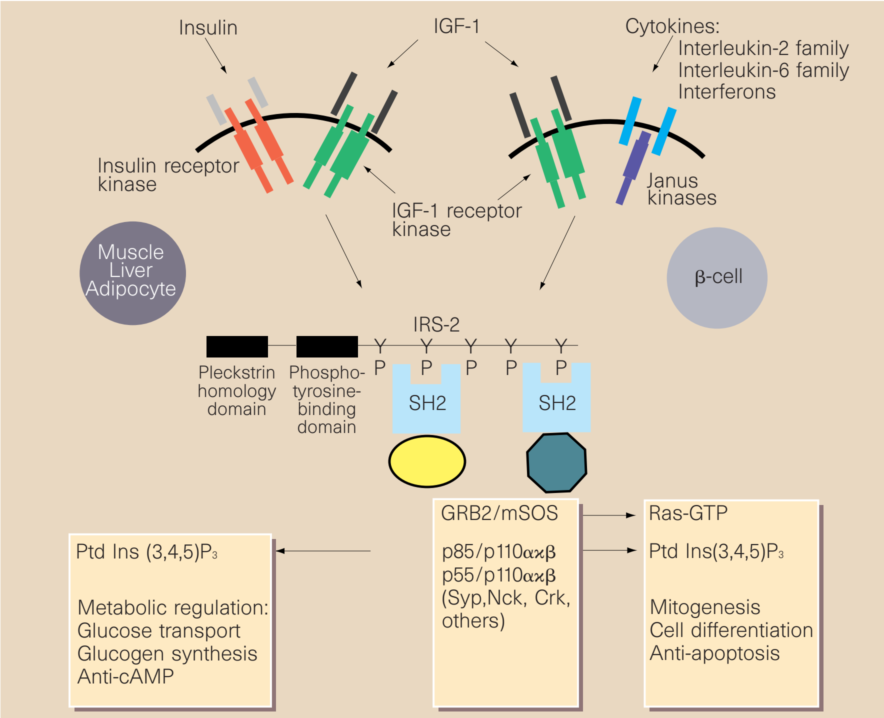

Figure 1 **Signal transduction through IRS-2 in the β-cell and in insulin-sensitive tissues. Withers *et al.*[2] have found that *IRS-2* knockout mice develop a syndrome that closely resembles human type 2 diabetes, implicating *IRS-2* as a candidate diabetes gene. Insulin, IGF-1 and cytokines bind to their respective receptors, resulting in tyrosine phosphorylation of IRS-2 and recruitment of signalling proteins. These include the phosphatidylinositol-3-OH kinases and the Ras-specific guanyl nucleotide exchanger, mSOS, which are likely to be important for the role of IRS-2 in β-cell compensation to insulin resistance. Generation of phosphatidylinositol-3,4,5-trisphosphate (PtdIns(3,4,5)P_3), and perhaps other signals, mediates the characteristic metabolic response to insulin in skeletal muscle, liver and adipose tissue.**

the transcriptional basis for β-cell development[11]. With the exception of hyperglycaemia, the signals that control the fate of β-cells — either during development or in adult life — are poorly defined. A 96-hour glucose infusion in the rat results in a 50% increase in β-cell mass, through increased replication and cellular hypertrophy[12]. Nevertheless, the mediators and mechanisms of this response to glucose are not known. Better insight into the control of β-cell fate is necessary to understand what ordinarily limits β-cell compensation in the face of insulin resistance, and to what extent these limitations are genetically programmed or environmentally imposed. The success of β-cell replacement therapies will also depend on such knowledge. For example, long-term β-cell function is much greater when islets are transplanted into human recipients in the context of an intact pancreas, compared with isolated islets. This undoubtedly relates to the capacity for β-cell neogenesis, and the ability of the β-cells to replicate and/or to avoid apoptosis under oxidative or anoxic stress. The contribution of IRS-2 and its partners to these processes will now come under scrutiny. ☐

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Errata

In the News and Views Feature "Galileo at Jupiter – meetings with remarkable moons" by William B. McKinnon (*Nature* **390,** 23–26; 1997), the heat flow from Io was given as 2.5 mW m^{-2}. It is actually 2.5 W m^{-2}, to compare with a terrestrial average of 90 mW m^{-2} (Pollack, H. N., Hurter, S. J. & Johnson, J. R. *Rev. Geophys.* **31,** 267–280; 1993). 'Size' in Table 1 refers to radius.

In the News and Views article "Fixed hotspots gone with the wind" by Ulrich Christensen (*Nature* **391,** 739–740; 1998), the Web-site address in reference 9 was misspelt. It should have read: http://www.ngdc.noaa.gov/mgg/image/seafloor.html

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Daedalus

Cold porridge

Last week Daedalus presented his new Hibernator. The subject is cooled down strongly enough to stop his heart, but his blood is kept moving by rhythmic hydrostatic pressures applied in sequence to his limbs and regions of his body. Thus his vital organs still receive their greatly reduced demand for oxygen and fuel. Monitoring equipment keeps him stable; at wake-up time, microwave heating swiftly restores his normal body temperature.

The primary beneficiaries of the technology are old people. A municipal Hibernatorium could see thousands of pensioners safely through the winter at far less cost than normal pension and social service provisions. Not only would they dodge the hardships of cold weather; they would live longer. Ageing, and the stealthy advance of degenerative diseases, will almost cease at hibernation temperatures. A pensioner with ten years of life in him could last for twenty years — and all that time would be summer. He would not need to relocate to some warm but dreary southern geriatric resort; he could stay around to follow the progress of his grandchildren, and experience and deplore what the world is coming to, for a much longer period.

