Millet then and now. Foxtail millet is still harvested near Xinglonggou, Inner Mongolia, the location of some of the earliest Neolithic records of foxtail and broomcorn millet.

with wild stands: The comparative levels of diversity in the domesticated and wild forms today can best be explained by a substantial exchange of genes (*10*). Crops from the other major old world center, the West Asian "Fertile Crescent," show a similar very gradual shift in the fragmentation patterns of the grain-bearing stem (*11*). In both regions, the weed species in the early assemblages are indicative of soil preparation (*6*, *9*, *12*).

Rather than a revolutionary shift from hunter-gatherers to farmers in a few human generations, the evidence now suggests that many generations of "affluent foragers" combined the gathering of wild fruits and nuts with the gathering of cultivated cereals (*13*). Incremental shifts to a different form of rice stem indicate that some rice was sown. Beyond that, we have to imagine harvested plots that were quite different from modern agricultural fields, and in which gene flow between plots was freer than it is today (*14*). The domesticated stem trait may have become fixed within the harvested plots only when such plots became sufficiently isolated from the wild stands. In other words, the fixation of the domesticated trait marks not the beginning of farming, but an early stage in its geographical spread (*15*).

Remains of millet chaff are rare before 7000 years ago, and it is thus not yet possible to chart domestication stem traits through time. The archaeological evidence for millet is, however, much more informative about another aspect of the crop's history: its long-distance spread. One of the earliest sites of millet cultivation is near Xinglonggou in Inner Mongolia, on a low foothill more than 600 km to the north of the Yellow River (*2*, *16*, *17*) (see the second figure), where 8000-year-old millet has been recovered. Just 1000 years later, broomcorn millet had spread widely, with more than 20 published occurrences west of the Black Sea (*16*)—much wider than rice around the same time (*1*). By 4000 to 5000 years ago, cereals were spreading in the opposite direction to millet, with finds of the Fertile Crescent crops wheat and barley in several regions in China (*18*, *19*).

The growing convergence between archaeological and genetic research has elucidated a series of episodes that can be followed in East Asia, just as they can in the more intensively studied Fertile Crescent. At various stages between 12,000 and 7000 years ago, key locations between the valleys and the foothills were chosen to cultivate the soil and optimize the seasonal use of water (*17*). The plants grown in these plots continued to exchange genes with wild stands for millennia before core morphological traits such as the change in stem form were fixed.

But the story does not end there. In East Asian crops, as in crops around the world, the change in stem fragmentation that linked the fate of these plants intimately with their human consumers is only one step in the evolutionary history of the relation between people and plants. Later steps include major changes to structure, ecology, and culinary chemistry (*20*). In the 12,000 years since rice phytoliths were deposited in Diaotonghuan Cave (*3*), the domestication of plants has been a continuing process, made up of episodes of both rapid and gradual change. It is a process that continues apace today.

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NEUROSCIENCE

The Sources of Human Volition

Patrick Haggard

Two regions of the brain contribute to the conscious experience of carrying out an action.

Every day we make actions that seem to depend on our "free will" rather than on any obvious external stimulus. This capacity not only differentiates humans from other animals, but also gives us the clear sense of controlling our bodies and lives. It therefore forms a key element of our personal identity. However, such voluntary actions are a puzzle for modern neuroscience. Where do they come from? A study by Desmurget *et al.* (*1*) on page 811 of this issue reveals how the brain may produce our experience of initiating voluntary action.

Neuroscientists have long recognized that instructions for all voluntary body movements pass through the final staging post in the primary motor cortex (see the figure). This area of the brain receives two important inputs. One, from the premotor cortex, is involved when animals move in response to visual signals (*2*). But when animals make the same movements spontaneously, without any specific external trigger, a different area—the presupplementary motor area—instead supplies the major input to the primary motor cortex (*3*). The presupplementary motor area is also a likely source of "readiness potential," a buildup of electrical activity in the brain during the period just before voluntary action.

