

Neural aspects of cognitive motor control

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Traditionally, motor and cognitive functions were studied separately; however, the investigation of processes at the interface between cognition and action has become more and more popular recently. Typical research goals include the identification of the processes involved using experimental psychological methods, and understanding the neural mechanisms underlying these processes using neurophysiological and functional neuroimaging methods. Specifically, there has been a special emphasis during the past few years on timing mechanisms, practice effects, and the application of rules in guiding action. New information concerning the neural mechanisms involved is being acquired at a rapid pace, albeit mostly within a descriptive framework. With respect to specific brain areas, a key finding has been the clear involvement of the primary motor cortex in complex tasks engaging diverse motor and cognitive dimensions.

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Current Opinion in Neurobiology 2000, **10**:238–241

0959-4388/00/\$ – see front matter

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Abbreviations

EEG	electroencephalography
fMRI	functional magnetic resonance imaging
ICMS	intracortical microstimulation
ISM	internal simulation of movement
M1	primary motor cortex
MEG	magnetoencephalography
PET	positron emission topography
TMS	transcranial magnetic stimulation

Introduction

Cognitive aspects in limb motor control were discussed succinctly by Hauert in 1986 [1] who argued with surprising foresight “in support of the view that motor function is a cognitive function”. Recent advances in the physiology of the motor cortex, a motor area *par excellence*, provide a good example of this assertion. Traditionally, the motor cortex has been regarded as nothing but an ‘upper motor neuron’. Contrary to that view, the case was made that the motor cortex was a crucial node in the processing of cognitive information related to motor function [2]. This hypothesis has been supported by the results of numerous and diverse studies, such as neurophysiological studies in monkeys [3–11,12**,13] and studies in humans using various methods including electroencephalography (EEG) [14], magnetoencephalography (MEG) [15], positron emission tomography (PET) [16], functional magnetic resonance imaging (fMRI) [17–20], and transcranial magnetic stimulation (TMS) [21–23]. These studies have documented the involvement of the motor cortex in spatial transformations, serial order coding, stimulus–response

incompatibility, motor learning and memory, and motor imagery. Overall, the picture that has emerged from these and other studies is that diverse aspects of a given action — cognitive and motor — are processed in several motor areas including the motor cortex. Therefore, the objective is not any more to show that a particular area is (or is not) involved in cognitive–motor processing (i.e. to show whether it is purely motor or not) but rather to discover which aspects of cognitive–motor function are processed by the given area in a specific task.

I discuss below these various aspects of cognitive–motor function, the tasks used to study them, and the main findings of neural studies with special emphasis on the motor cortex.

Cognitive factors in hand motor control

Even simple pointing movements to visual targets are not exactly ‘automatic’ in the sense that their initial direction can be interfered with by, for example, auditory stimuli applied during the response time. Frens and Erkelens [24] studied this problem for pointing (left/right) hand movements and saccades under three conditions. In the first condition, the target position was indicated for 2 s before the target was presented: both saccades and hand movements were directed towards the target without any error. In the second condition, the target was presented unexpectedly without any precueing: saccades were directed to the target without any error but in 1% of the trials hand movements were initiated in the wrong (opposite) direction. In the third condition, an auditory stimulus was given at the same time as the target appeared in an unpredictable location: saccades were still directed to the target without an error but the hand pointed in the wrong direction in 35% of the trials. These findings indicate that the process that specifies the direction of the hand movement, unlike that for saccades, is susceptible to interference, and is, therefore, attention-intensive and cognitive in nature.

