

tion with the striatum, neocortical *Dlx-1* expression is eliminated and there is a dramatic (fivefold) reduction in the number of cortical interneurons that express the inhibitory neurotransmitter  $\gamma$ -aminobutyric acid (GABA). Third, GABA-expressing cells in the *Dlx-1/2* double mutant neocortex are as heavily depleted as when the wild-type cortex is detached. Fourth, no cell migration from striatum into neocortex could be seen in dye-labeled slices of the double mutant forebrain.

This is compelling evidence that the GABA-containing, nonpyramidal interneurons of the neocortex—of which there are many—do not arise uniquely from neocortical proliferative regions; rather, there is also a significant source of these cells in the neighboring territory, from a proliferative region that also produces the GABA-containing, medium spiny neurons that populate the striatum. Equally compelling is the evidence that *Dlx-1* or *Dlx-2* homeobox gene function is required, presumably cell autonomously, for emigration from the striatal SVZ, both radially into the striatal mantle and tangentially into the neocortex.

These findings will provoke debate about the status of the cortico-striatal junction. Compartment formation presupposes the early allocation of defined assemblies of precursor cells whose borders are coextensive with the expression domains of genes involved in the acquisition of regional identity. Crucial to the compartment definition is the containment of cell polyclones at a boundary where cell mixing is restricted (3). Consistent with this notion is the finding that cells in the telencephalic VZ disperse tangentially, yet they never cross from neocortex to striatum (2). Furthermore, an adhesive difference has been shown between neocortical and striatal cells that would favor their segregation or nonmixing (8). However, clonal analysis has suggested extensive movement of cells between neocortex and subcortical regions (9), and now we see striatal precursors producing neocortical neurons. How can these apparently conflicting data be resolved?

Where there is no apparent restriction to movement, the cells involved may well be already-specified neurons that are migrating along preassigned vectors into their neighbor's territory, rather than passively stumbling into it. In the hindbrain, where a metamer series of compartments (rhombomeres) are formed, rhombomeric domains of the VZ remain completely lineage-restricted throughout neurogenesis, although inter-rhombomeric migration of cells occurs within the mantle (10). Lineage restriction thus exists only for the VZ (3), whereas the mantle is unrestricted. A similar situation may prevail in the forebrain, where no violation of the cortico-striatal junction has ever been noted for VZ cells. The adhesion prop-

erties responsible for holding incompletely specified precursor cells together would be lost as the cells acquire their regional identity and commence migration (8). The loss of compartment properties during differentiation may indeed be a prerequisite for organized migration, a process that would require a switch in cell-cell affinity.

How are *Dlx*-expressing cells guided into the cortex? Being orthogonal to the long axes of radial glial cells, their path is unlikely to be laid out by the glial scaffold customarily used by migrating neurons. *Dlx*-expressing cells may be guided by preexisting axon tracts (11): axons of cortical projection neurons do arrive in the striatum at the appropriate time (12). Time-lapse analysis of brain slices from *Dlx-GFP* transgenic mice might be useful here and could also show the full extent of the migratory cohort.

There are many examples of tangential migration by neurons, or their precursors, within the cortex (13), but the molecular regulators of migration, whether tangential or radial, are largely unknown; the particular significance of the new work by Anderson *et al.* (4) is the discovery that *Dlx* homeobox genes are (possibly direct) regulators of the

process. With this crucial step in place, the next will be to identify downstream targets of *Dlx* and thereby the cellular machinery required for migration.

## References and Notes

1. J. L. R. Rubenstein, S. Martinez, K. Shimamura, L. Puelles, *Science* **266**, 578 (1994).
2. G. J. Fishell, C. A. Mason, M. E. Hatten, *Nature* **362**, 636 (1993).
3. A. Lumsden and R. Krumlauf, *Science* **274**, 1109 (1996).
4. S. A. Anderson, D. D. Eisenstat, L. Shi, J. L. R. Rubenstein, *ibid.* **278**, 474 (1997).
5. S. A. Anderson *et al.*, *Neuron* **19**, 27 (1997).
6. M. H. Porteus, A. Bulfone, J. K. Liu, L. C. Lo, J. L. R. Rubenstein, *J. Neurosci.* **14**, 6370 (1994).
7. C. G. Van Eden, L. Mrzljak, P. Voorn, H. B. M. Uylings, *J. Comp. Neurol.* **289**, 213 (1989); J. A. De Carlos, L. Lopez-Mascaraque, F. Valverde, *J. Neurosci.* **16**, 6146 (1996).
8. M. Goetz, A. Wizenmann, S. Reinhardt, A. Lumsden, J. Price, *Neuron* **16**, 551 (1996).
9. C. Walsh and C. L. Cepko, *Science* **255**, 434 (1992).
10. R. Wingate and A. Lumsden, *Development* **122**, 2143 (1996).
11. N. A. O'Rourke, *Neuron* **16**, 1061 (1996).
12. C. Metin and P. Godement, *J. Neurosci.* **16**, 3219 (1996).
13. M. B. Luskin, *Neuron* **11**, 173 (1993); C. Lois, J.-M. Garcia-Verdugo, A. Alvarez-Buylla, *Science* **271**, 978 (1996).
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## PLANETARY SCIENCE

