secondary messengers (*9*). Unfortunately, cell culture is a condition far removed from the environment of the neuron in vivo, so the physiological relevance of these findings is still in doubt.

More recently, techniques combining newer fluorescent dyes (such as the lipophilic carbocyanine membrane stains, DiI and DiO) with confocal microscopy have enabled time-lapse observations of single cells within whole embryos and brain tissue slices (*10–13*). These studies show that extension and retraction of filopodia occur in tissue slices as well as in cell culture and provide evidence that this motility is modulated by neurotransmitters such as glutamate and electrical activity at synapses. Although these experiments provide access to neurons in appropriate tissue environments, interpretation of the results is restricted by the limits of detection inherent in confocal microscopy and the possible effects of excessive dye and light exposure.

Maletic-Savatic and co-workers have taken advantage of sophisticated new techniques in fluorescence microscopy to observe the dynamics of individual neurons in rat brain hippocampal slices at substantially higher resolutions than achieved before. They used a benign virus that infects neurons to shuttle the gene encoding a soluble green fluorescent protein (GFP) marker into hippocampal neurons. The principal advantage offered by GFP is that it provides excellent fluorescent signals with few toxic side effects (*14*). Finally, these investigators measured fluorescence with a two-photon laser scanning microscope. This new imaging method uses nonlinear fluorescence photoexcitation to achieve optical sectioning and three-dimensional imaging that is far more efficient (in terms of reducing noise and photodamage) than that achieved with the older confocal microscope.

With the improved image quality provided by the combination of these methods, the authors confirm and extend the results of confocal studies (*12*, *13*), including the observation of abundant filopodial protrusions (*13*). They then forged on to investigate the effects of the NMDA receptor blocker APV. Intriguingly, image analysis demonstrated that the firing of action potentials resulted in an increased rate of filopodial formation, which was abrogated by APV. Thus, they demonstrated that the possible morphological target of NMDA receptor activation is the initiation of filopodial extension. This provides an exciting link between NMDA receptor activation and neuronal morphogenesis because filopodial formation has been implicated in synaptogenesis (*7*) (see the figure). In this case, NMDA receptor activation might stimulate the extension of filopodia, which could then contact neighboring axons to initiate cell-cell adhesion and synaptogenesis. Alternatively, NMDA receptor activation might stabilize existing or nascent synapses, preventing their loss. As evidence accumulates that filopodial sprouting is important in synapse formation, it seems that both of these possibilities should be taken seriously. Of course, they are not mutually exclusive. Maletic-Savatic *et al.* note that the very localized control of dendritic filopodial activity by presynaptic action potentials could lead to an associative or "Hebbian" characteristic of synapse formation—that is, axons that fire and release glutamate, thereby triggering local filopodial protrusions, would seem to be more likely targets for synaptogenesis than nonfiring axons at other, more distant sites. These new findings bring to the fore many fascinating questions. What are the mechanisms by which dendritic filopodia protrude, and how are these processes linked to NMDA receptors and calcium influx? Almost certainly, the process involves the actin cytoskeleton (*8*, *15*), but the accessory proteins that generate mechanical force remain to be determined. In addition, filopodial protrusions are obviously accompanied by local rearrangements at the cell surface; these may include exocytotic delivery of membrane vesicles or clustering of molecules specialized for protrusion or adhesion. How do the basic cytomechanical and regulatory schemes for dendritic filopodial formation relate to those governing neuronal filopodial dynamics in other studies of neuronal (*6*, *8*, *13*, *16*) and nonneuronal cells (*17*)? Finally, this work only hints at the part played by filopodial protrusion in synaptogenesis. Much more work is required to establish a definite connection between these two events, and to identify alternative developmental or functional consequences. For instance, the motive forces evident in filopodial protrusion may have their major consequences in more subtle rearrangements of existing synapses rather than in the birth of new synapses (*18*).

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PERSPECTIVES: ORIGIN OF EARTH AND MOON

Colliding Theories

Alex N. Halliday and Michael J. Drake

How did Earth and the moon form? And what forces defined their basic physical structures? These key issues in Earth and planetary sciences have for many years been at the borderline of tractability. Advances have come mainly with progress in simulating the dynamics of planetary accretion, in measuring isotopes that act as chronometers for early solar system processes, in analysis of noble gas isotopes that yield clues about the early atmosphere, and in melting experiments at previously unattainable pressures and temperatures. A recent conference in Monterey, California (*1*), showed that, although a general picture may be emerging, many issues remain hotly debated.

