organs, mainly as a consequence of the slow diffusion of gases in water as opposed to in air[4]. The action of the two *SNORKEL* genes apparently occurs downstream of ethylene but upstream of gibberellic acid (Fig. 1a). Further study is needed to see if *SNORKEL* directs the marked rise in bioactive gibberellic acid that Hattori *et al.*[1] see in submerged tissues of deepwater rice.

The *SNORKEL* locus is the second example of a multigene region in rice that encodes ERFs and regulates underwater growth. The *SUBMERGENCE-1* (*SUB1*) gene region, situated on chromosome 9, encodes two or three ERFs (SUB1A, SUB1B and SUB1C) that determine the response to complete submergence[6]. *SUB1* was identified in a traditional variety prized for its ability to endure more than two weeks of inundation. In contrast to the rapid stem elongation manifested in submerged deepwater rice, lines that have the *SUB1A-1* gene can survive the stress by limiting ethylene-activated elongation growth (Fig. 1b), thereby conserving precious carbohydrates for regrowth when the flood recedes[6,7]. This is accomplished by minimizing the decline in a DELLA protein (SLENDER RICE-1, SLR1) and a related non-DELLA protein (SLR LIKE-1, SLRL1) in submerged shoots[8]. Strikingly, therefore, ethylene can trigger antithetical outcomes: the promotion (SNORKEL) or suppression (SUB1) of underwater elongation.

Fast submergence-induced shoot elongation is also a characteristic of some wild plants that grow in flood-prone ecosystems. Together with other traits, such as the possession of aerenchyma (the snorkel-like conduits for fast gas diffusion)[9], underwater elongation determines the distribution and abundance of species in river floodplains and similar environments. Fast underwater growth in wild plants is also regulated by the interaction between ethylene and gibberellic acid, with downstream target proteins such as the cell-wall-loosening expansins also having a role[4]. Submergence-induced elongation is observed in plants inhabiting locations characterized by prolonged but shallow floods. By contrast, species found in places where deep transient floods occur limit shoot elongation during submergence[4] — like rice that adopts the quiescence strategy.

Wetland species that are quiescent during submergence also accumulate ethylene in submerged tissues and can respond to gibberellic acid under non-submerged conditions[4]. This suggests that ethylene-driven shoot elongation, and thus the ecological distribution of many wetland plants, is regulated by molecular components that control the production and response to gibberellic acid in an ethylene-dependent manner. We speculate that transcription factors, related to the SNORKEL and SUB1 ERFs, regulate submergence responses — and thus survival in flood-prone environments — across plant species. The presence, function, timing and tissue-specificity of ERF expression could be targets of natural selection, and might thereby determine the remarkably varied growth responses mediated by ethylene at different doses and in distinct species[10].

Hattori and colleagues' delineation[1] of genes that control deepwater elongation has a practical edge: it provides a way to increase grain yields in areas prone to deep flooding by introducing the fast-elongation trait into high-yielding cultivars. This will complement the successful development of *SUB1* rice varieties that provide robust submergence tolerance in areas susceptible to flash floods[6]. Yields of rice cultivated in deep water may not reach those achieved in shallow paddies because carbon must be allocated to rapidly elongating underwater organs, and tall, grain-laden plants can topple if floodwaters recede. Nevertheless, the introduction of *SNORKEL* and *SUB1* into high-yielding varieties, using advanced breeding strategies, promises to improve the quality and quantity of rice produced in marginal farmlands.

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CHEMICAL PHYSICS

Electronic movies

Marc Vrakking

Strong laser fields can tear an electron away from a molecule, leaving a hole in the electronic wavefunction that races through the molecule. The ultrafast motion of such a hole has been traced at last.

The first event in a light-induced reaction is that the electrons in the irradiated molecule respond to the incident light. This response occurs on attosecond timescales (1 attosecond is 10^{-18} seconds), and even the fastest time-resolved measurements have been unable to probe the dynamics of the process. But on page 972 of this issue, Smirnova *et al.*[1] provide a glimpse into the fascinating world of attosecond electron dynamics, in effect revealing the opening frames of a movie that records the rearrangement of electrons when a molecule is ionized by a laser.

The authors make use of the fact that molecules exposed to intense laser fields emit soft (low-energy) X-rays, in a process that is generally referred to as high-harmonic generation (Fig. 1a). In this process, an electron is extracted from a molecule by the laser, leaving behind a molecular ion. The electron is then accelerated in the laser's oscillatory electric field, before recombining with the molecular ion[2]. The recombination results in the emission of an X-ray photon. Large numbers of (typically near-infrared) photons are thus converted into soft X-ray photons, which have frequencies that are multiples (harmonics) of the source laser's frequency.

