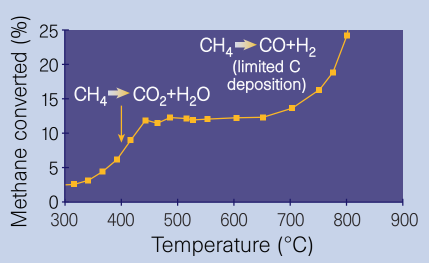

Figure 2 **Conversion of methane by an oxide catalyst[7]. The percentage conversion of CH_4 by $La_{0.8}Ca_{0.2}CrO_3$ powder is shown as a function of temperature when fed with a mixture of methane and oxygen (diluted in helium) in the ratio 5:1 (by volume). Methane is directly oxidized to CO_2 and H_2O at temperatures around 400 °C. At higher temperatures CH_4 is reformed to H_2 and CO fuel with minor carbon deposition on the oxide catalyst.**

In the SOFC research community, doped $La_{0.8}Ca_{0.2}CrO_3$ (LCC) and doped $Ce_{0.9}Gd_{0.1}O_{1.95}$ (CGO) have received the most attention. LCC is a promising anode material[7,9] because of its wide thermodynamic stability range, and existing use as an electrical connector between single fuel cells. Catalysts that contain ceria (such as CGO) have attracted interest[10] because it has been known for decades[11] that the use of doped ceria can improve the performance of SOFC anodes. Both LCC and CGO have good catalytic activity for methane oxidation. Steady-state measurements[7] with a limited supply of oxygen gas indicate that LCC oxidizes methane to CO_2 and H_2O at around 400 °C (Fig. 2). The reaction with CGO occurs at lower temperatures, around 300 °C. Exposure to residual excess methane confirms that only small amounts of carbon are deposited on both oxides at high temperatures (800–900 °C). Moreover, if carbon is intentionally deposited on the oxides it can be removed[12] at relatively low temperatures (300–400 °C) by the introduction of oxygen. The excellent catalytic behaviour of the ceria-based materials is not totally unexpected because CeO_2–ZrO_2 (CZO) catalysts are used in catalytic converters fitted to car-exhaust systems. It appears that CGO and CZO promote the reduction of Ce^{4+} to Ce^{3+}, which enhances oxygen-exchange processes[13] and associated catalytic reactions.

These catalytic studies suggest that the use of oxide electrodes instead of the standard composite nickel-ceramic anodes could have advantages in producing direct electrochemical oxidation of dry methane. But so far it has been impossible to synthesize a single-phase oxide material that satisfies all the criteria specified[14] for use at intermediate temperatures.

The experiments of Murray *et al.*[1] use electrodes consisting of a thin layer (0.5 μm) of yttria-doped ceria (YDC) together with a thicker layer (2 μm) of a nickel-ceramic composite as the current collector, demonstrating one way to overcome the relatively poor electronic conductivity of YDC. Yet although it works in the laboratory, this solution is unlikely to be adopted by SOFC developers for two reasons. First, natural gas usually contains higher alkanes (C_2H_6, C_3H_8 and so on) that are more easily dissociated than methane, resulting in carbon deposition on nickel at lower temperatures. Second, a number of investigations with intermediate-temperature SOFC stacks has revealed that when nearly all the fuel is converted to steam and CO_2 the nickel can be oxidized to NiO with a concomitant degradation in the anode performance.

A more promising strategy is to fabricate a composite anode in which doped CeO_2 is mixed with another oxide exhibiting good electronic conductivity, so avoiding the use of nickel altogether. This approach is being examined by a number of laboratories around the world and, if successful, is likely to speed up the commercialization of intermediate-temperature SOFC for small-scale applications. ☐

