fiberoptic paths. Also, the nonlinearity in the fiberoptic loops means that photons can interact. Thus, photons can jump from one pulse to another through nonlinear interactions and redistribute into different modes. The photons can thereby thermalize just like a gas. The result is a highly controllable thermodynamic testbed for designing a negative-temperature heat engine that uses a photon gas as a working substance. For instance, the total size of the lattice can be increased or decreased with the variable coupler, thus increasing or decreasing the number of modes. The internal energy of the system can also be changed while keeping the number of modes constant.

The time-synthetic lattice is described by lattice band theory, which is analogous to the energy bands of a crystal lattice. The upper energy bound within each band is necessary to realize negative temperatures. In this system, negative temperatures are created just by adding more energy. For example, by increasing the intensity of the laser light that is injected to the loop system of Marques Muniz *et al.*, the energy of the system can be increased, which leads to a negative temperature. The variable coupler allows the abrupt doubling of the number of occupied modes to realize a sudden expansion of a photon gas. By contrast, if the lattice time difference between modes is resized slowly, then isentropic compression and expansion can be implemented, which are the building blocks of a heat engine. Throughout these processes, the negative temperature is stable, thus confuting the notion that negative temperatures are not practically useful (*14*).

As negative temperatures become realizable in accessible experimental contexts such as nonlinear optics, a rapid exploration of their impact can be expected, from the design of nanoscale superefficient engines (*8*) to quantum transport devices (*14*) to the generalization of the many-temperature distributions found in quantum simulators and computing (*6*). ■

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ANIMAL BEHAVIOR

Bees learn to dance

Experience yields precision in the waggle dance of honey bees

By **Lars Chittka**[1] *and* **Natacha Rossi**[2]

Many animals can guide or call other members of their group to a rich foraging site (*1*–*3*). By contrast, honey bees have a distinctive form of communication that allows them to send nestmates to the location of a food source by using symbols. The coordinates are encoded by intricate movements (the "dance") on the vertical wax comb in the hive, using gravity and time as references. The motions are followed by recruits in the darkness of the hive, who subsequently decode the extracted flight vector information and follow the dancer's instructions once outside (*4*). Like many of the elaborate behaviors of social insects, this communication system was thought to be innate. However, on page 1015 of this issue, Dong *et al.* (*5*) reveal that honey bees only deliver precise spatial information in their dances if they previously had the opportunity to attend dances by experienced role models—the communication system must in part be learnt socially.

After the discovery of a rich food source, honey bee (genus *Apis*) foragers can recruit nestmates by performing a figure-of-eight–shaped dance (consisting of a central "waggle run" followed by alternating left and right semicircles) on the vertical wax combs inside the hive, with followers touching the dancer's abdomen with their antennae. The duration of the straight waggle run informs the others about the distance to the bounty. Direction of the target relative to the Sun is encoded in the angle of the waggle run, so that a waggle run straight up means "fly toward the Sun's azimuth" and a waggle run at an angle 20° to the right of the vertical means "fly 20° to the right of the Sun's azimuth" (*4*). The full dance circuit is repeated many times over to allow dance followers to average out variation of the display. There are indications that dance behavior is at least in part genetically encoded: All species of honey bees exhibit a form of this communication, and no other bee species do. Moreover, subtle variations of the dance code within the genus are species specific, and the information contents are largely preprogrammed in that they are limited to information about location and quality and cannot easily incorporate new "words" (new symbols with new meanings) in the same way that human language can (*6*).

However, if the waggle dance was fully innate, young bees would display the dance correctly even if they had never witnessed the behavior. Dong *et al.* created bee colonies composed exclusively of newly emerged bees; without any guidance from tutors, these bees began displaying waggle dances at the typical age of 1 to 2 weeks after emergence from the pupae (*7*). But the location indications from such inexperienced bees were highly variable from one dance circuit to the next and consistently indicated distances longer than the bees had actually traveled. Recruits would have struggled to find the indicated location. As the immature bees gained experience over the coming 20 days, the variation of their location codes gradually reached normal levels. However, distance indications remained abnormally high for life, indicating that after a critical time window, adjustments through social learning are no longer possible (*8*). Bees from control colonies, which had exposure to dances of seasoned foragers before initiating their own, displayed none of these shortcomings.

Why does any element of the dance language have to be learnt if the end point of the learning is always a dance of the same pattern and precision? There are two possible scenarios—one is similar to human locomotion, whereby everyone has to learn to walk, but the outcome is predictable. The alternative scenario is that there might be flexibility in the outcome of learning (the dance patterns displayed) depending on the environmental conditions encountered by bees. This indicates the exciting possibility that the link between symbol and meaning could be learnt, as in human communication.

