

rent). These back-of-the-envelope calculations suggest that receptor diffusion will have little effect at synapses with low to intermediate release probabilities and receptor occupancies.

The larger effects of AMPA receptor diffusion on short-term depression observed by Heine *et al.* could arise from higher receptor occupancies due to glutamate release from multiple vesicles per contact, a higher fraction of mobile receptors, and/or slower recovery from desensitization at the synapse. In general, larger effects of receptor diffusion will occur at synapses where a large fraction of receptors desensitize, as expected for connections with high release probabilities and receptor occupancies (see the figure). Receptor diffusion could explain the lack of desensitization at such

synapses (e.g., at the climbing fiber synapse) (6). Desensitization is prominent where the presence of glutamate in the synapse is prolonged (4, 11) and where strongly desensitizing AMPA receptors are expressed (12). However, counteracting desensitization with diffusion also requires abundant extrasynaptic AMPA receptors, which are not present in all neurons (8, 11).

Although further studies are required to determine the contribution of rapid AMPA receptor diffusion to short-term depression at different synapses in the brain, the present study changes our concept of the postsynaptic density, from an array of receptors that is fixed on a time scale of minutes, to a highly dynamic structure with the potential to rap-

idly refresh itself from the surrounding sea of extrasynaptic receptors.

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GEOCHEMISTRY

Toward New Uses for Hematite

Carrick M. Eggleston

The iron mineral hematite (see the figure) is common on Earth and has also been found on Mars (1). It acts as an adsorbent for natural and contaminant aqueous solutes in soils and sediments, is important in the redox cycling of iron and other metals, and acts as a respiratory electron acceptor for metal-reducing bacteria that may stem from early in the history of life (2). Hematite is also probably the cheapest semiconductor that absorbs substantial amounts of visible light, and is therefore a candidate component of inexpensive “artificial photosynthesis” systems for generating chemical fuels from sunlight (3). The results reported by Yanina and Rosso on page 218 of this issue (4) may bring these applications a step closer to reality.

Until recently, studies of hematite photocatalysis have given little cause for optimism. Hematite can use light energy to oxidize water, but does so inefficiently. In semiconductors like hematite, a gap exists between the valence band (electronic states occupied by electrons) and the conduction band (unoccupied electronic states). This gap normally contains no electronic states. When hematite absorbs light, electrons are elevated in energy from the valence band to the conduction band, leaving behind holes (electron vacancies) in the valence band that can move to surfaces and oxidize water. These holes are often filled



Hematite gets down to work. Hematite ($\alpha\text{-Fe}_2\text{O}_3$) is a natural mineral found on Earth and other planets; the specimen shown here is from Ouro Preto, Brazil. Results by Yanina and Rosso suggest ways in which the mineral may be used in photocatalytic applications.

before they can oxidize water. The electrons that fill the holes come from a poorly understood electronic state at an energy within the gap (an “intragap” state) (5).

Yanina and Rosso now show that hematite crystals—in the form of plates with narrow “edge” surfaces and larger “basal” surfaces—can, by means of conduction through the solid, reductively dissolve on edge surfaces while simultaneously oxidizing Fe^{2+} that interacts with basal surfaces so that the basal surfaces grow. Different crystal faces have different

New results suggest how the photocatalytic performance of hematite may be improved.

potentials at a given pH, which creates potential gradients within the crystal that can drive conduction from one crystal face to another. Their results are relevant to electrical processes in both natural and synthetic crystals generally and suggest, in particular, that the intragap state might be associated with the edge surfaces of hematite. This is important because surfaces can be modified, whereas states inherent only to the bulk structure could form an insurmountable obstacle to improving the photocatalytic efficiency of hematite.

Crystals will take advantage of any available kinetic pathway to evolve toward an equilibrium shape, and Yanina and Rosso have demonstrated one such pathway. Synthesis procedures already exist, however, for making hematite particles in spindles versus platelets by modifying surfaces with adsorbed molecules (6). Electric fields have also previously been observed in anisotropic solids (7). Earlier studies of hematite (8) noted dark currents and open-circuit potentials that were attributed to electrode corrosion. Yanina and Rosso show where this corrosion reaction probably happens. More important, they put many of these disparate pieces together to form a coherent picture of internal electrical currents between surfaces through conductive solids.

To discuss why their result is important for enhancing hematite photocatalysis, we take a closer look at the potentials reported by Yanina and Rosso for different hematite surfaces. The reported potentials do not coincide with either the valence or the conduction

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bands, but instead bracket the range of potentials reported for the intragap state (5). Only when sufficient electrons are available from aqueous solutes do the basal surfaces reach the more negative potential characteristic of the hematite conduction band.

