Central processes for the multiparametric control of arm movements in primates
Michael TV Johnson*, Carolyn R Mason* and Timothy J Ebner**†

Recent single-unit recording studies have clarified how multiple parameters of movement are signaled by individual cortical and cerebellar neurons, and also that multiple coordinate frames are utilized. Cognitive processes also modulate the firing of these neurons. The various signals and coordinate systems vary in time and evolve throughout a behavioral sequence, consistent with the demands of the task and the required sensorimotor transformations.

**Addresses**
*Department of Neuroscience, University of Minnesota, Lions Research Building, 2001 Sixth Street SE, Minneapolis, MN 55455, USA
†e-mail: ebner001@umn.edu


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Abbreviations
M1 primary motor cortex
PD preferred direction
PMD dorsal premotor cortex

Introduction
Almost 20 years ago, the paradigm of correlating primary motor cortical neuronal firing to movements about an isolated joint [1] changed to correlating neuronal firing to whole arm movements [2]. This experimental shift was paralleled by a conceptual shift. The correlations once sought between neurons and parameters of muscle activity or single-joint movements [3,4] were now sought between neurons and parameters of the hand trajectory [2,5]. The focus turned to whether global or executive features of movement were encoded [6]. The debates intensified as to whether movements/kinematics or muscles/dynamics were controlled [7,8,9••]. Moreover, questions concerning the coordinate system in use became prominent. Neuronal correlates to joint or muscle parameters imply the use of an intrinsic (relative to the arm) coordinate system. Correlations to hand position or path in space imply an extrinsic coordinate system [8,10,11].

This paradigm shift added an experimental richness not possible for single joint movements. Yet the debate remained largely focused on elucidating the one crucial parameter of movement encoded or the one crucial coordinate system used in a motor area. In contradistinction, this review examines the central processing of motor signals during multi-joint limb movements and emphasizes four points.

First, the search for a single, dominant, encoded movement parameter is unlikely to be fruitful. All available evidence suggests that neurons in motor structures signal many aspects of limb movements and are modulated by various motor and non-motor factors. Second, the correlations with specific motor parameters are unlikely to be invariant but rather change in time or over a behavioral sequence as required by the task. Third, the search for a single coordinate frame in which a neuron encodes these parameters is also unlikely to be fruitful. Processing motor, sensory and cognitive parameters will involve information represented in several coordinate systems. These coordinate systems are thought to evolve sequentially during the sensorimotor transformations occurring with limb movements [12–15]. Last, the parameters represented in the discharge of neurons reflect the tasks and paradigms being investigated. Task-specific processing may provide the flexibility needed to generate the vast repertoire of movements that human and non-human primates exhibit.

Directional tuning
Pivotal to the shift in the framework for studying the central control of arm movements was the observation by Georgopoulos et al. [2,5] that the discharge of primary motor cortex (M1) neurons is broadly ‘tuned’ to the direction of arm movement for reaching in two and three dimensions. Characterization of the directional tuning typically includes fitting firing to a cosine-tuning function to define the preferred direction (PD) at which the firing is greatest. Directional tuning is a prominent feature of central neurons. In dorsal premotor cortex (PMD) and M1, directional tuning has been described not only for reaching but also for curvilinear tracking movements [16–20], manual tracking of visual targets [21–23] and isometric force pulses [24–27].

Directional tuning of the firing is not limited to the movement but is also prominent during an instructed delay, in which the location of the upcoming target is visually presented [14,15,21,22,28,29•]. The activity of cerebellar cortical neurons is also directionally tuned during reaching [30,31] and manual tracking movements [32,33•]. Neurons in the parietal [34] and somatosensory cortices [35,36] exhibit directional tuning, as do basal ganglia cells [37] and cerebellar afferents [38].

In addition to its prevalence and robustness, the importance of the directional signal is underscored by the amount of controversy surrounding its interpretation [7,8,39,40]. In this review, we focus on single-unit recording studies in two frontal motor cortical areas, the PMD and M1, made during multi-joint arm movements. Studies of the cerebellar cortex are included, when direct comparisons are possible.

Encoding scalar parameters of arm movement
Accurate arm movements require the control of not only direction of movement but also other scalar parameters...
including speed, amplitude and accuracy. Human psychophysics point to the independent or serial processing of direction as well as other movement parameters [12,41–46]. Not surprisingly several non-directional scalars including amplitude [31,47,48,49••], speed [9••,16,19,22,32] and accuracy [29•] also modulate the discharge of motor cortical and/or cerebellar neurons. Importantly, subsets of direction, amplitude, speed and accuracy modulation occur commonly in the discharge of the same neuron [19,29•,33•,47,49••]. Certainly, the older concept of neurons as dedicated processors of a single parameter (i.e. movement direction, force, and so on) has been abrogated. Instead, mixtures of scalars, vectors and movement direction are signaled.

