

rodents have more than a thousand. A complete characterization of the repertoire of olfactory receptive ranges will require measurement of the responses of all receptors to all possible ligands. *Drosophila* seems to be the best model for such a venture because it has only about 60 odorant receptors<sup>7</sup>. These receptors are divided between two distinct chemosensory organs, the antenna and the maxillary palp. In their study<sup>2</sup>, Hallem and co-workers have characterized 31 of the 32 receptors expressed in the antenna. So perhaps the greatest merit of their work is its comprehensiveness: it describes, in remarkable detail, the receptive ranges of almost an entire chemosensory organ, albeit to a (necessarily) limited set of odours.

Most of the odorant receptors tested responded to a relatively broad, but nevertheless specific, spectrum of ligands. This is consistent with the response properties of sensory neurons in other organisms and with the tuning of neurons in the first olfactory processing centre in the brain. Precise odour information is therefore encoded combinatorially in activity patterns across multiple neurons. This notion was formulated

more than 50 years ago<sup>8</sup> and has since been examined in detail in many organisms<sup>9</sup>. The study by Hallem *et al.*<sup>2</sup> provides a molecular basis for this view of olfactory coding. Not only is this necessary for understanding the link between odorant receptors and the neural output of sensory neurons, but it will also allow further studies of receptor-ligand interactions — interactions that ultimately constrain olfactory coding strategies and constitute the keyholes through which the brain views the world of odours. ■

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## Superconductivity

# Why the temperature is high

Jan Zaanen

According to a new empirical law, the transition temperature to superconductivity is high in copper oxides because their metallic states are as viscous as is permitted by the laws of quantum physics.

**D**issipation is obvious in the human environment. The phenomenon describes how useful energy is eventually converted into microscopic disorder, which is perceived by us as a rise in temperature. But viewed from the fundamental perspective of quantum physics, dissipation is not at all obvious. A striking example is the superconductor — a quantum state of matter in which electrical currents flow without friction. Heat is the enemy of this state and above a certain temperature, the transition temperature, dissipation takes over again. Bardeen, Cooper and Schrieffer's 1957 explanation of superconductivity (in terms of paired electrons) seemed to be one of the great triumphs of twentieth-century physics — until the discovery in 1986 of a new class of superconductors with very high transition temperatures<sup>1</sup>. Despite years of intense research, these high-temperature copper-oxide superconductors are still on the list of the great mysteries of physics<sup>2</sup>.

On page 539 of this issue, Homes *et al.*<sup>3</sup> report their discovery of a simple but counter-intuitive empirical law for superconductors, a law that is so general it applies equally well to conventional and to high-temperature

superconductors. The law (let's call it Homes' law) states that transition temperature is proportional simply to the strength of the superconducting state at zero temperature (the superfluid density) multiplied by the quantity that expresses how efficiently electrical currents are dissipated in the normal state above the transition temperature (the electrical resistivity). The ramifications of this law for the copper-oxide superconductors are interesting. Although their transition temperatures are high, the superfluid densities of these superconductors are much smaller than those of the conventional superconductors. Why are the high-temperature superconductors so successful at fighting heat? Homes' law implies that it is because their normal states are extremely dissipative. In fact, according to the laws of quantum physics, it is impossible for any form of matter to dissipate more than these metals do; their transition temperatures are as high as they can be, given the ineffectual nature of the zero-temperature state.

Homes' law is exactly the kind of thing that physicists like: it is simple, quantitative, general, but at the same time surprising. It is no surprise, though, that transition temperature

is connected to the superfluid density — many copper-oxide superconductors are already known to obey Uemura's law, in which the two quantities are simply proportional<sup>4,5</sup> (all equations are given in Fig. 1). Instead, Homes' law relates the superfluid density to the product of transition temperature, conductivity (which is the inverse of resistivity) in the normal state at the transition temperature, and a universal constant (which has a value of roughly 40). Homes' law is valid when Uemura's law fails, even for conventional superconductors. The conductivity term reflects the capacity of the normal state to dissipate electrical currents, but why is it this quantity that ties the zero-temperature state (the superfluid density) to the transition temperature? Even for an expert this is puzzling. Although Homes' law can be rationalized for both high-temperature<sup>2</sup> and conventional<sup>6,7</sup> superconductors, the kinds of argument needed in each case are utterly different.