Under these circumstances, one would expect the basal surface to reductively dissolve. Yanina and Rosso show that this is true only if the basal surface is the only one exposed to solution. When both basal and edge surface are exposed to solution, the basal surface does not reductively dissolve but instead oxidizes aqueous Fe^{2+} . Reductive dissolution takes place at edge surfaces, not basal surfaces. Possible interpretations are that a state within bulk hematite—such as the intragap state—acts as an oxidant for basal surfaces and as a reductant for edge surfaces, or that the edge surfaces act directly as an oxidant for species at basal surfaces. Yanina and Rosso's result forces us to include the second interpretation among the possibilities.

Objections will be raised to the second interpretation because the intragap state is thought to be a bulk phenomenon, not a surface state (5). However, the two interpretations need not be mutually exclusive. Yanina and Rosso point out significant differences between hydroxyls on edge surfaces as compared to basal surfaces. Hematite crystals generally contain some hydroxyl as an impurity, and hydroxyl defects within hematite crystals may have similar electronic properties to hydroxyls on edge surfaces. If so, then the way is open to synthesizing hematites without an intragap state to limit photocatalytic efficiency. Bulk hydroxyl defects can be minimized using scrupulously dry synthesis techniques, and edge surfaces can be modified using a suitable adsorbate to create surface states at more negative potentials than those of unmodified edge surfaces.

More work will be needed to see whether edge surface modifications improve hematite photocatalytic efficiency, but recent results are encouraging. Kay *et al.* have reported a

new efficiency benchmark for photocatalytic water splitting by hematite (9) using nanocrystalline hematite films made by chemical vapor deposition (a nonaqueous process presumably resulting in low water content) and with a preferred orientation exposing edge surfaces to light. As for surface modification, Wang *et al.* have shown that photocurrents for hematite coated with SrTiO_3 are much higher than for hematite or SrTiO_3 alone (10). Maybe we can make hematite work for us after all.

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NEUROSCIENCE

Axons Seek Neighborly Advice

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Coordinating motor and sensory pathways in the nervous system ensures efficient execution of bodily movements. Motor neurons in the spinal cord extend axons that drive muscle contraction in the periphery. Sensory neurons (in dorsal root ganglia) adjacent to the spinal cord send feedback to the motor neurons about muscle position/stretch, touch, and pain. Anatomical coupling of the two pathways begins as axons from motor and sensory neurons join paths near the spinal cord and project together in related, but distinct, bundles on their way to muscle and dermis. Despite the known precision of sensory-motor connectivity, the mechanisms yielding this organization have remained unclear. On page 233 of this issue of *Science*, Gallarda *et al.* (1) report that subpopulations of motor and sensory axons directly

communicate with each other to prevent a biological short-circuit of this system.

Classical tracing and transplantation studies have shown that motor and sensory neurons exhibit closely associated projection patterns and can influence each other's outgrowth (2–4), but direct molecular evidence for their reciprocal communication during development has been lacking. Using advanced mouse genetics, Gallarda *et al.* simultaneously illuminated these pathways by expressing marker proteins. They observed that late-developing motor axons projecting to muscles of the trunk develop in close proximity to axons of sensory neurons from the dorsal root ganglia. Even at initial phases of growth, axial motor and sensory axons avoid each other before fully segregating within the same nerve. Interestingly, axons from axial motor neuron explants and sensory neuron explants refuse to intermingle, thus recapitulating their behavior *in vivo*. Moreover, motor neuron growth cones (the leading tips of axons) collapse on contact with sensory axons. These results suggest that molecular recognition events prevent inappropriate mixing of axons during development.

Among the factors that can mediate this type of recognition are the ephrins and Eph

Cell contact-dependent communication between adjacent motor and sensory neurons prevents miswiring of developing neural circuits.

receptors, cell surface-associated ligands and receptors whose interaction at sites of cell-cell contact facilitates intercellular communication (5). In general, these two protein families guide axons to their targets by enabling growth cones to communicate with surrounding cells. In the peripheral motor system, EphA4 signaling ensures proper pathway selection of motor axons to the limb (6–8). Compartmentalized Eph receptor expression within developing nerves, such as EphA4 in spinal nerves and EphB2 in the optic nerve of the chick embryo (9, 10), suggests that these proteins play an additional role in separating axon populations. However, their involvement in axon segregation has not been demonstrated.

Gallarda *et al.* analyzed the projections of axial motor and sensory neurons in mice lacking EphA3 and EphA4 and discovered that these receptors control the repulsion of axial motor axons from neighboring ephrin-A-expressing sensory axons. This repulsive signaling not only inhibits the intermingling of motor and sensory axons, but also blocks motor axons from projecting in the wrong direction along sensory axons and infiltrating the dorsal root ganglia (see the figure). Ultimately, these EphA-mediated guidance events

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