There seems to be a continuum in the involvement of cognitive processes in the visual control of movement. At one end of this continuum, a hand movement and its target may be strongly coupled so that changes in target location can alter the movement at short latencies, of the order of ~100 ms. This was demonstrated for the first time in monkeys [25] and later confirmed in people [26,27]. The strong dependence of the hand movement on its target was shown by the fact that when the target was left on for a variable period of time before changing location, the hand moved towards it for a proportionally longer time so that the target and movement duration were tightly coupled. These tight temporal relations were reflected in motor cortical cell activity [28]. At the other extreme, there is a host of tasks in which delays are imposed between stimulus and

movement and, in these cases, the presence of cognitive processing is evident. Rosetti [29**] has reviewed extensively the literature on this subject and has elaborated on the idea that the operation of the sensorimotor system can rely on cognitive spatial representations to a varying degree, depending on the constraints of a given task. Specifically, he has argued persuasively that the perceptual motor system can operate in a noncognitive mode in the absence of delays, whereas it switches to a cognitive mode when delays are interposed between stimulus and response. In that sense, the clear involvement of the motor cortex during instructed [30] and memorized [3,5,6,8,13] delay tasks is additional evidence for its role in cognitive motor processing.

It is interesting that a qualitatively similar idea of varying, task-related dependence of action on cognitive processes has emerged recently with respect to temporal aspects of motor control subserved by a network of interconnected areas [31]; amongst these areas the cerebellum [32] and the basal ganglia [33] seem to play special roles. Conceptually, at the ‘noncognitive’ extreme there are all kinds of movements that are not explicitly planned or instructed in their duration, such as swinging of the arms during walking or reaching to a target. The duration of these ‘natural’ movements could very well ‘fall out’ from the dynamics of motor performance [34]. At the other extreme, there are discrete ‘unitary’ movements, the timing of which can be explicitly instructed, such as tapping in a rhythm dictated by a previous metronome. The timing of these movements seems to depend on a central clock and motor delays [35], the presumed clock being on the cognitive side of time processing. This idea was supported by the results of experiments by Ivry and Hazeltine [36], which showed that the Weber timing function (i.e. the function relating timing variance to the square of the interval to be timed) was similar in perceptual timing and movement timing (tapping) tasks. Recent work on the timing of continuous drawing movements [37**] drew a clear distinction, however, between timing in drawing and timing in tapping tasks: timing in these two cases differed substantially, as shown by the fact that temporal precision in tapping was not related to temporal precision in continuous drawing, and the fact that the Weber function differed between the two tasks. Therefore, the ‘timing’ function will have to be qualified with respect to the specific task being performed.

Motor cognitive operations

The discussion above dealt with cognitive aspects of the motor plan *per se*. A different aspect concerns the rules that govern the translation of stimulus information to the appropriate motor output. The implementation of these rules typically involves cognitive processes of various sorts. A case in point is the stimulus–response (in)compatibility [38], which refers to “a hypothetical process of information transformation or recoding in the course of perceptual motor activity, and assumes that the degree of compatibility is at a maximum when recoding processes are at a

minimum”. Neural correlates of this process have been studied recently in monkeys trained to perform under conditions of varying degrees of stimulus–response incompatibility [10,11]. Interestingly, cells sensitive to the stimulus–response mapping rule were found in the primary motor cortex, and the temporal evolution of coding the stimulus, applying the re-mapping rule, and deriving the motor response could be identified in the temporal evolution of neuronal activity in a trial.

In a different paradigm [39], a fixed spatial transformation was required, namely the production of a movement at an angle from a stimulus direction. It was found that the response time increased as a linear function of the instructed angle and that in the motor cortex the population vector (a measure of the directional tendency of the neuronal ensemble) rotated from the stimulus to the movement direction through the smaller angle [2]. This rotation took the larger part of the response time and its rate was comparable to the rotation rate calculated from the response time experiments [39]. These results demonstrated the processing of cognitive–motor information in the motor cortex.

Obviously, one can move in a direction other than that of a stimulus under various circumstances. The transformation required above was just one of several possibilities, and it was based on a spatial rule by which the movement direction was at a fixed angular offset from a variable stimulus direction. In recent experiments [7,13], a serial order rule was imposed, as follows. First, a number of stimuli were presented in a certain sequence, and then one of them changed color (test stimulus): a movement has to be made in the direction of the stimulus that followed the test stimulus in the sequence. It was found that, unlike the rotation transformation, cell activity and the population vector in the motor cortex changed direction abruptly (within ~50 ms) during the response time [7], which indicates a switch between directions without passing through the intervening directional space. Moreover, the serial order of the stimuli presented was encoded in the activity of single cells and could be uniquely recovered from small ensembles of neurons recorded simultaneously [13].