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Neurobiology

Oscillations in the basal ganglia

Thomas Wichmann and Mahlon R. DeLong

The basal ganglia constitute a network of brain structures that are components of larger loops connecting cortical and subcortical structures. Like many neuronal assemblies in the mammalian nervous system, this network seems to have two distinct operational modes. Classic studies of neuronal activity in the basal ganglia have focused on the single-spike mode, where neuronal discharge reflects information transfer or processing. But it has become clear that basal ganglia neurons can also discharge in a rhythmic, oscillatory-burst mode, in which individual bursts are unrelated to external events. As suggested for other systems that involve burst discharges, these bursts may signal and facilitate changes in functional states of the nervous system, or they could provide a representation of time[1,2]. But what is the origin of these oscillatory bursts? On page 677 of this issue, Plenz and Kitai[3] show that, in a cell-culture environment, synchronized oscillatory-burst discharges in one of the main basal ganglia structures, the subthalamic nucleus (STN), may depend on anatomical projections from another — the external segment of the globus pallidus (GPe; Fig. 1, overleaf).

Oscillatory discharge in subcortical regions, conveyed from the thalamus to the cortex via the thalamo-cortical network, may have powerful effects on cortical processing. To date, these changes have been studied mainly in areas of the thalamus concerned with sensory processing. For example, under conditions of little or no sensory input — such as during non-REM sleep — the oscillatory activity of the thalamo-cortical system is dominated by synchronized, low-frequency oscillations generated in the thalamus[2]. Waking is associated with desynchronization of thalamo-cortical activity, unmasking the less synchronized, higher-frequency[4] rhythms that prevail within the cortex during wakefulness, and allowing faithful transfer of information to the cortex. Changes of cortical function on a smaller scale (such as the changes that underlie selective attention[4]) could be mediated by precisely controlling the degree of synchronized oscillatory activity along specific parts of the thalamo-cortical network. The time-signalling aspects of the oscillatory activity may help to coordinate activity patterns in spatially separate regions of cortex[5]. In this way, for instance, sensory features detected by spatially segregated areas of the cortex could be integrated perceptually (a process known as 'binding')[6].

In all current models of basal ganglia function, the STN drives activity in the basal ganglia output nuclei — the internal segment of the globus pallidus (GPi) and the pars reticula of the substantia nigra (SNr) — and is a port of entry to the basal ganglia for cortical inputs (Fig. 1). Activity changes in the STN strongly affect the average rates and

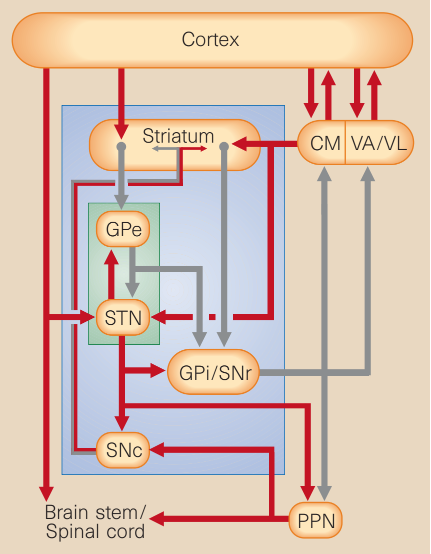

Figure 1 **The basal ganglia/thalamo-cortical circuitry (simplified). The basal ganglia (blue box) consist of the striatum, the external and internal segments of the globus pallidus (GPe and GPi, respectively), the pars compacta and pars reticulata of the substantia nigra (SNc and SNr, respectively), and the subthalamic nucleus (STN). These structures are linked via a complex network of excitatory and inhibitory connections (shown as red and grey arrows, respectively). Their external connections include cortical areas, the thalamic centromedian (CM), ventral anterior (VA) and ventral lateral (VL) nuclei, and the pedunculopontine nucleus (PPN). The GPe/STN 'pacemaker' circuitry proposed by Plenz and Kitai[3] is shown inside the green box.**

occurrence of non-oscillatory bursts in the GPe and GPi[7]. Plenz and Kitai[3] now show that the STN — and its link with the GPe — may also be important in generating synchronized oscillatory discharge in the basal ganglia. Previous brain-slice-recording studies have emphasized that individual neurons in the STN and GPe can generate oscillatory discharge through their intrinsic membrane properties[8,9]. In the STN, this occurs particularly during hyperpolarization[8]. Plenz and Kitai provide evidence that the STN/GPe circuitry may generate the necessary conditions for such burst discharges to occur and be maintained in synchrony.