The mental effects of the Hibernator remain to be explored. Will six months of hibernation seem like six months to the memory? If not, hibernating pensioners will hardly notice their periods of torpor. But if so, the Hibernator could revolutionize the prison service as well. Most prisoners would be happy to serve their time unconscious; and most prison governors would be only too pleased to let them. At the end of (say) ten years' hibernation, the criminal would wake up to recall his crime and late way of life as a distant folly. He could reasonably vow to leave all that behind, and start life afresh. Unconsciousness would be a far better form of rehabilitation than sharing a gaol with an ever-changing crew of lively expert criminals, all keen to swap ideas.

The Hibernator could serve still other purposes. The long-term unemployed could sleep out an economic downturn; unrequited lovers might embrace it as a way to forget. Those valiantly predicting a religious revival, or the resurgence of Socialism, or invasion by aliens, could use it to await (or sleep safely through) these social revolutions. And the younger child's hopeless threat to his big brother — "Wait till I'm older than you!" — would at last have a chance of coming true.

David Jones

Galileo at Jupiter — meetings with remarkable moons

William B. McKinnon

The four large moons of Jupiter form the most coherently organized planetary system known. Over the past two years, the Galileo spacecraft has illuminated both the interconnections between these worlds and the uniqueness of each, challenging theories of moon formation and evolution.

In January of 1610, Galileo Galilei turned his newly fashioned telescope upon Jupiter, finding "... four stars that wander around Jupiter as does the moon around the earth..."[1]. These were not stars, of course, but satellites of the great planet; and it is fitting that four centuries later a sophisticated robot named in his honour orbits Jupiter as well. Its mission: to seek out new knowledge of the planet, and by means of nearly a dozen close passes, to explore in detail the four Galilean moons – Io, Europa, Ganymede and Callisto.

Most of the basic parameters of Jupiter's satellite system have been known since the Voyager flybys of 1979 (see Table 1, overleaf). The inner two Galilean moons (Fig. 1), Io and Europa, are about the size of our Moon, and composed mostly or entirely of rock and metal. Ganymede and Callisto are larger, equal to or greater than Mercury in size, and roughly half ice by mass. This division is reminiscent of the Solar System as a whole, where the rock- and metal-rich inner planets are distinct from the much larger gas- and ice-rich outer planets. Jupiter's satellite system is, however, more 'systematic', in that most properties vary continuously with distance from Jupiter. All of the bodies are essentially solid, like the Earth, but vary by water-ice fraction. Io is ice-free, Europa has a surface shell of ice (and possibly water), and although Ganymede and Callisto are both ice-rich, outermost Callisto has more.

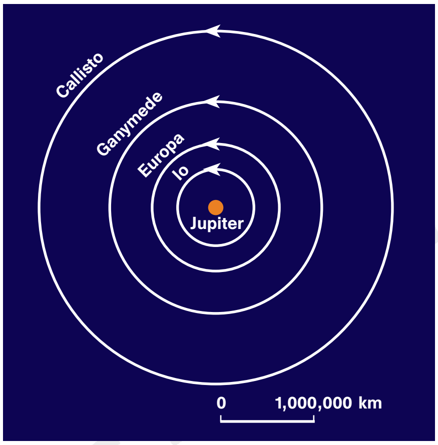


Figure 1 **The orbits of the four large satellites of Jupiter. Many much smaller moons are also known.**

