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Motor systems

Editorial overview

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Introduction

For many years research on the sensory systems, and the visual system in particular, dominated the field of neuroscience. Although research on the motor system provided tremendous insight as sophisticated as that in the sensory systems, these results seemed much more difficult to relate to other fields of neurophysiology and, in particular, to the rapidly developing cognitive neurosciences. Motor system research was firmly in the domain of the specialists and clinical neurologists investigating the devastating effects of motor system damage. This is certainly not the case today. Following the seminal work of Mountcastle [1] and Hyvarinen [2], it became evident that the cortical areas involved in motor control are not only the frontal agranular areas — the traditional motor region — but also the parietal cortical areas. Thus, the notion of association parietal cortex changed. The view that the parietal cortex was the place where different sensory modalities were 'put together' was substituted by the notion that the parietal cortex is the place where different modalities are integrated with action representations. At the same time new and more sophisticated computational models provided the tools that enabled a deeper understanding of how actions are planned and performed. Furthermore, these same models provided fundamental tools for understanding cognitive functions. As a consequence, the studies of the motor system acquired a much broader scope and motor systems became a crucial system for cognition. The wide range of topics selected for the present issue illustrates the advances that have recently been made in understanding various aspects of cortical motor organization, in addition to that of cerebellum and basal ganglia. Most of the reviews concern experiments on the motor system of humans and monkeys, one is devoted to motor organization in invertebrates. 'Small brains' are an important tool for understanding the complexity of motor organization in anatomically and functionally complex motor systems.

Motor cortical functions: the parietal lobe

As already mentioned, the notion that the posterior parietal lobe has motor functions is by no means new, yet this notion has still not fully penetrated current thinking. The issue of the motor functions of the parietal lobe is addressed in the review by Fogassi and Luppino. They discuss experiments showing that neurons in the inferior parietal lobule (IPL) discharge during specific motor acts, such as grasping. Most interestingly, the discharge of most of these neurons is influenced by the motor act that follows grasping. These findings, and the receptive field properties of IPL neurons, suggest that actions (e.g. take food and bring it to the mouth) are organized as 'chains' of simpler motor acts. Neurons coding grasping are linked with neurons coding the act of bringing food to the mouth, with neurons coding placing, or with neurons coding other motor actions, and so on. According to the intention of the acting individual, one action chain is selected. The authors also review

anatomical data showing links between inferior parietal and temporal lobe. These data indicate that the parietal lobe motor representation receives semantic information from the temporal lobe and suggest that this information could play an important role in the selection of appropriate motor chains. Another important finding concerns the role of parietal neurons in intention understanding. Several IPL grasping neurons have mirror properties; that is, they fire both during action execution and during action observation (see Rizzolatti and Craighero [3]). What is new is the demonstration that most of these neurons discharge selectively when the observed motor act (e.g. grasping) is embedded in a given specific action (e.g. eating). The authors propose that this differential activation, determined by context observation, might give clues as to what is the most likely future action of the observed individual and, thus, constitute a basic mechanism enabling the observer to understand the intention of others.

Imitation

In his review, Iacoboni addresses the neurophysiological basis of imitation. Imitation is a fundamental human ability that underlies much of human culture. The processes underlying imitation are very complex, requiring a translation of a message coded in sensory, typically visual, coordinates into a representation coded in motor coordinates. Thus, in spite of its importance and with the exception of birdsong learning, a detailed study of the neural correlates of imitation has only started to emerge in the past few years, mainly inspired by the discovery of mirror neurons (see above). Iacoboni reviews a series of brain imaging experiments showing that at the basis of imitation of actions, already present in the motor repertoire of the observer, is the activation of the two nodal areas of the human mirror system; that is, the inferior parietal lobule, the ventral premotor cortex (plus the posterior sector of the inferior frontal gyrus), and the region around the superior temporal sulcus (STS). He argues that STS provides a higher order visual description of the observed action. This description is fed into the fronto–parietal mirror neuron circuit, where the goal of the actions and motor specification of how to achieve it are coded. Efferent copies of planned motor actions are then sent back to STS for matching the predicted sensory consequences of the planned action with the visual description of the observed action. Iacoboni also addresses the problem of the neural basis of imitation learning, stressing the importance of the prefrontal lobe for this type of imitation. Finally, experiments are reviewed in which transcranial magnetic stimulation (TMS) has been used to selectively block cortical areas involved in imitation. These experiments crucially confirm the role of the frontal lobe mirror neuron system in imitation.

Basal ganglia

Graybiel reviews the fast growing (or ''exploding'' as she describes it) field of the basal ganglia. She selects some of the fundamental issues of the basal ganglia and discusses them in detail. Among them are the role played by the basal ganglia in learning action sequences, the relation between the striatum and the cortex in different learning processes, and the role of reinforcement signals in basal ganglia functions. Subsequently, she examines the conventional view on the role of basal ganglia in releasing or inhibiting actions. These actions are determined by the opposing influences of the two main pathways that originate in the striatum: the movement-releasing 'direct pathway', and the movement-inhibiting 'indirect pathway'. Graybiel then presents evidence that challenges, or at least partly modifies, this view. Six challenges are discussed. Some concern the anatomical substrates that are at the basis of a segregation of the targets of the direct and indirect pathways, and the type of information that direct and indirect pathways receive from the cortex. Further challenges are functional and concern, for example, the validity of the notion that cerebellum is involved in supervised learning, whereas the fundamental role of basal ganglia is in reinforcement learning. Graybiel ends her review by presenting an interesting series of problems to be further examined, the solutions of which will provide a better comprehension of the role of basal ganglia in the control of movement and cognition.

