Modular features of motor control and learning

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The study of complex motor behaviours has highlighted the role of modular representations both in the planning and in the execution of actions. Recent findings suggest the presence of functional modules within a variety of neural structures. Computational investigations are now addressing the issue of how these modules may act concurrently to generate a wide repertoire of behaviours.

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Introduction

The most exciting advances in the study of motor systems have been brought about by a shift in attention from simple to complex behaviours. Indeed, the class of behaviours that one elects to consider drastically affects the perspective on neural computation. When the investigations focus on the rich repertoire of actions in which living organisms engage, the number of states and of motor commands to be represented appears to be tremendously large. Then, computational analyses may provide valuable insights on constraints that must be satisfied by the neural circuits of the brain. The focus on complex dynamical behaviours has also been a feature of recent progress in the control of artificial systems. There too, the attention has moved from highly constrained manipulations to more complex tasks, such as controlling a bouncing ball with a paddle [1•], guiding objects by pushing and rolling [2,3] and, more generally, handling objects without grasping them [4•]. Understanding how this complex yet ordinary motor competence may be represented and implemented in robots is of great value for the study of biological motor systems. This review describes some of the advances that have been recently brought about in neurobiology by dealing with the complexity of 'real' motor behaviours. Among these advances is the formulation of new hypotheses about the building blocks, or 'modules', that the central nervous system (CNS) uses to form useful representations for planning and control of actions [5].

The acquisition of complex skills is facilitated by internal models of limb dynamics

The ability to generate a variety of complex behaviours cannot be attained by simply storing randomly the control signals for each action and then recalling these signals when needed [6,7]. Simple considerations about the geometrical space of motor behaviours are sufficient to establish that this approach would be inadequate because the number of possible configurations of the human body grows exponentially with the number of its degrees of freedom [8]. The number of possible movements, like the number of rice grains on a Chinese checkerboard, is larger than the number of synapses in the brain. Therefore, one's past experience of movement is necessarily confined to a negligible portion of this space. To achieve its typical competence, the motor system must be capable of generalising beyond the set of movements that it has experienced in the past. This operation is possible only through the construction of some internal representation of the dynamics of the body and of its environment. These representations allow us to generate new behaviours and to handle situations that have not yet been encountered.

A vivid illustration of how internal dynamical models may facilitate motor learning is offered by Schaal and Atkeson (see [9,10,11•]), who studied the task of balancing an inverted pendulum on the hand of a robotic arm. Humans have no difficulty executing this balancing task. Therefore, it seemed that the simplest way to teach a robot arm the same task was to have it copy every movement made by a human. When Atkeson and Schaal [10] tried this direct imitation approach, it failed: even if the human hand movements were carefully copied by the robot, the smallest amount of uncertainty associated with sensing and acting did not allow the pendulum to remain balanced.

This does not mean that imitation of successful behaviour is not a valid strategy [12–14]. On the contrary, robots can learn to copy behaviour successfully when the data from the observed demonstrations are used not to mimic the expert's movements but to build an internal representation of the motor dynamics associated with the task [9,10,11•]. Such a representation can be constructed using a computational method called a search procedure. This method involves starting with an arbitrary initial model that specifies which action should be taken at every possible state. Then, the data from trial and error experiences are used to iteratively update the model parameters until some optimal or at least satisfactory performance is attained. It turns out that, in most cases, search procedures are effective only if the starting point — the initial assumptions about the dynamic model — is not too far from the correct representation. Therefore, the work of Atkeson and Schaal [10] shows that imitation is a useful strategy when it provides the learner with a good starting point for the subsequent development of an internal model using a search procedure.

In the study of biological motor behaviour, the term 'internal model' refers to two distinct mathematical transformations: first, the transformation from a motor command to the consequent behaviour, and second, the transformation from a desired behaviour to the corresponding motor command [15–20]. The first type of

transformation is described by 'forward models'. These models provide the control centers in the brain with the means not only to predict the expected outcome of a command, but also to estimate the current position and velocity of the moving limbs in the presence of feedback delays (delays associated with the neural processing of sensory information) [21]. A representation of the mapping (or transformation) from planned actions to motor commands is called an 'inverse model'. Wolpert, Kawato and Miall (see [22••,23]) propose that the neural structures within the cerebellum perform sensory–motor operations equivalent to a combination of multiple forward and inverse models.