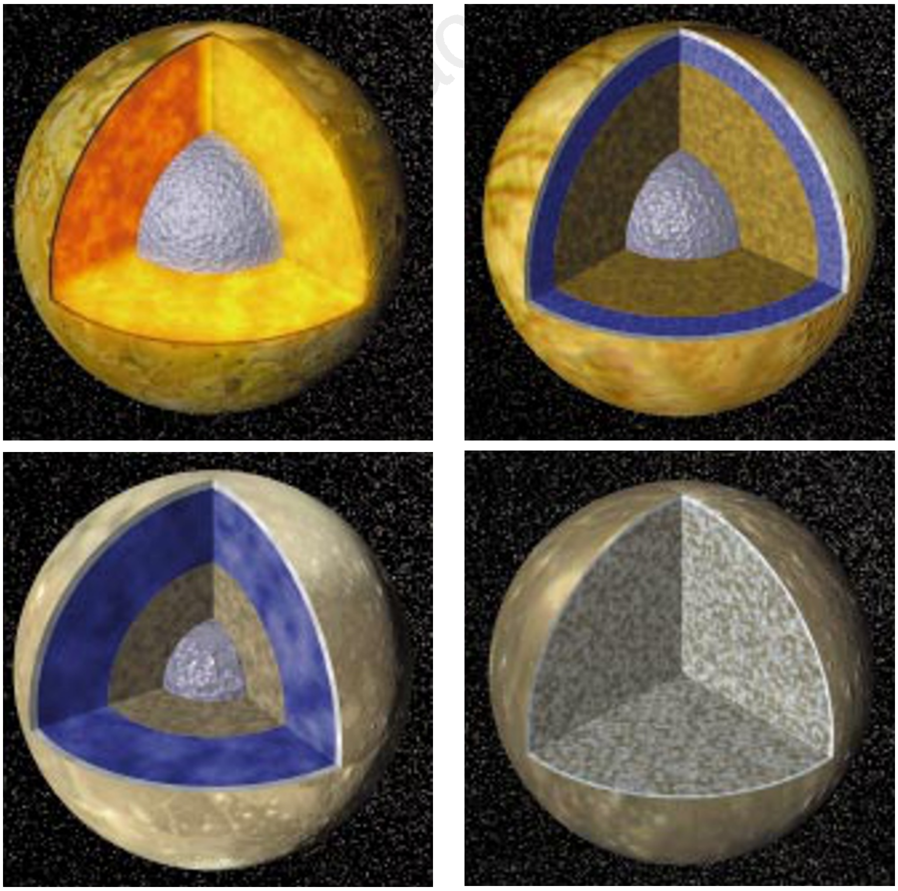


Figure 2 **Cut-away drawings of the four Galilean satellites, based on gravity and magnetic data. Metal, rock and ice (where appropriate) have separated according to density in Io (top left), Europa (top right) and Ganymede. Callisto remains an undifferentiated mixture of ice and rock. (Images by Zareh Gorjian and Eric M. DeJong, JPL Digital Image Animation Laboratory.)**

This compositional gradient has curious geological parallels. Io is extremely geologically active (an understatement, actually), Europa seems also to be active, though on a more modest scale, and Ganymede has undergone bouts of activity in its geological past. Only Callisto appears to have refrained from revealing any hints of internal activity. Correspondingly, Callisto's surface is very heavily cratered, Ganymede is heavily cratered in parts but more or less resembles the Moon in terms of the range of crater densities, Europa is very lightly cratered, and Io lacks any detected impact craters at all, so far. This is all the more remarkable given that Jupiter's gravity concentrates the flux of comets and asteroids passing near it, which substantially increases the bombardment rate of the inner moons with respect to the outer ones[2].

Jupiter is principally responsible for these patterns. Early in its history, Jupiter was larger and more luminous than it is today (ref. 3, for example). As proto-Jupiter acquired its vast gaseous envelope from the solar nebula, excess angular momentum forced some of the material into a flattened disk orbiting in the planet's equatorial plane, forming a planetary counterpart to the much larger solar nebula. The condensable material in the protojovian nebula, once gathered together (accreted) by gravity, created the satellite system. So it is by birth as well as by organization that the Galilean satellites, along with Jupiter, can be called a miniature planetary system.

Jupiter's early luminosity ensured that the inner regions of the protojovian nebula remained relatively warm. Rock and metal, but not water ice, should have condensed in the inner nebula, accounting for Io's lack of ice and Europa's modest endowment[3]. At the positions of Ganymede and Callisto, water ice condensed, but 'supervolatile' ices such as methane and N_2 did not, because the outer protojovian nebula would have been kept warm by the surrounding solar nebula.

Table 1 Basic properties of the moons

	Io	*Europa*	*Ganymede*	*Callisto*
Distance from Jupiter[26] (Jupiter radii)	5.9	9.4	15.0	26.4
Size[27] (km)	1,821	1,565	2,635	2,405
Density[7,9,10,17] (g cm^{-3})	3.53	3.02	1.94	1.85
Orbital period[26] (days)	1.77	3.55	7.16	16.69
I/MR^2 (refs 7,9,10,16)	0.378 ± 0.007	0.347 ± 0.014	0.311 ± 0.003	0.406 ± 0.030

Tides and migration

Jupiter also influences the levels of geological activity on its satellites through the tides it raises, which flex the solid moons, and so heat them. So powerful are these tides that their heating usually overwhelms the heating due to the decay of uranium, potassium-40 and thorium in the rock of these worlds. The tides occur because the satellite orbits are eccentric (rather than circular), and the tides would tend to reduce the orbital eccentricities — but these are maintained, for the inner three satellites, by mean-motion resonances: Europa's orbital period is nearly twice that of Io, and Ganymede's period is nearly twice that of Europa. This is collectively termed the Laplace resonance. The resonance could be primordial, dating back to the time of the satellites' accretion, but mean-motion resonances are not characteristic of other satellite systems (those of Saturn, Uranus or Neptune). So the orbits of Io, Europa and Ganymede probably evolved into their present resonant configuration.

We expect that such orbital evolution is possible, because the tides that the satellites raise on Jupiter exert torques that cause the satellites' orbits to expand over geological time. Io has evolved outwards faster than Europa, and Europa faster than Ganymede. Given enough dynamical evolution, it was all but inevitable that the Laplace resonance would form (ref. 4, for example). And dynamically speaking, the Galilean satellites are an extraordinarily ancient system. If we were to scale outermost Callisto to the position of Neptune, the Galilean satellites would take 16 trillion years to reach their present dynamical age! A lot can happen in such an eternity, and from this perspective the unusual body is the only one not entangled in any resonance – Callisto.

The intensity of tidal heating goes as the square of orbital eccentricity (which ranges from zero for a circle to one for a parabolic orbit) but inversely as a large power of the orbit size. So Io receives a prodigious amount of tidal heating[5], enough to keep its volcanic surface in a more or less permanent state of upheaval[6]. Europa is less intensely heated, but tidal energy may be responsible for maintaining Europa's bright, flat and young ice surface[5]. Ganymede is farthest from Jupiter of the three resonant satellites, and as the most massive of the Galilean moons it acts as a kind of gravitational anchor for the others, so its eccentricity is not at present being resonantly forced strongly enough to provide much tidal heating. Yet numerical simulations of the satellites' orbital history suggest that during a previous resonant configuration Ganymede's eccentricity may have been nearly as high as 0.1, and the resulting tidal heating at that time could have been substantial[4]. It is tempting to link Ganymede's past tectonic and volcanic activity with this tidal heating episode[4]. Callisto, uninvolved in any of this, and with a nearly circular orbit, is negligibly heated.

