

Cortical control of reaching movements

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Recent studies provide further support for the hypothesis that spatial representations of limb position, target locations, and potential motor actions are expressed in the neuronal activity in parietal cortex. In contrast, precentral cortical activity more strongly expresses processes involved in the selection and execution of motor actions. As a general conceptual framework, these processes may be interpreted in terms of such formalisms as sensorimotor transformations and 'internal models'.

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Abbreviations

AIP	anterior intraparietal cortex
LIP	lateral intraparietal cortex
MDP	medial dorsal parietal cortex
MI	primary motor cortex
MIP	medial intraparietal cortex
PET	positron emission tomography
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
PO	parieto-occipital cortex
VIP	ventral intraparietal cortex

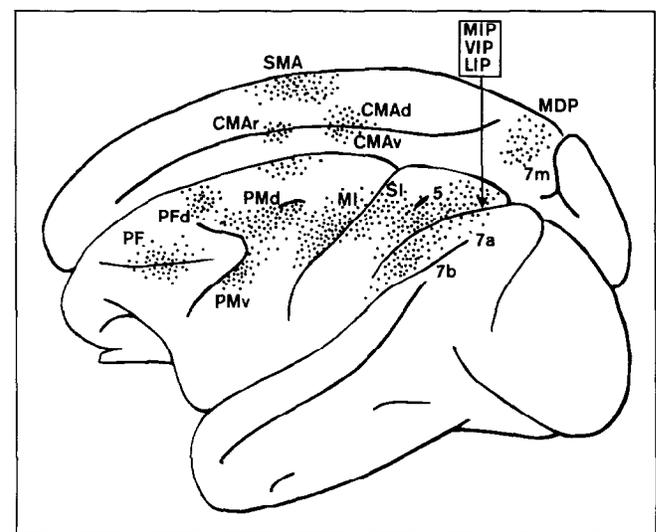
Introduction

The central neuronal processes that control eye and arm movements aimed at visual targets are often described as a sequence of sensorimotor co-ordinate transformations between a signal of spatial location and a pattern of muscle activity [1–3,4**]. From this perspective, one experimental goal is to identify the intervening reference frames, parameter spaces, and co-ordinate transformations by which the motor system accomplishes this task. A literal interpretation of this conceptual model would predict a serial cascade of recruitment of separate neuronal populations, each with uniform response properties and each performing a discrete operation.

In this review, we survey recent studies of the distributed cortical network controlling reaching movements (see Figure 1). These studies show that simplistic predictions of the serial co-ordinate transformation model are not literally correct. Nevertheless, analysis of cell activity

in terms of reference frames, co-ordinate systems and transformations captures reasonably well how cell activity in different cortical areas is coupled to sensory and motor events during reaching movements. Therefore, although the co-ordinate transformation model may be only a metaphorical description of the underlying causal mechanisms, it retains heuristic value.

