

Such palmitate incorporation has also been reported in bacteria carrying mutations in components of the transport systems that move LPS towards the outer membrane⁹ and phospholipids away from it^{10,11}. What can these observations tell us about the function of PbgA? They could fit with the proposal^{12,13} that PbgA is a transport protein for the phospholipid cardiolipin. However, directly blocking LPS biosynthesis can also lead to LPS depletion, and to incorporation of palmitate in outer-membrane LPS^{14,15}. As such, PbgA's apparent influence on cardiolipin transport seems to be a secondary consequence of its role in regulating LPS biosynthesis. In support of this idea, Clairfeuille *et al.* confirmed the finding¹⁶ that PbgA was required for the outer membrane to retain its integrity, whereas eliminating cardiolipin had no effect.

Clairfeuille and colleagues' key advance was to analyse the structure of PbgA at a resolution of 1.9 Ångströms, using a technique called X-ray crystallography. They found that PbgA belongs to a family of enzymes that also includes EptA – a protein that adds a phospholipid-derived molecular modification to the lipid A domain of LPS¹⁷. Lipid A is made of two phosphorylated sugars. By modifying these phosphate groups, EptA provides cells with resistance to antibiotics that bind to lipid A, called polymyxins.

The authors showed that the external surface of PbgA was tightly bound to an LPS molecule. They then re-evaluated a lower-resolution structure of PbgA¹³ and – on the basis of the distance between its phosphate groups – verified that it was bound to the lipid A domain of LPS. Although a phospholipid partially occupies a site near the bound LPS, PbgA has lost the amino-acid side chains used by EptA to catalyse LPS modification. Whether or not PbgA retains enzymatic activity remains to be determined.

The picture of PbgA that emerges from Clairfeuille and colleagues' structure is of a protein that has been adapted as a receptor to sense LPS at the external surface of the inner membrane. The structure supports the model that a PbgA–LapB–FtsH–LpxC regulatory circuit acts as a control mechanism, modulating LPS biosynthesis to meet the physical demands of the cell's interconnected double membranes. Indeed, the researchers also confirm the finding⁴ that a direct physical interaction occurs between PbgA and LapB in membranes. But how LPS–PbgA binding relaxes the inhibition that PbgA exerts on the LapB–FtsH interaction remains unknown.

Clairfeuille and co-workers' structure reveals that PbgA binds the lipid A moiety through a linker domain, using an amino-acid sequence that has not been reported in any other LPS-binding protein. Mutations in this LPS-binding motif compromised PbgA function. In a final set of experiments, the

authors demonstrated that a synthetic peptide based on this sequence could bind LPS and inhibit bacterial growth. Through rational design, they improved the peptide's antibiotic spectrum and potency.

The polymyxins bind lipid A by interacting with both of its phosphorylated sugars¹⁸, but PbgA binds to just one. The polymyxin antibiotic colistin is used as a last resort for treatment of infections in the clinic, but it can also increase outer membrane permeability, thereby sensitizing bacteria to more-effective antibiotics¹⁸. Clairfeuille and co-workers' show that the PbgA-derived peptide also sensitizes bacteria to other antibiotics, acts in synergy with colistin, and is not hampered by the LPS modifications catalysed by EptA.

PbgA was one of the few essential proteins in *E. coli* without a well-characterized function⁴. The discovery that PbgA is the LPS signal transducer provides insights for antibiotic development, in addition to illuminating a remarkable lipid balancing act in the bacterial membrane.

Russell E. Bishop is in the Department of Biochemistry and Biomedical Sciences, and at the Michael G. DeGroot Institute for Infectious Disease Research, McMaster

University, Hamilton, Ontario L8S 4K1, Canada.
e-mail: bishopr@mcmaster.ca

1. Bertani, B. & Ruiz, N. *EcoSal Plus* <https://doi.org/10.1128/ecosalplus.ESP-0001-2018> (2018).
2. Clairfeuille, T. *et al.* *Nature* **584**, 479–483 (2020).
3. Guest, R. L., Guerra, D. S., Wissler, M., Grimm, J. & Silhavy, T. J. *mBio* **11**, e00598-20 (2020).
4. Fivenson, E. M. & Bernhardt, T. G. *mBio* **11**, e00939-20 (2020).
5. Nguyen, D., Kelly, K., Qiu, N. & Misra, R. J. *Bacteriol.* <https://doi.org/10.1128/JB.00303-20> (2020).
6. Xie, R., Taylor, R. J. & Kahne, D. J. *Am. Chem. Soc.* **140**, 12691–12694 (2018).
7. Nikaido, H. *Chem. Biol.* **12**, 507–509 (2005).
8. Jia, W. *et al.* *J. Biol. Chem.* **279**, 44966–44975 (2004).
9. Wu, T. *et al.* *Proc. Natl Acad. Sci. USA* **103**, 11754–11759 (2006).
10. Malinverni, J. C. & Silhavy, T. J. *Proc. Natl Acad. Sci. USA* **106**, 8009–8014 (2009).
11. Chong, Z.-S., Foo, W.-F. & Chng, S.-S. *Mol. Microbiol.* **98**, 1133–1146 (2015).
12. Dalebroux, Z. D. *et al.* *Cell Host Microbe* **17**, 441–451 (2015).
13. Fan, J., Petersen, E. M., Hinds, T. R., Zheng, N. & Miller, S. I. *mBio* **11**, e03277-19 (2020).
14. Helander, I. M., Hirvas, L., Tuominen, J. & Vaara, M. *Eur. J. Biochem.* **204**, 1101–1106 (1992).
15. Helander, I. M., Lindner, B., Seydel, U. & Vaara, M. *Eur. J. Biochem.* **212**, 363–369 (1993).
16. Qiu, N. & Misra, R. J. *Bacteriol.* **201**, e00340-19 (2019).
17. Anandan, A. *et al.* *Proc. Natl Acad. Sci. USA* **114**, 2218–2223 (2017).
18. Vaara, M. *Front. Microbiol.* <https://doi.org/10.3389/fmicb.2019.01689> (2019).