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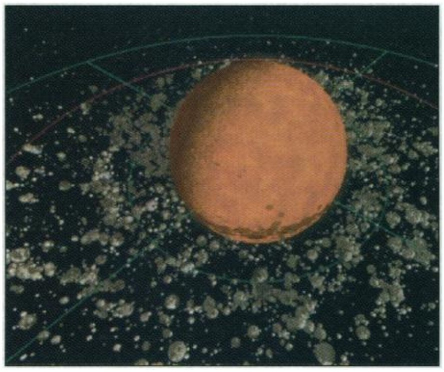
Planet formation is thought to start with sticking and frictional coagulation of dust particles in a gaseous nebula that persisted in the circumstellar disk. The particles grow in size until there is substantial gravitational attraction between kilometer-sized bodies, which coalesce further. Major collisions between small proto-planets eventually result in objects the size of Earth. The energy of late-stage planet-building impacts would be colossal, sufficient to melt the entire planet. Magma oceans would be formed, and some volatile elements would escape into space.

The most widely accepted theory for the origin of the moon is that it coalesced from a ring of debris produced by such a late-stage collision between two Earth-forming proto-planets (see the figures) (*2*). This "Giant Impact Theory," established over a decade ago, has received more support than earlier models, partly because it explains the rotational speed of the Earth-moon system, a critical feature that has to be reproduced by any satisfactory model.

The making of a moon. This simulation starts from a disk of debris generated by a collision between proto-planets.

Recent model refinements have improved the estimates of the geodynamic constraints under which the Giant Impact Theory can be correct, but the results are still equivocal. According to simulations of planetary accretion (Robin Canup, Southwest Research Institute, Boulder), the accretion of bodies with a size distribution like that in the inner solar system is to be expected. However, a substantial uncertainty surrounds the timing of accretion of the terrestrial planets relative to the gaseous outer planets and the effects of the gaseous planets on the terrestrial ones. We also do not know at what stage the nebula gas remaining after the collapse of the solar nebula to form the sun was lost, what the temperatures were at different stages, or what effects the temperature had on accretional processes. Some dynamic simulations (Al Cameron, Harvard University) of the impact now invoke a proto-Earth that—at about half its modern size—is smaller than previously estimated and that collides with another body that is larger than expected, perhaps three times the mass of Mars (*3*). This impact would produce sufficient energy to provide the right angular momentum for the Earth-moon system and eject material into a stable orbit. However, Jay Melosh (University of Arizona) argued that we do not know the equations of state well enough to calculate the energy of such an impact and that we may have grossly underestimated them, to the point that specific dynamic models are currently unjustified. A striking feature of all of these energetic scenarios is that they should evaporate moderately volatile elements such as potassium. Munir Humayan (University of Chicago) has shown that the isotopic composition of potassium in inner solar system objects has not been fractionated and that this precludes certain models of loss of volatiles by evaporation (*4*). However, new evidence presented by Yutaka Abe (University of Tokyo) showed that escape would be so vigorous that there would be no isotopic effect.

In spite of a growing consensus, some workers still dislike the entire Giant Impact Theory, on both dynamical and geochemical grounds. Model-independent estimates

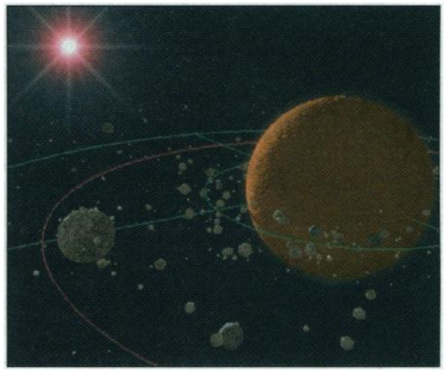


About 20 hours later, a spiral-arm structure forms due to gravitational instability.

of the time and speed of Earth formation relative to that of the moon and the rest of the solar system would provide a powerful test of the theory. However, the direct evidence has been destroyed by mantle convection and plate tectonics, and we have to rely on model ages for important isotopic fractionations related to early physical processes such as accretion, Earth core formation, and outgassing—the transfer of volatiles from Earth's interior to the atmosphere and hydrosphere (Frank Podosek, Washington University, St. Louis) (*5*, p. 1863). All isotopic data are consistent with Earth being fully formed within 50 to 100 million years after the start of the solar system. The isotopic record from moon rocks is consistent with its formation at about the same time. The newest insights (*6*) come from measurements of tungsten isotopic compositions (*5*).