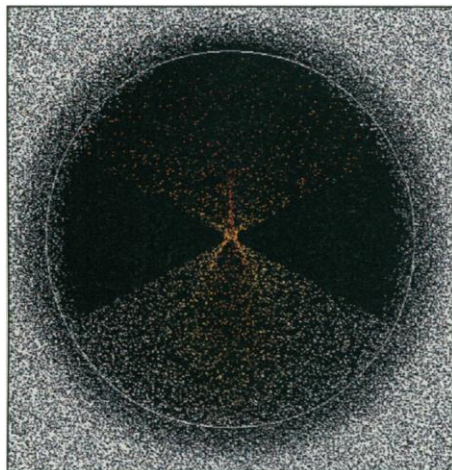
# Lensing by Triton's Atmosphere

William B. Hubbard

During a total lunar eclipse, Earth-based observers can see the moon glowing with a coppery color as it passes through the center of Earth's umbra. An observer on the moon at the same time would see Earth's limb illuminated as a ring of refracted, reddened sunlight. On much larger spatial scales, and much more rarely, a more distant planet occults a more distant star in an alignment similar to a total lunar eclipse. In this case, when the stellar image is within a critical distance from the planet-observer line, light from the star refracts in unison around the planet's limb, forming a phenomenon known as the central flash. Central flashes have been observed during stellar occultations by Mars, Neptune, Saturn, and Saturn's largest moon, Titan. On page 436 of this issue of *Science*, Elliot *et al.* report the first observation of a central flash produced by Neptune's large and interesting moon Triton (1).

When Voyager 2, so far the only spacecraft to visit Neptune, encountered that planet in 1989, investigators detected a tenuous nitrogen-rich atmosphere on Triton (2). They measured the density and surface pressure by observing the bending of radio waves transmitted through Triton's atmosphere to Earth as the spacecraft was occulted. The spacecraft occultation was not close to central, and no central flash could have been seen in any case because the bending was very slight (maximum of about  $10^{-6}$  radians). The geometry of a stellar occultation by Triton as seen from Earth is vastly different. In this case, the maximum bending angle, still only about  $3 \times 10^{-7}$  radians, is large enough to give a deflection of one Triton radius by the time the ray gets to Earth, enough for a central flash. Bending of light into the shadow is enormously sensitive to the atmospheric structure, for it depends on spatial second derivatives of the atmospheric density. In the central flash region, the global second derivatives determining the atmosphere's projected radius of curvature become most important.

The author is at the Lunar and Planetary Laboratory, University of Arizona, Tucson, AZ 85721, USA. E-mail: hubbard@lpl.arizona.edu



**Simulation of the distribution of starlight** in the occultation shadow of a satellite with a dynamically distorted atmosphere and nonuniform hazes. The density of points is proportional to the stellar flux at that point in the shadow. The solid curve shows the geometrical limb of the satellite. The central caustics have been exaggerated by a factor of 4 for clarity.

Even without an atmosphere, a spherical occulter can produce a bright spot in the center of its shadow, the so-called Poisson spot, produced by constructive interference of wavelets diffracted around the sphere's edge.

No airless planet can be so perfectly spherical, but an imperfectly spherical atmosphere refracts light into central caustics (that is, regions where light rays cross over one another), with the positioning and size of the caustics determined by the varying curvature of the atmosphere along the limb. Such varying curvature must be produced by atmospheric dynamics if the underlying gravity has spherical symmetry. For more distant occultations, with the propagation distance measured in light years rather than astronomical units—the so-called microlensing events used to search for unseen objects in our galaxy—the main source of bending is gravity rather than refraction in neutral gas, and the caustics are formed by asymmetries in the gravity field (3).