However, most neuroscientific studies of voluntary action in humans face a methodological and a conceptual problem. The for-

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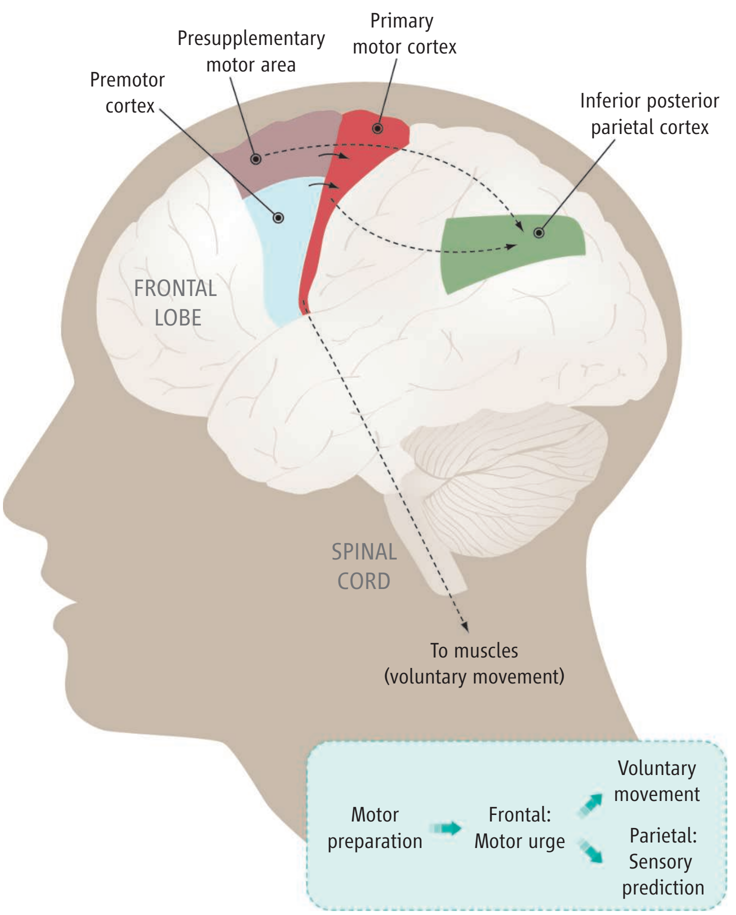
mer is that voluntary action seems to vanish in laboratory experiments designed to investigate it. Volunteers can be asked to choose what action to make, when to make it, or even whether to make it at all (*4*). But these instructions—which amount to "Have free will now!"—have something unsatisfactory, even paradoxical, about them. Scientists typically investigate systems by delivering controlled inputs and measuring outputs, but in volition, the experimenter cannot control the input, almost by definition. The conceptual problem is consciousness. Voluntary actions appear to start with a kind of thought—a "conscious intention." As the philosopher Ludwig Wittgenstein asked, "What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" (*5*). Conscious intention is one partial answer to his question (although not one that he himself would have welcomed). But how does conscious intention relate to the intended movement? Neurosurgeons sometimes directly stimulate the awake patient's brain during clinical exploration before surgery. This situation partly resolves both of these problems: The neurosurgeon's electrode delivers a precisely known input to the motor system; when applied to the presupplementary motor area, this electrical stimulation can produce a distinct conscious experience of an "urge to move" (*6*). Desmurget *et al.* now report that stimulation of another area, the inferior part of the posterior parietal cortex, also generates experiences of intention. The parietal cortex has traditionally been considered a sensorimotor association area—linking visual stimuli to appropriate responses, for example—and quite distinct from the frontal lobe areas responsible for voluntary action.



Voluntary action. (**Top**) The premotor cortex prepares commands for voluntary actions triggered by external stimuli, whereas the presupplementary motor area prepares commands for internally generated "intentional" actions, which are then executed by the primary motor cortex. Signals containing copies of prepared motor commands are also sent to the parietal cortex, where they are used to predict sensory consequences of movement. (**Bottom**) The preparation of motor commands for voluntary movement by the presupplementary motor area causes a sense of urge. The inferior part of the posterior parietal cortex generates sensory representations of the predicted consequences of the movement.

