A Brief Historical Review of Motor Control Theory

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In this edition, we begin a series of primers on motor control. Topics to be covered include the motor cortices, basal ganglia and cerebellum. Naturally such a series cannot be comprehensive, but we hope our contributors, drawn from the UK and farther afield, will convey both some of the fundamentals and some of the exciting new developments in motor neuroscience. We start with an historical overview. Rather than take the traditional perspectives of neurophysiology and neuroanatomy, we have chosen to review what seem to us some of the key conceptual advances in thinking about motor control since the late nineteenth century. Although Charles Sherrington will (we hope!) be a familiar name, some of the other authors discussed may not be to those of you who benefitted from a traditional medical school curriculum.

Martyn Bracewell, Series editor

Introduction

The field of motor control explores the ways in which the nervous system co-ordinates the musculoskeletal system to produce movement. This review describes some key theoretical contributions to the field from the nineteenth century through to the present day.

From Sherrington to Bernstein

For Sherrington[1] the reflex arc, consisting of a receptor, a conductor and an effector motor neuron, was the basic unit of analysis. The motor neuron acted as the final common path for stimuli from other reflex arcs throughout the organism. Reflexes might be combined simultaneously, with one dominant and multiple subordinate arcs converging on the common path. They could also form a consecutive chain, with one reflex initiating the next, as in the process of swallowing. Sherrington also demonstrated that the simultaneous excitation and inhibition of synergistic muscles acting at a joint was a product of the same reflex, a phenomenon labelled reciprocal innervation. Overall, voluntary and automatic movements were seen as resulting from such co-ordinated reflex responses.

Other researchers questioned this emphasis on movement as a reaction to external stimuli. Woodworth,[2] for example, investigated human hand movements and noted that the accuracy of very rapid movements seemed unaffected by visual or muscular feedback. Woodworth concluded that these movements were guided by impulse control, independent of sensory feedback. This initial impulse, he argued, comprised the action goal and the concomitant muscular activations, and therefore encompassed the whole movement. Lashley[3] explored this idea in a case study of a man with complete anaesthesia in the left lower limb. When deprived of visual feedback the patient could nonetheless place his leg following instruction, demonstrating accuracy comparable with a healthy control. Lashley maintained that these movements were controlled centrally, with the impulse spreading from its origin to downstream motor centres.

Bernstein[4] made a number of contributions that built on earlier ideas and pointed in new directions. He shared the view that movements are directed towards a pre-specified goal and therefore the central nervous system (CNS) must contain a guiding engram or advance program for the entire movement. While this implied a hierarchical organisation for the nervous system, Bernstein stressed that movement resulted from the interaction of the CNS, the musculoskeletal apparatus and environmental forces. A further development was a closed circle model of motor control including, among other components, a central command, sensory receptors and a comparator which assessed the discrepancy between the motor program and the unfolding action. Movement could be initiated from any point in this circle and Bernstein suggested this overcame the opposition of centrally directed and reactive movements which had marked earlier debates. Finally, he noted that the abundance of available articular configurations, muscle elasticity and the unpredictability of external influences meant that any motor problem was solvable in a potentially vast number of ways. He contended that an overarching goal for research was to specify how the motor system co-ordinated these factors. Generally known as the degrees of freedom problem, it has remained a key challenge in the field.

From World War Two to the 1970s

Experience of war led to interest in human-machine interaction and the development of cybernetics, the study of control and communication systems.[5] With this came a tendency to see human motor and machine engineering problems as analogous. Craik,[6] for example, portrayed the motor system as an intermittent correction servo, meaning that trajectory corrections in human movements were predictive and based on extrapolation from earlier feedback rather than current conditions. Fitts,[7] also working in this tradition, was concerned to understand the information capacity of the human motor system. He defined this as the ability to generate a uniform movement response when faced with a range of alternatives; the greater the number of available alternatives, the higher the information capacity of the response. The minimum information needed for a specific movement was labelled its index of difficulty (Id). In his studies of movement amplitude and duration, Fitts noted that Id was a function of the width of the target and the distance to be moved. Thus speed, distance and accuracy requirements were interlinked. These interrelationships were given a mathematical formulation, now known as Fitt's Law, which is still widely applied in motor research.