Within the basal ganglia/thalamo-cortical network, oscillatory discharge has been directly recorded in corticostriatal neurons[10], tonically active striatal interneurons[11,12], the substantia nigra pars compacta (SNc)[13], both pallidal segments and the STN[8,14] (Fig. 1). Hypotheses about the physiological importance of oscillatory discharge in the basal ganglia are tentative at best. But its role is better defined under pathological conditions such as Parkinson's disease. In patients with this condition, dopaminergic (dopamine-producing) neurons in the brainstem degenerate, resulting in a loss of dopamine throughout the basal ganglia. The dopamine loss in Parkinson's disease results in prominent oscillatory-burst discharges in the STN, GPi and SNr at oscillation frequencies of 3–8 Hz[14,15]. Lesion studies[16] indicate that these oscillations may contribute to the development of the tremor seen in patients with Parkinson's disease. Plenz and Kitai studied oscillatory-burst discharges in a co-culture environment containing neurons from the striatum, GP and STN, in which the different neuronal groups connect with each other appropriately. Because this co-culture did not contain dopaminergic cells, the culture conditions may better reflect the pathological condition (parkinsonism) rather than the normal state.

Neuronal oscillations as a property of local or extended networks are also thought to be important in some of the proposed rhythm generators within the thalamus and the cortex[17]. In these positive-feedback systems, reverberations may occur with resonant frequencies that depend mainly on transmission times and synaptic delays. But the STN/GPe system differs because the polarity of its connections makes it a negative-feedback system, which would dampen rather than facilitate oscillations (Fig. 1). This, and the fact that the observed primary oscillation frequencies are relatively low, indicates that oscillatory bursts in the STN/GPe network are probably not the result of a simple, reverberating circuit. Instead, these bursts seem to result from specific, pro-oscillatory membrane properties of STN neurons.

In support of this idea, Plenz and Kitai[3], as well as previous studies[8], show that oscillatory discharge can be induced in the STN neurons by hyperpolarizing them with GABA (γ-aminobutyric acid). Many types of neuron in the basal ganglia share such membrane properties. Moreover, output nuclei of the basal ganglia participate in a variety of feedback loops, which may create the right conditions for oscillations to occur. So Plenz and Kitai's findings may be just the tip of the iceberg, with other potential independent oscillators in the basal ganglia still waiting to be discovered. Some may be involved in normal function, whereas others may contribute to pathological changes. ☐

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Ecology

Sprucing up beaver meadows

Peter D. Moore

In ecology there is no such thing as community spirit. Cooperation and altruism, we are told, are illusory, or simply the outcome of the activity of selfish genes. Yet the interdependence of species in communities is often extremely complex. One example is the complexity that characterizes the ecology of beaver ponds once they have been abandoned by the animals that first constructed them. This is discussed in the journal *Oikos* by John Terwilliger and John Pastor[1], who set out to discover why it takes so long for old beaver ponds to revert to forest.

When beavers dam streams and create their own aquatic environment, they inadvertently set in motion a directional process that eventually leads to re-establishment of the forest. The ponds begin to accumulate silt and are abandoned by the beavers. Then, once the dams are breached, the ponds drain and are soon invaded by herbaceous vegetation, especially grasses and sedges. This is how the beavers create grassy openings in the forest — in much the way that high winds and fire create clearings, which are subsequently recolonized by species that prefer open habitats. But with fire and tree falls, healing is usually rapid, resulting in the invasion and growth of a new tree generation within a few years. Old beaver ponds, on the other hand, may remain as damp grassland patches for decades — often 70 years or so — before trees that can tolerate these wet conditions, such as black spruce (*Picea mariana*), eventually manage to establish a forest cover.

Why should this vegetation succession become stuck at the grassland stage, and not progress smoothly in its development? In most successions, 'facilitation' is observed. This is where certain species, simply by existing at a site, modify the local environment and make it more suitable for invasion by other species. Plants with associated nitrogen-fixing bacteria, for example, enrich the