On the outside looking in

What new insights has the Galileo spacecraft brought? Unheralded in comparison with the eagerly awaited high-resolution imaging and the atmospheric probe, some of the most important results derive from measurements of gravity and magnetism. Powerful constraints on the internal structure of all four Galilean satellites have been obtained.

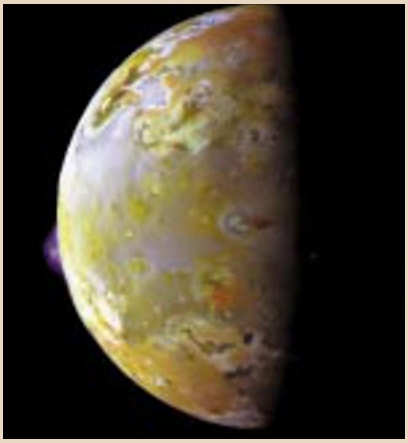
Although Newton showed that any spherically symmetric arrangement of matter behaves gravitationally as a point source, if the arrangement is distorted by rotation or tides, asymmetries are created in the gravity field. These can be measured if a spacecraft passes close enough to a body, as Galileo has, and broken down into their geometrical components – among which the quadrupole terms dominate.

Assuming that the body is in hydrostatic equilibrium[7], the quadrupole terms can then be used to find the moment of inertia *I* of the body, and thus give a hint at its structure. Different radial-density profiles can result in the same moment of inertia, but as long as physically and chemically sensible configurations are chosen *a priori*[8], the implied structure should be reasonably close to the truth. So the satellites are assumed to have layers of water ice (except for Io), silicate rock, and metal (predominantly iron), or various mixtures thereof, with the density of each layer increasing from the outside in.

Based on one close pass by Io, and two apiece by Ganymede and Europa, the moment-of-inertia factors I/MR^2 (where M and R are the satellite mass and radius, respectively) for these satellites have been determined to be 0.378 ± 0.007, 0.311 ± 0.003, and 0.347 ± 0.014, respectively[7,9,10] (Table 1). Given that I/MR^2 for a uniform sphere is 0.4, this is unambiguous evidence that all three bodies are centrally condensed. That is, they have differentiated into distinct layers of material, like the rocky planets. Io appears to have a metallic core and rock mantle[7], which is not surprising given Io's level of tidal heating, but the result for Ganymede is particularly striking. Its I/MR^2 is the lowest yet obtained for any solid body in space, and implies that Ganymede is strongly differentiated, with its ice forming an 800–900-km mantle above a rock and metal core, with little or no room for any intervening mixed ice and rock layer. Furthermore, Ganymede has been found to possess a relatively strong dipole magnetic field, and the most physically plausible explana-

Io

Io is the most geologically and geophysically active body in the Solar System. Io is strongly tidally heated, and undergoes more-or-less-continuous volcanic resurfacing[6]. Plumes, hydrodynamically more akin to geysers, are the most spectacular volcanic phenomena (one can be seen erupting on the limb in this view from the Galileo spacecraft, and another, called Prometheus, on the line between night and day), but a wide range of volcanic landforms are found, such as vents, calderas (collapsed craters) and flows, along with mysterious, isolated mountains up to 10 km high. Heat from individual eruptions can be monitored from Earth, and Galileo has now measured both the heat and visible light from various eruptive centres; eruption temperatures can reach 1,100–1,500 K, indicating silicate volcanism[6]. The surface is covered, however, with sulphur



and sulphur compounds, including SO_2 frost. The heat flow from Io[6] is about 2.5 mW m^{-2}, nearly 30 times the terrestrial average.

tion is dynamo action in a convecting, liquid portion of an inner metallic core[11,12].

The moments of inertia measured during the two Europa encounters differ, but even the larger value (listed in Table 1) implies that Europa, too, is quite centrally condensed[10]. This indicates a deep (~100–200 km) ice layer[13], a dehydrated rocky interior, and probably an inner metallic core. Magnetic-field measurements at Europa are hard to interpret because of the strength of Jupiter's magnetic field closer to the planet, but an internally generated dipole field (implying a metallic inner core) is a possibility[14].

But Callisto bucks this trend. There, all is quiet on the magnetic front[15], and its I/MR^2 is consistent with an undifferentiated interior[16]. The lack of an intrinsic magnetic field is also consistent with, but does not require, an undifferentiated interior — as Venus and Mars demonstrate. How Callisto could have remained undifferentiated is a great puzzle (see below).

Interestingly, an undifferentiated Callisto would have an ice/dry-rock mass ratio of ~55/45, whereas a differentiated Ganymede, despite its similar size and density, has the opposite ratio of ~45/55 (this is possible because much of the ice in Callisto would be deep inside the planet, compressed into dense phases)[17]. This is a substantial difference in composition, not just in surface appearance, between the two bodies.

All these worlds but one

The new gravity and magnetic-field data seem to fit together in a rather neat package. All of the tidally heated satellites have separated their rock and ice, and the rock has further differentiated into metallic inner cores and silicate outer cores. Convection in the liquid portion of the metallic inner core of Ganymede, and possibly that of Europa and Io as well, generates a dipole magnetic field. Only Callisto, having never been tidally heated, retains its primordial undifferentiated character (Fig. 2).