Functional organization of the smooth pursuit movements

The functional organization of smooth pursuit movements is a clear case in favor of the view that the cortical motor system includes parietal and frontal areas. In their review, Thier and Ilg show that five parietal areas (MT, MSTl, MSTd, LIP and VIP) and two frontal areas (FEF and SEF) are involved in the organization of smooth pursuit movements. Some of these areas probably play a minor role in smooth pursuit, such as LIP, which is more involved in the organization of the saccadic eye movements. Yet, in this area and in area 7a, not discussed in the review, activity is related to smooth pursuit movements. Unlike FEF and SEF, where there is segregation between saccade and smooth pursuit-related signals, LIP does not to appear to have such segregation. Note, however, that a clear anatomical, possibly cytoarchitectonical and histochemical, analysis of LIP is still lacking, despite the large number of neurophysiological experiments devoted to it. Next, the authors review the extremely complex organization of the projections of the various cortical areas involved in smooth pursuit movements to the pontine nuclei and the nucleus reticularis tegmenti pontis. From these nuclei information arrives at the cerebellum where two regions are involved in smooth pursuit movement organization: the flocculus–paraflocculus complex and the posterior vermis, including lobules VI and VII. The rich variety and large amount of data reviewed in this chapter shows how much we have learnt in the past few years on the anatomy and on the functional organization of smooth pursuit movements. However, we

are still lacking exhaustive data on the ascending branch of the system originating in the cerebellum. Initial experiments suggest that this pathway — back to the cortex — might provide an efference copy of the pursuit eye command that is needed for the coordinate transformation leading to representation in non-retinal coordinates.

Motor learning to altered dynamics

Although the problem of motor control, choosing a series of motor commands to achieve a desired goal, might seem simple, it is dramatically complicated by the ever changing relationship between our motor commands and the ensuing movement. This changes as the properties of our bodies change with growth or fatigue and when we interact with objects in the environment. These changes affect the dynamics of our arm. Lackner and DiZio review recent advances in the study of motor learning in which the dynamics of the arm are altered. Although previous studies have often treated learning of novel dynamics as one entity, Lackner and DiZio stress that there are different mechanisms at play when we adapt to changes in dynamic that are intrinsic to the properties of the arm and others in which the arm operates on an external tool. They show significant differences between the properties in the adaptive process, and these differences reflect adaptive self-calibration of motor control versus learning the behavior of an external object or 'tool'. Lackner and DiZio end with a suggestion that much of the work on motor behavior involves a small number of paradigms being intensively mined, and that future progress will be enhanced by new paradigms with direct relevance to natural behavior.

Motor primitives in primitive and complex neural systems

Flash and Hochner review evidence that motor actions and movements in both vertebrates and invertebrates are composed of elementary building blocks or primitives. The key idea is that in the same way as we can construct an enormous repertoire of sentences from the building blocks of words, the motor system might construct movement from a limited number of elements or 'movemes'. Flash and Hochner review new techniques for extracting the representation of such primitives form recorded movements in addition to muscle and neural activity. They provide evidence for the existence of such primitives in organisms ranging from locusts through octopus to primates, and they assess the value of such primitives in robotic control. The authors stress the need for the development of new mathematical tools to analyze and decompose movements into primitives, in addition to the need to unravel their neural representations.

Cerebellar memories

Despite containing more than half the neurons in the brain, the cerebellum is still a mysterious structure. However, studies of simple movements are beginning to reveal the working of memory processes that rely on the cerebellar circuitry. De Zeeuw and Yeo review recent advances in our understating of the learning mechanisms in the vestibulo-ocular reflex and in eyeblink conditioning. The review highlights both the similarities and the differences in the learning mechanism of these two control systems. They review the evidence for long term depression (LTD) and long term potentiation (LTP) mechanisms, and whether learning involves the cerebellar nuclei and cerebellar cortical sites. They stress that in all cases the evidence that is presented is correlational and does not conclusively indicate causality. But a solution might be close at hand with new studies that will examine mutant strains that might finally unravel the mechanism of cerebellar memory formation.

Engineering an understanding of neural control

To what extent is it useful to understand the control mechanisms inside a space shuttle or your DVD player to understand the neural basis of control? Schaal and Schweighofer review the links between the engineering fields of cybernetics and control theory and the insights they provide in reverse-engineering the brain. They highlight recent research directions in computational neuroscience for motor control in which the computational foundations have strong overlap with theories in robotics and artificial intelligence. These include internal models, control in the presence of noise, motor learning, coordinate transformation, task space control, movement planning with motor primitives, and probabilistic inference in sensorimotor control. They highlight two trends. The first is a growing acceptance of complex computational models of brain information processing. The second is a dramatic increase in the number of model-based experiments, in which complex models function as a guide to the experiment design and subsequent data analyses.

Conclusions

Although the topics covered in the reviews in this issue all deal with the theme of motor control, they currently form important, yet discrete, sets of knowledge with rather little overlap with the other reviews. The global challenge for the future of motor control will be to provide a unified account of motor control that can provide strong links among these themes linking neurophysiological, behavioral and computational levels of understanding of how the brain controls movements.

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