High-harmonic generation has recently attracted great interest for at least two reasons. First, the soft X-ray photons are not emitted continuously, but in short bursts that have attosecond durations[3,4]. These attosecond pulses can be used to investigate fundamental questions about the interactions of light with matter. The number of research groups working in the field of harmonics-based attosecond science is thus growing exponentially, making it one of the most vibrant areas of laser physics and chemistry.

Second, harmonics contain a wealth of information about the atoms or molecules from which they are generated. Experiments have already suggested that high-harmonic generation allows information about molecular orbitals[5] and molecular structure[6] to be retrieved. The experimental and theoretical work reported by Smirnova *et al.*[1] represents a new milestone in this respect. The authors argue that high-harmonic radiation carries information about the amplitudes and phases of electron 'hole states' that are formed during the ionization event; holes are positively charged 'quasiparticles' formed by the absence of an electron. High-harmonic radiation can provide insight into hole migration in the ion during the timescale of up to several femtoseconds (1 femtosecond is 10^{-15} seconds) when the ionized electron is away from the ion, before recombination occurs.

Smirnova *et al.* used the fact that intense laser fields can force molecules to point in any desired direction — a process known as dynamic alignment[7]. By studying the interference

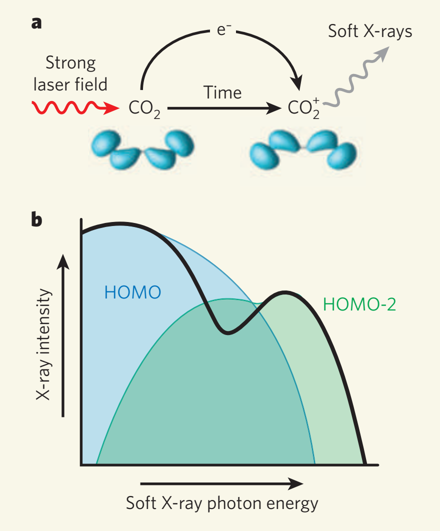

Figure 1 | High-harmonic generation. a, In high-harmonic generation, an electron is extracted from an atom or molecule, accelerated in a laser field, and directed back towards the resulting ion; soft X-rays are emitted during the course of electron–ion recombination. Smirnova *et al.*[1] show that the electronic wavefunction left behind by the ionization of CO_2 is different from the one encountered by the electron when it recombines with the CO_2^+ ion. Wavefunctions are shown in blue. **b,** The existence of different electronic states of the CO_2^+ ion gives rise to the formation of a minimum in the combined intensity of the X-ray emissions, caused by destructive interference of contributions from the different states (in this case, the HOMO and HOMO − 2 states). Blue and green areas are the X-ray emission spectra of the HOMO and HOMO − 2 states; the black line indicates the sum of these spectra after they have interfered destructively.

patterns of harmonic emissions from aligned and non-aligned carbon dioxide molecules, Smirnova *et al.* obtained the amplitude and phase of the harmonics as a function of the laser intensity, the alignment angle and the harmonic order (the multiple of the source laser's frequency that defines each harmonic frequency). In this way, the authors provided compelling evidence that, on ionization, the CO_2^+ ion is formed in both the ground state of the ion (corresponding to the removal of an electron from the highest occupied molecular orbital, known as the HOMO) and in the second excited state (corresponding to removal of an electron from a lower-energy orbital known as HOMO − 2). This challenges the widely held notion that strong-field ionization processes remove electrons only from the HOMO. A similar conclusion was recently reached in a study of harmonic generation from nitrogen molecules[8].

If more than one ionic state is populated in the ionization, this suggests that the electronic wavefunction of the molecular ion evolves between the moment of ionization and the moment of recombination, when the hole vacated by the electron moves. During recombination, the structure of the hole is encoded in the harmonic spectrum, which thus in effect provides a 'movie' of the hole's development. By working back from the information in the spectrum — playing the electronic movie in reverse — Smirnova *et al.* determine that the original ionization must have occurred by a 'tunnelling' process. Tunnelling is one of two models often used to describe the ionization of atoms or molecules influenced by a strong laser field.