Beneath this beautiful architecture, however, lie deeper mysteries. It sounds simple: heat a rock core and the metal will melt and drain to the centre. But the rock core of an icy satellite forms when ice melts and rock falls inwards, and such a core is necessarily relatively oxidized. Under pressure and increasing core temperature, and in the presence of carbon (which must also have accreted), any iron oxides will react to join iron-bearing silicates[18], leaving iron sulphide[19]. As a single metallic phase, its melting temperature is quite high — more than 1,500 K at core pressures. Under tidal or radiogenic heating, this means that solid-state convection in the rock sets in before melting occurs, moderating any further temperature increase and thus preventing metal-silicate separation.

Obviously, the Earth has formed its core, so it can be done. But the Earth is different in two important ways. First, it formed from materials closer to the Sun and therefore rather chemically reduced, resembling to first order the ordinary chondrite meteorites. They contain iron sulphide and free iron, and the presence of these two phases ensures that a low-melting-point (eutectic) metallic liquid can be formed. Second, the Earth was probably melted during a giant, Moon-forming impact[18], enabling core formation no matter what the oxidation–reduction state of the proto-Earth. The growing Galilean satellites could also have been supplied reduced material by heliocentric (solar-orbiting) planetesimals, the small bodies from which the planets grew. Unfortunately, equilibration with ice and water during core formation should still have oxidized any rock and metal, regardless of its origin.

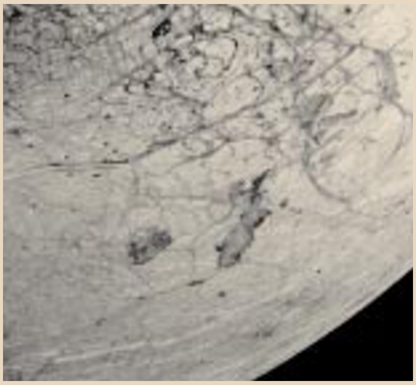
Furthermore, substantial accretion of

Ganymede

Ganymede is the largest and most massive satellite in the Solar System. Its surface is predominantly water ice, and divided more-or-less equally into two terrain types, a more cratered dark terrain and a less cratered bright terrain. Both can be seen in this 54-by-90-km Galileo image. Voyager images indicated that bright terrain replaced dark terrain by the volcanic infilling of broad rifts with cleaner ice, which were then extended and fractured to form parallel sets of ridges and valleys, or grooves[22]. Galileo confirmed the role of extensional faulting in grooved terrain formation and the degraded nature of the dark terrain[28]. The dark terrain seen here is irregular, knobby and cut by faults. The nearby lanes of bright terrain contain smooth swaths, supporting a volcanic origin. The parallel lineations at the upper left are grooves, and strongly resemble 'horst and graben', an extensional formation familiar on Earth. The coupled creation of bright terrain and grooves — the main geological event in the history of Ganymede — has been variously attributed to Ganymede's differentiation, the freezing of its ice mantle, and a past era of tidal heating[4,22].

Europa

Europa's surface is almost entirely water ice. From the rarity of impact craters, its surface is young, perhaps less than 10 million years old[29]. Relief is extraordinarily low (<200 m), which reflects both the weakness of ice as a geological material and tidal heating within the satellite. This view of a portion of the southern hemisphere (with its contrast enhanced) nevertheless shows a variety of geological units and structures. Prominent are dense assemblages of ice plates, bounded by lineaments and lanes of darker, younger ice that have accommodated the separation, rotation and translation of the plates. Long dark and bright lineaments also cross the scene, and when seen at high resolution turn out to be ridges or ridge sets[29]. Small, dark spots may be caused by hot ice rising buoyantly from below[28]. The irregular dark splotches at the centre of the image appear to be some type of icy volcanic flow. Evidence for an ocean on Europa, below ~10–30 km of surface ice, has been accumulating for some time[29]. The ocean could be maintained by vigorous tidal heating in the ice above and, to a lesser degree, in the rocky interior. Europa's ocean/ice layer is deep (~100–200 km), and the moon's interior may have differentiated into a metallic core and an overlying rock mantle[10,14]. Thermal evolution models indicate that tidal heating may have kept the rock mantle convecting, perhaps with active volcanism at the mantle/ocean boundary[19]. In overall structure and activity, Europa is curiously similar to the Earth.



Callisto

Callisto is distinguished from the other Galilean satellites by showing little or no geological activity generated from within. Its ancient surface has been heavily cratered without respite, and would be monotonous were it not that the largest impacts left vast, multi-ringed fracture patterns in the crust. This Galileo image shows a close-up, 38 km across, of one of the scarps in the outer portion of the ~4,000-km-diameter Valhalla multi-ringed structure. A black cliff-shadow stretches across a ruined landscape of icy hillocks and small craters, partially buried by dark, smooth material. This 'blanketing' is not seen on Ganymede's dark terrain. It may be the result of the loss of ice over geological time to sublimation and sputtering by magnetospheric charged particles[30], allowing rocky material originally bound in the ice to accumulate. This makes sense if the rock component is substantial, such as would be true for a primordial ice and rock mixture of 20–30% rock by volume[17].

heliocentric planetesimals would compound another deep mystery — how to keep Callisto from differentiating. Both Ganymede and Callisto are large enough bodies that the gravitational potential energy of their formation is more than enough to have melted all their ice[20]. Only by accreting gradually enough, or from bodies small and/or slow enough that the heat released by the collisions is not deeply buried, can accretional heat be efficiently radiated or convected (via nebular gas) away from a growing satellite surface[3,20]. Unfortunately, heliocentric planetesimals move on high-velocity, hyperbolic trajectories with respect to the satellites, and release one to two orders of magnitude more energy upon collision than local planetesimals orbiting Jupiter — a large enough heliocentric impact could even trigger wholesale (satellite-wide) ice–rock differentiation[21]. No one has yet come up with a convincing mechanism to prevent ice melting and differentiation within Callisto[20,22].

