News & views

the cryptochrome CRY4 lacks such signs of circadian cycling, suggesting that it has a different biological role, possibly that of magnetoreception[10,11]. CRY4 is found only in birds, fishes and amphibians, which are types of animal with well-documented magnetically guided behaviours. CRY4 has therefore emerged as the leading candidate for enabling cryptochrome-based magnetoreception in vertebrates.

Previous analysis[10] of chickens (*Gallus gallus*) and migratory European robins (*Erithacus rubecula*) indicates that CRY4 is located in the outer segments of two types of photoreceptor cell in the retina – double cones and long-wavelength single cones. This is an ideal location for receiving the light that would excite cryptochromes and thus aid magnetic sensing. Further evidence consistent with a possible role for CRY4 in magnetoreception is that its expression level in the robin retina rises as the migratory season approaches, whereas its level remains permanently low in non-migratory chickens[10].

Xu and colleagues' major advance is the demonstration that the version of CRY4 (dubbed *Er*CRY4) in the migratory European robin has a crucial property needed to sense Earth's magnetic field: the ability to form radical pairs that have high magnetic sensitivity. Radical pairs arise when the FAD bound to *Er*CRY4 is reduced (gains an electron) in the presence of light. Radicals contain an odd number of electrons, and a radical pair consists of two radicals that have been created simultaneously, usually by a chemical reaction. In *Er*CRY4, the radicals' odd electrons are supplied through sequential electron-hopping along a chain of three or four tryptophan amino-acid residues (termed Trp_A to Trp_D) that are located between FAD and the surface of the cryptochrome.

In the case of FAD, the odd electron that arises from reduction in the presence of light makes the radicals intrinsically magnetic. This is because electrons behave as microscopic magnets, with a property that physicists call spin (typically symbolized by an arrow ↑). In a molecule with an even number of electrons, the spins of each electron pair exactly cancel each other out, rendering the molecule non-magnetic.

If the spins of the odd electrons in each of the two radicals in a radical pair are antiparallel (↓↑), the radical pair is said to occupy a singlet state, but when they are parallel (↑↑), the pair occupies a triplet state. When cryptochrome becomes photoexcited, it always forms a radical pair in the singlet state, but it doesn't stay that way for long. Owing to a quirk of quantum mechanics, the radical pair rapidly converts to the triplet state, and then continues to bounce between these two states millions of times per second. Each of these two states can produce a reaction product – the form of CRY4

that contains the radical FADH•, which is the proposed signalling molecule for magnetoreception (Fig. 1). But the singlet state can also revert to its oxidized, non-excited ground state, thereby reducing its relative contribution to the generation of reaction products. Thus, if the interconversion of the singlet and triplet states can be manipulated to change the relative amounts of time spent in each of the two states, so too can the yield of the reaction products be manipulated, because a greater fraction of time in the triplet state leads to a higher yield of reaction products.

Herein lies the heart of the proposed cryptochrome-based magnetosensor: the relative amounts of time spent in the singlet and triplet states and the yield of reaction products are directly manipulated by the direction of Earth's magnetic field. The interaction between a single *Er*CRY4 molecule and the field is, on its own, at least one million times too weak to create the radicals and influence their stability[2], but the energy required is provided by the photon absorbed by FAD. However, for this to work at all, the radical pair must be sufficiently magnetically sensitive, and the reaction product must exist for long enough and have a sufficiently high yield to realistically act as a sensory signalling substance. In a tour de force of biophysical chemistry, Xu and colleagues used a wide range of techniques, such as spectroscopic methods and molecular-dynamics simulations, to show that all of these conditions are satisfied by *Er*CRY4, at least *in vitro*.

Not only does *Er*CRY4 have a much higher magnetic sensitivity than do CRY4 proteins in non-migratory pigeons and chickens, but site-specific mutations of amino-acid residues in *Er*CRY4 also reveal that its Trp_D is probably responsible for generating high and long-lasting (of greater-than-millisecond duration) yields of reaction products that would be needed for magnetosensory signalling. Although the evidence provided by Xu and colleagues is not definitive proof that *Er*CRY4 is the elusive magnetoreceptor *in vivo*, the authors have brought us ever closer to solving this abiding mystery of sensory biology.

