OBITUARY

Vitaly Ginzburg (1916–2009)

Nobel-prizewinning success in physics achieved in the Soviet system.

Vitaly Lazarevich Ginzburg, who died on 8 November, played a leading part in many aspects of theoretical physics during the Soviet era and after the dismantling of the Soviet Union in 1991. His research contributions were vast and of the highest order, culminating in the award of the Nobel Prize in Physics in 2003, jointly with Alexei Abrikosov and Anthony Leggett, for pioneering studies in superconductivity and superfluidity.

Ginzburg was born in 1916 into a Jewish family in Moscow just before the Russian Revolution. His formal school education began only at the age of 11. In 1931, Evgeni Bakhmet'ev, a professor at Moscow's Technical University, helped him to get a job as a laboratory assistant in the university's X-ray laboratory. This experience whetted his appetite for physics and he entered Moscow State University in 1933 to study this discipline. Strongly attracted to theoretical physics, he was unsure of his mathematical ability and decided to work in optics under the supervision of Grigory Landsberg. He went on to take his PhD in 1940 and, having transferred to the Lebedev Physical Institute of the Soviet Academy of Sciences (FIAN) in Moscow, completed his science doctorate there in 1942. He was to remain a member of the FIAN for the rest of his life.

The scope of Ginzburg's research can be appreciated from his own attempt at a scientific autobiography, in which he listed, roughly chronologically, his range of interests in theoretical physics: classical and quantum electrodynamics, Cherenkov and transition radiation, the propagation of electromagnetic waves in plasma, radio astronomy and synchrotron radiation, cosmic-ray and γ-ray astrophysics, the scattering of light in crystals, the theory of ferroelectrics, and superfluidity and superconductivity.

In all of these areas, he wrote prolifically and made original contributions. For example, his work on transition radiation, a phenomenon that occurs when high-speed charged particles cross two media of different electric permittivity, followed on from his deep interest in electrodynamics, and his comprehensive treatment of the topic was truly pioneering. His studies of synchrotron radiation were highly influential in establishing that this process is the dominant non-thermal radiation mechanism in high-energy astrophysical phenomena in radio astronomy. These diverse interests were reflected in a series of influential books.

The pinnacle of his scientific achievement was his groundbreaking research with Lev Landau on the theory of superconductivity, published in 1950. This work built on Landau's theory of second-order phase transitions. Ginzburg had already applied Landau theory to ferroelectric phenomena. The crucial advance in the Ginzburg–Landau theory was the concept that, in the transition from the normal to the superconducting state, the phenomenon of symmetry breaking in a metal, a characteristic of Landau theory, was associated with the wavefunction of the metal's superconducting electrons, a non-gauge invariant process. This new paradigm was to have profound implications for many aspects of quantum physics beyond superconductivity, including the Higgs phenomenon, which gives particles mass.

His broad interests in theoretical physics were reflected in the famous Ginzburg seminars, which were held each week at the FIAN. Ginzburg stated that the topics for discussion should include all theoretical physics, except particle physics. His leadership at these seminars was impressive: he regularly interrupted the speaker to summarize what had just been said so that all listeners could follow the argument. These were celebrated weekly events, with most of Moscow's physicists making an effort to attend.

Ginzburg lived through a turbulent era. The Soviet Union entered the Second World War in 1941, and the Soviet Academy of Sciences was evacuated to Kazan, where Ginzburg worked for the next two years. In 1937, he had married his fellow student Olga Zamsha, but they divorced in 1946. In the same year he married Nina Ermakova, who had been arrested in 1944 on a trumped-up charge of plotting to kill Stalin. She was given a lenient sentence and released under an amnesty in 1945, but was not allowed to return to Moscow.

In 1945, Ginzburg was invited to become a visiting professor at the newly established radiophysical department at Gorky University in what is now Yekaterinburg, and he subsequently became chair of a group studying the propagation and radiation of radio waves. Living mainly in Moscow, for seven years Ginzburg made annual applications for his wife to be allowed to return there, but these were refused until after Stalin's death in 1953.