Homes' law has a deep but simple meaning in the case of high-temperature superconductivity (in conventional superconductors it is much more complicated). Its subtlety is clear through the straightforward technique of dimensional analysis: both sides of the equation should be expressed in the same units, and these units are inverse seconds squared, or  $s^{-2}$ . Starting on the left-hand side of Homes' equation (Fig. 1), what has the strength of the superconductor, its superfluid density, to do with time? Well, electromagnetic radiation cannot enter a superconductor when its frequency is lower than the 'superconducting plasma frequency' (which has units of  $s^{-1}$ ). The square of this quantity is a quantitative measure of the strength of the superconductor (it can be expressed in terms of the density of electrons participating in the frictionless currents) and has units of  $s^{-2}$ .

Turning to the right-hand side of Homes' equation, the normal-state conductivity quantifies dissipative electrical transport. This conductivity can also be related to a plasma frequency, but this time the plasma frequency is associated with the density of mobile electrons in the normal state; another poorly understood empirical relation, Tanner's law<sup>8</sup>, insists that in high-temperature superconductors the density of mobile electrons in the normal state is four times the density in the superconducting state. In the normal state, there is another timescale, as well as the plasma frequency: it takes a characteristic period of time (the relaxation, or inelastic-scattering, time) to dissipate electrical currents into heat. So conductivity has the dimension of inverse seconds, corresponding to the square of the plasma frequency multiplied by the relaxation time (Fig. 1).

To balance Homes' equation dimensionally, we need one more factor on the right-hand side with dimension inverse seconds. This must come from the transition temperature. Temperature is easily converted into

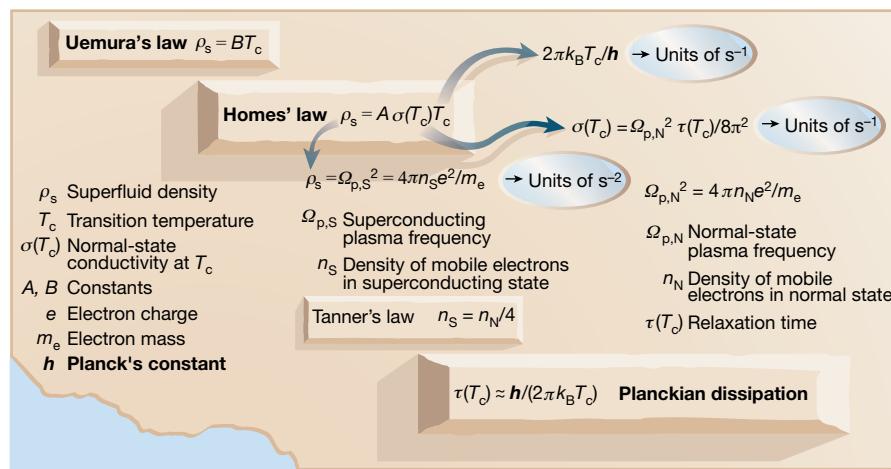


Figure 1 Planckian dissipation and high transition temperatures. Homes *et al.*<sup>3</sup> have established a universal relation between the superfluid density, the normal-state conductivity and the transition temperature for high-temperature, copper-oxide superconductors. Further insight comes from a dimensional analysis of the equation: given that both sides of the equation must have units of  $s^{-2}$ , the identification of the transition temperature with units of inverse seconds brings Planck's constant into play. This quantum connection is the crux of the matter. Bearing in mind Uemura's law<sup>4</sup>, the quantum physical constraint on the relaxation time — planckian dissipation — explains why the transition temperature for copper oxides is so high.

units of energy, through Boltzmann's constant ( $k_B$ ). But to convert energy into time requires quantum physics: the uncertainty principle relates energy and time through Planck's constant,  $h$ . Putting all these pieces together, we arrive at a rather surprising outcome: Homes' law reduces to the statement that the characteristic timescale for dissipation in the normal state of high-temperature superconductors arises from expressing the transition temperature in units of time through Planck's constant.

