opacity which governs the outward transport of energy by radiation and which depends on the star's temperature and density. If this is the true explanation of the giant phenomenon it depends on rather detailed physics. Iben and Renzini point out that it cannot explain all giants, for in stars less massive than about 1.2 solar masses, most of the energy in the relevant region is carried by convection.

Alternatively, the relationship between the pressure P and density ϱ inside the stars could be a factor. This can be expressed in terms of an index n defined as a function of the pressure–density gradient: $n/(n+1) = \mathrm{d}(\log \varrho)/\mathrm{d}(\log P)$. Although the interdependence of ϱ and P, and hence n, varies inside a star, some insight can be gained by studying models with constant n.

In homogeneous stars, n is usually in the range 1.5–3; as $n \rightarrow 5$, the model radius of the star tends to infinity. Eggleton and Faulkner argued that the combination of a shell of hydrogen burning and a discontinuity in chemical composition at the core surface can produce a local value of n greater than 5, which is sufficient to produce a very large star[7]. Or, according to Yahil and van der Horn, a steep density gradient, equivalent to a large n, at the edge of the core generates the same effect[8].

Applegate[1] now argues that it is the increase in luminosity of the hydrogen-burning shell that is the crucial factor. There is a maximum luminosity which can be carried by an overlying envelope whose opacity is given by Kramers' formula. If this luminosity is exceeded, the star expands rapidly until the energy can be radiated away. His detailed discussion applies to a star the mass of the Sun, for which the arguments of Iben and Renzini[6] are not valid. Although Applegate singles out the rise in luminosity as the crucial factor he indicates that there must be an abrupt reduction of density at the surface of the core, in agreement with the n-dependent models[7,8].

I suspect that the argument about what causes what is not yet over. As there should be a few thousand million years before the Sun becomes a red giant and extinguishes life on Earth, there will be time for some further thoughts. □

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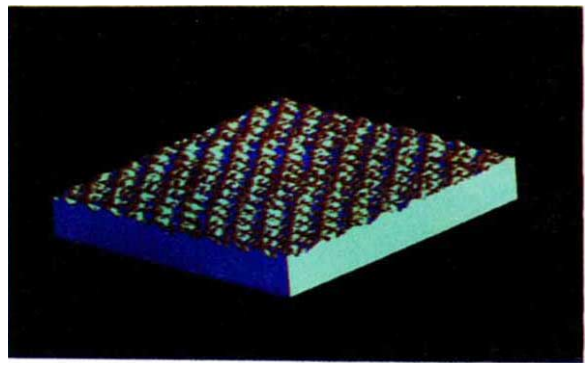
Microscopy

Electrons that make waves

C.F. Quate

SCANNING tunnelling microscopes, recently developed high-resolution devices that trace the form of surfaces using an atomic-scale tip, typically reveal atomic and molecular details, often with surprising clarity. But because the technique is sensitive to variations in the density of charge at the sample surface, usually determined by the ion positions, other electronic effects can also become apparent. On page 55 of this issue[1], Wu, Zhou and Lieber present images of charge density waves, spontaneous fixed or mobile corrugations of the charge distribution, at the surface of the metal tantalum disulphide.



Projected view of an image of TaS_2 taken with a scanning tunnelling microscope at 236 K. The large hill-like structures are the maxima of the triclinic charge density wave (CDW) present at this temperature and the smaller modulation arises from the surface sulphur atoms (lattice constant 0.33 nm). In this view, the discommensurations forming the boundaries between two commensurate CDW domains are clearly seen as jogs introduced into the lines of CDW maxima. (For the best view of the discommensurations, hold the page up to eye level and look along the diagonal.) The image is 15 nm square. (Courtesy of John Clarke.)