The highly energetic final stages of accretion are expected to be associated with the formation of deep oceans of magma. Most of the direct evidence of this is likely to have also been eliminated by 4.5 billion years of mantle convection and plate tectonics, but the effects of large-scale fractionation may still be present, particularly in the concentrations of siderophile elements. Siderophile or metal-loving elements are those that like to go into Earth's core in preference to the silicate outer portion of Earth. The exact proportion that stays behind is a function of the temperature and pressure at which the metal and silicate were last in equilibrium. Recent melting and partitioning experiments (Mike Walter, Okayama University) fit equilibrium at about 700-km depth, implying a magma ocean that extended to the bottom of the upper mantle (*7*). However, Kevin Righter (University of Arizona) pointed out that his model for such a magma ocean only works if large amounts of water are present. Late additions of chondritic material to the silicate Earth are an alternative explanation for siderophile abundances (*8*). The debate on this issue continues unabated.

Planetary outgassing and the earliest conditions on Earth and the moon are typically investigated with noble gas isotopic



Within 200 hours, a single large moon forms by accreting material from the disk. This remaining debris is accreted by the moon or falls to Earth.

measurements (*9*). A critical discovery of the past decade has been the identification of solar He and Ne within Earth, identified by comparison with the He/Ne ratio of the solar wind. We do not know how much solar gas was originally trapped by Earth. The most obvious way to introduce such components is by terrestrial accretion in the presence of a nebula. The nebula is unlikely to have lasted more than 10 million years, and this finding needs to be reconciled with tungsten isotope evidence that Earth may have only been accreted to about 20% of its current mass at this stage. Perhaps Earth did not need to be very big to retain a substantial amount of gas. But how did this solar gas survive the Giant Impact? It has been proposed that Earth's atmosphere and hydrosphere (which are clearly nonsolar) are secondary, added later by cometary impacts. However, all of the D/H data for comets acquired so far preclude this possibility. Accreting planetesimals and residual nebula gases appear to have provided Earth's inventory of volatiles. It is hard to envision such an origin for these elements because the probability of a collision with comets,

CREDIT: E. KOKUBO AND H. MIURA, HTTP://GRAPE.C.U-TOKYO.AC.JP/GRAPE/INDEX-ANIME.HTML which come from beyond the furthest reaches of the solar system, is so low (Tobias Owen, University of Hawaii, and Kevin Zahnle, NASA, Ames Research Center).

A solution may come from the idea (Takuo Okuchi, Nagoya University) that the volatile budget of Earth has been affected by the dissociation of water, the extraction of large amounts of hydrogen into the core, and the oxidation of the iron in Earth's mantle. An excellent new model has been developed (Don Porcelli, California Institute of Technology) for Xe isotope data in terms of late catastrophic volatile loss about 100 million years after the start of the solar system. Did this happen during a Giant Impact–like event? Perhaps there were several such events and the final damage happened after the moon formed. It is unlikely that the moon did not form until 100 million years after the start of the solar system. If Earth had only half formed at this late stage the accretion rates must have been very slow. Furthermore, the W isotope heterogeneity on the moon would have to be an inherited feature because it can only be produced within the first 60 million years of the solar system. Such inherited heterogeneity is hard to reconcile with the energetics of the Giant Impact.

We have recently come a long way in obtaining hard constraints on the origin of Earth and the moon. The issues have changed from discussion of whether or not there was a giant moon-forming impact to debates about the accretion rates of the Earth and the chemical, isotopic, and physical effects of such castastrophic accretionary scenarios.