Are these scalar parameters encoded independently of direction as the psychophysical results suggest? Simultaneous encoding may not be possible, because the directional signal in the motor cortices can account for a large fraction of the available depth of modulation, leaving little residual channel capacity for the additional encoding of scalars [19,33•]. In PMd and M1, evidence favors the sequential and relatively independent coding of different parameters in single neurons over time. First, the amplitude encoding during step movements does not occur preferentially along the PD [47]. Second, the direction of best speed modulation occurring during manual tracking is not coupled to the PD [33•]. Third, the addition of speed coefficients does not improve the fit of directional tuning curves [50]. However, others have argued that simultaneous encoding of speed and direction (i.e. a velocity vector) occurs in M1 during curvilinear drawing, on the basis of non-directional residual of the firing [19]. In that study [19], speed and curvature co-vary by the two thirds power law, confounding the interpretation of the residual.

Last, an additional set of observations favors the independent signaling of direction, amplitude, speed and accuracy in PMd and/or M1: the firing correlations with direction, amplitude, speed and accuracy are processed serially over time across a behavioral sequence. This was demonstrated for the encoding of direction and amplitude in a step reaching task, in which the pre-movement processing was limited to the reaction time and target location information was provided throughout the trial [48]. A serial order to the correlations was observed with direction specified first and then amplitude, consistent with the psychophysical observations that the direction of movement is processed independently and usually before amplitude [12,41,44].

Recently, a similar serial processing scheme for direction and amplitude was described for a different reaching task [49••]. The firing correlations with amplitude began in the memorized-delay period, earlier than found for the step reaching task [48]. One interpretation is that the task required amplitude and direction information to be processed early, thus illustrating that the processing of specific parameters is task dependent. Additional examples of time- or context-dependent processing in PMd and M1 include the observation that accuracy-related modulation occurs preferentially at the end of a reach, whereas directional tuning occurs early, consistent with the timing of the corrective movements [29•].

In a manual tracking task, correlations with target speed were more prominent in the cue period, with directional tuning dominating the track period [33•]. The speed modulation in the cue period was interpreted to be used for the timing of movement onset (a similar timing signal was found in another interception task [25]). These examples of ‘temporal parcellation’ in PMd and M1 suggest that such parameters are processed independently and indicate that the directional signal is not only task dependent but also varies over time and behavioral sequence.

Cerebellar Purkinje cells also signal direction [30–32], amplitude [31] and speed [32,33•]; however, these neurons do not have the same limit on channel capacity because the non-directional proportion of the simple spike firing accounts for 60% of the firing variability [33•]. Therefore, simultaneous admixtures of directional (i.e. vector) and non-directional (i.e. scalar) signals are possible. For lateral and intermediate cerebellar Purkinje cells, the direction and speed signals can be argued to represent a preferred velocity vector [32,33•]. First, there is no evidence for the decomposition of the velocity vector into its components of direction and speed [33•] or direction and amplitude [31]. Second, each Purkinje cell encodes direction at only one of a range of speeds, evidence for a one-to-one mapping of a specific speed and direction [32]. In contrast, neurons in PMd and M1 encode direction irrespective of movement speed [33•]. Last, the polarity of speed encoding is related to the PD of Purkinje cells. Positive speed regression slopes occur preferentially along the PD and negative speed slopes occur along directions opposite to the PD [33•]. Again, this relationship was not found to hold for the motor cortices.

Encoding other directionally sensitive parameters of arm movement

When neurons in the PMd and M1 signal both direction and a scalar, the directional tuning is not altered. The directional tuning of PMd and M1 neurons changes over time and during a behavioral sequence, consistent with the encoding of multiple directional parameters or vectors. In PMd and M1, the PD is influenced by arm posture [51–53] and starting position [54]. Eye position can shift the PD of these neurons [55,56], as can visual target location [14,15,57] and selective attention [58]. Also, altered dynamics such as tonic loads [59] and force fields [60••] influence the directional tuning of M1 neurons.

The discharge of M1 neurons is also correlated to velocity and acceleration [23,61]. Therefore, the discharge of PMd and M1 neurons can signal several directional parameters or vectors, which shift the directional signal. The change in directional signal may be seen as the result of vector arithmetic: multiple vectors are summed to yield one resultant
vector, which can be signaled by the limited channel capacity of motor cortical neurons [62].