The study by Desmurget *et al.* investigates the experience that a patient has during electrical stimulation of specific brain areas. Experimental subjects were patients undergoing brain surgery; thus, stimulation took place with the patient awake but immobilized in a stereotactic frame, with the parietal cortex exposed—not an ideal setting for considering the nature of consciousness. However, stimulating this part of the brain led to experiences of intention that were clearly linked to specific body parts (patients reported wanting to move their arm, lips, or even chest). Moreover, experience of intention was a direct result of the electrical stimulation, not just of experimenter suggestion: When the neurosurgeon did not actually apply any current, patients did not report an urge to move.

The results of Desmurget *et al.* suggest that the parietal cortex, and not just the frontal cortex, may be involved in the experience of conscious intention. Other studies confirm that the parietal cortex contributes to the sense of controlling our actions (*7*), and also to conscious intention before movement. However, stimulation at one site may have remote effects elsewhere (*8*). Thus, stimulation of the presupplementary motor area could evoke urges indirectly, by remotely activating the parietal cortex, or vice versa. But if stimulation at the two sites produces qualitatively different effects, this would suggest that the two areas house distinct components of the experience of voluntary action.

In fact, there are important differences between frontal and parietal stimulation. Stimulation of the presupplementary motor area at low current caused an experience of urge, whereas stronger stimulation caused actual movement (*6*). By contrast, Desmurget *et al.* found that parietal stimulation, even at high intensities, never caused movements, though it could produce the illusion that a movement had occurred. This difference suggests that there may be two distinct aspects to conscious intention (see the figure). One would be a conscious correlate of preparing motor commands in the presupplementary motor area. Another would be a sensory prediction, in the parietal cortex, of the consequences of those commands. Sensory predictions could help to establish a sense of authorship over one's own voluntary movements (*9*). This view predicts that parietal cortex lesions should make one's actions feel involuntary, perhaps like delusions of control in psychosis (*10*). Low-level sensorimotor measures, such as the perceived time of intention, fit this prediction (*11*). But when patients with parietal lesions explicitly judged whether visual feedback reflected their own action or another person's action, they overattributed observed actions to themselves, contrary to the prediction (*12*). It remains unclear why stimulation of the parietal cortex causes conscious intention, yet damage to the same areas causes an excessive, rather than a reduced, sense of control over voluntary movement.

Could the conscious experience that patients call "urge" really be a sensory feedback from slight muscle contraction? Desmurget *et al.* exclude this long-standing alternative explanation by demonstrating that parietal stimulation does not produce any muscle activity (yet patients clearly experienced a desire to move). By contrast,

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stimulation of the premotor cortex produced large limb movements, yet the patients never reported any sense of urge, nor awareness of such movement. Therefore, conscious intention—or at least the parietally generated aspect of it—seems to be a specific class of experience generated within the brain, rather than a sensation of slight tension in the muscles. Thus, Desmurget *et al*. confirm that the parietal cortex contributes to conscious experience of volition. Just how the frontal, motor aspect of this experience differs from the parietal, sensory aspect is the next question.

