PLANETARY SCIENCE

Io and the Plasma Torus

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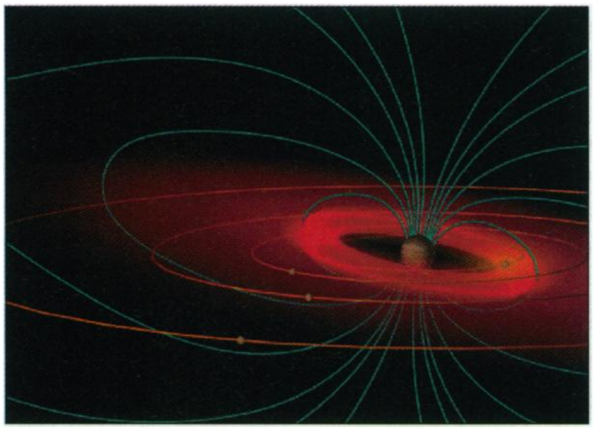
Io, one of the moons of Jupiter discovered by Galileo in 1610, is a bizarre and enigmatic world (*1*). Io's geologic history was once thought to be similar to that of our moon, but Jupiter is 300 times more massive than the Earth and consequently has a much more powerful tidal influence on its tiny satellite. Just a few days before the first Voyager spacecraft encountered Io in 1979, a landmark theoretical report published in *Science* by Peale *et al.* addressed the dissipation of tidal energy on Io and predicted "...widespread and recurrent volcanism..." (*2*, p. 892). The spectacular results of the Voyager spacecraft flybys provided stunning confirmation of this prediction, revealing a dramatic landscape devoid of impact craters, richly colored by volcanic deposits, and littered with active volcanic plumes and hot spots (*3*). Whereas our moon has been geologically inactive for eons, Io is teeming with activity, a dynamic planetary body that presents a rich array of puzzles.

Io's presence has a profound impact on the environment around Jupiter. A unique manifestation of this is the Io plasma torus, a donut-shaped volume of ionized gas concentrated near Io's orbit (see figure). It has long been believed that the torus results from Io's prodigious volcanic activity (*4*). The similarity between the composition of the plasma and the surface of Io, and the fact that the torus envelops Io's orbital corridor, leaves little doubt that torus material has escaped from the satellite. Yet, we also know that material from Io's volcanoes does not have sufficient velocity to escape the satellite directly. Io's volcanic plumes are like fountains, with little hope of ejecting material beyond the gravitational influence of the satellite, much as a fountain is unlikely to eject material from the surface of Earth into interplanetary space. A multistep escape process is required, making it less obvious that there is a direct connection between volcanic outbursts and the plasma torus. Despite many years of trying to prove that a volcanic eruption would result in observable changes to the plasma, that proof has, until now, been elusive. On page 268 of this issue, Brown and Bouchez present results of an observational program that has provided the first evidence that volcanic activity on Io results in observable changes in the plasma torus (*5*).

These observations are particularly important because they show how material escapes from Io to populate the jovian magnetosphere. Generally speaking, the volcanoes are believed to be a primary source of material for Io's tenuous atmosphere (it's surface pressure is about one billionth that of Earth's atmosphere) and much more extended "clouds" of un-ionized atomic particles around the satellite, called "neutral clouds" (*6*). Active volcanic plumes form localized "umbrella atmospheres" and deposit onto the surface volatile material, which takes the form of frost at the generally cold surface temperatures found on Io. Daytime temperatures on Io are, however, warm enough to sublimate some of the frost into the atmosphere. Meanwhile, plasma from the torus, which is confined and propelled at high velocity by the Jupiter magnetic field, is continuously slamming into the satellite, dislodging and energizing surface material and effectively lifting it into the atmosphere, removing it to the neutral clouds. The atmosphere and clouds, which are far too tenuous to significantly impede the plasma, are stripped by knock-on collisions with the plasma particles. The multistep escape scenario depends, then, on (i) volcanoes, as a primary source of gas for the atmosphere and clouds, and (ii) the plasma, which strips the atmosphere and clouds of particles that are subsequently ionized and swept up by Jupiter's magnetic field, themselves becoming part of the plasma torus.