The implications of an undifferentiated Callisto reach further. As discussed above, the conventional explanation of the satellites' compositional gradient involves the luminosity of proto-Jupiter, but this assumes that the satellites accreted not far from their present orbital distances. This may not be true in general for satellites or for planets. Evidence is accumulating that the planets migrated great distances inward or outward as they formed[23], and inward migration may explain the 'hot Jupiters' around other stars, discovered over the past few years[24]. And because of the high density of the protojovian nebula, gas drag or other dynamic satellite–nebula interactions could have caused the satellites to spiral in towards Jupiter after they formed. The satellites we see today would have then been left stranded when the nebula dissipated, and may only be the last in a long line of worlds, most of which were consumed by proto-Jupiter[3,20].

In this picture, each satellite presumably accreted from a similar mix of ice and rock as it migrated, so Io and Europa would have needed some way to shed unwanted ice. The late E. M. Shoemaker hypothesized that the early bombardment of Jupiter's system (more than four billion years ago) would have been fierce enough to completely strip Io of an original ice mantle and remove most of Europa's as well. But an undifferentiated Callisto imposes stringent conditions on the nature of any such bombardment, leaving the whole 'orbital migration' picture in question. Yet from a theoretical standpoint it is difficult to make the young Galilean satellites sit still in their nebular nursery[3]. Perhaps there were hardly any comets large enough to melt Callisto. Or perhaps Callisto is differentiated after all, but is fooling us with non-hydrostatic components in its gravity field[17]. There is as yet no attractive solution to the mystery of Callisto.

A mission from the Pope

Last winter a meeting called "The Three Galileos" was held in Padua, Italy, to celebrate the man, the spacecraft and the new Italian national telescope. A highlight was the official presentation of a volume of images from the Galileo Project to Pope John Paul II. The Pope was reported to be interested and perceptive, and encouraged continued exploration of the Universe[25]. Happily, Galileo (the spacecraft) should in this instance have no trouble acceding to papal wishes. The Orbiter completes its nominal mission this December, but the US space agency NASA plans to let it continue, taking advantage of the final orbital geometry to repeatedly encounter Europa, and then, by using Callisto for several gravity assists, to encounter Io. Much more of Europa will be imaged at high resolution, and Io will be for the first time. Moreover, the additional gravity and magnetic field measurements should greatly improve the interior models, providing a richer portrait of the satellites' geophysical personalities. Understanding the origin and evolution of the Galilean satellites will doubtless take time and require further explorations, but it will be a vital element in building a comprehensive theory of planet formation. ☐

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Fixed hotspots gone with the wind

Ulrich Christensen

Island chains such as Hawaii are produced by hotspots — points of volcanic activity driven by plumes of hot rock. New analyses reveal that hotspots are much more mobile than had been thought.

Ever since we have known that the Earth's tectonic plates are in relative motion, the search has been on for fixed points to which absolute plate motion can be referred. For a while it was assumed that hotspots, long-lived centres of volcanic activity, provide such a reference frame. Hotspots are commonly explained by mantle plumes, narrow conduits of upwelling hot rock that probably originate near the core–mantle boundary and rise close to the surface. But it seems unlikely that plumes can be firmly anchored in a convecting mantle. Writing in *Geophysical Journal International*[1], Steinberger and O'Connell now describe how they have used kinematic models to tackle the issue — they show how plumes have swayed, drifted and twisted in the large-scale mantle flow, yet have produced the observed hotspot tracks at the Earth's surface.

The chain of islands and seamounts originating at the Hawaiian hotspot is the best example of such a track. Radiometric dating shows that the rocks become progressively older with increasing distance from Hawaii. The present distances and ages reveal how the Pacific plate has moved, with respect to the hotspot, during the past 80 million years (Myr). For example, the sharp bend at the link between the Hawaiian chain and the Emperor seamount chain (Fig. 1) is thought to have resulted from an abrupt change, at 43 Myr, from northerly plate drift to the current, more westerly, motion.

In 1971, Morgan[2] recognized that the various hotspot tracks on the Pacific plate can be explained by assuming that the hotspots are fixed relative to one another, and he introduced the concept of deeply anchored mantle plumes. It was later shown, however, that the Pacific hotspots move relative to those in the Atlantic[3] at rates of 1–2 cm yr^{-1}. This is less than the speed of fast-moving plates (10 cm yr^{-1}), but enough to make the hotspot frame of reference suspect.

Results from seismic tomography[4], a technique for imaging the Earth's internal structure using waves generated by earthquakes, imply that much of the return convective flow that balances plate motion occurs in the lower mantle, which therefore cannot be the immobile groundwork through which fixed plumes rise. In a first step, Steinberger and O'Connell[1] calculate a global mantle-circulation model for the past 68 Myr, using buoyancy forces inferred from tomographic anomalies and taking the present and past plate motions as boundary conditions. In the second step, they insert plume conduits and calculate how these conduits are advected by the 'mantle wind' (a process comparable to the advection of a trail of smoke in the atmosphere). The tendency of tilted plume conduits to straighten out because of their own buoyancy is also accounted for. Strictly speaking, plumes and the large-scale circulation are parts of a single convective system. But because plume conduits are comparatively narrow (50–100 km across), they can probably be considered as separate entities that do not affect the global circulation.

