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## Motor systems

### Editorial overview

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Roger Lemon's research is focused on the sensorimotor control of skilled hand movements in human and non-human primates, movements that are particularly vulnerable to cortical and spinal injury. His work has established the importance of the corticospinal system for such movements and the cortical mechanisms involved in visual control of grasp. He uses neurophysiological, behavioural and neuroanatomical approaches.

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Paul Bolam's research focuses on the neurobiology of the basal ganglia in normal conditions and in models of Parkinson's disease. He uses a combination of a broad range of approaches in attempt to elucidate the functional organisation of the basal ganglia. These include advanced anatomical techniques, *in vivo* electrophysiology and single cell analyses. The outcome is an understanding of the position and role of an individual neuron in network activity.

#### Introduction

Everyday movements are carried out flawlessly and apparently with little need for any conscious intervention. The covert nature of the brain processes underlying such movements has rendered them particularly difficult to study. There are a number of drivers that prompt us to want to 'open the box' of motor control. First, over 100 years of clinical neurology and pathology has demonstrated the characteristic disruption to movement that results from damage to different brain areas. A better understanding of motor control is now beginning to inform neurotherapeutic approaches to rehabilitate patients with a damaged motor system. Second, modern brain imaging approaches have firmly established the distributed nature of the control system. The explosion of interest in cognitive neuroscience has made it all the more imperative that we understand how cognitive activity leads to selection and execution of action. Meanwhile, work in animal and insect models has greatly helped to elucidate how motor networks might function together; in particular, work in non-human primates has helped us to get close to the neural machinery that underpins some characteristic features of human motor behaviour including skilled grasp and manipulation of objects and tools. Computational approaches have helped to model how neural control systems interact with the complex biomechanics of moving limbs and bodies, and helped us to identify the operational principles to look for in studies of motor control. With advances on these many different fronts, we are in a better position than ever to 'open the box' of motor control.

#### Muscle synergies and motor behaviour

As Sherrington put it 'From felling the forest to the faintest whisper, the sole executant is muscle', organisms have a single set of muscles with which to perform their entire motor repertoire. In their review 'Neuromechanics of muscle synergies for posture and movement', [Lena Ting and Lucas McKay](#) argue that we use flexible combinations of just a few muscle synergies, that is, the elements from which complex muscle activation patterns are constructed, to produce the wide repertoire of motor behaviour. They make the case for muscle synergies being the main feature determining the organisation of the CNS motor system. They suggest that muscle synergies are generalised across tasks: the synergy remains the same. While sensory inputs, other central processes and even local cellular properties may alter the level of activation of the different components of the synergy, the synergy remains the same. The authors emphasise the importance of biomechanical modelling studies to help resolve the crucial questions relating to muscle synergies.

#### Motor behaviour in insects

The seemingly simplicity of the insect nervous system is belied by the fact that insects have remarkable capacities for adaptive motor behaviour, having

to navigate through a remarkably tortuous and unpredictable environment in three dimensions. In their article on 'Adaptive motor behavior in insects', Roy Ritzmann and Ansgar Büschges demonstrate some of the key interactions between sensory input and central motor structures. Both behavioural and neurobiological observations suggest that modifications in sensorimotor function are often dictated by commands descending from the brain, and the loss of these descending influences compromises the insect's ability to navigate a complex terrain. The parallels with mammalian motor control seem obvious; the advantage of the insect model is already apparent in terms of the ease with which different components of the control system can be genetically modified.

### The control of grasp in humans and non-human primates

Two reviews deal the control of precision grasping, and both emphasise the importance of grasp in primates. In their review 'Cortical control of grasp in non-human primates', Thomas Brochier and Alessandra Umilta state that 'The skilled use of the hand for grasping and manipulation of objects is a fundamental feature of the primate motor system' and Olivier and colleagues cite Tallis, 'The special relationship we indubitably enjoy with the material universe is to a very great extent the result of the special virtues of our hands'. In their review of data from non-human primates Brochier and Umilta stress the importance of multiple areas in the parietal and frontal lobes in the visuomotor transformation related to grasp. The functional organisation of these areas encodes not only the control of grasping movements but also the goal of such movements.

