

essentially spherical space³ and is composed of inner and outer nuclear membranes. The two membranes are periodically joined at annular junctions, forming channels that connect the inside of the nucleus with the cell's cytoplasm. These channels are occupied by multiprotein nuclear pore complexes (NPCs), which regulate the trafficking of macromolecules across the envelope.

The outer nuclear membrane is also connected to a membrane network called the endoplasmic reticulum, which permeates much of the cytoplasm. As such, the inner and outer nuclear membranes and the endoplasmic reticulum constitute a single continuous membrane system. When the nuclear envelope breaks down during cell division, NPCs disassemble and the nuclear membranes are peeled open. This causes the constituents of the nuclear membrane to disperse into the endoplasmic reticulum, where the proteins of the two structures become intermingled⁴ (Fig. 1a).

The nuclear membranes start to re-form as the chromosomes segregate to opposite poles of the cell. Membranes from the endoplasmic reticulum attach to and spread out over the surfaces of the mass of chromosomes, a process that is mediated by proteins of the inner nuclear membrane (Fig. 1b). But what mechanism is in place to close gaps within the membranes that eventually surround the daughter nuclei? Perhaps these holes are never actually sealed, but are instead plugged by reassembled NPCs. But this cannot be the whole story, because a sealed envelope can form even in the absence of NPCs⁵. Indeed, the enzyme p97 can drive fusion at annular junctions between the inner and outer nuclear membranes⁶ to seal NPC-free holes in the nuclear envelope. However, a full understanding of this fusion process has remained out of reach.

The ESCRT-III complex is known^{7,8} to have roles in the formation of certain intracellular vesicles, in the budding of retroviruses from the membranes of infected cells, and in the abscission process that separates two daughter cells at the end of cell division. What all these seemingly disparate events have in common is that they involve membrane fusion, which generates a membrane-bound compartment that is separate from, but topologically identical to, the cell's cytoplasm. In each case, components of ESCRT-III act as a molecular drawstring that constricts the neck of a membrane bud (or even of an entire cell) to promote annular fusion. This process is strikingly similar to the topological changes that occur when holes in the re-forming nuclear membranes are closed.

The current studies^{1,2} demonstrate that components of ESCRT-III accumulate transiently at the edge of gaps in re-forming nuclear membranes — just as would be expected if the complex mediated the fusion of nuclear membranes. Such a role is borne out by the observation, made by both groups, that depletion of the components of ESCRT-III results

in failure to seal the nuclear envelope. Olmos *et al.* also show that p97 and its cofactor protein, UFD1, are essential for the recruitment of key ESCRT-III subunits to the re-forming envelope.

Vietri *et al.* further reveal that ESCRT-III has a complementary role in disassembling the mitotic spindle. The microtubule structures that make up much of the spindle are attached to separating chromosomes, so they must be eliminated before the nuclear envelope can be sealed. Vietri and colleagues show that this elimination is carried out by spastin, a microtubule-severing protein that is attracted to the spindles by ESCRT-III.

These authors find that interference with spastin results in delayed disassembly of the spindle, and prolonged association of ESCRT-III with the re-forming envelope. Not surprisingly, interference with ESCRT-III also impairs spindle disassembly. So ESCRT-III and spastin coordinate spindle disassembly with closure of the nuclear envelope. This represents a striking parallel with abscission, in which spastin severs the spindle microtubules that pass between the two daughter cells.

Together, the current studies reveal a previously unknown role for ESCRT-III in re-forming the nuclear envelope. The association, albeit transient, between ESCRT-III and nuclear membranes raises the question of whether this complex, or a functional equivalent, might have other roles in envelope maintenance. Indeed, there are several situations in which such activity might be required.

For instance, some macromolecular complexes in fruitflies are exported from the nucleus by budding through the inner nuclear membrane, bypassing NPCs⁹. Capsid

structures containing DNA from herpes simplex viruses exit the nucleus in a similar manner¹⁰. These movements involve the type of membrane remodelling that is a hallmark of ESCRT-III. More dramatically, the Vpr protein, which is produced by HIV, is associated with transient ruptures of the nuclear envelope¹¹, and the membrane is again probably resealed through a similar mechanism. Finally, the elimination of misassembled NPCs in yeast has been shown¹² to depend on ESCRT-III. In the light of these phenomena, it would be no great surprise if ESCRT or ESCRT-like complexes were shown to have other, hitherto unappreciated, roles in nuclear-envelope dynamics. ■

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NANOPHOTONICS

Bright future for hyperbolic chips

The unusual properties of hyperbolic metamaterials, such as their ability to propagate light on the nanoscale without diffraction, have been realized in two-dimensional devices, heralding improved photonic circuits. SEE LETTER P.192

GUY BARTAL

Devices known as photonic integrated circuits^{1,2} could succeed electronic circuits in future data-storage, computation and communications technologies, because they would allow improved data bandwidths and lower energy consumption. But such devices lag behind their electronic counterparts because they are limited by diffraction effects that restrict their

applications to micrometre scales, whereas electronics have already reached the nanometre scale. This shortcoming is due to the fact that the electromagnetic properties of typical optical media hinder the relay of tiny optical features. If a beam narrower than (or comparable to) the wavelength of light travels through such media, it will either be distorted when it reaches its destination, because of diffraction, or it will not get there at all, because of exponential decay. This is a