This article was published online on 12 August 2020.

Electronics

One-way supercurrent achieved in a polar film

Toshiya Ideue & Yoshihiro Iwasa

Diodes are devices that conduct electric current mainly in one direction. An electrically polar film that acts as a diode for superconducting current could lead to electronic devices that have ultralow power consumption. **See p.373**

An essential process in modern electronics is rectification, whereby bidirectional electric current is converted to unidirectional current. Electronic devices that enable rectification are called diodes and are widely used to transform alternating current into direct current, protect electric circuits from excess voltage and detect electromagnetic waves. Extending this concept to a superconducting current, which flows with zero resistance, is a fascinating challenge from both fundamental and technological viewpoints. On page 373, Ando *et al.*¹ report the achievement of this superconducting diode effect and its magnetic control in an electrically polar film that is non-centrosymmetric – lacking symmetry under a transformation known as spatial inversion. The authors' findings demonstrate that charge can be transported

in a single direction without energy loss.

In a conventional diode, rectification is realized using a heterojunction (an interface between two different semiconductors), such as a p–n junction (Fig. 1a). For a p–n junction, one of the semiconductors is p-type, containing an excess of positively charged electron vacancies called holes, and the other is n-type, containing an excess of negatively charged electrons. Electric current flows easily only from one side of the interface to the other². Although such a structure is a fundamental component of many devices today, it is difficult to achieve the superconducting-diode effect by this strategy because a non-zero electrical resistance at the junction is inevitable.

Non-centrosymmetric conductors can exhibit an intrinsic rectification effect, even if they are uniform and junction-free

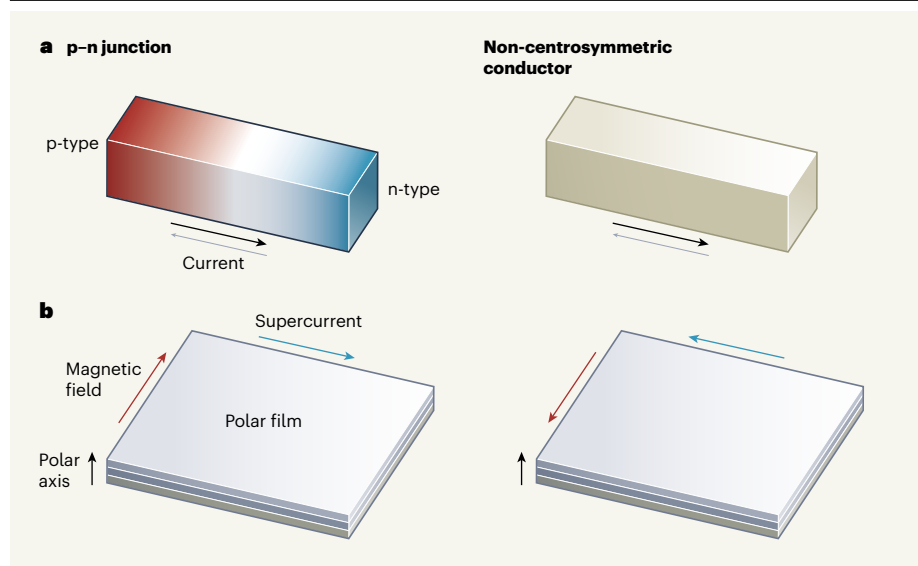


Figure 1 | Different types of rectification. **a**, Rectification is a process that causes electric current to flow freely in one direction but only slightly (or not at all) in the opposite direction. This process can be realized at a p–n junction, which is the interface between two types of semiconductor known as p-type and n-type. It can also be achieved in an electrical conductor that is junction-free and non-centrosymmetric – lacking symmetry under a transformation known as spatial inversion. **b**, Ando *et al.*¹ made an electrically polar film that consists of stacked layers of three metals. The authors applied a magnetic field perpendicular to the polar axis of the film and observed a superconducting current in a single direction perpendicular to the directions of both the magnetic field and the polar axis. They found that the direction of this rectified supercurrent could be inverted by reversing the direction of the magnetic field.