In their article 'Precision grasping in humans: from motor control to cognition' Etienne Olivier, Marco Davare, Michael Andres, and Luciano Fadiga address similar issues in humans. Using data derived from the use of transcranial magnetic stimulation (TMS) which induces transient 'virtual' lesion of discrete brain regions, they review data relating to the neural correlates of precision grasping. They describe the roles of distinct parietal and frontal areas in the control of both the kinematics and dynamics of precision grasping and hypothesise that the same cortical network may contribute to language and number processing, which supports the idea of tight interactions between processes involved in cognition and action, and the possible contribution of the motor system to higher cognitive functions.

### Oscillations in motor systems

Virtually every biological system oscillates to varying degrees and at varying frequencies and the nervous system is not an exception. This can be at the level of current flow, the firing rate of an individual neuron or the activity large groups of neurons in networks. Oscillations at a frequency of about 20 Hz ('the beta band') in field

potential recordings are a consequence of fluctuations in both sub-threshold and supra-threshold activities of large groups of neurons spread over distant regions of the brain. They are the subject of two of the reviews. In his article 'Oscillatory interactions between sensorimotor cortex and the periphery', Stuart Baker reviews recent data on beta-band oscillations in the motor system. Beta oscillations are present in the motor cortex and are coherent in the electromyogram of contralateral muscles and are most prominent during rest or periods of steady contraction but are absent during dynamic movement. He reviews data on the generation of the oscillations in the cortex and describes recent work demonstrating that corticomuscular coherence does not simply involve motor cortex; oscillations are synchronised with those in somatosensory cortex which involves feedback from the periphery. Finally he discusses possible functional roles of these oscillations as sensorimotor phenomena.

In contrast to the role of beta oscillations in normal motor behaviour, Peter Brown in 'Abnormal oscillatory synchronisation in the motor system leads to impaired movement' reviews evidence that *exaggerated* oscillations in the beta band are pathological and may contribute to the bradykinesia observed in patients with Parkinson's disease. Thus exaggeration and abnormally synchronised beta oscillations that are present in the motor cortex and basal ganglia of Parkinson's patients, and in models of Parkinson's disease, are lost following dopamine replacement therapy. Direct stimulation of the basal ganglia at beta band frequency slows movement. In addressing the question 'Is oscillatory synchrony causally important in Parkinson's disease?', he raises some crucial issues that must be resolved and draws upon data from the syndrome of cortical myoclonus in which pathologically synchronised discharges of pyramidal neurons lead to rhythmic jerking. He concludes with the statement 'Nevertheless, it remains to be proven whether pathological beta-band synchrony is an exaggeration of physiologically important synchrony or an exaggeration of an emergent property of networks that has no physiological function per se, but when exaggerated becomes pathological.'

### Parkinson's disease and L-DOPA-induced dyskinesias

Although there are many pharmacological and surgical therapies for Parkinson's disease, the principal strategy for treatment is to elevate the level of endogenous dopamine by the administration of the precursor of dopamine, dihydroxy-phenylalanine (L-DOPA). This therapeutic approach gives remarkable alleviation of the motor (and other) symptoms of the disease but its success is tempered by the fact that prolonged treatment L-DOPA itself leads to motor disturbances, the L-DOPA-induced dyskinesias. Despite extensive study the precise mechanisms of L-DOPA-induced dyskinesias have remained elusive. Angela Cenci and Hanna Lindgren review recent

advances in our understanding of the mechanisms underlying these 'side effects' and, as one might predict, the chronic exposure to L-DOPA of a disordered system, as occurs in Parkinson's disease, leads to many changes that can contribute to aberrant movement. Thus chronic L-DOPA treatment leads to presynaptic changes in dopamine release and clearance, molecular and synaptic adap-

tations in the striatum, alterations to the microvasculature and changed firing patterns in the basal ganglia. Of course, the hope for the future is that these advances in our understanding will lead to therapeutic strategies and targets to prevent the emergence of dyskinesias and thus a longer period of effective anti-parkinsonian therapy with L-DOPA.