In the scanning tunnelling microscope (STM), a sharp metal tip is placed close to the sample and mechanically scanned across the surface. The tip is tapered to a single atom at the apex, which sets the limit on resolution. The apex is held 5–10 Å from the surface, a distance comparable with the spacing between atoms in the solid (2–3 Å). In this configuration, the moving electrons can tunnel either to adjacent atoms in the surface or to the single atom at the tip. The current to the tip is proportional to the density of electronic charge at the characteristic 'Fermi' energy of the conducting electrons. The charge density can be imaged by scanning the sharp tip across the surface of the sample. Contours of constant brightness in the image correspond to contours of constant electron density on the surface.

On the surface of semiconductors and of many other materials, the contours of maximum electron density surround the nuclei of the atoms or are associated with molecular orbitals involved in the bonding between atoms. For these surfaces, the observed topography directly reflects the atomic structure. For other surfaces the periodicities in distribution of charge can differ from the periodicity of the lattice, and for these surfaces topographical data are not available. The work of Wu *et al.* reported in this issue[1] is a graphic illustration of the distinction between these two situations. The authors studied the surface of tantalum disulphide (TaS_2), a material easily cleaved to expose a fresh, clean surface that is inert and not easily oxidized. At high temperature, TaS_2 is a metal with a resistivity that is 100 times that of copper. At lower temperatures, the material undergoes a first-order phase transition to a new electronic state[2,3]. The new phase, called a charge density wave (CDW), is a result of the strong coupling between the electrons and the vibrating ions in the lattice. The distribution of charge in the new state is modulated with a periodicity much larger than the periodicity of the ions. Superimposed on the ionic lattice there is an 'electron lattice' that is revealed in the new STM images of Wu *et al.*. The ionic lattice, determined by the positions of the atoms in the solid, does not show in the images.

In a second experiment, Wu *et al.* use a crystal chemically modified by replacing 10 per cent of the tantalum atoms with titanium atoms. With this substitution, the CDWs are suppressed and the ionic lattice reappears in the STM images, furnishing dramatic evidence that the tunnelling current in the STM is a measure of the surface charge density.

Electronic phase transitions, such as the transitions to ferromagnetism, to superconductivity and to charge density waves, are problems central to solid-state physics. The transition to CDWs is a significant effect: nearly one electron from each atom is transferred to the new state[4] producing the strong modulation observed in the charge density.

When first introduced[2], charge density waves seemed to be very esoteric objects

with little relevance to the real world. They can be seen in X-ray diffraction patterns as satellite 'wings' to the principal Bragg diffraction peaks generated by the ion lattice. They can dramatically alter the resistivity and magnetoresistance (variations of resistance in applied magnetic fields) of aligned metal wires. And because CDWs are a result of interactions between electrons and ion-lattice vibrations, they can affect the elasticity of samples.

Coleman, Hansma and co-workers were the first to show[5] that all forms of CDWs can be studied with the STM. Several groups[6-8] find that the properties inferred from diffraction studies[4] can be obtained directly from the STM images. It turns out also that a small defect in the substrate can suppress the CDW near the defect[8].

Clarke and co-workers[9] have studied the four different charge density wave phases that occur in TaS_2 in the range of temperatures 77–370 K. At the highest temperatures the waves are incommensurate — the wavelength is not an integral multiple of the ion-lattice spacing. At the lowest temperatures, the waves are wholly commensurate. In between there are two nearly commensurate phases, one of which (the triclinic phase, see figure) is obtained on warming only. Significantly, the transition temperatures at the surface as measured with the STM coincide with those measured for the bulk, meaning that CDWs extend to the surface layer unaltered in character.

This body of work is extensive but incomplete. The motion of CDWs has not yet been observed with the STM. In materials such as $NbSe_3$, a modest electric field will dislodge the standing waves of charge density from their 'pinning' sites and convert them to travelling waves that carry current through the sample. It would be fascinating to study this mobile "lattice within a lattice"[4] with the STM. □

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RNA processing

The post-RNA world

Miranda Robertson

INTRONS, in the light of the recently recognized catalytic properties of RNA, have come to be widely regarded as the legacy of a primordial RNA world[1], now largely expunged by bacteria in the interests of economy, exploited by metazoa for versatility, and tolerated by yeast. As part of this general scheme, it has been argued[2] that the self-splicing introns of latter-day organisms such as *Tetrahymena*[3] are the direct descendants of autocatalytic introns in the original RNA genome; and that in the course of evolutionary time the catalytic function of introns has escaped into the ribonucleoprotein particles (snRNPs) that in modern metazoa mediate their removal, leaving behind only a minimum of conserved bases to guide cleavage and splicing. Yeast introns, whose sequences are more conserved, can be interpreted as an intermediate-to-late stage in the release of the intron from the constraints imposed by its catalytic origins; and other variant species of intron (see Fig. 1) can be understood as intermediates of different kinds in the same progression[2].

