quired (*17*). Nonetheless, the new reports identifying the importance of NgR in preventing neuronal regeneration represent a big step forward in our understanding of the molecular pathways that impede regeneration in the CNS. The fact that these reports provide a point of convergence—and therefore a potential reduction in the number of interventions necessary to promote nerve regeneration—is also good news.

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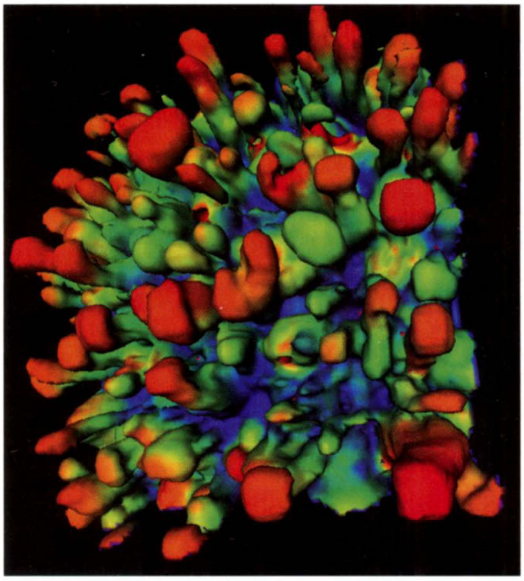
PERSPECTIVES: ASTRONOMY

The Secrets Behind Supernovae

H.-Th. Janka

Once every second, somewhere in the universe a massive star is disrupted in a supernova explosion. Visible even at cosmic distances, these stellar catastrophes provide valuable information about the history of star formation in the universe. Ejecting several solar masses of stellar debris, they enrich the interstellar medium with heavy elements from millions of years of quiescent nuclear burning, and with radioactive nuclei that are freshly synthesized during the star's violent death.



Three-dimensional supernova simulation. The perspective image shows convective mixing in a newly formed neutron star. The mushroom-shaped structures are a result of hydrodynamic instabilities (*19*). The colors represent different fluid entropy values (blue, low; red, high) on a surface of constant proton-to-neutron ratio. [Adapted from (*19*)]

As brilliant as it may be, a supernova explosion is only a weak side effect of a much more energetic event. Theory suggests that as the iron core of the exploding star collapses to form a neutron star or black hole, most of the gravitational binding energy is carried away by neutrinos. This prediction was confirmed by the detection of two dozen of the 10^{58} neutrinos from Supernova 1987A in the underground experiments of Kamiokande, Irvine-Michigan-Brookhaven, and Baksan. Typically, only 1% of the released energy goes into kinetic energy of the ejecta, and only a small fraction of this energy is converted to electromagnetic radiation.

How is energy transferred from the collapsing compact remnant to the matter that gets ejected? Understanding this driving force of the explosion is crucial for predicting remnant masses, explosion energies, and nucleosynthetic yields. It is thus essential for establishing the theoretical link between the properties of massive stars and the observables of supernova explosions. Unfortunately, observations have so far been unable to constrain the processes that take place in the collapsed core of a star.

Future measurement platforms may provide the required data by allowing thousands of neutrinos and possibly gravitational waves to be measured in a future supernova in our Galaxy. But current knowledge is based mainly on numerical simulations and analytic analysis. Despite more than 30 years of research and increasingly detailed computer models, there is still no satisfactory understanding of the start of the explosion.

Stellar iron cores become gravitationally unstable when energetic photons begin to split iron-group nuclei into α particles and free nucleons (protons and neutrons). At the same time, electrons are captured by nuclei and free protons, thereby reducing the pressure even more and producing large numbers of electron neutrinos. The latter can leave the star unhindered until they get trapped as the density grows. Within less than a second, the inner part of the core collapses to nuclear densities and then resists further compression due to the onset of nucleon degeneracy and repulsive nuclear forces.

At this moment, a hydrodynamical shock wave is launched and propagates outward through the still supersonically infalling outer core. There is general agreement that this shock cannot cause an explosion directly. It suffers from severe energy losses by photodisintegration of iron nuclei and neutrino emission and therefore stalls at a radius of 100 to 200 km.

But just fractions of a second later, the situation has changed. The temperature behind the standing shock has dropped so much that energetic neutrinos, which leave the hot, nascent neutron star in large fluxes, are readily absorbed by free nucleons in the postshock layer (the layer right behind the supernova shock). If this energy deposition is large enough, it can revive the stalled shock and lead to a successful "delayed" explosion (*1*, *2*). Because the ultimate fate of the shock is determined by a delicate rivalry between competing processes, detailed computer models are needed to answer the question of whether the energy transfer to the shock by neutrinos is sufficient to lead to an explosion.

Wilson and Mayle (*3*) have successfully simulated such neutrino-driven explosions by making two assumptions, which are, however, not generally accepted. They assumed that convective mixing by neutron-finger instabilities (*4*) in the neutron star boosts neutrino emission. Moreover, they considered high densities of pions (strongly interacting elementary particles that are built from a quark and an antiquark) in the neutron star medium to obtain explosion energies in the observed range (*5*). Both assumptions favor an explosion because the energy transfer by neutrinos increases sensitively with higher neutrino luminosities and energies.