The involvement of the motor cortex in these more complex processes was also documented using fMRI in human subjects [19]. In addition, these studies revealed the participation of other areas in these tasks. By its nature, however, fMRI cannot provide information about the cellular mechanisms underlying a neural operation; therefore, the two methods are complementary in the sense that fMRI can pinpoint the areas likely to be involved in a task, and the neural mechanisms can then be investigated using single cell recordings [40*].

Motor learning and memory

The results of the studies discussed above demonstrated the involvement of the motor cortex in cognitive–motor processing of spatial and temporal (i.e. serial order) information.

A number of recent studies have also documented the involvement of the motor cortex in motor learning both in people [16–18,20–23] and in monkeys [12••]. With respect to cellular mechanisms, clear evidence has been found for an ongoing change in motor cortical cell activity during visuomotor adaptation in the monkey [12••]. Interestingly, changes in cell activity continued to occur after the adaptation was ended. These results identified the motor cortex as a focus of motor learning.

In between single cell recordings (which provide the finest grain), brain lesions (which drastically alter the system) and artificial neural network modeling (which is a theoretical construct) lie other frequently used methods for studying brain function, including EEG, MEG, PET, fMRI, TMS, and intracortical microstimulation (ICMS). All of these methods operate at an intermediate level, by measuring aspects of the activity of (or stimulating) ensembles of neurons. Although data obtained with these methods need to be interpreted cautiously with respect to the possible cellular mechanisms contributing to the measurements, they have nevertheless provided converging evidence on the involvement of the motor cortex in complex motor functions as well as an insight into the effects of motor learning and/or practice on motor cortical maps. Thus, using EEG and MEG, it was found that the motor cortex is engaged during imagination of hand movements [14] and during internal simulation of movement (ISM) [15], a condition presumably reflecting ‘internal programming’ of movements in the absence of their execution. As Lang *et al.* [15] state, “brain systems involved in ISM or ‘programming’ were hypothesized to be superior to and separable from [an] ‘executive system’ including M1”. The finding that M1 was active with ISM rejected this hypothesis and suggested instead that the motor cortex is an integral part of multifaceted aspects of motor function, which is in accord with the results of others studies discussed above.

Finally, three different techniques (fMRI, TMS, ICMS) have provided congruent results on a different aspect of the involvement of motor cortex in motor learning and practice. Nudo *et al.* [41] trained monkeys to skillfully use their digits (in a small-object retrieval task) or their forearm (in a key-turning task). Using ICMS, they found that the motor cortical representation of the digits (or the forearm) expanded following motor practice at the expense of the representation corresponding to the nonpracticed movements. As these changes were progressive and reversible, it was concluded that “M1 is alterable by use throughout the life of an animal” [41]. Similar findings were obtained in the rat [42]. Using TMS in human subjects, Pascual-Leone *et al.* [43] found an expansion of the motor cortical areas targeting specific hand muscles used in a practiced motor task as well as a decrease in their activation threshold. Finally, Karni *et al.* [17] documented an enlargement of the area of activation of the motor cortex following practice of rapid sequences of finger movements.

Conclusions

The conjunction of motor control and cognition is now an established and very active field; however, this decade can be regarded as still exploratory of the many dimensions of the issues, the vast richness of motor–cognitive intersection, and the wealth and evasive nature of the relevant brain mechanisms. This review touches upon only a few selected topics to exemplify directions of evolving research rather than to summarize settled knowledge. In due time, the connections between brain development and the development of motor cognitive functions will also be made and rigorously investigated. And if speech is to be included within the motor family, it will be a large family indeed, with practically unbounded horizons.

Acknowledgements

This work was supported by United States Public Health Service grants NS17413, PSMH48185, and NS32919; the United States Department of Veterans Affairs, and the American Legion Brain Sciences Chair.

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