In Steinberger and O'Connell's model, the plume conduits are twisted and substantially tilted from the vertical (it is assumed that plumes break up and become extinct when the tilt gets larger than 60°). The model hotspots migrate at a rate of about 1 cm yr^{-1} in a reference frame of zero mean plate drift. However, all the Pacific hotspots move more or less consistently towards the south-east. After adjusting the drift of the Pacific plate, the model explains the observed hotspot tracks equally well as the assumption of fixed plumes does. Because the mantle wind blows differently in other parts of the world, hotspots in the Atlantic and Indian Oceans are predicted to migrate independently from those in Pacific, in agreement with observations.

Plume advection is sensitive to the variation of mantle viscosity with depth. Steinberger and O'Connell's results are consistent with observed hotspot tracks only for a comparatively low viscosity of 1.5×10^{20} pascal seconds (Pa s) between 100 km and 400 km depth, and a high viscosity of the order of 10^{23} Pa s below 1,500 km. If the lower mantle is less viscous than that, hotspots should wander around at a higher rate than is compatible with surface observations. The low viscosity at shallow depth is required to explain the sharpness of the bend in the Hawaii–Emperor chain. In a model with a stiffer upper mantle, the plume conduit reacts to the sudden change of plate drift direction by performing a wide swing, which would result in a smoothly curved hotspot-track.

Although the idea of a viscosity increase with depth is not new, its magnitude has been disputed. A modest rise, less than an order of magnitude, had been inferred from the uplift of the Canadian land surface in response to the removal of the glacial load at the end of the last Ice Age. In contrast, the interpretation of long-wavelength anomalies of the Earth's gravity field related to subducted plates favours a stronger increase of viscosity with depth. This conclusion is now reinforced by the modelling of plume migration.

The new results put some long-standing ideas about plume migration on a more quantitative basis. What are the conse-

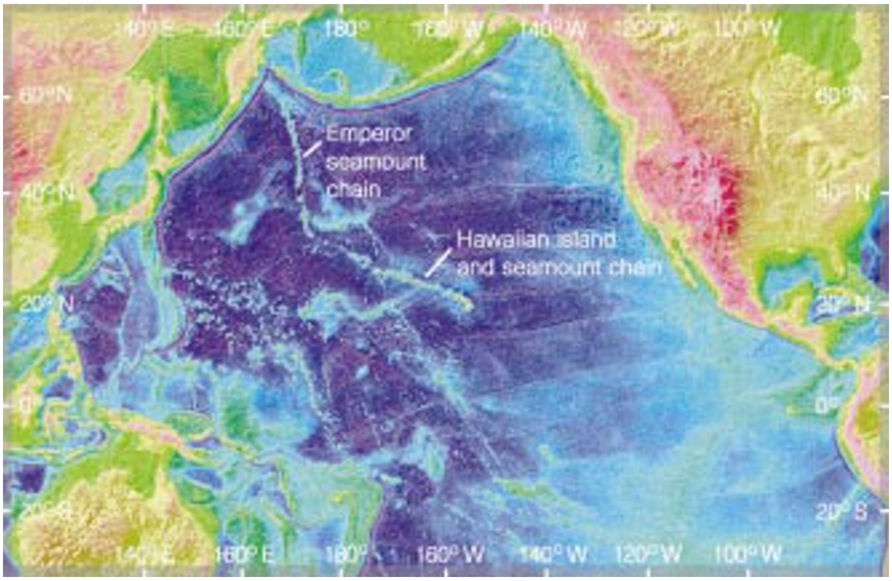

Figure 1 **Topography of the northern Pacific seafloor, showing the chain of islands and seamounts originating at Hawaii, and the Emperor seamount chain. The sharp kink between the two is customarily taken to reflect a sudden change in the direction of plate motion about 43 million years ago. (Map reproduced from ref. 9, courtesy of Walter H. F. Smith.)**

quences? It seems that we must abandon the convenient concept of fixed hotspots as reference points for past plate motions. Ironically, this jeopardizes some lines of argument in Steinberger and O'Connell's work. The only good evidence that we have for an abrupt change in the motion of the Pacific plate 43 Myr ago is the kink in the Hawaiian hotspot track. No other major tectonic event occurred at that time[5] and geodynamic models based on buoyancy forces derived from subduction history, which do a good job of explaining present-day plate motions, fail to predict the change[6]. Could it be that the hotspot, rather than the plate, suddenly changed its state of motion?

To decide on this question, we need a reference point that is independent of plates and hotspots. The Earth's magnetic dipole axis, which wanders around but coincides with the rotation pole when averaged over some thousand years, provides just such a reference. The direction of magnetization acquired when a volcanic rock is cooled below its Curie temperature, the temperature at which magnetization becomes fixed, is often preserved over geological time, allowing determination of the rock's palaeolatitude — that is, its latitude at the time that the magnetic field was frozen in.

