

microtubule plus ends renders a region of the plasma membrane incompatible with microtubule PPB formation, thereby orienting cell division.

As in plant cells, division orientation in animal cells often prescribes daughter cell polarity by determining whether a cell inherits a cortical polar domain. For division-plane specification in animal cells, the orientation of the nucleus and/or mitotic spindle emerges from physical constraints that are sensed by microtubules, leading to bisection of the spindle axis in cytokinesis. To bias geometrical rules to break symmetry, polar domains typically recruit or activate cytoskeleton-associated proteins at the cortex, yielding net forces that reorient the mitotic structures such as the astral microtubules, which extend from the spindle poles (8). In the context of asymmetrical division in plant cells, the study by Muroyama *et al.* suggests that the orientation of the asymmetric division is not obtained through an effect of astral microtubules, because plants do not have them, but rather through effects on cortical microtubules transitioning toward the formation of a PPB before mitosis. Moreover, in plant asymmetric cell division, the polar domain does not specify a position for cytokinesis but acts as a forbidden landmark where microtubules cannot align, preventing the division plane from colliding with it.

The proposed mechanism by which polarity proteins could specify the division plane by creating a microtubule-depleted zone raises the questions of how the BASL-BRXf complex is recruited to the plasma membrane and how it excludes microtubules. Based on preliminary genetic evidence (9), BASL and BRXf are mutually required for the polarization of each other. In the current model, BRXf proteins reversibly associate with the plasma membrane through palmitoylation at their N termini (9). BASL is recruited through an interaction between BASL and the BRX domains that define the BRXf proteins. The nature of the upstream signal that defines the location of BASL-BRXf polarization remains to be discovered.

It is likely that the scaffold proteins BASL and BRXf recruit a microtubule-associated protein to affect microtubule dynamics rather than directly mediating plus-end de-

polymerization. The critical microtubule-associated proteins might not be cell division specific because the same microtubule depletion is observed after division in SLGCs for as long as the polar domain persists. But how can the component responsible for the direct effect on microtubules be identified? The establishment of asymmetry in animal cells often involves both biochemical and mechanical processes (8). Because microtubules were proposed to be tension sensors (10), the mechanical constraints and subsequent signaling might be aspects to consider.

During pavement cell differentiation, specific small guanosine triphosphatases (GTPases) called Rho of Plants (ROPs) act as master regulators of cell polarity, mediating the recruitment of microtubule-

associated proteins in the polar domain to shape cytoskeleton distribution. Upstream, ROPs are regulated by several stimuli, including the receptor-like kinase FERONIA (FER) pathway, which participates in sensing and/or transducing mechanical signals (11–13). Investigating the cross-talk between ROP signaling and symmetry breaking in the context of asymmetric cell division might be key in the future. Overall, the study by Muroyama *et al.* highlights the singular mechanism used by plants to control the inheritance of fate regulators by connecting polarity with microtubule interactions. ■

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PHYSICS

Probing fundamental particles with molecules

Molecular spectroscopy constrains the size of the electron's electric dipole moment

By Mingyu Fan and Andrew Jayich

The discovery of the Higgs boson in 2012 marked the completion of the Standard Model (SM) of particle physics. The SM remains the best theory of the known fundamental particles and how they interact, but there is evidence that the SM is incomplete. A shortcoming is that the SM predicts nearly equal amounts of matter and antimatter after the Big Bang, which would result in a cosmos full of light after the matter and antimatter particles mutually annihilate. The physicist Andrei Sakharov outlined the basic conditions that are needed to create the matter imbalance, called the baryon asymmetry of the Universe (BAU), that allows for our existence (1). One of the Sakharov conditions, time symmetry violation (TSV), suggests that other particles and interactions beyond those of the SM await discovery. On page 46 of this issue, Roussy *et al.* (2) report the most stringent limits to date on the size of the electron's permanent electric dipole moment (EDM), which may help explain the BAU.

Time symmetry ensures that when we imagine reversing time, the physical laws follow their time-reversed paths. TSV is needed to generate the BAU because it is a necessary condition to convert antimatter to matter, which may have happened in the early Universe just after the Big Bang, leaving more matter than antimatter. After annihilation of particles with their antiparticles, the excess amount of matter formed the current Universe. The physics that describes the SM mostly obeys time sym-

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metry; although there is TSV in the SM, it is not nearly enough to account for the BAU. TSV interactions arising from undiscovered particles can generate permanent EDMs of SM particles such as the electron. An EDM in an electric field causes an energy shift when its orientation is flipped with respect to the field. An electron EDM (eEDM) violates time-reversal symmetry: If time were reversed, its magnetic moment would flip and the EDM would not, looking fundamentally different from before time-reversal (see the figure). All eEDM measurements so far are consistent