Figure 1

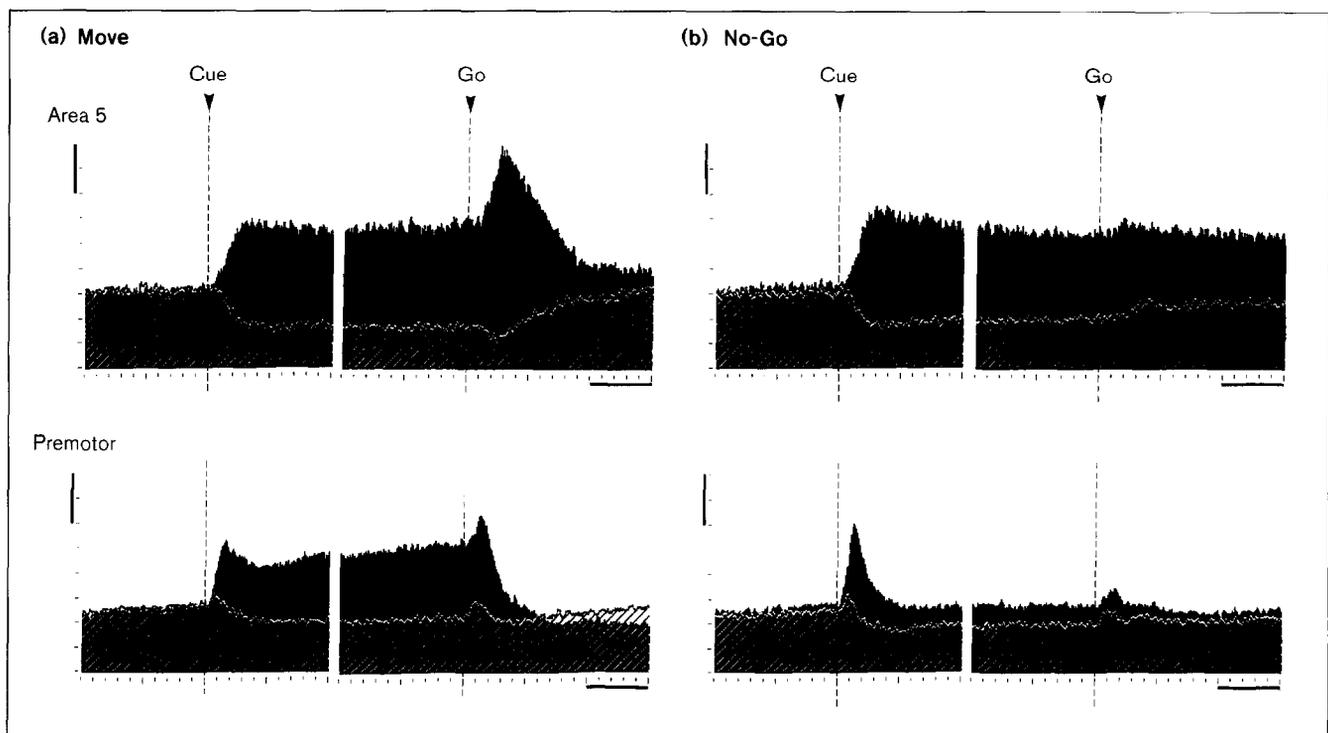


Distribution of the movement-related cell populations in the cerebral cortex of the macaque monkey, implicated in the planning and execution of visually guided reaching movements of the arm, as well as those activated by reafferent mechanoreceptive signals from the limb. 5, superior parietal area 5; 7a, posterior parietal cortex area 7a; 7b, posterior parietal cortex area 7b; 7m, posterior parietal cortex area 7m; CMA, cingulate motor area; CMAAd, dorsal CMA; CMAr, rostral CMA; CMAv, ventral CMA; PF, prefrontal cortex; PFd, dorsal PF; SI, primary somatosensory cortex; SMA, supplemental motor area. Modified from [8*].

Parietal cortex – representations of spatial locations and potential motor actions?

The parietal cortex plays a critical role in the processes linking sensation and action [4**–6**,7,8*,9*,10]. It generates representations of both the posture and movement of the body and eyes and of the spatial location of the stimuli. It also contains neuronal correlates of higher cognitive functions such as directed attention and 'working memory'. Moreover, there is a growing consensus that the representations in parietal cortex signal not just where an object is but also the animal's potential motor actions on it [4**–6**,7,8*,9*,10]. Therefore, the parietal cortex could contribute to the spatial representations and early sensorimotor transformations underlying action.

Figure 2



Mean population histograms of the activity of samples of cells in parietal area 5 and PMd in an instructed-delay task. Visual cues in different spatial locations instructed the monkeys either **(a)** to move to the cue after a delay ('Move') or **(b)** not to move ('No-Go'). Activity is shown for trials in which cues appeared at the preferred movement direction of each cell (solid histograms) and at the opposite direction (diagonal hatched histograms). Activity is oriented to the appearance of the cue at the left and to the go signal at the right in each histogram. During the delay period in Move trials (a), cells in both areas generated strong directional signals in anticipation of the movements after the go signals. Activity in PMd was much less directional within 300 ms after the cue in No-Go trials than in Move trials, a presumed neuronal correlate of the monkeys' decision not to move. In contrast, area 5 cells continued to generate strong directional signals in No-Go trials (b), as if signalling the potential movements that the monkeys were not permitted to make after the 'go' signal. Horizontal calibration bars=500ms. Vertical calibration bars=10spikes/s. Modified from [29].

