say, CH_4 or NH_3 near Neptune's orbit would have been comparable to the photodissociation rates these molecules experience today in the vicinity of the Earth. This scenario would favor the formation of strongly bonded molecules such as CO and N_2 over the more easily photolyzed CH_4 and NH_3 in all regions of solar system. Contrary to the statements of Prinn and Fegley (*2*), it seems that solar photochemistry *was* important in the early solar nebula and that the IPM-backscattered source of Lyα should be represented in future chemical models of solar system formation.

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Kasting reiterates (*1*) a traditional view that the global Archean atmosphere and ocean [Stage I, before about 2.4 billion years ago (Ga)] was a reducing environment without free O_2. Relevant data (*2*) and geochemical and biochemical arguments (*3*) that support alternative views are not mentioned by Kasting, who addresses two items. (i) Some O_2 should have been available to generate a minimum ozone screen for early life against a stronger-than-modern UV flux (*4*) at that time. (ii) Some O_2 should have been available in amounts sufficient to support global aerobic respiration in order that organic C be recycled at a time when the C isotopic evidence seems to require a more-or-less constant burial rate for organic C (*5–7*). To minimize the first difficulty, he follows a suggestion of Lovelock (*7*) that a photochemical hydrocarbon smog generated in an anoxic atmosphere containing about 100 ppm methane could have absorbed UV radiation as efficiently as ozone. To minimize the second problem, Kasting makes the unrealistic suggestion that global marine primary productivity may have been smaller than the already miniscule value that I have suggested for the early Archean (*8*).

In dismissing these two potential difficulties for the anoxic Archean models, Kasting produces inconsistencies. A low marine productivity cannot support a methane-rich atmosphere, and the photosynthetic productivity that would be adequate to support such an atmosphere would generate more O_2 than could be consumed by the available reductants in the absence of aerobic processes that use O_2 (*8*). The following calculations illustrate this dilemma.

Kasting, Zahnle, and Walker (*9*) and Zahnle (*10*) have calculated that in order to sustain atmospheric levels of methane under anoxic conditions (100 ppm), a surface flux of CH_4 of about 4×10^{11} molecule cm^{-2} sec^{-1} would have been necessary. This flux is the equivalent of an annual global source equal to 1.1×10^{14} mol of CH_4 or 1.3×10^{15} g of C. Because 2 mol of organic C must be completely recycled to generate 1 mol of methane, 2.6×10^{15} g of organic C should have been recycled by methanogens each year to generate and maintain a UV-absorbing, methane-smog atmosphere (*11*). When this value is then added to the accepted (*5, 6*) burial rate of C of 10^{13} mol or 1.2×10^{14} g $year^{-1}$ (a rate that is needed to account for C that escaped all modes of recycling), a minimum global primary productivity of C of 2.7×10^{15} g $year^{-1}$ is obtained. Dividing by the area of the world oceans, a mean productivity of C of 6 to 8 g m^{-2} $year^{-1}$ results. This is smaller by a factor of 50 than the productivity suggested by Kasting recently for the Archean in "stagnant" upwelling zones (*12*), smaller by a factor of 3 than the production he had earlier calculated (*9*) for the world oceans, yet is larger by an order of magnitude than the tiny value he now suggests should be even lower (*1*).

Nevertheless, if one accepts the methane-smog idea to minimize the UV problem, an additional and larger inconsistency for the anoxic model arises: the minimum 2.7×10^{15} g of C per year primary productivity would have produced a net 2.3×10^{14} mol of O_2 per year that must also be accounted for. The modern process of aerobic C recycling is incompatible with global anoxia and therefore cannot act as a sink for this O_2 as it does today. Accordingly, it is usually posited that Archean O_2 has been taken up by "virtually limitless" Fe^{2+} (6×10^{-5} to 8×10^{-5} M) from the deep oceans (*6, 7, 13, 14*). However, as 4 mol of Fe^{2+} are needed to sequester 1 mol of O_2 (*14*), this rate of O_2 production would have required an *annual* sink equivalent to 5.2×10^{16} g of total Fe. The average sedimentary rock contains about 5% total Fe (*14*). It follows that for the Stage I atmosphere proposed by Kasting to have been viable, and in order to accommodate this huge amount of Fe, the mean global sedimentation rate would have to have been about 10^{18} g $year^{-1}$—an increase of two orders of magnitude over most estimates (*14, 15*). As a result, an average Archean sedimentary rock should contain less than 0.01% organic C. Furthermore, at this rate of Fe utilization, the deep oceans should have been depleted of their Fe stores in less than their 1000-year turnover time, leading to an O_2 "runaway."