Could it be that what is socially learnt is not just the precise choreography, but the translation of the information provided by other bees' dances into the actual coordinates of food sources subsequently encountered by the dance attendees? In

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support of this possibility, one species of honey bee was found to learn to read the distance code of another species, even though these two species normally encode distance differently (*9*). Bees' flight distance estimation is in part determined by the amount of contrast in the environment and thus differs between, for example, forests and steppes. Therefore, it is at least plausible that there might be subtly different, socially acquired local "cultures" of the dance language that depend on visual characteristics of the landscape or the spatial distribution of food sources (*10*).

The study of Dong *et al.* adds to the growing evidence that complex behaviors are seldom entirely innate. For example, although the regularity and optimality of the honey bee comb construction were regarded by Darwin as "the most wonderful of all known instincts" [(*11*), p. 235], it turns out that how workers build comb is affected by the comb structures that they experienced when young (*12*). Even specialist bee species, supposedly innately tied to certain species of flowers, must learn to manipulate these flowers (*13*).

Some scholars assume that instinct is by default the ancestral (or primitive) state and that learning is more advanced. The opposite is more rarely considered: Individual learning might be at the root of some behavior innovations that are now partly innate. Bees can learn even relatively arbitrary behaviors, such as string pulling or ball rolling, by observing skilled conspecifics (*14*). It is therefore plausible that some of their most advanced behavioral innovations (including elements of the dance language) might have emerged at least in part by individual innovation and subsequent social learning, becoming instinctual later in evolutionary time (*14*, *15*). Therefore, the observed flexibility of species-specific behavior might simply reflect the ancestral condition. ■

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CELL BIOLOGY

Watching biomolecules stride in real time

A noninvasive imaging technique tracks the motion of single biomolecules in live cells

By **Jinyu Fei** *and* **Ruobo Zhou**

A long-sought goal for scientists is to directly watch motions and interactions of all individual biomolecules within a cell, which would substantially increase our understanding of life processes at the molecular level. On pages 1004 and 1010 of this issue, Wolff *et al.* (*1*) and Deguchi *et al.* (*2*), respectively, take us one step closer to this goal. They report an improved version of MINFLUX, a nanoscope concept introduced 6 years ago (*3*), that increases the spatiotemporal resolutions of light microscopy to nanometer and millisecond scales. They apply this technique to study the molecular mechanisms of kinesin walking on microtubules under unprecedented physiologically relevant conditions.

In the journey to view objects inside cells with light microscopes, great successes have been made for visualizing cell organelles, which are typically 1 to 10 μm across. However, visualizing the crowded, single proteins inside cells with light microscopy is challenged by the diffraction limit of visible light (*4*). Light microscopes can distinguish between two fluorescent objects divided by a lateral distance of approximately half the wavelength of light used to image the objects, and hence the smallest feature size that light microscopes can resolve is ~250 nm, whereas proteins are only ~5 nm. A group of superresolution imaging methods, collectively called fluorescence nanoscopy, have recently been developed that circumvent the diffraction limit and have pushed the spatial resolution down to 10 to 30 nm (*4*).

There are two main categories of fluorescence nanoscopy approaches. The first category, such as stimulated emission depletion microscopy (STED), surpassed the light diffraction limit with patterned illumination, in which an additional coaxial donut-shaped depletion laser beam is added to the point-scanning confocal excitation laser beam to inhibit fluorescence emission everywhere other than at the very center of the diffraction-limited illumination region. This allows the center region, which is much smaller than the diffraction-limited region, to emit fluorescence. The second category, such as stochastic optical reconstruction microscopy (STORM) and photo-activated localization microscopy (PALM), is based on single-molecule localization, in which a superresolution image is constructed from a camera-recorded series of time-separated image frames, each of which contains only a sparse set of fluorescent molecules so that the centroid positions of these molecules can be individually localized by using two-dimensional (2D) Gaussian fitting to find the peak position of each molecule's fluorescence intensity profile. The precision of this peak finding (localization) is inversely proportional to the square root of the photon number collected for building the single-molecule fluorescence intensity profile (*5*). The spatial resolution of these traditional camera-based localization nanoscopy approaches is also limited to the maximum photon number that a fluorophore can emit per localization, which is an intrinsic property of fluorophores.

In 2017, MINFLUX was introduced to push the spatial resolution down to 2 to 3 nm, enabling true molecular-scale fluorescence imaging (*3*). In contrast to traditional camera-based localization that uses the fluorescence intensity maximum, MINFLUX shifted a donut-shaped illumination spot over an area of a few hundred nanometers around each fluorescent molecule to localize these molecules by using the fluorescence intensity minima. This requires 10 to 100 times fewer photons compared with that of camera-based localization to achieve the same localization precision. The unprecedented spatial resolution of MINFLUX is achieved by combining the strengths from both categories of nanoscopy approaches: Using photo-switchable dyes to excite only a small subset of dyes at a time for single-molecule localization, as used in STORM and PALM, while using a point-scanning donut-shaped beam as used in STED to localize the fluorescence intensity minimum. MINFLUX has been successfully used to visualize cellular ultrastructures—such as the multiprotein mitochondrial contact site and cristae organizing system (MICOS) (*6*), the nuclear pore complex (*7*), and neuro-

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