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ically separated before, but the connection to subcellular compartments is new. The authors tie these points together with previous results (8, 11) in a model (see the figure).

The most surprising finding from these studies is that EDS1 interacts with AvrRps4 and another bacterial effector protein HopA1. Bhattacharjee *et al.* show that AvrRps4 and HopA1 interact directly with EDS1 in vitro and disrupt interactions between EDS1, SRFR1, and TIR-NB-LRR proteins at the endomembrane. Heidrich *et al.* demonstrate that AvrRps4 binds directly to EDS1, but not RPS4, in vivo. These results suggest that AvrRps4 and HopA1 evolved independently to target EDS1 and thereby interfere with immunity. Subsequently, multiple TIR-NB-LRR proteins evolved to guard EDS1.

In this context, EDS1 could be considered a co-receptor in a surveillance complex. Does this contradict the long-standing model that predicts a downstream signaling role for EDS1? In principle, the necessity of EDS1 for resistance triggered by RPS4, RPS6, and SNC1 could be explained simply by its role as a guarded virulence target. That is, the absence of the target/guardee in *eds1* mutants

renders the surveillance complex incompetent. However, it is important to consider the conservation of EDS1 in monocots (which do not have TIR-NB-LRR proteins), along with its role in basal resistance (presumably independent of TIR-NB-LRR proteins) and experiments from previous studies of EDS1 that support a signaling role in effector-triggered immunity (11). The two functions are not mutually exclusive and could be reconciled by an evolutionary model in which EDS1 has a relatively ancient signaling function in basal resistance that was targeted by effectors and also co-opted to support effector-triggered immunity. This could be further resolved, such as by testing whether EDS1 is guarded by other TIR-NB-LRR proteins.

Bhattacharjee *et al.* and Heidrich *et al.* provide important clues to the mystery of how plant immune surveillance proteins perceive pathogen effectors and activate downstream responses. Additionally, the targeting of EDS1 generalizes the prediction that pathogens exploit "points of vulnerability" in the immune network, which in turn can be guarded by NB-LRR proteins (*12*). Attention can now be focused on plotting the sequence of events in RPS4 activation and understanding how effectors manipulate EDS1 to enhance virulence. The effector proteins might serve as probes to investigate how EDS1 and partners regulate immunity in different cellular compartments. Because EDS1 supports resistance against diverse pathogens in divergent plants, results from these experiments can inform breeding for disease resistance in crops.

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CHEMISTRY

Optimizing Perovskites for the Water-Splitting Reaction

Aleksandra Vojvodic^{1,2} and Jens K. Nørskov^{1,2}

lectrochemical splitting of water into molecular oxygen (O_2) , protons, and electrons could provide a way to store the electricity generated from sustainable but intermittent energy sources, such as wind and solar power, as fuels (1). Hydrogen would be the simplest fuel to make, but the protons and electrons could be used to produce hydrocarbons and alcohols from CO₂ or ammonia from N₂. A major challenge is that efficient catalysts for water electrolysis are expensive and contain rare noble metals, so costeffective approaches will require the discovery of efficient electrocatalysts that contain only Earth-abundant elements. On page 1383 of this issue, Suntivich et al. (2) describe a method for rational design of metal oxide catalysts for the oxygen evolution reaction. They discovered perovskite-structure cata-

lysts based on non-noble metals that work with a higher efficiency than one of the stateof-the-art catalysts, iridium oxide.

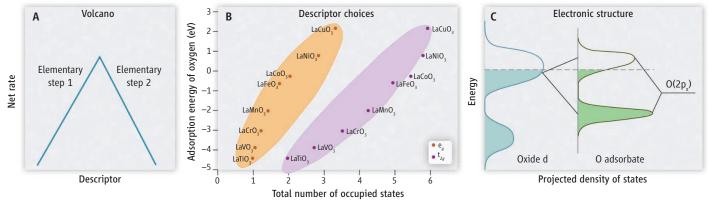
Most catalyst development has been based on trial-and-error approaches. To rationally design a catalyst, we need to understand which intrinsic material characteristics, or descriptors, control catalysis. One approach, for example, is to change the electronic properties of the material through the deliberate addition of other elements. Finding a descriptor can be very challenging because of the complexity of a chemical reaction involving several subreactions with numerous intermediates. When a descriptor is identified, the catalytic rate typically has a "volcano"shaped dependence on the descriptor with a maximum at the optimum value of this descriptor (see the figure, panel A) (3).

Suntivich *et al.* conducted a systematic investigation of several transition metal oxides and deduced that the number of occupied d orbital states of a specific symmetry The electron occupation of orbitals in transition metal oxides guided the identification of an efficient oxygen evolution catalyst based on Earth-abundant elements.

 (e_g) of the active metal can be used as the descriptor (see the figure, panel A). They then searched for compositions with a descriptor value near the predicted optimum and identified Ba_{0.5}Sr_{0.5}Co_{0.8}Fe_{0.2}O_{3- δ} perovskite as a good candidate. Subsequent synthesis and testing revealed this hypothesis to be correct.