All of this is implausible. There are many difficulties associated with any model of Earth's early atmosphere, but the body of data (*2*) not mentioned by Kasting suggests that, if Kasting's proposed Stage I atmosphere ever existed on Earth, it was short-lived, having been eliminated most likely by Isua time (3.8 Ga) and almost certainly by 3.5 Ga. A two-stage model is a plausible alternative solution that is more compatible with current observations.

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Response: Gladstone suggests that scattering of solar Lyα by the IPM might have provided the energy needed to drive hydrodynamic escape from Earth's early atmosphere. This suggestion is welcome. I pointed out in my article that the high $^{22}Ne/^{20}Ne$ ratio in the atmosphere as compared with that of the mantle or the solar wind is best explained by preferential depletion of the lighter isotope during rapid hydrodynamic escape of hydrogen. (Indeed, it is not clear how else this situation could have come about.) The hydrogen escape flux needed to drag off ^{20}Ne is $\sim 2 \times 10^{13}$ H_2 molecule cm^{-2} s^{-1} (*1*). By comparison, the maximum (or energy-limited) escape flux that could be driven today by solar extreme ultraviolet (EUV) energy is $\sim 6 \times 10^{11}$ H_2 molecule cm^{-2} s^{-1} (*2*). Thus, the EUV flux incident on the upper atmosphere must have been approximately 30 times greater than it is today in order for ^{20}Ne to have been lost. Gladstone's estimate of a tenfold increase in solar Lyα resulting from scattering off the IPM is not quite high enough to have driven hydrodynamic escape, but it is close. This scenario appears to circumvent the problem of dust opacity in the ecliptic plane during the latter stages of planetary accretion.

Towe's argument that the Archean atmosphere must have contained free O_2 is based on three premises: (i) a UV screen was required to protect Archean life against solar UV radiation; (ii) a hydrocarbon screen produced by methane photolysis would probably not have been maintained under anoxic conditions; and (iii) the global O_2 budget in an anoxic, Stage I atmosphere would not have been balanced.

First, whether or not a UV screen was needed during the Archean is a topic that has been widely debated in the literature. I tend to agree with Towe that a UV screen would have been useful (*3*) but others who have examined this problem have reached different conclusions (*4, 5*). Rambler and Margulis (*5*) point out, for example, that modern prokaryotes are much more UV-tolerant than are eukaryotes; furthermore, the tendency of many single-celled organisms to form mats may have provided additional protection against solar UV. Benthic organisms that lived at depths of several meters or more could have been shielded by dissolved substances (for example, organic compounds or minute amounts of Fe^{3+}) in seawater. It is not clear whether an atmospheric UV screen was required during the Archean.

If a UV screen was necessary, could such a screen have been provided by hydrocarbon particles formed from methane photolysis? This calculation has not yet been done, so one cannot give a definitive answer. However, the chance that such a screen existed is better than Towe's numbers would suggest. We see no reason to assume, as Towe does, that 100 parts per million of atmospheric methane are required. Towe references Lovelock (*6*), but he does not seem to have attempted this calculation. Thus, the figure of 1.1×10^{14} mol of CH_4 per year required to maintain the screen is suspect from the outset. This figure was also calculated from computer models (my own or variants thereof) that did not include particle production. Including the particles would reduce the rate of methane photolysis by shielding the lower atmosphere from UV. So, the actual methane flux required might well have been an order of magnitude lower than the value quoted, putting it on a par with Towe's own estimate (*7*) for methane production in an anoxic system. (For comparison, the present methane flux is on the order of 3×10^{13} mol year^{-1}, if one assumes a 10-year atmospheric lifetime.)