Many reaching models propose that signals about limb starting position and target location must be combined to specify movement parameters such as direction or final arm posture [3,8[•],10,11[•]]. The parietal cortex appears to play a critical role in integrating visual and somatic inputs [10,12[•],13[•]]. This is illustrated by a study on adaptation to lateral-displacing prisms during pointing movements, which is usually presumed to require realignment of central representations of target and limb position. Using PET techniques in humans, Clower *et al.* [14^{••}] reported that part of the parietal cortex was the only supraspinal structure differentially related to the adaptation process itself. As adaptation in a task often does not transfer well to other task situations [15[•],16[•]], Clower *et al.* [14^{••}] concluded that the parietal activation involved a specific adjustment of representations of the limb and the target used to guide the pointing movements, rather than a global perceptual realignment of visual and proprioceptive reference frames.

One way to define the relative spatial location of the target and limb would be to converge signals about both onto single cells, as has been observed in ventral intraparietal

cortex (VIP) and area 7b [17[•]]. Similarly, preliminary reports have described cells in area 7m on the medial surface of the hemisphere whose discharge covaried with the direction of both eye and arm movements, and was modified by visual feedback during movement in reaction-time tasks [18[•]] and before impending movements in instructed-delay tasks [19[•]]. Parietal cells related to grasping movements also exhibit complex interactions between visual inputs and motor functions [7,9[•]]. The convergence of visual- and limb-related inputs might be a means to match attributes of the stimulus, such as target location or object form, with attributes of the appropriate motor response, such as the direction of reach or the general type of grasping action required [7,9[•],18[•],19[•]].

Alternatively, this interaction might be the neuronal basis of a sensorimotor co-ordinate transformation [4^{••},5^{••},17[•]]. For instance, cells in lateral intraparietal cortex (LIP) and area 7a generate a representation of the spatial location of stimuli, but do not explicitly signal their location in any obvious spatial co-ordinate system. Instead, they generate an implicit distributed representation of stimulus location in head-centred co-ordinates by combining a signal about

the retinal location of stimuli and a multiplicative gain signal covarying with the orbital position of the eyes [4**]. Recently, the converging signals have been expanded to include auditory and vestibular inputs, and gain fields covarying with head position and body orientation (reviewed in [4**]). This suggests that the posterior parietal cortex may generate multiple simultaneous representations in eye-, head-, body-, and even world-centred frameworks, rather than a single monolithic reference framework for spatial localization. The co-ordinate systems may vary in different parts of the parietal cortex according to the nature of the actions evoked by the sensory input [5**,6**]. The multiplicative gain-field interactions between converging inputs appear to be a powerful and efficient mechanism to produce the co-ordinate transformations that integrate the diverse inputs in different co-ordinates into a distributed polymodal spatial representation [4**,20*,21].

Controversy remains, however, as to how activity in parts of the posterior parietal cortex relates to motor action. Some evidence suggests that it specifies the spatial location of behaviorally relevant stimuli but not the nature of the motor response [5**,17*]. Other evidence indicates that it also signals potential actions in motor co-ordinates [4**,9*,23*,24**].

The superior parietal cortex has traditionally been regarded as a somatosensory region representing body posture and movement [8*]. Lacquaniti *et al.* [25] showed elegantly that area 5 cell activity signalled arm postures and movements in a body-centred reference frame. When cell activity was evaluated in different co-ordinate systems, the discharge of most cells covaried mainly with only one of the parameters (co-ordinate axes) of each co-ordinate system. However, the highly stereotypical behaviour of the animals made it impossible to distinguish which co-ordinate system best accounted for cell discharge.

It is increasingly evident that the superior parietal cortex also has important visuomotor planning functions, especially those parts embedded in the medial wall of the sulcus (medial intraparietal cortex; MIP) and on the medial surface of the hemisphere (areas 7m and medial dorsal parietal cortex [MDP]) [8*,26**].

One line of evidence supporting the role of area 5 in visuomotor planning is the presence of directionally tuned activity during the delay period of instructed delay tasks [27–29,30**]. Much of this delay activity appears to be expressed in the motor co-ordinates of arm movements rather than the sensory co-ordinates of visual inputs [8*,28,29].

A striking new finding is that the delay activity in parietal cortex may signal potential movements even when the monkey decides not to perform those actions. This was first shown in area 5 [29]. Many cells that discharged during the delay period before reaching movements in

particular directions continued to discharge in no-go trials in which visual stimuli in the same spatial locations instructed the monkeys not to move (Figure 2). This was in sharp contrast to the behaviour of dorsal premotor cortex (PMd) cells, which differentially signalled the monkeys' intention to move (or not) shortly after the appearance of the instructional signal.