The inner region of the jovian magnetosphere. The Jupiter magnetic field is shown with blue lines, and the Io torus, located at the orbit of Io, is shown in red. The locations of the orbits of the other Galilean satellites, Europa, Ganymede, and Callisto, are also shown in brown. [Figure: courtesy of John Spencer, Lowell Observatory]

But there is a conundrum. In the scenario described, the plasma generates and maintains itself by constantly scavenging particles from Io's atmosphere and neutral clouds. The plasma ions impacting the satellite were themselves sputtered from Io and ionized only days or weeks before. A sporadic perturbation such as a volcanic outburst that increases the density of particles in the atmosphere and clouds provides a larger source of material to supply the plasma. An unstable runaway of plasma density buildup is then implied: More atmosphere and cloud particles generate more ions, which in turn produce more atmospheric particles, ad infinitum, unless some process inhibits this positive feedback. Until the work by Brown and Bouchez (*5*), there has been no general agreement on the limiting process and no consensus on the expected effect of increases in volcanic output on the torus plasma.

Brown and Bouchez (*5*), considered two basic types of limiting processes. First, an increase in plasma density resulting from an atmospheric perturbation causes a much more rapid increase in plasma loss, limiting the buildup of plasma density. Usually plasma is lost when it is hurled outward by the rapid rotation of the confining magnetic field. This outwardly diffusing material encounters the more distant satellites, particularly Ganymede and Europa. Some of the plasma embeds itself into the surfaces of these satellites and, just as on Io, the plasma also sputters material from the surfaces of these satellites to form atmospheres even more tenuous than Io's. Evidence for tenuous atmospheres on Ganymede and Europa has recently been discovered by Hubble Space Telescope observations (*7*) and observations by the Galileo spacecraft, which is currently in orbit around Jupiter (*8*). A second possibility for preventing runaway in the plasma is a mechanism that shields the atmosphere from the plasma. The discovery of a possible magnetic field on Io by the Galileo mission (*9*), for example, provides such a shielding mechanism for the atmosphere.

The Brown and Bouchez work (*5*) clarifies for the first time that the first of these two possibilities, a rapid increase in plasma loss as

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a result of increases in the densities of the atmosphere and neutral clouds due to a volcanic eruption, appears to be operating at Io. If accepted and verified, these observations provide an important piece of the puzzle in the continuing quest to untangle the web of activity that manifests itself on one of the most compelling objects in the solar system.

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IMMUNOLOGY

Reuse of B Lymphocytes in Germinal Centers

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The remarkably diverse immunoglobulins (Igs), which can exist either as secreted antibodies or as membrane-bound antigen receptors on B lymphocytes, can recognize a broad universe of foreign antigens. This is primarily because the gene coding for the Ig antigen-binding site is constructed by a combinatorial joining of several distinct germline gene segments—V, D, and J for the Ig heavy chain, and V and J for the light chain (*1*). V(D)J recombination is initiated by the proteins encoded by recombination-activating genes 1 and 2 (RAG1 and RAG2), which recognize the recombination signal sequences adjacent to each of the V, D, and J coding segments. These proteins generate double-stranded DNA breaks and hairpin structures. After deletion and addition of nucleotides at the coding ends, a DNA binding protein complex that contains Ku70, Ku80 subunits, RAG1, RAG2, and DNA ligase executes V(D)J joining (*2*). The expression of RAG1 and RAG2 is restricted to T and B cells. During early B cell development in fetal liver and bone marrow, RAG1 and RAG2 are induced by an unknown signal or signals at the pro- to pre–B cell stage and initiate Ig gene rearrangement. They are then down-regulated once developing B cells express surface IgM, to prevent expression of two or more antigen receptors (*3*).

It has been thought that B lymphocytes have only one chance to undergo a productive Ig rearrangement during their lifetime. But in fact RAG1 and RAG2 can be induced again in sIgM-positive immature B cells within bone marrow as a consequence of antigen receptor triggering (*4*). This leads to a secondary Ig gene rearrangement, allowing autoreactive B cells (otherwise destined to die) to replace their "bad" autoreactive antigen receptors with new antigen receptors and to become mature normal peripheral B cells.