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PERSPECTIVES: ORIGIN OF EARTH AND MOON

A Couple of Uncertain Age

Frank A. Podosek

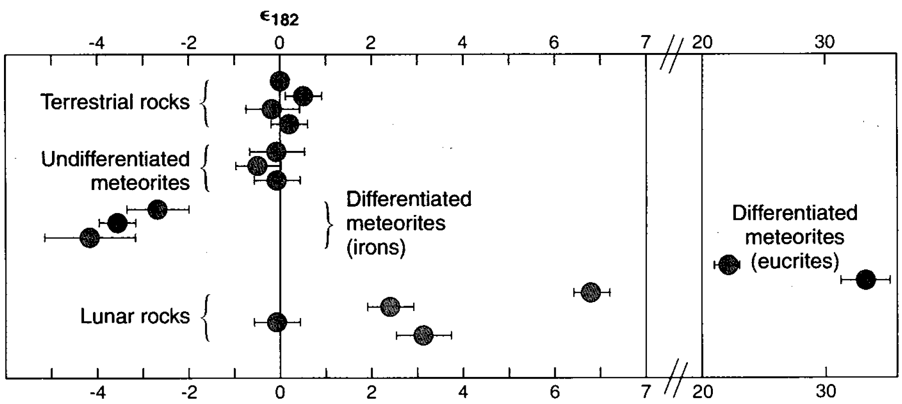
The age of our planet is interesting in its own right and has a bearing on other questions such as early conditions on Earth and the origin of life. In modern practice, geologic ages are determined by measuring the accumulated amount of some daughter isotope that is produced in radioactive decay and relating it to the abundance of the parent radionuclide. In this century, Earth's age has been progressively more constrained as a result of better understanding of natural radionuclide parent-daughter systems and advances in analytical technology. But despite such progress, some thorny issues remain, not only in dating but also in identifying the key processes associated with Earth and moon formation (*1*, page 1861).

The age of the solar system as a whole is easier to determine than the age of Earth. The former is reliably inferred from the age of refractory element–rich inclusions in undifferentiated meteorites to be about 4.57 billion years (*2*), thus providing an upper limit to the age of Earth. These inclusions are the oldest known objects in the solar system, and their content of very short-lived radionuclides such as ^{26}Al (with a half-life of 0.74 million years) indicates that the solar system did not exist for more than about 1 million years before the inclusions formed (*3*).

In contrast to these ancient extraterrestrial objects, there are no known terrestrial rocks or minerals whose formation essentially coincides with formation of Earth, and therefore its age must be inferred indirectly. Several independent approaches indicate that Earth formed about 100 million years later than the solar system as a whole. This is rather a long time compared with theoretical estimates for early solar system evolutionary time scales and for formation of other terrestrial-type planetary bodies, both around 10 million years or less (*4*).

One line of evidence, pursued over several decades, emerges from measurements of the proportions of ^{206}Pb and ^{207}Pb, which are produced at different rates from ^{238}U and ^{235}U, respectively. Models for the evolution of Pb isotopic composition in terrestrial mantle samples almost always give an age of Earth several tens to more than a hundred million years younger than that of the solar system (*5*). Another approach that leads to the same conclusion (*6*) is based on the observation that the amounts of excess ^{129}Xe and ^{136}Xe in the atmosphere are much less than would be expected from early solar system–estimated abundances of their short-lived parent radionuclides ^{129}I and ^{244}Pu, respectively. Similarly, decay of ^{87}Rb for several tens of million years is required to produce Earth's estimated initial $^{87}Sr/^{86}Sr$ ratio (*7*). The most recent isotopic system applied to the problem is based on the decay of short-lived ^{182}Hf (half-life of 9 million years) to ^{182}W (see the figure); it too suggests formation after several tens of million years (*8*).

The reader will note my frequent use of qualifiers. All of the above-mentioned isotopic chronometers are intrinsically capable of considerably higher precision, but this precision cannot yet be realized. It is not even clear whether the chronometers are consistent or in conflict with each other. One reason is that the issue is not so simple



Tungsten isotope survival. Relative abundance of ^{182}W, the daughter of short-lived ^{182}Hf (half life of 9 million years), in various solar system materials [data from (*8*)]; the abscissa scale is in units of 0.01%. If a planetary body experiences metal-silicate fractionation while ^{182}Hf is still present in substantial amounts, W in the metal should be depleted, and W in the silicate enriched, in ^{182}W. This appears to be the case for meteoritic metal and for lunar and meteoritic silicate but not for Earth's mantle and crust.

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