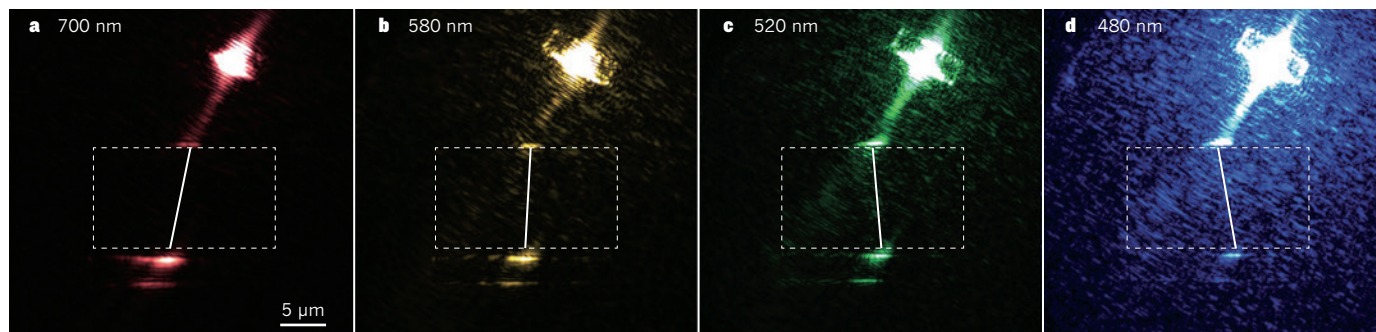


Figure 1 | Normal versus negative refraction in a hyperbolic metasurface (HMS). This set of images illustrates the effect of wavelength on the refraction of optical beams as they impinge on the interface of a silver film with the HMS grating, in a device built by High and colleagues³. The grating consists of nanoscale grooves. In **a** and **b**, a beam is refracted in the normal sense, whereas in **c** and **d** negative refraction occurs

(the respective wavelengths are labelled). In each case, the dotted box indicates the area covered by the HMS and the solid line indicates the angle of refraction. Devices based on nanoscale photonic circuits will be able to exploit this phenomenon to facilitate wavelength-based switching and routing of light and to increase the amount of information transferred.

fundamental limitation of propagating waves.

On page 192 of this issue, High *et al.*³ report the first experimental realization of two-dimensional ‘hyperbolic metasurfaces’ (HMSs)^{4,5}. The authors’ HMSs exhibit a range of unconventional properties, including colour-dependent negative refraction and diffraction-less propagation, coupled with low optical-transmission losses — all packed in a tiny chip.

Hyperbolic metamaterials (HMMs) are artificial structures whose optical properties are highly direction dependent. They are made of ultrathin multilayers⁶ or dense nanowire arrays⁷, and are renowned for their ability to overcome the diffraction limit by enabling the propagation of ultra-small features of electromagnetic waves^{4,8–10}. Moreover, they can support greater photon energy densities than can conventional materials, thereby enhancing the interaction of light with matter^{11,12} — a property that can lead to improved signal modulation and decreased energy consumption. These are key ingredients for bringing HMMs to the front line of integrated circuitry, on a par with electronics. Their unusual properties could also expand their applicability beyond that of run-of-the-mill optical media.

Until recently, HMMs have been fabricated only in three-dimensional configurations, making them unsuitable for integration on flat chips. Furthermore, these composite devices often contain metallic parts that absorb light and cause losses from resistivity, weakening their electromagnetic-power throughput. Also, preventing diffraction requires a certain design that inevitably maximizes the damping of electromagnetic waves¹⁰, reducing the waves’ effective propagation distances to less than 1 μm.

High and colleagues overcame these issues by fabricating an HMS consisting of a nanoscale grating on a single-crystal silver film — a design that can prevent diffraction without causing excessive losses from resistivity. Moreover, using sophisticated crystal-growth techniques and cutting-edge patterning methods, the authors were able to further minimize

both resistivity and scattering losses and to achieve operational propagation distances.

What new on-chip functionalities result from this work? The hallmark property of HMMs is negative refraction, the ability to bend a beam that crosses from one medium into the HMM in the ‘wrong’ direction — essentially, breaking the law of refraction. Negative refraction is not typically observed in naturally occurring materials, but it has been demonstrated in various metamaterials in the past 15 years^{6,13,14}. Not only have High *et al.* produced the first chip to exhibit negative refraction, but they have also shown that the effect can be wavelength dependent (Fig. 1); that is, their device allows certain colours of visible light to be refracted in the ‘wrong’ sense, whereas others refract normally.

This property could facilitate wavelength-based switching and routing of light in photonic circuits. No less importantly, it could be used to counter the natural tendency of a tightly focused light beam to expand as it travels, because the transition from normal to negative refraction occurs at a certain wavelength that depends on the material’s design. At this wavelength, the beam impinging on the HMS does not diffract, but propagates unimpeded without sideways loss of energy, irrespective of the beam’s launch angle or width (see Fig. 3a, b of High and colleagues’ paper³). The devices built by the authors take advantage of this effect, so that each groove of the grating can channel this particular wavelength, regardless of how closely spaced the grooves are or how small their intrinsic width is compared with the wavelength in question. In fully fledged HMS devices, this would allow a substantial increase in the information capacity transferred across small chips. Diffraction-less 2D imaging could be one of many other potential applications.

High and colleagues further demonstrate that they can selectively route light beams of visible frequency not only by the beams’ colour, but also by the photons’ spin. Spin is a fundamental signature of photons, and is

associated with the circular polarization of electromagnetic waves (the direction of rotation of the electric field in time and space). In one of the devices demonstrated in the current work, a beam of left-handed polarization is diverted to a direction opposite to that of a right-polarized beam. Although this phenomenon has been previously demonstrated in metasurfaces¹⁵ and HMMs¹⁶, what is unique here is the combination in prototype devices of colour sensitivity, polarization-dependent refraction, enhanced light–matter interaction and significant reduction in optical losses. The ability to encapsulate these desirable properties on a chip could form the backbone of a robust photonic system, suitable not only for high-capacity data transmission, but also for quantum-communications and quantum-memory applications. ■

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