This timescale turns out to be very, very short — in fact, the laws of quantum physics forbid the dissipation time to be any shorter at a given temperature than it is in the high-temperature superconductors. If the timescale were shorter, the motions in the superfluid would become purely quantum mechanical, like motion at zero temperature, and energy could not be turned into heat. In analogy with gravity, this timescale could be called the 'Planck scale' of dissipation (or 'planckian dissipation'). That the normal electron fluid in high-temperature superconductors is at the quantum limit of dissipation does not come as a surprise. To reach this limit, the quantum system has to fulfil very specific requirements<sup>9</sup> — it must be 'quantum critical', with dynamics that seem the same on all scales in time and space. There is, in fact, evidence for the quantum-critical nature of the normal state in high-temperature superconductors<sup>10</sup>, including an independent confirmation of planckian dissipation.

What is so surprising about Homes' law is that it relates planckian dissipation to the transition temperature. Uemura's law had already signalled the connection of the superfluid density to the transition temperature, through a simple constant. But what sets the

value of that constant for each compound? Uemura's law and Homes' law are both valid for high-temperature superconductors, so Uemura's constant of proportionality must match the corresponding term in Homes' law — the normal-state conductivity multiplied

by a universal constant (Fig. 1). Because the normal state is a planckian dissipator, with conductivity as small as is permitted by Planck's constant, the transition temperature for copper oxides is consequently high.

Uemura's law, Tanner's law, planckian dissipation — these are extremely simple, empirical relations, particular to high-temperature superconductivity. Conventional superconductivity lacks this kind of simplicity. This is even true for Homes' law. Although it applies to conventional superconductors, it works there for entirely different — and far more complicated — reasons than planckian dissipation<sup>6,7</sup>. Why should there be this extraordinary simplicity for high-temperature superconductivity? We have as yet no clue, which is why this phenomenon is still on that list of mysteries. ■

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## Cell biology

# How to build a cell junction

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Structures of the protein vinculin reveal drastic conformational changes associated with binding to its partners in cell-adhesion contacts. These changes might let vinculin regulate the assembly of these complexes.

The development and organization of tissues depends on adhesive junctions, structures that enable cells to stick to one another and to attach to the extracellular matrix. These highly dynamic multi-protein complexes reach from the cytoplasm through the cell membrane to the outside of the cell. Linking intercellular adhesion proteins to the cytoskeleton enables, for example, remodelling of epithelial sheets during development. Similarly, cell migration depends on coordinating adhesion to the extracellular matrix with changes in actin polymerization. Papers by Liddington and colleagues (Bakolitsa *et al.*, page 583 of this issue<sup>1</sup>) and by Izard and co-workers<sup>2–4</sup> show how vinculin, a protein found in the cytoplasmic regions of certain types of junction, might regulate the assembly of these complexes.

Vinculin is found in two varieties of junction: adherens junctions and focal adhesions. Adherens junctions mediate

cell–cell adhesion using proteins called cadherins that span the cell membrane, contacting cadherins on other cells and linking to the actin cytoskeleton inside the cell. Focal adhesions, meanwhile, fasten cells to the extracellular matrix, with other proteins — integrins — forming a bridge across the cell membrane from matrix to cytoskeleton.

Vinculin consists of a 'head' region (Vh) of about 850 amino acids linked to a 'tail' (Vt) of roughly 200 amino acids. When the head and tail regions are made as separate proteins, they can bind to other components of the junction complexes. Vh binds to talin, a protein that interacts with the tails of integrins in focal adhesions; it can bind to  $\alpha$ -catenin, a homologue of vinculin found in adherens junctions; and it can bind to  $\alpha$ -actinin, another actin-binding protein found in both focal adhesions and adherens junctions. The Vh–Vt linker is a binding site for VASP, a regulator of actin polymerization. And Vt binds to filamentous actin.