Extensive experimental evidence for the biological and behavioral relevance of internal models has been provided by numerous recent studies [16,24–27,28•,29]. Some studies examined the adaptation of arm movements to a perturbing force field generated by an instrumented manipulandum. The major findings of these studies are briefly summarized here. First, when exposed to a complex but deterministic field of velocity-dependent forces, arm movements are first distorted but, after repeated practice, the initial kinematics are recovered [16]. Second, if the force field is suddenly removed following adaptation, after-effects are clearly visible as mirror images of the initial perturbations [16,24]. Third, the CNS achieves adaptation by forming a local map that associates the states (i.e. positions and velocities) visited during the training period with the corresponding forces [30,31••]. Finally, after adaptation, this map (i.e. the internal model of the field) undergoes a process of consolidation [25].

In order to generate the appropriate command for a desired movement of the arm, an inverse model must take into account that multi-joint inertia depends on limb position and velocity. Therefore, an inverse model must be informed about the current state of motion of the limb. This information may come in one of two ways: first, from the input to the inverse model that specifies where the limb should be or, second, from a prediction of the current state based on delayed sensory feedback and on the past history of motor commands. Bhushan and Shadmehr [32••] have found compelling evidence for the second way. Their experimental results are consistent with the hypothesis that we learn to compensate for changes in limb dynamics through a process that involves the combined adaptation of a forward and of an inverse model of the limb.

What are internal models made of? The concept of motor receptive fields

Once established that the motor system creates internal representations of complex multi-joint dynamics, it remains to determine how these representations may come about. As pointed out by Marr [33], any mathematical transformation may be carried out in different ways depending on which elementary building blocks or 'primitives' are employed. To identify a set of possible primitives, one can use one of two approaches: a top-down approach, which is based on the nature of the problem to be solved, or a bottom-up approach, which is based on the properties of the motor output. As detailed below, these approaches can lead to opposite conclusions about an important feature of motor primitives.

The goal of a control system is to define a policy [34] — that is, a function that assigns to every possible state of the system, and its relevant environment, a specific action, such as the force to be produced by the limb muscles. Schaal and Atkeson [35••] demonstrated that complex policies can be learned by tuning the parameters of local controllers. Their approach to motor learning falls within the broad mathematical framework of function approximation [36]. The construction of an optimal (or, simply, of a 'good') policy from experience is equivalent to the reconstruction of an unknown function from a set of sampled data — in this case, the combination of states and actions experienced during training. These data are used for tuning the parameters of predetermined basis functions — such as local linear controllers in [35••], radial basis function in [37] or Gaussian fields in [38]. A local controller operates only over a limited region of state space, which is called a receptive field in analogy with visual and somatosensory receptive fields. The computational analysis of Schaal and Atkeson [35••] shows that on-line learning of complex behaviours is successful only when the receptive fields are sufficiently small. If each local controller had a large region of influence, the tuning of its parameters might interfere disruptively with neighbouring regions.

In contrast to top–down analysis, bottom–up analysis has revealed that the likely building blocks used by the central nervous system for the generation of motor behaviours have large domains of influence. I call such building blocks 'motor primitives'. Like primitives in natural and computer languages, motor primitives may be combined by the central nervous system to generate a grammar of more complex constructs that is, in this case, of more complex motor behaviours. Some important properties of biological motor primitives have emerged from the results of two electrophysiological studies. These studies, which involved the stimulation of muscles and of the spinal cord in spinalized frogs [39,40] presented three main findings: first, that the focal stimulation of a site in the lumbar spinal cord results in the activation of multiple muscles acting on the ipsilateral leg; second, that synergistic muscle recruitment generates a field of viscoelastic forces over a broad region of the leg workspace; and third, that the simultaneous activation of multiple spinal sites leads to the vectorial summation of the corresponding force fields. A computational analysis of electromyographic (EMG) activities induced in frogs by cutaneous stimulation of the leg has provided additional support to the hypothesis that the spinal cord organises a small set of motor primitives that are expressed by fixed synergies of leg muscles. [41••].

Taken together, these studies indicate that motor commands are not directed at controlling the forces of

individual muscles or single joint torques. Instead, it appears that the descending commands that are directed at spinal interneurons modulate the viscoelastic force fields produced by specific sets of muscles [42]. These force fields influence broad regions of the limb state space as each active muscle within a synergy contributes a significant force over a large range of positions and velocities. Simulation studies have shown that broadly tuned nonlinear force fields similar to those elicited by stimulation of the spinal cord can generate — by linear combination — the kinematic and dynamic repertoire of reaching movements [38]. However, as shown by Schaal and Atkeson [35••], broadly tuned force fields would lead to negative interference if their parameters were modified so as to optimize locally one movement at a time. In this respect, it is worth pointing out that human subjects display a significant degree of negative interference when adapting to a novel force field [16]: after adaptation is completed in a region of workspace, after-effects are clearly observable in different regions.