Why does the e_{g} occupation act as a good descriptor of the catalytic activity for the oxygen evolution reaction? Suntivich et al. suggest that it must be related to the ability of the surface to bond oxygen, given the suggestion, based on density functional theory (DFT) calculations, that oxygen adsorption energy is a good descriptor for this reaction (4). The reason is that all of the reaction intermediates (*OH, *O, *OOH, where the asterisk indicates a bond to the surface) interact with the surface through an O atom. Some reaction steps (such as the formation of *OH or *O from H₂O) become easier when O atoms interact more strongly with the surface, whereas other steps (such as $*O + H_2O \rightarrow OOH^- + H^+ + e^-$)

¹Department of Chemical Engineering, Stanford University, Stanford, CA 94035, USA. ²SLAC National Accelerator Laboratory, Menlo Park, CA 94205, USA. E-mail: norskov@stanford.edu; alevoj@slac.stanford.edu



Discovering descriptors for catalyst performance. (A) For many catalytic reactions, intrinsic catalyst parameters, or descriptors, can be identified (such as changes in electronic properties created by using different metals) that lead to a "volcano plot" for the reaction rate. (B) Suntivich *et al.* identified the occupation of d states with e_q symmetry as a good descriptor for the oxygen evolution reac-

tion over metal oxide catalysts. We include DFT calculations (7) to show that the descriptor can also be the t_{2g} symmetry occupation or the adsorption energy of oxygen. (C) Schematic of the formation of a bond between an oxygen adsorbate level and the d states of the oxide, explaining why the occupancy of the d states correlates with the oxygen adsorption energy and hence with the catalytic activity.

become more difficult because surfaceoxygen bonds are ruptured.

This tradeoff was exploited and led to the identification of an optimum surface-oxygen interaction energy that maximizes the overall rate. This approach follows the Sabatier principle (5), which states that the interaction between the catalysts and the adsorbate should be neither too strong nor too weak, but introduces the important new aspect of quantifying this interaction strength (3). The electronic structure of these solid oxides is described by band theory. Unlike an isolated molecule, the valence bands and conduction bands can be partially filled with electrons, which is described as a density of states (DOS).

We show in the figure, panel B, that the notion that the surface-oxygen bond energy scales with the e_g occupation is borne out by direct DFT calculation. In addition, there is a similar correlation with the occupancy of the other d symmetry component, t_{20} . A more detailed analysis of the electronic structure reveals that the occupation of e_{a} and t_{2a} states has two contributions, one from occupied valence band states and one from occupied conduction band states. The best correlation is with the number of occupied conduction band states. Hence, it is the reactive states near the Fermi level (which separates the occupied from the unoccupied states) that are responsible for the occupancy of e_{o}/t_{20} states being a good descriptor.

The interaction between these surface states and the O 2p adsorbate levels gives rise to bonding and antibonding O states (see the figure, panel C). The adsorption strength will depend on the occupancy of these bonding and antibonding O states and will be strongest when the O bonding states are completely occupied while the O antibonding states are completely unoccupied. This bonding interaction resembles the ones between an adsorbate and a transition metal surface, in which the d-band center of the metal is a descriptor (3), and between an adsorbate and a transition metal carbide surface, in which the center of the surface resonance states is a descriptor (6).

The work of Suntivich *et al.* provides a new approach for science-based catalyst design and for finding cheap and efficient alternatives to the known inorganic catalysts for water splitting. Their work is an important step toward sustainable fuel production, and could also provide insights into more direct approaches in which incident light helps to power the water-splitting process.

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ECONOMICS

Can Integration Tame Conflicts?

Lorenz Goette¹ and Stephan Meier²

Integration efforts can increase cooperation between ethnic or religious groups if competition is avoided.

ivil wars between ethnic or religious groups have cost millions of lives in recent history (1). In Bosnia and Herzegovina alone, tens of thousands were killed and millions displaced in the war between 1992 and 1995. However, although intense hatred against other groups can lead to tragedy, it often seems to come in tandem with stronger altruism and cooperation within one's own group (2, 3). This combination may have played a key role in early human development (4). Are there ways to mitigate group conflict while at the same time harvesting the potential benefits from stronger cooperation within groups? A report by Alexander and Christia on page 1392 of this issue (5) suggests that the answer is yes, under the right circumstances.

The conditions under which conflicts emerge between groups are not well understood. Two African tribes—the Chewas and the Tumbukas—provide a stark example: They get along with each other in Zambia, but relations are hostile in the neighboring state of Malawi (6). Ethnoreligious diversity alone does not always create conflict. The environment in which different groups interact seems to matter for whether the dark side of group membership emerges.

It has been suggested that integration of different previously warring groups can mit-

¹Faculty of Business and Economics, University of Lausanne, 1015 Lausanne-Dorigny, Switzerland. ²Graduate School of Business, Columbia University, 3022 Broadway, New York, NY 10027, USA. E-mail: lorenz.goette@unil.ch; sm3087@ columbia.edu