In another paper, published last year, Tarduno and Cottrell[7] presented palaeomagnetic data for a 81-Myr-old seamount near the northern end of the Emperor chain, which indicate that it was formed at a latitude of 36 °N. Another seamount further south in the Emperor chain was created 16 Myr later at 27 °N. If the Hawaiian hotspot had remained fixed with respect to the rotation axis, both should have formed at 19 °N, the present latitude of Hawaii. The latitude change could be explained by a movement of the entire Earth relative to the rotation axis, called true polar wander. But although this phenomenon is indeed thought to occur (driven by slight changes in the Earth's moment of inertia), its path, derived from independent data[8], does not explain the rapid latitude shift of the Hawaiian hotspot in the time between the formation of the two seamounts.

Setting true polar wander aside, the palaeomagnetic data are consistent with a southward drift of the hotspot at a rate of at least 3 cm yr^{-1} before 43 Myr, much faster than Steinberger and O'Connell's model predicts, and little drift after 43 Myr. These data therefore challenge the usual interpretation, also adopted by Steinberger and O'Connell for calculating their time-dependent circulation model, that the kink in the hotspot track reflects a change of plate motion. Of course, if there is no obvious reason why the motion of the Pacific plate should change, a sudden stop of hotspot migration is equally enigmatic.

Although two data points may not be enough to make a strong case, and the possibility of true polar wander complicates the interpretation, Tarduno and Cottrell show that the way to disentangle plate drift and hotspot migration is to study the magnetization of volcanic rocks along a hotspot track in some detail. Palaeomagnetic data are abundant for the continents, but most hotspot tracks lie in the oceans and can only be sampled by ocean drilling. So the difficulties in obtaining reliable magnetization directions are far greater for seamounts than for land-based rocks. But it seems well worthwhile for palaeomagnetists to take up the challenge. ☐

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Immunology

Signal sequences stop killer cells

Eric O. Long

Most proteins destined for the surface of eukaryotic cells possess a signal sequence, which includes a stretch of several hydrophobic amino acids that guide protein translocation into the endoplasmic reticulum during protein synthesis. The fate of amino-terminal signal sequences, found in certain transmembrane proteins, is thought to be much like that of ticket stubs: torn off by an endopeptidase and trashed by further proteolysis.

In an unexpected twist, Braud *et al.*, on

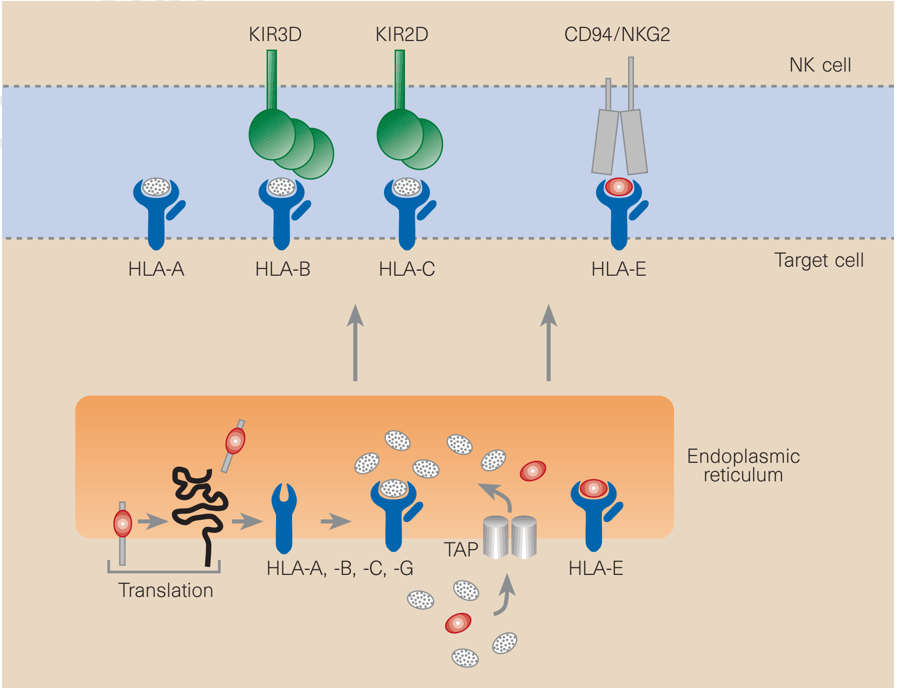

Figure 1 **The ABC...E of natural killer (NK) cell tolerance to self. Two types of receptors specific for self HLA class I molecules inhibit NK cells, each having a distinct mode of HLA class I recognition. The lectin-like heterodimer CD94/NKG2 binds to HLA-E molecules[1], whose transport to the cell surface is limited by the availability and binding of a specific peptide (indicated in red) derived from signal sequences of other HLA class I molecules. The killer cell inhibitory receptors with three (KIR3D) or two (KIR2D) immunoglobulin domains recognize HLA-B and -C, respectively. HLA-B and -C bind many different peptides (stippled), most of which are compatible with recognition by KIR3D and KIR2D. The lower left portion of the diagram illustrates the first steps in synthesis of HLA class I molecules. An amino-terminal signal sequence directs translocation into the endoplasmic reticulum during translation of HLA class I messenger RNA. After cleavage of the signal sequence by an endopeptidase, the HLA class I polypeptide folds and assembles with β_2-microglobulin and a short peptide delivered into the endoplasmic reticulum by the transporter for antigen presentation (TAP). Binding of the signal-sequence-derived peptide to HLA-E is also TAP-dependent[4]. The signal sequence of HLA-E lacks amino acids necessary for binding to HLA-E.**