(Fig. 1a). This effect is currently recognized as a fundamental feature of these materials and as an emergent physical property that reflects the characteristic electronic states, magnetic structure, interaction effects and geometric or topological nature of electrons in non-centrosymmetric solids.

If this intrinsic rectification effect occurs alongside broken time-reversal symmetry (a lack of symmetry when the direction of time is reversed), it is known as magnetochiral anisotropy. Since this phenomenon was first reported³ in 2001, it has been studied in a variety of quantum materials and interface systems^{4–7}. A key aspect of magnetochiral anisotropy is that, in principle, it can occur in any quantum phase of matter, including a superconducting phase under appropriate symmetry conditions. Moreover, the direction of the rectified current can be inverted by reversing the direction of the magnetic field or magnetization.

In 2017, scientists observed magnetochiral anisotropy in two-dimensional non-centrosymmetric superconductors⁴. They suggested that the effect is a hallmark of exotic superconducting states, such as those in which the Cooper pairs (the electron pairs responsible for superconductivity) have an unconventional pairing symmetry. Therefore, magnetochiral anisotropy could provide a powerful experimental probe of non-centrosymmetric superconductors⁴. Moreover, a relatively large rectification effect has been detected in superconducting

films that have microstructures, such as triangular magnets through the motion of vortices⁵ – magnetic fluxes that pierce superconductors. However, the realization of an ideal superconducting rectifier, in which the zero-resistance state is retained in only one direction, has been both lacking and highly anticipated.

Ando *et al.* produced an artificial film called a superlattice that is composed of stacked alternating layers of niobium, vanadium and tantalum. The superlattice has an electrically polar structure because mirror symmetry

“The authors’ work opens the door to a new era of superconductivity research.”

along the stacking direction is broken. The authors focused on electric transport along the film’s plane, which is uniform and junction-free. In previous studies on interfaces⁶ and polar crystals⁷, an intrinsic rectification effect was observed along the plane when a magnetic field was applied perpendicular to both the current and the polar axis. Using a similar set-up, Ando and colleagues detected ideal superconducting diode behaviour in their film (Fig. 1b).

Because the authors’ film is relatively thick (120 nanometres), it can be regarded as a 3D superconductor. It shows a sharp transition

between conducting and superconducting states when it is cooled to temperatures below 4.4 kelvin, which is needed for the current to completely switch between these states. Moreover, the direction of the rectified current can be reversed by inverting the direction of the magnetic field, which is useful for practical applications (Fig. 1b).

The authors’ results indicate the great potential of non-centrosymmetric superconductors for producing devices that have ultrahigh sensitivity to electromagnetic fields or ultralow power consumption. The findings could also pave the way to unexpected device capabilities that are even more intriguing. The use of a superlattice is advantageous because the superconducting-diode effect should be controllable by tuning the superlattice’s structure. For example, by choosing appropriate constituent elements and optimizing the film’s thickness or number of stacked layers, it might be possible to obtain samples that have, relative to the authors’ film, a higher superconducting transition temperature or a higher resistance in the opposite direction to that of the rectified current; such samples would be desirable for applications. Another possibility is that the direction of the rectified current could be reversed by merely inverting the stacking order.

An important future issue is to clarify and fully understand the superconducting state in this superlattice and the microscopic mechanism of the superconducting diode effect. Ando *et al.* focus on a well-documented interaction in polar systems, known as the Rashba effect, and discuss the possible impact of the unconventional pairing symmetry in the superconducting state. However, there might be other contributions to the film’s behaviour from vortex motion or electron-scattering processes. Despite these remaining issues, there is no doubt that the authors’ work opens the door to a new era of superconductivity research.

Toshiya Ideue and **Yoshihiro Iwasa** are at the Quantum-Phase Electronics Center and in the Department of Applied Physics, University of Tokyo, Tokyo 113-8656, Japan.
e-mails: ideue@ap.t.u-tokyo.ac.jp;
iwasa@ap.t.u-tokyo.ac.jp

1. Ando, F. *et al.* *Nature* **584**, 373–376 (2020).
2. Sze, S. M. *Semiconductor Devices: Physics and Technology* (Wiley, 1981).
3. Rikken, G. L. J. A., Fölling, J. & Wyder, P. *Phys. Rev. Lett.* **87**, 236602 (2001).
4. Wakatsuki, R. *et al.* *Sci. Adv.* **3**, e1602390 (2017).
5. Villegas, J. E. *et al.* *Science* **302**, 1188–1191 (2003).
6. Rikken, G. L. J. A. & Wyder, P. *Phys. Rev. Lett.* **94**, 016601 (2005).
7. Ideue, T. *et al.* *Nature Phys.* **13**, 578–583 (2017).