Now a second exception is described in two reports on pages 298 and 301 of this issue (*5, 6*). Secondary Ig rearrangement also occurs in germinal centers (GCs) during T cell–dependent antibody responses. In the GC, B cells further increase the diversity and improve the affinity of their antigen receptors by somatic hypermutation in rearranged IgV region genes (see the figure). The somatic mutants undergo affinity selection by antigens presented by follicular dendritic cells (FDCs). High-affinity Ig variants pick up antigen from FDCs, present the antigen to T cells in the GC, and differentiate into memory B cells and plasma cells. B cells with low-affinity Ig receptors fail to acquire sufficient antigen and die by apoptosis (*7*). The first hint that mature B cells may undergo secondary Ig gene rearrangement in GCs comes from the observation that GC B cells express RAG (*8–10*). The ability of mature B cells to reexpress RAG was further supported by the demonstration that lipopolysaccharide (LPS) and interleukin-4 (IL-4) are able to induce RAG expression in mature naïve B cells (*9*). Now, using a locus-specific, ligation-mediated polymerase chain reaction assay, Han *et al.* and Papavasiliou *et al.* detected J_κ breaks and new VJ_κ junctions in GC B cell populations, but not in naïve B cell populations from immunized mouse spleen. Signals such as LPS and IL-4 that are capable of inducing RAG expression in naïve B cells induce J_κ breaks and VJ_κ joints in these cells in culture (*5, 6*).

Does secondary V(D)J recombination in activated mature B cells result in the replacement of "old" antigen receptors with "new" ones? Using an antibody that recognizes the idiotype produced by a unique VDJ region (the antigen-binding site), Nussenzweig and colleagues (*5*) showed that secondary Ig rearrangement within these mature B cells correlates with the disappearance of a preexisting idiotype on the cell surface. However, this does not occur in LPS- and IL-4–stimulated B cells whose Ku80 gene involved in V(D)J joining is deleted. These experiments suggest

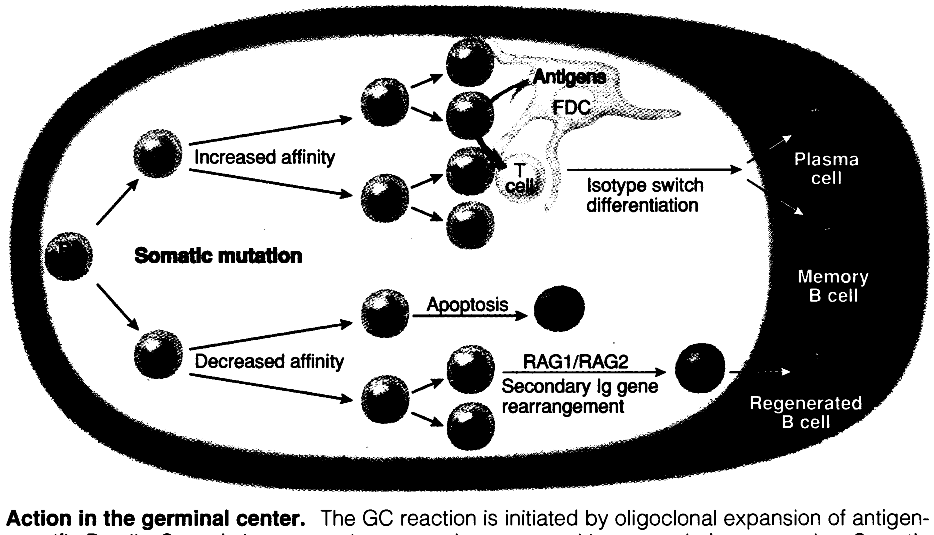

ILLUSTRATION: K. SUTLIFF

Action in the germinal center. The GC reaction is initiated by oligoclonal expansion of antigen-specific B cells. Somatic hypermutation occurs in rearranged Ig genes during expansion. Somatic mutation can increase the affinity of antigen receptors on some B cells. These B cells pick up antigen from FDCs, present it to GC T cells, and differentiate into memory B cells and plasma cells. Somatic mutation can also decrease the affinity of antigen receptors. These low-affinity B cells undergo either apoptosis or secondary Ig gene rearrangement by RAG1 and 2 to become new B cells.

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