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ECOLOGY

Some Like It Cold

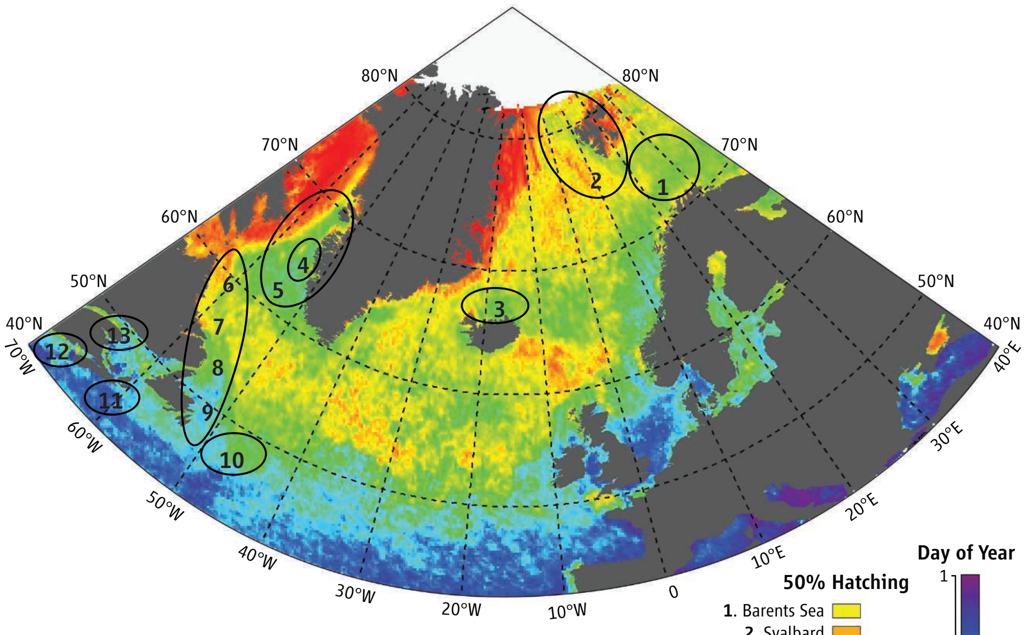
Northern shrimp stocks thrive when climatic conditions lead to cold bottom waters.

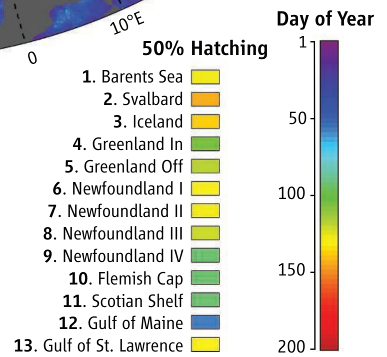
Charles H. Greene,* Bruce C. Monger, Louise P. McGarry

The northern shrimp, *Pandalus borealis*, makes up ~70% of the 500,000 tons of cold-water shrimp harvested annually from the world's oceans. Commonly captured in shelf waters deeper than 100 meters, it supports major fisheries throughout the North Atlantic. On page 791 of this issue, Koeller *et al*. (*1*) report that the reproductive cycles of most northern shrimp stocks are finely tuned to match the timing of egg hatching with that of the local spring phytoplankton bloom (see the figure). This remarkable degree of local adaptation on a basin scale is achieved by females regulating the initiation date of their temperature-dependent egg incubation period so that eggs hatch on average within a week of the expected spring bloom. Thus, in typical years, eggs hatch at the time of maximum food availability. The potential downside of this reproductive strategy is its sensitivity to climate-associated changes in the ocean environment.

A species' sensitivity to the vagaries of climate is often most evident at the limits of its distributional range. In the Gulf of Maine, the northern shrimp's southern limit in the northwest Atlantic, the temporal match between egg hatching and the spring bloom is relatively poor (*1*). Here, the deeper offshore waters are warmer than in other parts of the species' range because they are partially derived from the relatively warm and salty slope waters entering the gulf from the North Atlantic (*2*). Because northern shrimp are bottom dwelling and eggs develop faster at higher temperatures, eggs hatch earlier in the gulf stock than in any other stock investigated, and well before the spring bloom. Egg hatching would occur even earlier if gulf females did not exhibit a behavior seen nowhere else in the species' range. During winter, egg-bearing females migrate from offshore into the colder, shallower nearshore waters, a behavior that Koeller *et al*. suggest is an adaptation to delay egg development and improve the match between egg hatching and the spring bloom.

Bottom temperatures in the northwest Atlantic's shelf waters often respond to climate-associated changes in ocean circulation, and such responses can impact the population biology of northern shrimp. The North Atlantic





Good timing. Koeller *et al.* (*1*) show that in most parts of the North Atlantic, egg hatching for northern shrimp stocks occurs within a week of the initiation of the spring phytoplankton bloom (*9*). Average spring bloom initiation dates were determined from satellite-derived surface chlorophyll data collected from 1998 to 2006. The average timing of 50% egg hatching for each stock area is shown with circles that use the same color bar as that used for spring bloom initiation dates.

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