This finding has now been confirmed in a task that dissociated eye and hand movements [24**]. When monkeys were instructed to make only eye or arm movements toward visual targets in a delayed-response task, a sizeable minority of cells appeared to discharge nonspecifically before both eye and arm movements toward particular targets (cf. [18*,19*]). When the same 'nonspecific' cells were tested in a dissociation task requiring simultaneous eye and arm movements in opposite directions, their activity was unconditionally coupled to the direction of only the eye or arm movements. This indicated that in the first task, many of the 'nonspecific' cells were in fact always signalling the direction of potential eye or arm movements, whether or not the animal had been instructed to perform those actions.

Both studies suggest that the appearance of a behaviourally relevant visual stimulus could evoke neuronal correlates of a number of alternative and potentially competing motor actions in the parietal cortex—motor intentions that may never be expressed overtly. This supports a role for the parietal cortex in the early processing of sensory inputs in terms of potential motor actions, with the final selection of the overt motor response being made elsewhere, possibly in PMd and primary motor cortex (MI) for limb movements.

Premotor and primary motor cortex – selection and implementation of motor actions?

Recent reviews provide an excellent overview of the response properties of PMd cells [31*,32**,33*]. They also survey evidence that the sources of visuospatial information to PMd include parietal areas 7m, MIP, MDP and PO [26**,30**,31*,33*,34].

Two studies of ventral premotor cortex (PMv) [35*,36*] reported that it contains a hybrid body-centred representation of peripersonal space composed, in part, of single cells that possess a somatic receptive field and also respond to visual stimuli in locations adjacent to the somatic receptive field. These responses have features in common with cells in areas VIP and 7b, which project to PMd. By signalling the spatial location of visual stimuli relative to body parts, these cells may contribute to transformations from extrinsic to intrinsic co-ordinates to guide movement directed to objects in peripersonal space [35*,36*].

The co-ordinate framework for PMd activity is less clear. PMd cells appear to lack bimodal somatic/visual receptive

fields [36•]. Like some parietal cells, PMd cells may be affected by the angle of gaze and direction of attention ([37]; reviewed in [32••,33•]), but the implications of this feature for co-ordinate frameworks in PMd are unclear. Any differences between the co-ordinate systems in PMd and PMv probably reflect differences in their respective roles in visually guided movements [31•,35•].

Wise *et al.* [32••,33•] propose that PMd plays a critical role in the context-dependent selection and planning of movements in conditions that involve arbitrary stimulus–response mappings. Shen and Alexander [38••,39••] have provided new insights into that process. Monkeys displaced a cursor on a computer screen by moving a lever with their arm in two instructed-delay tasks. In one task, the motions of the arm and cursor were collinear (i.e. nonrotated). In a second task, cursor motion was rotated 90° counterclockwise from that of the arm. Before movement onset, most PMd activity covaried only with the direction of cursor motion, or was significantly influenced by the context (degree of rotation between cursor and arm motions) in which the movements were performed. Activity unambiguously coupled to limb movement direction independent of task context was relatively minor until after movement onset. In contrast, a representation of limb-specific signals was more prominent in MI, but neuronal correlates of cursor movement and task context could also be seen [39••]. This implicated PMd in several different putative stages in the sensorimotor transformation between stimulus and response. Shen and Alexander [38••] concluded that PMd plays a preferential role in generating a representation of the extrinsic visuospatial objectives of the task (cursor displacement) and of the context-dependent stimulus–response associations required to select the appropriate motor response. In contrast, MI appeared to be more involved in transforming that information into signals that specify the required limb movement itself [38••,39••]. Crammond and Kalaska [40•] came to similar conclusions about the differential nature of the movement representations in PMd and MI in a more indirect manner.