The only previous observation of a central flash by a satellite was in 1989, when the center line of a stellar occultation by Saturn's satellite Titan passed over western Europe and yielded seven closely spaced observations of Titan's central flash, along with six more-distant observations of the shadow (4). The central caustics were unexpectedly large and gave evidence for rapid and complex zonal flows in Titan's high atmosphere, along with an equally complex distribution of high haze particles. The figure shows a numerical simu-

lation of Titan's occultation shadow based on these measurements.

Although several stellar occultations by Triton have been observed to date, the 1995 event observed from Hawaii by Elliot *et al.* is the only one where observers were fortuitously located close enough to the center line to see the central enhancement of the signal; their path did not penetrate within the central caustics but came close enough to reveal their presence. If Triton's atmosphere were in perfect hydrostatic equilibrium rotating with the solid surface, it should be almost perfectly spherical, and the shadow should have circular symmetry. Evidently it does not. Effects from the hazes that Voyager 2 found in Triton's atmosphere have not yet been revealed in any of the stellar occultation data, but the results of Elliot *et al.* suggest that the analog of the illustration for Triton will be equally complex when enough data have been obtained to construct it. The underlying model for Triton's atmosphere is likely to be a dynamical one.

#### References

1. J. L. Elliot, J. A. Stansberry, C. B. Olkin, M. A. Agner, M. E. Davies, *Science* **278**, 436 (1997).
2. G. L. Tyler *et al.*, *ibid.* **246**, 1466 (1989).
3. S. J. Peale, *Icarus* **126**, 269 (1997).
4. W. B. Hubbard *et al.*, *Astron. Astrophys.* **269**, 541 (1993).

#### SOLID-STATE CHEMISTRY

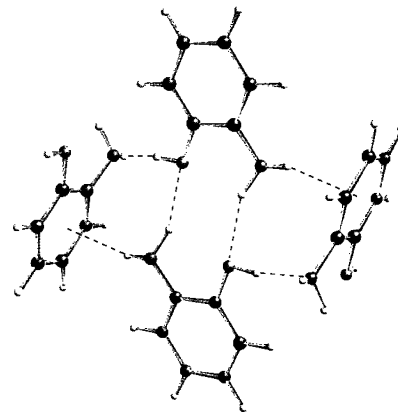
## Crystal Gazing: Structure Prediction and Polymorphism

Gautam R. Desiraju

Crystal engineering, the design of organic solids with specified architectures and therefore particular physical or chemical properties, continues to elicit intense interest (1, 2). Crystals are built with molecules, and ideally one would like to predict the crystal structure of an organic substance from nothing more than its molecular structure. Indeed, given the molecular basis of organic chemistry, such a goal seems almost intuitive. A particular molecular structure can also yield more than one crystal structure, and this phenomenon of polymorphism (3) has been in the forefront, most notably in litigation surrounding the widely used ulcer medication Zantac (4).

The major obstacle in routinely predicting crystal structures from molecular struc-

tures is that in any kind of molecular recognition, and this includes the recognition between identical molecules during crystallization, it is the dissimilar functionalities that come into closest contact and not the similar surfaces (5). Steric and electronic complementarity thus characterize the crystallization event. The functional group approach, so central to molecular chemistry, is of limited applicability because the supramolecular behavior of a particular functional group depends acutely on the nature and even the location of the other functionalities in the molecule. This issue is greatly complicated by the fact that hydrocarbon residues, not normally considered functional groups in molecular chemistry, are quite respectable supramolecular functionalities. All this means that the crystal structures of many "simple" organic compounds need not be simple at all. What is surprising, however, and this is what provides the vital impetus to



**Odd bonds.** An unusual N-H... $\pi$  hydrogen bond is found in the crystal structure of 2-aminophenol. Although conventional O-H...N and N-H...O hydrogen bonds are also seen, saturation of the hydrogen bonding capabilities of the -NH<sub>2</sub> and -OH groups with conventional hydrogen bonds, as predicted (6, 7), is not observed.

the subject, is that although the energy differences between the plethora of putative crystal structures for a given molecule can be quite small, many organic compounds are not polymorphic. Molecules seem to know exactly how to crystallize, even as chemists seem unable to accurately foresee such events.

Sometimes, it is possible to predict the outcome of crystallization. In seminal papers, Ermer (6) and Hanessian (7) and their col-

The author is in the School of Chemistry, University of Hyderabad, Hyderabad 500 046, India. E-mail: grdch@uohyd.ernet.in