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1. Mouritsen, H. *Nature* **558**, 50–59 (2018).
2. Hore, P. J. & Mouritsen, H. *Annu. Rev. Biophys.* **45**, 299–344 (2016).
3. Xu, J. *et al. Nature* **594**, 535–540 (2021).
4. Lohmann, K. J. *Nature* **464**, 1140–1142 (2010).
5. Qin, S. *et al. Nature Mater.* **15**, 217–226 (2016).
6. Nimpf, S. *et al. Curr. Biol.* **29**, 4052–4059 (2019).
7. Schulten, K., Swenberg, C. E. & Weller, A. *Z. Phys. Chem.* **111**, 1–5 (1978).
8. Ritz, T., Adem, S. & Schulten, K. *Biophys. J.* **78**, 707–718 (2000).
9. Griffin, E. A., Staknis, D. & Weitz, C. J. *Science* **286**, 768–771 (1999).
10. Günther, A. *et al. Curr. Biol.* **28**, 211–223 (2018).
11. Pinzon-Rodriguez, A., Bensch, S. & Muheim, R. *J. R. Soc. Interface* **15**, 20180058 (2018).

The author declares no competing interests.

Condensed-matter physics

Plasmons dragged by drifting electrons

Hugen Yan

Plasmons are combinations of light and collective electron oscillations. The demonstration that plasmons can be dragged by drifting electrons in the 2D material graphene could lead to advances in optical physics. **See p.513 & p.517**

A wave passing through a moving medium can be dragged by that medium. Depending on the relative velocity directions of the wave and medium, this effect can either increase or decrease the wave's speed. For a light wave, which typically travels at an enormous speed, the drag effect of a moving medium is negligibly small. Only sensitive optical-interference techniques can detect such a speed change – as shown by a celebrated experiment performed by the French physicist Hippolyte Fizeau in 1851, in which light passes through

moving water[1]. On pages 513 and 517, respectively, Dong *et al.*[2] and Zhao *et al.*[3] demonstrate an analogous effect in which plasmons (combinations of light and collective electron oscillations) are dragged by drifting electrons in solids. The groups show that this effect is much more pronounced than that for light travelling through a moving medium.

Waves are said to be transverse if they oscillate perpendicularly to their direction of propagation, and longitudinal if they oscillate parallel to that direction. Light is a transverse
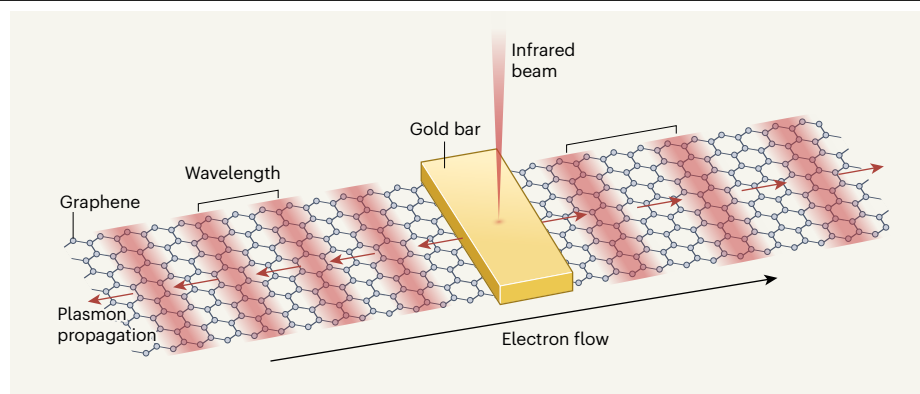
Figure 1 | Plasmons in graphene dragged by drifting electrons. Dong *et al.*[2] and Zhao *et al.*[3] directed a beam of infrared light at a gold bar, which launched propagating waves called plasmons (shown by red shading) in a single sheet of carbon atoms, known as graphene. The two groups found that plasmons moving in the opposite direction to the flow of drifting electrons in the graphene had a shorter wavelength (and, thus, a lower speed) than those travelling in the same direction. This observation suggests that plasmons can be dragged by drifting electrons in solids.

wave, whereas a plasmon is a longitudinal wave. In Fizeau's experiment, the light and the moving water are separate constituents, and the light can travel without a medium. However, for a plasmon, the light and the electrons are inseparable. As a result, a plasmon can be efficiently dragged by its constituent electrons if these electrons are drifting in an electric field. Crucially, this drag effect is easier to observe than that for light passing through a moving medium, because plasmons travel much slower than light.

Dong *et al.* and Zhao *et al.* fired a beam of infrared light at a gold bar, which launched plasmons in graphene[4] — a single sheet of carbon atoms. They directly visualized the plasmons at cryogenic temperatures using an imaging method known as near-field infrared nanoscopy. The groups found that plasmons travelling in the opposite direction to the electron flow in the graphene had a shorter wavelength (and, therefore, a lower speed) than those propagating in the same direction (Fig. 1). They conclude that the drag effect alters the plasmon wavelength by a few per cent. Such a change is remarkable because it can be directly measured without needing to resort to sensitive optical-interference techniques.