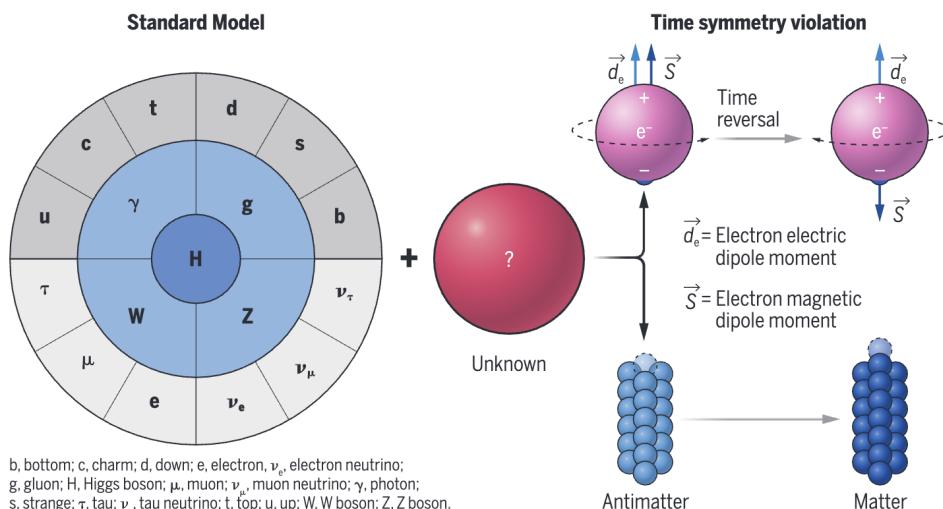
with anti-aligned to the molecule's massive electric field. They probed the molecular energy shift that arises between the two configurations, allowing them to limit the eEDM to be no larger than $4.1 \times 10^{-30} e \text{ cm}$. With their vacuum apparatus that fits on a table, they were able to probe for undiscovered particles up to a mass of 40 TeV, which is 10 times the energy of particles than can be observed in the Large Hadron Collider at CERN, which costs about \$4.75 billion to build and \$1 billion to run annually. Considerable effort by Roussy *et al.* went into meticulously studying their

analysis of multiple measurements in different systems narrows down the contributions from the individual TSV sources and provides more stringent bounds to test theories. Knowledge from EDM measurements across multiple systems would help guide the requirements of a future high-energy particle collider that could create the TSV particles responsible for the BAU.

The SM predicts a very small eEDM of less than $10^{-38} e \text{ cm}$, which is roughly a billion times smaller than the limit reported by Roussy *et al.* This extremely small SM contribution to the eEDM gives future experiments operating at higher sensitivities plenty of room for discovery. In parallel with the ThO and HfF⁺ eEDM experiments, there has been progress toward next-generation TSV measurements that aim to improve sensitivity by using more-sensitive molecular species, larger numbers of a given species, and longer measurement coherence times. These include using polyatomic molecules (7), exotic isotopes with deformed nuclei (8), and even probing TSV in solids where larger numbers of atoms are trapped in a crystal (9). Technological improvements to allow such advances include laser cooling and trapping of polyatomic molecules (10), spectroscopy of radioactive molecules (11), and fine-grained control of molecular ions with quantum logic spectroscopy (12, 13). A combination of such approaches could allow the detection of high-energy particles perhaps at PeV energies (1 PeV = 10^{15} eV), and along the way the sought-for undiscovered particles may be detected. Such experiments will constrain high-energy theories beyond the SM. But upgrades of both the ThO beam experiment and the trapped molecular ion technique, including a switch from HfF⁺ to ThF⁺, are poised to enhance the particle-mass reach of eEDM experiments in the near future. ■

Trying to understand the missing matter

The Standard Model does not explain important problems such as the baryon asymmetry of the Universe (BAU), which requires undiscovered particles for additional time symmetry violation (TSV) interactions to convert antimatter to matter in the early Universe. Such particles may be discovered by precision measurements of the electron electric dipole moment, which is a TSV moment induced by an asymmetry of the charge distribution in the electron.



with zero, indicating that no particle has been found to induce enough TSV to generate an eEDM that is within the current experimental sensitivities. However, tighter experimental bounds on the eEDM probes increasingly higher particle masses, analogous to how higher-energy particle colliders can search for more-massive particles.

Roussy *et al.* measured eEDM by precision spectroscopy of HfF⁺ molecules. They produced and trapped HfF⁺ molecules in an ion trap and polarized them with a rotating electric field. The polarization controls the orientation of the large internal molecular field that the molecule's valence electron experiences. With an additional applied magnetic field, lasers, microwaves, and radiofrequency fields, Roussy *et al.* measured the energy of HfF⁺ molecules in two configurations: when the electron's magnetic moment was aligned and when it

experimental apparatus and measurement technique so they could understand systematic uncertainties in minute detail to ensure that no spurious signals were mistakenly introduced (3).

Sensitivity in the detection of the eEDM increased when molecules were used instead of atoms (4). The two previous eEDM limits come from brief measurements of many thorium oxide (ThO) molecules (5, 6) using a cryogenic beam as compared to the trapped molecular ion approach of Roussy *et al.*, in which fewer molecules are measured for much longer times. The combined ThO and HfF⁺ measurements set more stringent limits on sources of TSV than either measurement does on its own. This is because measurements in different molecules have different sensitivities to underlying sources of TSV. In the event of a nonzero eEDM measurement, a combined

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