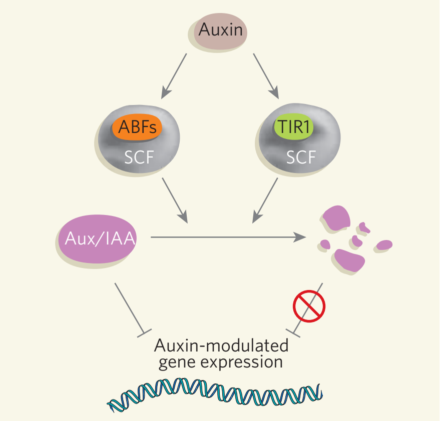

Figure 2 | Model of auxin action. Auxins act directly with SCF complexes containing either transport inhibitor response protein 1 (TIR1) or the related auxin-binding factors (ABFs). This catalyses the destruction of Aux/IAA proteins, which directly inhibit the genes that carry out the auxin response. The inhibitory effect of Aux/IAA is thus relieved, allowing auxin responses to occur.

advance in understanding auxin perception in plants[5]. Developing plants that lack ABP1 show defective cell elongation, fail to organize the basic plant body plan, and subsequently degenerate[5]. However, cell division still occurs in these plants, indicating that an auxin pathway to regulate cell division is still working. Finally, after ardent searching, comes the discovery of a surprising mode of auxin perception[2,3]. The key proteins involved have been studied for several years, but they now show a direct and unexpected ability to 'sense' auxin.

Auxins cause rapid changes in gene expression, and two families of proteins have been identified in this response: auxin response factors (ARFs) and Aux/IAA proteins[6]. The genes encoding Aux/IAA proteins initially seemed to fit the mould of 'early response genes', because their expression increased rapidly following exposure to auxin. According to this model, Aux/IAA proteins would modulate the expression of 'late response genes' that encode factors directly involved in cell division and growth. But it turned out that these proteins actually suppress auxin-induced gene expression[7], and that high auxin accelerates their destruction[8,9]. So, rather than functioning solely as positive downstream messengers, Aux/IAA proteins also act as negative regulators, and their abundance must decline, at least initially, if auxin is to be sensed. How, then, does auxin mediate changes in Aux/IAA protein destruction?

The 'transport inhibitor response 1' protein (TIR1), previously shown to be a part of this response pathway, is now confirmed as the vital link[2,3]. TIR1 was previously isolated in a genetic screen looking for mutant plants that show an altered response to auxin. The function of TIR1 was suggested by the presence of an 'F-box' motif in its protein sequence. This short sequence of amino acids is found in proteins that form part of a protein complex called the SCF, named after the first three of its subunits to be identified: SKP1, cullin and F-box protein. This complex catalyses the covalent addition of a ubiquitin molecule to proteins, targeting them for destruction. The ubiquitin pathway is highly conserved among species, being found in all animals, fungi and plants — only bacteria lack it. Thorough biochemical work established that TIR1 was indeed part of a plant SCF complex[10] that interacts with Aux/IAA proteins[8]. But how does auxin communicate with the SCF complex to alter Aux/IAA destruction? None of the precedents established for the regulation of SCF activity in animal or fungal systems seemed to apply.

Dharmasiri *et al.*[2] and Kepinski and Leyser[3] show that auxin simply binds to TIR1 in the presence of an Aux/IAA protein, and somehow changes TIR1 activity. When plant TIR1 is made in animal cells, such as insect[2] or frog (*Xenopus*)[3], auxin still binds to TIR1 in the presence of Aux/IAA, implicating TIR1, or TIR1 together with the Aux/IAA protein, as the sole components required to sense auxin by this pathway. Auxin perception is thus unique among SCF-mediated pathways. In the canonical SCF pathway, covalent modification of the target protein promotes its interaction with the SCF complex. In the auxin response, no target modification has been observed. Instead, it is the alteration of the TIR1-containing SCF complex by non-covalent auxin binding that is responsible for the increased destruction of Aux/IAA proteins (Fig. 2).

Much remains to be done. The biochemical nature of the SCF–auxin–Aux/IAA interaction and the relationship between auxin perception by SCF and by ABP1 clearly merit further examination. Can the interaction of auxins with SCF account for the myriad auxin responses in growth and development? Let us hope that we will soon be able to answer the rhyme: yes, you and I can know how oats and beans and barley grow! ■

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PARTICLE PHYSICS

Electrons are not ambidextrous

Andrzej Czarnecki and William J. Marciano

The best low-energy measurement yet obtained of the electroweak mixing angle — a central parameter of the standard model of particle physics — is the last hurrah for Stanford's powerful two-mile linear accelerator.