Plasmons exist in many materials, including noble metals (such as silver and gold), and the conventional 2D electron gas found in semiconductor stacks called heterostructures. However, plasmons in graphene have three distinctive attributes that are relevant to the drag effect. First, their drift velocity can be large — a few orders of magnitude larger than in noble metals. That's because electrons in graphene are highly mobile and relatively sparse. This feature allowed Dong and colleagues to observe the complex (nonlinear) drag effect in their experiments.

Second, the plasmon-drag effect in graphene is well described by Einstein's special theory of relativity and not by classical physics[5]. For the conventional 2D electron gas, the drag effect satisfies a classical relationship in which the plasmon's final velocity is simply the sum of its initial velocity and the electron drift velocity. However, for graphene, as for Fizeau's experiment on light passing through moving water, special relativity is needed to determine the final velocity, as shown by both groups of researchers. Third, electrons in graphene are highly mobile even at room temperature, suggesting that the drag effect might be observable under ambient conditions. For the conventional 2D electron gas, cryogenic temperatures are required before such an effect can be studied.

The two groups' plasmon-drag experiments provide insight into electron–electron scattering in graphene[6]. A measured quantity known as the drag coefficient reflects the scattering rate. If this rate (given in units of energy) is low compared with the plasmon energy, the drag coefficient is 0.25, as observed by Dong and colleagues. However, if the scattering rate is high relative to the plasmon energy, the drag coefficient is 0.5. Therefore, the plasmon-drag effect provides a measurement of the electron–electron scattering rate, which is particularly valuable for analysing interactions involving many electrons.

The progress made by these two groups has profound implications. The drag effect causes forwards- and backwards-propagating plasmons to have different wavelengths and speeds, introducing a property called non-reciprocity. As a result, time-reversal symmetry is broken: the physical characteristics of the system would change if the direction of time was reversed. Typically, an external magnetic field or a process known as chiral pumping[7] is needed to break such symmetry. However, the first of these approaches would not be useful in the context of a plasmonic device, because a magnetic field strong enough to

break time-reversal symmetry could not be applied to individual photonic components in the device: it would affect all of the components. The groups' results show that a current of drifting electrons can efficiently break time-reversal symmetry; this effect could be readily applied to a targeted photonic component, thereby improving the controllability and multifunctional capabilities of the device.

To fully unleash the potential of these non-reciprocal plasmons in graphene or other plasmonic systems, many further experimental studies would be needed. First, the difference in propagation length between forwards- and backwards-moving plasmons should be determined. Theoretical work[8] suggests that forwards-moving plasmons have a much longer propagation length than do backwards-moving ones; and, in the extreme case, backwards-moving plasmons cannot propagate. Such unidirectional plasmons are immune to being scattered back by material defects and obstacles. Second, with respect to the groups' experiments, achieving an even stronger drag effect requires a higher drift velocity, which would cause severe heating — a problem that might be alleviated using a pulsed current.

Third, the two groups studied only single-frequency plasmons. Measuring the drag coefficient for plasmons that range in frequency from the far- to the mid-infrared would provide a more complete picture of the plasmon-drag effect. Finally, the method of near-field infrared nanoscopy could be applied to the conventional 2D electron gas, which has been investigated using techniques based on infrared absorption[9] and a process called Raman scattering[10]. A careful comparison of nanoscopy images for the conventional 2D electron gas and graphene would be rewarding, directly revealing the difference in drag coefficients.

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1. Fizeau, H. *C. R. Acad. Sci.* **33**, 349–355 (1851).
2. Dong, Y. *et al. Nature* **594**, 513–516 (2021).
3. Zhao, W. *et al. Nature* **594**, 517–521 (2021).
4. Novoselov, K. S. *et al. Science* **306**, 666–669 (2004).
5. Borgnia, D. S., Phan, T. V. & Levitov, L. S. Preprint at https://arxiv.org/abs/1512.09044 (2015).
6. Sun, Z., Basov, D. N. & Fogler, M. M. *Proc. Natl Acad. Sci. USA* **115**, 3285–3289 (2018).
7. Song, J. C. W. & Rudner, M. S. *Proc. Natl Acad. Sci. USA* **113**, 4658–4663 (2016).
8. Morgado, T. A. & Silveirinha, M. G. *ACS Photonics* **5**, 4253–4258 (2018).
9. Tyson, R. E. *et al. Int. J. Infrared Millim. Waves* **14**, 1237–1249 (1993).
10. Súilleabháin, L. C. Ó. & Hughes, H. P. *J. Appl. Phys.* **76**, 1701 (1994).