This work[1] also sheds light on a fascinating controversy that has created quite a stir in the high-harmonics community. In 2002, the theoretical physicist Manfred Lein proposed[9] that harmonic generation from aligned molecules is influenced by the wave-like nature of the returning electron. He predicted that destructive interference could occur between harmonic emissions that originate from different atomic centres in a molecule, analogous to that observed in interfering light waves by Thomas Young in the classic double-slit experiment of 1801. The interference minima in harmonic spectra should depend only on the angle of alignment between the molecular axis and the electric field of the source laser beam, the wavelength of the returning electron and the internuclear distances of atoms in the molecules. Because the first two variables can be determined or controlled, this would allow the internuclear distances to be calculated. Remarkably, however, experiments in Tokyo[6] and Milan[8] observed interference minima for aligned CO_2 molecules at substantially different harmonic orders. Surely, the structure of CO_2 in these two cities could not be different?

Smirnova *et al.*[1] now reconcile these conflicting observations[6,8] by suggesting that the interference minima in the harmonic spectra of CO_2 have primarily a dynamical rather than a geometrical origin. They argue that the harmonic spectra consist of overlapping contributions from ionization of the HOMO and HOMO − 2 states. These two contributions interfere with each other, creating a minimum at a harmonic order that is determined by the intensity of the laser used in the experiment (Fig. 1b). The authors present a convincing comparison of numerical simulations of harmonic spectra with experimental data over a wide range of laser intensities, and show that their explanation might account for the different results of the Tokyo and Milan experiments.

Does this mean that the structural interpretation of minima in harmonic spectra — and hence the prospect of using such spectra to determine molecular structures — goes out of the window? Not quite yet. Two recent papers[10,11] have argued that interference patterns can have a structural origin. This proposal is based on the experimental confirmation of a distinctive feature, known as a phase-jump, on either side of the interference minimum. Intensive research thus continues around the world, aiming to disentangle geometrical and dynamical effects in harmonic generation and searching for conditions under which the two can more easily be separated. The ultimate outcome may well be that high-harmonic generation leads to interference minima that have both a dynamical and a geometrical origin. For now, the jury is still out. ■

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NEUROSCIENCE

Activity acts locally

Jonathan B. Demb and Marla B. Feller

How does neuronal activity affect the development of neural circuits? Work on the retina shows that blocking activity at the synapses between neurons reduces local synapse assembly without affecting global cellular structure.

Nervous system function depends on the organization of underlying neural circuits — groups of neurons whose ability to perform specific functions depends on an organized pattern of intercellular communication at neuron junctions (synapses). The importance of synaptic activity in the assembly of circuits during development has been a long-standing debate in neurobiology: a dominant model in the field[1,2] suggests that the amount of neurotransmission at synapses during maturation of the nervous system affects the large-scale arrangement of neural circuits, and even the structure of their component neurons. On page 1016 of this issue, Kerschensteiner *et al.*[3] present exciting work that revises this model. The authors show that, in the retina of mice, excitatory synaptic activity determines the density of synapses at individual neurons (a local effect), but does not affect cellular structure on a global scale.