Von Holst,[8] also influenced by cybernetics, was concerned to identify mechanisms by which a visual signal produced by moving the eyeball with an external force could be distinguished from a visual signal produced by an active eye movement. The problem was to explain why, in the first case, the visual world appears to move, whereas in the second it remains still. He proposed that when the CNS issues a command to move, or an efference, then a replica of that command, the efference copy, is stored in a lower CNS mechanism. Reafference from an active movement cancels out the efference copy and the visual world remains static. Ex-afference from an externally produced movement, however, does not have this effect and the visual world appears to move. This concept of efference copy has continued to be crucial in movement theory.

An influential paper by Keele[9] reviewed many earlier studies and helped spark renewed academic interest in the field. This paper also outlined a modified version of Fitt's Law suggesting that, as very rapid movements are not reliant on visual feedback, so movement time would not depend on accuracy requirements. This modification was widely referenced in subsequent discussion. Ultimately, however, the chief legacy of this paper was a broader awareness of the concept of the motor program. Keele defined the program in terms reminiscent of Bernstein and Woodworth, although only the latter author was referenced in the paper.

In 1975 Schmidt[10] criticised earlier models, arguing that cerebral storage capacity did not allow for every individual movement to have its own motor program, as previously suggested. Rather there were generalised motor programs for categories of movement, with adjustable parameters, for example for force or speed. During repeated movements the interrelationships of certain components, such as sensory feedback and accuracy, were abstracted from to form a motor schema for the movement. The schema would then allow the selection of an appropriate response to achieve a desired result. This selection involved the specification of the parameters to be modified and the triggering of the appropriate motor program. Schmidt's multifaceted model addressed problems with existing approaches and has continued to provoke debate.

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Motor theory today

The dominant concept in contemporary theory is that of the internal model which simulates movement. This has two constituents. First, a forward model predicts the future state of the system by combining knowledge of its present condition with an efference copy of the motor command. Second, an inverse model calculates the motor command needed to cause a desired sensory state, allowing feedforward control of action in advance of feedback.[11] The internal model thus facilitates a two-way transfer of motor and sensory information, allowing the acquisition of motor skill.

Jeannerod[12] has argued that motor simulation is based on the activation of hard-wired motor rules, and is central in predicting the outcome of action and in understanding the actions of others. His model relies heavily on evidence regarding mirror neurons. These were an accidental discovery by Rizzolatti and colleagues,[13] who identified neurons in monkey pre-motor cortex which are active during the execution and observation of goal-directed hand movements. They are now thought to occur in primate (including human) inferior parietal, ventral pre-motor and caudal inferior frontal cortices[14] and, in Jeannerod's view, underpin the formation of the internal model.

One dissenting position in contemporary discussion is that of the equilibrium point hypothesis (EPH). Feldman and Latash, advocates of EPH, suggest internal models are unable to explain a mundane problem in movement control identified by Sherrington.[15] That is, how can movement take place against a background of postural stability without the stabilising mechanisms dragging the limb back to its initial posture? EPH posits that this can be achieved by one centrally controlled variable, the point λ at which the tonic stretch reflex activates the muscle as it is stretched. The ratio of muscle force and length, when muscle force is balanced by an opposing force and posture is stabilised, is labelled the equilibrium point (EP). EP and its attendant torques and joint angles are considered emergent properties which cannot be pre-programmed as the internal model approach suggests. The ratio can be changed by a voluntary adjustment of λ, leading to a shift to a new EP, overcoming postural inertia and allowing movement.

Conclusion

This has been a necessarily selective review of an extensive literature. We hope to have highlighted some of the key contributions over the last 115 years and shown how similar concerns have occupied researchers in that time. Both motor program and internal model concepts, for example, sought to answer how rapid movements are controlled without sensory feedback. EPH, on the other hand, has placed renewed emphasis on reflex control in movement. This suggests that, while the field progresses, investigators will still be compelled to draw on the past achievements we have outlined. ◆

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