The trade-off between learning and stability

As pointed out by Hogan [43], another critical issue in defining the properties of motor primitives is the issue of stability (see also [44]). A controlled behaviour is stable when errors induced either by inaccuracies in planning or by unexpected perturbations are automatically corrected so that the behaviour is rapidly restored. A number of experimental and theoretical studies provide support for the equilibrium point hypothesis, according to which reaching movements, as well as other behaviours, are generated by the CNS shifting the static equilibrium of a limb along a continuous trajectory [45]. From a mechanical standpoint, this theory emphasizes stability: movements are constructed and represented as smooth transitions among stable postures. In this respect, the hypothesis that the CNS combines spinal force fields to generate stable behaviours is an extension of the equilibrium point hypothesis.

Lohmiller and Slotine [46••] have used an elegant paradigm from nonlinear fluid dynamics to show that in the control of a nonlinear system, such as a multijoint arm, the linear combination of stable dynamical primitives leads to stable behaviours. They found that the force fields generated by muscle synergies are indeed stable primitives within regions that correspond to the receptive fields defined above: these are regions within which external perturbations are compensated for by elastic forces. From this analysis it follows that stable behaviours are enforced over broad domains of a limb's state space by combining stable synergies with large receptive fields.

Higher-order primitives

While the internal representation of limb dynamics is vital for the execution of complex tasks, movements are planned in ways that may be independent from the details of movement execution. Indeed, the computational modules that are needed for movement planning may have features that are distinct from the modules for movement control. In early groundbreaking work, Georgopoulos *et al.* [47] investigated the activities of motor cortical neurons in relation to the direction of hand movements. They found that the firing rates of individual neurons are broadly tuned to preferred hand directions and that the linear combinations of preferred directions weighted by the cells' activities provide a good estimate of movement direction. The importance of Georgopoulos' approach lies in the attempt to establish a direct relation between neural activities and kinematic variables related to movement planning (see [48,49]). These findings, however, were controversial as they may be consistent both with coding of variables related to movement execution, such as muscle activities, and with coding of variables related to movement planning, such as hand kinematics [50,51]. Whereas some recent studies suggest a strict relation of motor cortical activity with the action of muscles [52–54], others have shown dissociation between cortical activity and movement execution [55,56••,57••].

The presence of separate neural representations for movement planning and movement execution raises interesting questions regarding the relationship between these representations. Rizzolatti and Fadiga [58] suggest that the representation of action supported by 'mirror neurons' in area F5 is a representation of action goals rather than of motor outputs. If these neurons form the basis for a 'vocabulary' of actions [59••] — that is, if they support planning modules — then it is of great importance to understand how the words of this vocabulary may be combined with each other by the brain to span a repertoire of purposeful behaviours. At present, we know that force fields implementing the execution of motor commands are combined by vectorial superposition. However, the rules that govern the combination of goals appear to be more complex. If there is a system of higher order primitives that codes for goals, then it remains to be established how these goals may be translated into movements so that their concurrent activation leads to meaningful actions.

Conclusions

The latest progress in the study of the motor system has been characterized by an increased focus on the complex dynamics of natural tasks in conjunction with the development of new experimental paradigms for the investigation of motor learning. There is a convergence of theoretical and experimental studies on the concept that complex control problems may be solved by a combination of independent modules. From a functional perspective, these modules implement control policies by associating an action to each state (position and velocity) visited during past limb movements. From a neurophysiological perspective, these modules organize specific synergies of muscles. Finally, from a mechanical perspective, these modules generate force fields upon the controlled limbs. The range of action of a module has been defined as a receptive field. There is a significant trade-off between the demands for

stability and the mechanics of muscles, both of which lead to broad receptive fields, and the demands of learning, which suggests narrow receptive fields in the interest of reducing unwanted interference across the state space. This trade-off defines an important area for future investigations into the interactions between higher and lower centers of the motor system.

Acknowledgements

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The paper describes both in formal and in intuitive terms an elegant approach to implementing complex manipulation skills in robot manipulators. In particular, this study focuses on problems such as controlling the bouncing of a ball on a paddle, where it is difficult for an engineer to define a single control procedure that may work across the entire state space. To deal with these problems, the authors divide the state space of the controlled system (for example, the space of all possible positions and velocities of the paddle and of the ball) into smaller non-overlapping regions. If a region is sufficiently small, then a simple control procedure – called a 'local controller' – is sufficient to ensure that the controlled system, once it has entered the region, can be bought to a pre-defined state. After this fragmentation is completed, the local controllers are combined into a single composite procedure that is capable of bringing the system from any state to the desired final state. The work makes use of the formalism of differential geometry to develop this idea.

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