Synaptic organization has been studied

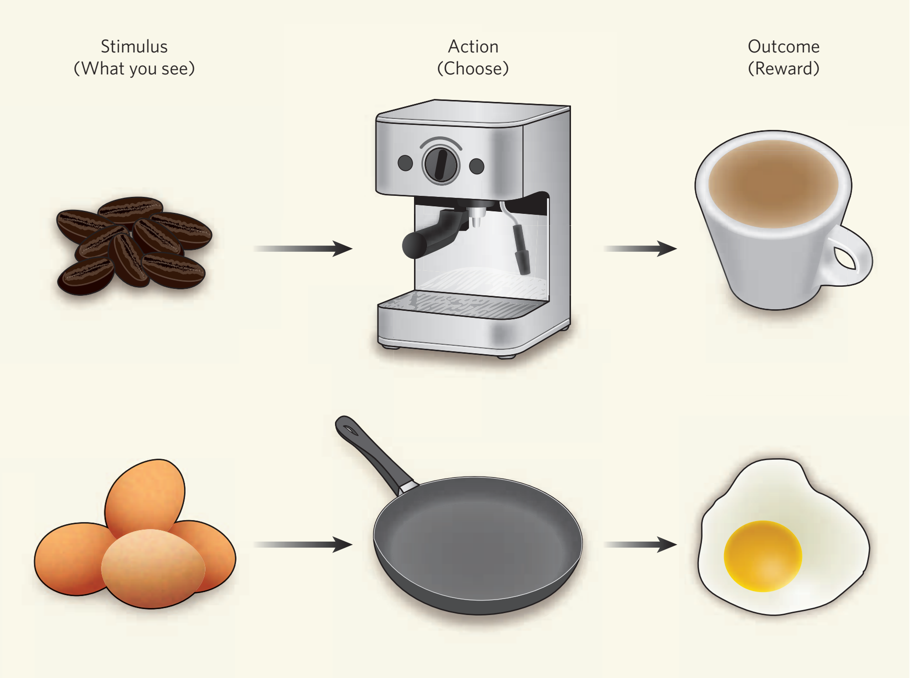

Figure 1 | Stimulus–action–outcome associations. Histed and colleagues[2] study how the brain stores information about the relationship between a stimulus, an action and its outcome. Their work shows that learning the outcomes of specific actions might be facilitated by persistent neural activity in the prefrontal cortex and basal ganglia.

experience the same sequence of sensory stimuli, actions and outcomes repeatedly. Moreover, the sensory and motor events that need to be remembered together are often transient, whereas the outcome of an action may be revealed only after a long delay. Therefore, the information about various sensory and motor events must be stored temporarily before the long-lasting memory about their relationship can be formed.

At least two mechanisms have been proposed to store such information in the brain. First, the relationship between two events, such as the tendency for separate sensory stimuli to occur together, might be reflected in the strength of synapses within a population of neurons[3,4]. Although the properties of such synaptic plasticity are becoming better characterized, how they encode behaviourally relevant information during the learning of a specific task is poorly understood. In addition, this mechanism requires the activity of the pre-synaptic and post-synaptic neurons to overlap within a relatively narrow time window, and therefore might not be able to deal with a long delay between relevant events[3]. A second, alternative mechanism for storing information about the relationship between multiple events might be persistent neural activity, which is sustained beyond the duration of the initiating event[5,6].

The best-known example of persistent neural activity is the 'delay activity' observed during the delay period of a working-memory task[5,6]. The activity of neurons in the primate prefrontal cortex often alters while the animal remembers the location or identity of a particular stimulus in order to use this information for guiding subsequent behaviour. The results from more recent studies[7–11], however, suggest that persistent activity might serve broader functions than working memory. For example, persistent activity is observed[7] in the prefrontal cortex, even when the animal is not performing a working-memory task. Also, during a dynamic decision-making task in which the animal has to discover an optimal behavioural strategy by trial and error, the activity of neurons in the prefrontal and parietal cortex often changes according to the outcomes of the animal's previous choices[8–11].

Histed and colleagues' work[2] shows that persistent neural activity might have an important role in learning the correct actions, even when the animal needs to repeatedly revise the associations between a sensory stimulus, an action and its outcome. In their study, monkeys learned which of two alternative actions (looking to the left or to the right) was required to gain a reward after viewing a particular visual stimulus. Once the animal learned the rewarded or 'correct' actions, the associations between stimuli and the correct actions were unpredictably reversed, requiring the animal to re-learn the relationship. The authors found that individual neurons in the prefrontal cortex and basal ganglia showed changes in activity depending on whether the action was correct or incorrect. And these neurons often displayed persistent activity during the inter-trial interval, signalling whether the animal had performed correctly or not in the preceding trial. Histed *et al.* also found that the activity in the prefrontal cortex and basal ganglia that is related to the animal's upcoming choice was enhanced, and the animal was more likely to choose the correct action when its choice in the previous trial was correct.

Histed and colleagues' results indicate that persistent neural activity might have more diverse roles in relating multiple events separated in time than previously thought. Studies have shown that some neurons in the prefrontal cortex and basal ganglia carry information about previous actions[8,11–13]. Combined with the authors' findings[2], these data suggest that the prefrontal cortex and basal ganglia might be essential brain areas for storing information about action–outcome associations[12–14]. However, how the signals related to an action and its outcome can be bound to a particular stimulus remains unknown. For example, in the task used by Histed *et al.*, the animal had to learn the relationship between a particular stimulus and an action. But neurons in the prefrontal cortex and basal ganglia predominantly encoded the outcome of the animal's choice between trials rather than the corresponding stimulus or action. To build on these findings, more studies are needed to further characterize the neural circuitry responsible for forming appropriate associations necessary for adaptive and flexible behaviours. ■

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Correction

The News & Views article "Chemical physics: Electronic movies" by Marc Vrakking (*Nature* **460,** 960–961, 2009) stated at the end of the fifth paragraph that "A similar conclusion was recently reached in a study of harmonic generation from nitrogen molecules", and incorrectly cited reference 8 of the article. This should have cited B. K. McFarland *et al. Science* **322,** 1232–1235 (2008).