A. ZEMLIANICHENKO/AP

In 1947, he was personally attacked in an article in the *Literaturnaya Gazeta*, which blamed him for non-patriotic citations in his papers and for 'idealism'. Despite this attack, Igor Tamm, in need of physicists of the highest quality, arranged that he join the Soviet nuclear-weapons programme. The leaders of this project — Yulii Khariton, Igor Kurchatov and Yakov Zeldovich — assembled a brilliant team of physicists and mathematicians, including Andrei Sakharov, Israil Gel'fand, Alexander Kompaneets, Landau and Ginzburg, to develop nuclear weapons in response to the United States' development of the atomic and hydrogen bombs. Ginzburg's major contribution was to propose the use of lithium-6 as the fuel for the Soviet hydrogen bomb, a quite different process from that adopted in the United States. But he did not remain long in the nuclear programme.

After Stalin's death, Ginzburg was elected a corresponding member of the Soviet Academy of Sciences and his wife returned to Moscow. He became a full member of the academy in 1966 and, on the death of Tamm in 1971, became head of the theoretical physics department at the FIAN. During this period, Sakharov had become politically active and was classed as a dissident, being exiled to Gorky in 1980. The FIAN provided a scientific home for him, but, as a member of the theoretical physics department, this placed significant constraints on Ginzburg, who was not allowed to travel abroad for many years. Matters changed significantly with the period of perestroika that started in 1985, with Ginzburg being appointed a member of the Congress of People's Deputies from 1989 to 1991, when the body was dissolved.

Ginzburg was a strong personality, with deeply held humanitarian views that he maintained throughout the years of Soviet rule. He kept an open mind on issues in theoretical physics, but based his opinions on a strongly developed intuition for the underlying principles. He will be remembered with gratitude by all who experienced his kindness, and as an inspirational figure who carried out world-leading research against a background of significant political oppression.

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must self-organize, using some intrinsic, probably physical, property of the axoneme to regulate dynein. Computer simulations showed that regulation of dynein by local curvature of the axoneme, or by modifying the sliding distance between doublets, could both work in principle[7]. Jülicher and colleagues have combined theory and experiment to provide decisive support for the sliding-control model. Their work builds on a simple idea, first proposed by Brokaw[8], for how sliding might regulate motor activity to generate self-organized oscillations, an idea conceptually involving a system of opposed motors and springs (Fig. 2).

Jülicher and colleagues' initial insight[1] was to conceptualize the axoneme as an 'active material', making no assumptions about its microscopic properties. A rod of ordinary material resists a bending force by its stiffness and by frictional resistance to its movement. An axoneme, in contrast, can respond by actively deforming in the direction of the applied force, owing to activation of its internal dyneins by the deformation. This type of response can be quantified using negative values for the stiffness and viscosity parameters. For certain values of these parameters, an instability will propagate down the rod, and it will beat spontaneously[1].

An initial implementation[1] of this concept predicted waveforms that propagated in the wrong direction. This problem was fixed[2] by allowing some relative movement between doublets at the base of the cilium (stiffness of the base enters the mathematics as a boundary condition), leading to the interesting prediction that cells might control beat direction by regulating the stiffness of inter-doublet links at the cilium base. The improved model[2] was compared with experimental data from tethered bull sperm using a 'sperm equation'. This equation predicts sideways oscillations as a function both of distance from the base of the flagellum and of several parameters that describe the physical properties of the axoneme.

Any oscillation can be described as a sum of sinusoidal oscillations of increasing frequency, called Fourier modes; sideways oscillations can be described by the temporal Fourier modes of tangent angles. Power-spectrum analysis showed that experimentally observed oscillations in tangent angles were well approximated using only the first (fundamental) Fourier mode, so the sperm equation could be analytically solved using values of this mode. Tangent angles quantify the curvature of the axoneme at a given position, and the curvature is geometrically related to the sliding distance between doublets at that position. The sperm equation thus relates time-dependent angular movement at each position to the extent and rate of inter-doublet sliding at that position, and to the local forces that either oppose or promote further sliding.