Finally, Towe's figures on O_2 recycling and demands on Fe^{2+} in an anoxic Archean system are misleading; most of these ideas were published in 1990 (*7*) and were subsequently criticized by me (*8*). The rock record provides, at best, an estimate for the organic C burial rate; it does not give us primary marine productivity. But one does not need to know primary productivity in order to determine whether the Archean atmosphere was anoxic. Whether or not free O_2 was present depends on the relative rates at which photosynthetic O_2 and reduced gases were vented into the atmosphere. (Reactions between O_2 and reduced gases are fast, so that one or the other could have been present in abundance, but not both.) Photosynthesis generates O_2 and organic C at the same rate.

In an anoxic system, the organic C that is not buried is likely to decay either by fermentation followed by methanogenesis (schematically, $2CH_2O \rightarrow CO_2 + CH_4$) or by bacterial sulfate reduction ($2CH_2O + SO_4^{2-} \rightarrow 2CO_2 + S^{2-} + 2H_2O$). The CH_4 produced by methanogens would have reentered the atmosphere, where it would have been oxidized to CO_2 by OH radicals produced by water vapor photolysis. This results in an effective H_2 source, as the overall reaction is $2H_2O + CH_4 \rightarrow CO_2 + 4H_2$. Because oxidative weathering of the land surface would, by presumption, have been negligible, the sulfate used in bacterial sulfate reduction must have derived from oxidation of volcanic H_2S or SO_2 in an analogous manner (for example, $SO_2 + 2H_2O \rightarrow H_2SO_4 + H_2$). This process would also have left H_2 behind in the atmosphere. The H_2 generated by these and other possible anaerobic decay processes would have neutralized all of the O_2 produced by photosynthesis, except for that which corresponded to buried organic C.

Thus, to determine whether the Archean atmosphere was reducing or oxidizing, one needs only to compare the burial rate of organic C (the net O_2 source) with the volcanic flux of reduced gases and with the rate of reaction of O_2 with dissolved Fe^{2+} in the oceans (the net O_2 sinks). If these O_2 sinks were exceeded, then O_2 would have accumulated in the atmosphere until balanced by weathering of reduced minerals on land surfaces. If not, then the reduced gases released from volcanos would have accumulated in the atmosphere until balanced by the escape of H to space.

Let us apply some numbers to see which outcome is more likely. In Towe's earlier paper (*7*), he assumed that organic C was buried at a rate of 5×10^{12} mol year^{-1}, which generated an equivalent amount of O_2, and that $\sim 2.2 \times 10^{12}$ mol of O_2 per year might have been consumed by reaction with Fe^{2+}. The difference between these figures, 2.8×10^{12} mol of O_2 per year, is the amount of O_2 that would need to have been consumed by volcanic gases to keep the system anoxic. This latter figure drops to 0.3×10^{12} mol year^{-1} if DesMarais *et al.* (*9*) are correct, and the organic C burial fraction during the Archean was only half its present value. These figures should be compared with a present O_2 sink of $\sim 8 \times 10^{11}$ mol year^{-1} from reduced volcanic gases (*8, 10*). The higher estimate for the Archean O_2 production rate exceeds the present volcanic O_2 sink by a factor of ~3.5 (*8*); the lower estimate is less than half of the present volcanic sink. Because all of these numbers are uncertain, I conclude [see also (*8*)] that one cannot reliably predict whether the Archean atmosphere was reducing or oxidizing on the basis of mass balance calculations of this type. One has to rely on the rock record which, as I was careful to point out in my review (reference 87), has been interpreted differently by different workers. The interpretation that I follow is based on the work of Cloud and Walker *et al.* (references 71 and 77 in my article) and is, I believe, the majority view. My theory (*11*) is that a gradual reduction in the H_2/CO_2 ratio in volcanic gases caused by progressive mantle oxidation resulted in the critical threshold atmospheric O_2 being reached around 2 Ga.

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