The quest for unity in the diverse taxonomy of surviving introns is of more than academic interest; for if yeast and mammalian mechanisms (for example) are only minor variants of one another, then the mammalian mechanism becomes susceptible to investigation by yeast genetics, and the extensive biochemistry of mammalian splicing pathway components becomes available to yeast geneticists.

On the whole, the unified view has been increasingly upheld by the search for homologues of the mammalian snRNPs, a trend that was maintained at this year's Cold Spring Harbor Meeting on RNA processing* where the differences between mammals and yeast continued to evaporate while trans-splicing, an eccentricity of trypanosomes and nematodes, emerged as an interesting variation on the metazoan theme, as foreseen by Sharp[4]; and an important focus for the future was signalled by the inclusion of a talk on the central part played by alternative splicing in the determination of sex in *Drosophila*.

Taxonomy of introns

Introns are removed from mammalian RNA precursors (pre-mRNAs) by two successive cleavage and splicing reactions. In the first, a conserved guanosine at the 5′ end of the intron is joined to an adenosine a short distance from its 3′ end to form a lariat, freeing the 3′ end of the upstream exon. In the second reaction, the 3′ end of the upstream exon is joined to the 5′ end of the downstream exon with the release of the intron lariat (see Fig. 1). These reactions are mediated by snRNPs designated U1, U2, U4, U5 and U6 whose assembly into a spliceosome is outlined in Fig. 2 and its legend.

Yeast introns are distinguished from mammalian introns principally by the possession of a conserved sequence termed the UACUAAC box which specifies the branch point for the lariat and to which U2 binds by complementary base-pairing[5]. Although mammalian introns do not contain UACUAAC boxes, a degenerate consensus sequence can be derived from bases adjacent to the adenosine at the branch point; and that and the fact that mammalian cells will remove yeast introns has strongly suggested that despite the difference in sequence conservation, and the fact that the yeast U2 is six times larger than its mammalian homologue, branch formation in the two is essentially the same process.

Further support for this inference has been provided by manipulation of the branch-point sequences in synthetic globin constructs in which the first exon is joined to tandem duplicates of intron 1 and exon 2 so that one 5′ splice site has a choice between tandemly duplicated 3′ sites. Normally, exon 1 will become spliced to the closer of the two 3′ sites; but Robin Reed (Harvard University) reported that alterations to the adjacent branch-point sequence (presumably disrupting complementarity to U2) can induce splicing to the distal exon. Using a similar construct, Yuan Zhuang (Yale University) has been able to achieve the same result by inserting a UACUAAC box in an appropriate position in the more distal intron. Thus, mammalian U2 has the same sequence preference as the yeast U2 but is more tolerant. Moreover much of the substantial size difference between the yeast and the mammalian U2 RNA is attributable to a ~ 1-kb dispensable domain in the yeast U2 that intervenes between two regions of conserved secondary structure (Elizabeth Shuster, University of California, San Francisco), and so seems unlikely to signify any fundamental functional distinction[6].

Plethora of proteins

Plainly, complementary base-pairing plays an important part in the binding of U2 (and other snRNPs) to intron sequences; but an increasing number of protein factors is now known to have intervened in the assembly of the spliceosome since its (putative) ribozymal origin. One such, U2 snRNP auxiliary factor (U2AF), is thought to account for a second import-

*The Cold Spring Harbor Meeting on RNA Processing, Cold Spring Harbor, 11–15 May 1988.