The model contains two adjustable parameters — stiffness and friction of the active material inside the axoneme that deforms and exerts force during bending. It also contains several fixed parameters that Jülicher and colleagues independently measured and fed into the equation. These include the hydrodynamic drag of the moving flagellum and its ordinary stiffness, both of which oppose active deformation, and the beat frequency. The authors obtained an excellent fit to the data, with both internal stiffness and friction taking the negative values expected for an active material. Importantly, a microscopic model of dynein behaviour, incorporating the force-dependent detachment concept illustrated in Figure 2, predicted negative values for stiffness and friction similar to those obtained by fitting the sperm equation.

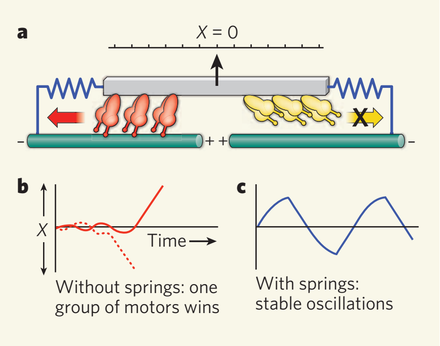

Figure 2 | Self-organized oscillations in a system of opposed motors and springs. a, Thought experiment using an artificial geometry to illustrate how sliding control leads to oscillations, a principle now further refined by Jülicher and colleagues[1–3]. Two groups of dynein motors anchored to a rigid scaffold walk outwards on two static microtubules oriented with their minus ends outwards. The system can omit or include springs (blue zig-zags). **b,** If the springs are absent, the system is unstable and one group of motors wins: the winning motors (solid curve) exert force on the losing motors (dotted curve) in a direction opposite to their walking direction, increasing the likelihood that the losing motors will become detached from the microtubule[8]. **c,** If the springs are present, as in **a**, the system undergoes stable oscillations. Oscillations are self-organized in the sense that no external control of the motors is required. The geometry is more complex in real axonemes, but the same concept applies: dyneins on opposite sides of the axoneme oppose each other, and crosslinking proteins supply the springs. (Redrawn from a presentation by F. Jülicher to illustrate a concept for self-organized oscillations proposed by C. J. Brokaw[8].)

Jülicher and colleagues first solved the sperm equation analytically using a linear approximation corresponding to small displacements[2], but a full, nonlinear solution was subsequently shown to predict similar waveforms[3]. Overall, the model fits the experimental data well and provides a conceptually satisfying explanation for how cilia and flagella beat that unites Brokaw's mechanistic proposal for controlling sliding[8] with the active-material concept. Predicting beat frequency is a challenging future goal for theorists, but this will probably require a detailed treatment of the microscopic details.

What further experiments are needed to test and refine the model, and what are its biological implications? Single-molecule measurements[9] could test whether experimental force–detachment relationships for axonemal dyneins are within the range required by the theory. Piston-like movement of doublets at the base of cilia, required by the model, has been observed in some systems[10], but needs to be tested more generally. More ambitiously, it might be possible to nano-fabricate simplified model systems, such as those shown in Figure 2, and test their properties.

Further testing will probably require a genetic approach. Here, theory meets medical genetics in a potentially fruitful way. Primary ciliary dyskinesias are inherited diseases characterized by paralysis or defective waveforms in epithelial cilia and sperm flagella due to ultrastructural abnormalities[11]. These are caused most often by mutations in ciliary dyneins, but sometimes in other axonemal proteins[12]. The theory opens up the prospect of formulating causal explanations of the effect of mutations on beat waveform, and the flagellated single-celled organism *Chlamydomonas* provides an ideal model for theory–structure–function studies. Key to this approach will be careful experimental measurement of aberrant waveforms, which the theory can relate to internal molecular behaviour[2].

Could any of this help patients with primary ciliary dyskinesias? In some patients, cilia lacking central pairs still beat, albeit abnormally[12]. Guided by mechanistic understanding of the underlying defect, it might be possible to correct this by using small molecules that weaken or strengthen dynein. ■

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Correction

In the obituary of Vitaly Ginzburg by Malcolm Longair (*Nature* **462,** 996; 2009), editorial intervention introduced the statement that Gorky University was "in what is now Yekaterinburg". That should have read "in what is now Nizhny Novgorod".