The visual direction of the target is another such vector that influences the PD. During reaching or tracking tasks with an instructed delay period, the PD diverges as much as 180° between cue and the actual movement [21,63–65]. The direction of a visual target and subsequent arm movement serially influences the PD in step movements under altered visuomotor mappings [14,15,28,57], consistent with the proposed sequential nature of visuomotor transformations [10]. Force is another vector that may alter the unloaded PD. The PDs of caudal M1 neurons shift rapidly during reaching but not during an isometric task, in which a controlled force is produced by the arm without actual movement. This is suggestive of a task-specific multiplexing of a force vector with the direction signal. Here, multiplexing is used in the engineering sense to designate the processing of two or more independent signals over a single channel or neuron. Thus, a multitude of both scalar and vector quantities modulate motor cortical neurons.

**Coordinate systems and transforms**

Whether intrinsic (e.g. joint angles or muscles) or extrinsic (e.g. hand- or workplace-centered) coordinate systems are used by M1 has been extensively debated [7,8,10,40]. Because motor cortical neurons signal kinematic, dynamic, postural, visual and oculomotor information, the neural substrate exists for representing signals in multiple coordinate systems. Altering the required pronation–supination (forearm rotation) and flexion–extension movements of the wrist to move a cursor to a visual target demonstrated that a large group of M1 neurons did not shift their PDs, reflecting representation in an extrinsic coordinate frame [53]. But for a substantial fraction of the cells the PD shifted, consistent with a muscle-like intrinsic coordinate frame.

Similar fractions of M1 cells shift and do not shift their PDs when reaching in a force field [60••], also consistent with representations in both intrinsic and extrinsic frames. For reaching in three dimensions [9••], the stereotypic relationships between the hand and joint movements show that the extrinsic and intrinsic parameters are tightly correlated. Accordingly, population vectors constructed from hand-centered and joint-centered coordinates yield almost the same trajectories, which makes it difficult to distinguish between these two coordinate systems. The existence of several coordinate systems may facilitate information transfer and task-dependent processing. The postulated role for the PMd cortex in mapping arbitrary stimuli into movements would require such flexibility [66].

Psychophysical evidence points to an evolution of coordinate systems from an early, visually based system to a later limb-segment-based system during a visually cued reach to target movement [10,13]. This transformation involves changing from extrinsic to intrinsic coordinates. Movement parameters also seem to be processed independently and serially through a visuomotor transform [44,45]. At the single-neuron level, the PD should be altered during the postulated coordinate transformations. Consistent with this prediction, the PD rotates as much as 180° during a prolonged visual instruction period before movement [21] and shifts from visually directed to motorically directed over time or a trial sequence [14,15,28,57].

**Higher cortical processes also modulate PMd and M1 neurons**

The relations of motor cortical neuronal firing to arm movements are not rigid; they depend not only on task-specific behavioral but also cognitive content [57,67]. The changes in PD that occur with learning to move in a force field [60••], or with altered visuomotor relationships, illustrate how complex coordinate transformation alters the directional signal. Other higher cortical processes modulate motor cortical neuronal activity. The rotation of the PD of individual cells and the population vector in M1 during a visuomotor transformation task was the first and one of the more dramatic demonstrations of this concept [68,69].

Motor cortical neurons may also provide a short-term storage of sequential stimuli about forthcoming movements. During the instruction of a two-movement sequence, the PD was found to signal the direction of the first or second movement in the series [70]. In a context-recall task, M1 activity reflected the serial order of five visual stimuli, consistent with a memory scanning operation [71]. Similarly, processes related to decision making influence both PMd and M1: M1 neurons respond bimodally to the need to make a decision about a moving tactile stimulus [72], and PMd neurons encode signals related to the decision to ‘move’ or ‘not to move’ [22,73]. Therefore, many different non-motoric signals modulate PMd and M1 neurons.

**Conclusions**

The firing of PMd, M1 and cerebellar neurons contain many motor and non-motor signals. The most studied of these, directional tuning, is a robust phenomenon that has proved useful not only for understanding the planning and execution of movements but also for evaluating occult cognitive processing. But there is no single directional signal; instead, directional kinematic and kinetic variables contribute to the directional tuning. Within a behavioral context, the directional signal may vary in time with other movement-related parameters. The behavioral context influences the nature of the directional signal, as does the experimental design. Both extrinsic and intrinsic coordinates are represented.

From an engineering standpoint, it might seem that other parameters are multiplexed with the directional signal. Rather, the encoding of multiple coordinate systems and multiple parameters may simply reflect the contributions of the different sensory and motor neural networks operating to control movements [74,75]. The challenge is to understand the time-varying and adaptive directional information flows in these networks.
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References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:
* of special interest
** of outstanding interest

Motor systems