But important other physics was missing from the models of Wilson and colleagues, as suggested by spectral observations of

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Supernova 1987A, which showed that radioactive nickel was moving at unexpectedly high velocities in Supernova 1987A. This observation suggested that large-scale flows had carried matter from near the neutron star to the outer shells of the exploding star. Multidimensional simulations indeed revealed the development of violent overturn motions between the newly formed neutron star and the supernova shock where neutrino heating creates a convectively highly unstable layer. While ongoing accretion maintains large neutrino fluxes from the neutron star, rising hot matter helps to push the shock farther out. Both effects seem to be crucial for the success of the delayed explosion mechanism described above (*6–9*).

Most recently, the first three-dimensional computations of this sort have been performed (*10*), marking another milestone for the growing sophistication of supernova modeling. The results essentially confirmed those of previous two-dimensional models (*9*). Mushroom-shaped structures (see the figure) develop and grow to large scales. Creating seed perturbations, this neutrino-driven postshock convection can explain the anisotropic distribution of nucleosynthesis products in many supernovae (*11*). In combination with rotation, it might also produce global asymmetries (*12*) and the large recoil velocities measured for young pulsars (*13*).

However, no simulation to date is sufficiently accurate to provide conclusive evidence for the viability of the neutrino-heating mechanism. In the best two- and three-dimensional models, the neutrino physics is still grossly simplified. The stars explode fairly rapidly, leaving behind small neutron stars and ejecting large amounts of strontium, yttrium, and zirconium, in disagreement with the abundances of these elements in our Galaxy. Neutrinos dominate the supernova energetics and determine the conditions for nucleosynthesis. Describing their transport and interactions accurately is therefore essential for resolving these problems.

A new level of refinement has been achieved by integrating the Boltzmann equation for the neutrino transport in Newtonian (*14*, *15*) and general relativistic (*16*) hydrodynamical models. But no explosions could be obtained in spherically symmetric (one-dimensional) models.

The next step must be two- and three-dimensional simulations with such an accurate treatment of the neutrinos (*17*). Improved descriptions of neutrino interactions in dense matter should ultimately be included (*18*). Increasing interest in studying the properties of hot neutron star matter is also highly desirable. The role of magnetic fields in the explosion is still poorly understood and deserves further exploration. Only an adequate inclusion of all these aspects of the problem will bring us closer to a standard model for the explosion of massive stars.

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PERSPECTIVES: DEVELOPMENT

Doublesex in the Middle

Kenneth C. Burtis

The morphology of male and female organisms is often strikingly different. From the time of Aristotle (*1*), biologists have attempted to elucidate the mechanistic basis of this sexual dimorphism. Mutants that display aberrant sexual phenotypes, most notably those of the fly *Drosophila* and the worm *Caenorhabditis elegans*, have allowed the definition of elaborate genetic hierarchies that control sex determination and somatic sexual differentiation (*2, 3*). However, a crucial question is: What are the target genes and biological processes controlled by these genetic hierarchies during the creation of sexually dimorphic animals? Biologists addressing this question in *Drosophila* have focused their efforts on a regulatory gene called *doublesex* (*dsx*) at the "bottom" of the sex determination hierarchy (*4–7*). Yet, as Ahmad and Baker illustrate in a recent issue of *Cell* (*8*), *dsx* is not at the bottom of a cascade of regulatory genes but instead sits right in the middle of a complex web of regulation. Their results, together with findings from other studies (*4–7*), lead us to consider *dsx* from a new angle as the linchpin that imposes sexual identity on developmental events in many tissues through its complex interactions with other regulatory hierarchies.

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In the fly, the sex determination hierarchy of regulatory genes begins with a counting mechanism based on X chromosome control elements (*9*). These elements regulate expression of the Sex lethal protein (Sx1), a splicing factor required for expression of the transformer protein (Tra) in female flies. Tra, in its turn, regulates expression of the female isoform of the Doublesex protein (DsxF). In males, the X chromosome signal does not activate Sxl expression, Tra is not produced, and *dsx* mRNA is spliced by default to encode the male isoform, DsxM. Both Dsx proteins are transcription factors that bind to DNA through a unique zinc-binding domain (see the figure) (*10, 11*). In the only confirmed direct molecular interaction of Dsx with a target gene, Dsx binds to an enhancer that regulates the expression of two yolk protein genes, resulting in either repression (DsxM) or stimulation (DsxF) of the transcription of these genes (*12*). Because the yolk proteins do not regulate other genes, *dsx* is commonly described as the last regulatory gene in the sex determination hierarchy. Reality, however, is far more complex.

A remarkable example of this complexity is revealed by Ahmad and Baker (*8*), who show that Dsx controls the differentiation of specific male genital tissues (the paragonia and vas deferens) by regulating the expression of the *Drosophila* fibroblast growth factor (FGF) gene. The fly FGF signaling pathway is known to direct development of the trachea (*13*), but its new role in sexual differentiation is unexpected. In males, the paragonia and vas deferens are derived from a group of mesodermal cells that migrate over the epithelia of the genital imaginal disc late in larval development and come to rest in two invaginations on the surface of the disc. Ahmad and Baker demonstrate that this unprecedented (in *Drosophila*) incorporation of mesodermal cells into the epithelia of the genital disc is dependent on expression of Branchless/FGF (the ligand for the FGF receptor) in the target regions of the disc. They also show that in female flies DsxF represses *branchless* expres-