Like speeding rifle-bullets, high-energy electrons can spin about the direction of their motion. Electrons spinning clockwise are said by convention to be left-handed; those spinning anticlockwise are right-handed. Researchers on experiment E158 at the Stanford Linear Accelerator Center (SLAC) in California have announced[1] that, in contrast to bullets, the probability of an electron hitting a target depends slightly on whether its spin is right- or left-handed. This is a manifestation of a phenomenon known as parity violation — the difference between a fundamental interaction and its mirror image.

Most physical theories — from Newton's mechanics and Maxwell's electrodynamics, to relativity and quantum mechanics — are perfectly symmetric with respect to left–right interchange, or parity. But in 1956, Lee and Yang[2] suggested that the so-called weak interaction, responsible for the β decay of unstable nuclei and the feeble force of the accompanying neutrinos, might exhibit a left–right preference — a feature soon established experimentally. In fact, the weak interaction was found to be maximally parity violating: only left-handed electrons participate in such reactions.

Through the work of Sheldon Glashow, Abdus Salam and Steven Weinberg[3], the weak interaction was later unified with electromagnetism in what is now called the standard model of 'electroweak' phenomena. In this theory, electric and magnetic forces are mediated by massless photons, and parity is conserved: photons do not distinguish the handedness of electrons or any other elementary particles. Because electromagnetism dominates almost all physical, chemical and biological phenomena, the parity violation of weak interactions is not evident in the world around us. The very short-range weak force, on the other hand, is mediated by heavy, electrically charged analogues of the photon — W bosons — that interact with the left-handed

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components of particles, but not with right-handed components. Thus, the maximal parity violation of weak interactions is easily accommodated. But why nature chose to violate parity remains a mystery, as do possible connections with the evolution of life (Box 1).

The unified electroweak theory also predicted the existence of another heavy, but neutral particle called the Z boson. Like the W, the Z also mediates weak interactions and violates parity. But, unlike that in W-mediated interactions, the degree of parity violation in Z-mediated interactions is not maximal, because of mixing effects that can be expressed in terms of the 'weak mixing angle', θ_W. And because the Z boson, like the photon, is electrically neutral, it also interferes with electromagnetic reactions, resulting in a small — usually unobservable — degree of parity violation in these processes.

The first definitive observation of a parity-violating effect caused by the Z boson — measured as $\sin^2\theta_W$, at an uncertainty of around 10% — was made some 30 years ago by the E122 experiment, a forerunner of E158 at SLAC[4]. E122 measured the difference between the scattering of left- and right-handed polarized electrons on a deuterium target; the observed asymmetry was consistent with theoretical expectations and was a historic confirmation of the standard model. Nowadays, W and Z bosons are routinely created at high-energy accelerators, and their properties have been thoroughly scrutinized — experiments at SLAC and at CERN in Geneva have used colliding electron and positron beams tuned to the Z boson mass at around 91 GeV (9.1×10^{10} electronvolts) to measure the weak mixing angle, appropriate for high-energy studies, to an accuracy of less than 0.1% at high energies (Fig. 1).

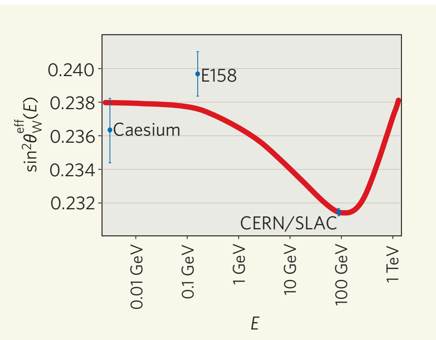

Figure 1 | Measurements of the weak mixing angle. The effective weak mixing angle θ_W^{eff}, the fundamental parameter of parity violation involving the Z boson, is expected to vary ('run') depending on the energy scale (E) probed by a given experiment. Using the very precise value obtained by high-energy studies at CERN and SLAC, the expected running at lower and higher energies is illustrated. Pictured at low energies is the new E158 result[1], as well as an earlier, somewhat less precise measurement of the weak mixing angle obtained from a study of parity-violating interference effects in atomic caesium[6]. Together, they nicely confirm the theoretically predicted running. (It should, however, be noted that data from a high-energy neutrino experiment at Fermilab[7] suggest a significant, currently unexplained, deviation from the curve.)

Like its E122 predecessor, the E158 experiment[1] used the two-mile-long linear accelerator at SLAC — currently the world's highest-energy electron accelerator — to accelerate left- and right-handed electrons separately to about 50 GeV and scatter them off other electrons in a liquid-hydrogen target. This allowed the number of interactions between left-handed accelerated electrons and left-handed target electrons to be compared with the analogous number of right–right scattering events — no mean feat, as the average deflection of an electron after collision was less than 0.3°.

The observation of an asymmetry in event numbers at E158 — at an expected level of about 1.5 events in every 10 million scattered electrons — would mark the first discovery of parity violation in a simple electron–electron system and provide a novel determination of θ_W. The E158 researchers, led by spokesmen Emlyn Hughes (Caltech), Krishna Kumar (University of Massachusetts), Paul Souder (Syracuse University), and the analysis leader Yury Kolomensky (University of California, Berkeley), having recorded a staggering 10^{16} electron–electron collisions, did indeed observe an asymmetry of the anticipated magnitude, a technical tour de force. The resulting experimental constraint, effective at relatively low energies (eff), of $\sin^2\theta_W^{eff} = 0.2397 \pm 0.0013$ (about 0.5% accuracy) provides the best existing determination of the weak mixing angle at low energy.

The value obtained by E158 for the effective low-energy weak mixing angle is considerably larger than that obtained in experiments at higher energies, such as those that created real Z bosons at CERN and SLAC. But should this value always be the same? The answer is, 'not quite'. Quantum effects, particularly 'clouds' of quark–antiquark excitations surrounding the electrons at short distances, modify the mixing of the photon and Z boson. This causes the effective weak mixing angle to change slowly as a function of the energy scale probed, a phenomenon known as 'running' (Fig. 1). The value of that parameter is expected to decrease by about 3% as one goes from relatively low-energy phenomena to the 'Z pole' of the CERN and SLAC measurements, and then to start increasing again at higher energies owing to quantum excitations of the heavy, charged W bosons. (That change of direction is incidentally analogous to the source of asymptotic freedom in quantum chromodynamics, which won its discoverers the 2004 Nobel prize[5].) Results from E158 (ref. 1) and an earlier experiment on caesium atoms[6], when compared with the more precise higher-energy determination, nicely establish the predicted low-energy running.

The relatively good agreement between the E158 and caesium results on the one hand, and theory on the other, allows one to rule out or constrain 'new physics' appendages to the standard model. For example, some theories invoke additional 'Z′' bosons that could also couple to electrons and provide an added source of parity violation. The lack of any apparent deviation from the expectations of the standard model implies that the Z′, if it exists, must have a large mass that suppresses its effect — indeed, it would have to be at least ten times heavier than the known Z boson.

Box 1 | Parity violation and life

Could fundamental parity violation have macroscopic consequences in our living world? Some organic molecules, such as enzymes and amino acids found in living organisms, are maximally optically active. When subjected to linearly polarized light, they will rotate the plane of polarization in only one direction; that is, they have a definite handedness. This is not fundamental parity violation, because molecules with the opposite handedness can be created artificially. But why don't they participate in life's processes? This preference of life-giving molecules for one type of handed structure is called homochirality. Although homochirality does not seem to have any direct connection to parity violation, some scientists[8] have speculated that parity violation in the weak interactions may have played an early role in evolution through some as yet undetermined enhancement mechanism. Such ideas are provocative but controversial. Should large organic molecules be found in extraterrestrial samples, it would be interesting to check the handedness of their optical activity. **A.C. & W.J.M.**

The glorious history of the SLAC two-mile accelerator, encompassing many great discoveries, such as the first conclusive evidence for quarks, is now drawing to a close. E158 is the last high-energy fixed-target experiment at SLAC: the accelerator is now being converted into the Linac Coherent Light Source, the world's highest-energy free-electron laser. This bright source of X-rays will, literally, shed new light on a variety of questions in condensed-matter physics and the life sciences. The results from E158 provide a precision test of the standard model and establish the predicted running of the weak mixing angle via quantum quark effects, a fitting end to a distinguished career. ■

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