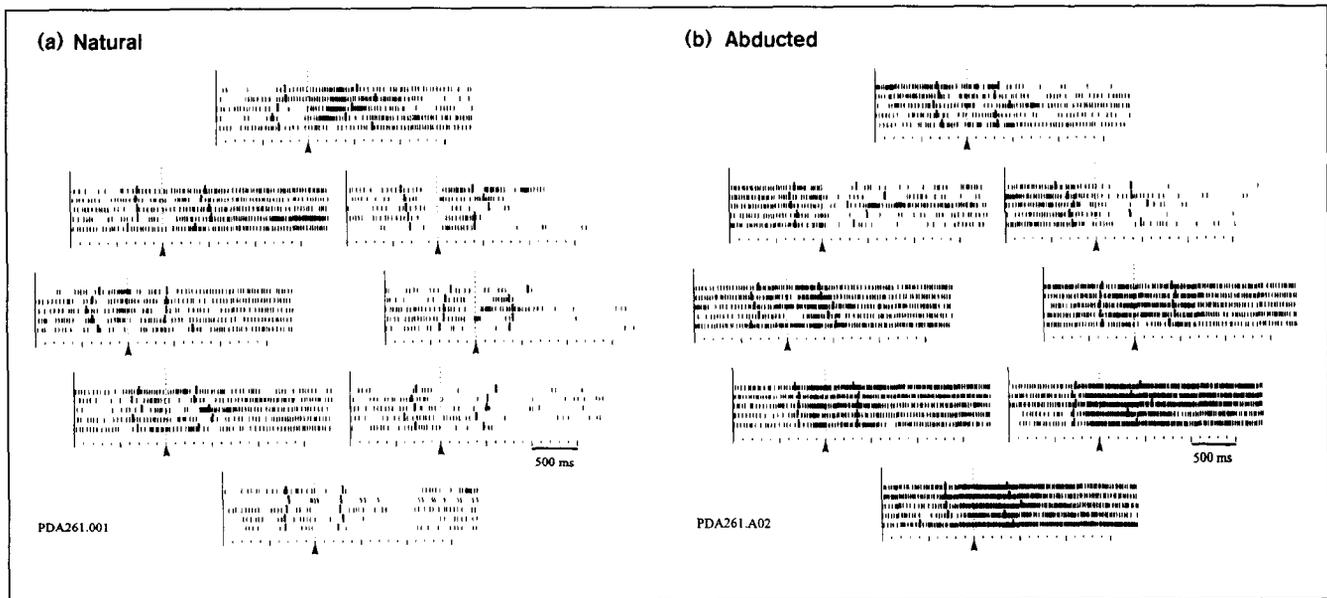
Zhang *et al.* [41•] likewise reported the presence of representations of stimulus location, movement target location and stimulus–response associations in MI activity using a reaction-time task that dissociated the location of visual stimuli and movement targets. Both Shen and Alexander [38••,39••] and Zhang *et al.* [41•] propose that PMd and MI resolve the sensorimotor transformation required in their tasks by performing a sequence of discrete functional operations. This is very different from the transformation mechanism proposed by Lurito *et al.* [42] for MI cells in a similar visuomotor dissociation task. The latter authors proposed that all the cells are functionally equivalent and represent the direction of motor output. Their sensorimotor transformation model involves a continuous sweep of activation across the vector space of MI cell directionality, from cells oriented toward the stimulus to

those oriented toward the intended target. These very different hypotheses about the transformation mechanism may have resulted partly from the analytic methods used in each study. Shen and Alexander [38••,39••] and Zhang *et al.* [41•] categorised cells into distinct functional classes based on an analysis of the relative degree of coupling of cell activity to attributes of sensory input or motor output. In contrast, Lurito *et al.* [42] analysed the gradual change both in the net directional signal generated by a population of cells and in the timing of cell activation as a function of their directional tuning.

A prominent theme in several recent articles has been the extensive overlap and gradual rostrocaudal gradient of response properties across PMd and MI [30••,34,38••,39••,40•]. Correlates of ‘higher-order’ visuospatial processes and ‘lower-order’ output-specific signals are distributed across the entire rostrocaudal extent of the precentral gyrus, with the former more prominent rostrally and the latter more prominent caudally. Johnson *et al.* [30••] found a corresponding but oppositely oriented gradient across the rostrocaudal (or dorsoventral) extent of the medial bank of the superior parietal cortex. Moreover, cell populations with corresponding response properties in the precentral and parietal gradients were interconnected by corticocortical projections. Activity within the distributed frontoparietal network may gradually transform extrinsic visuospatial information about target location and movement trajectory into limb-centred motor commands [26••,30••,33•], by local interactions within the frontal and parietal gradients, and long-range interactions via the corticocortical projections. The higher-order representations in PMd are probably generated, in part, by inputs from visuospatial representations in parietal areas 7m, MDP, PO and MIP. In contrast, the more limb-centred representation in MI may result partly from the input it receives from proprioceptive/somatomotor representations in areas 2 and 5. Similarly, PMv and the parts of the parietal cortex with which it is connected (AIP, VIP, area 7b) may comprise a second distributed frontoparietal network to resolve movement-related sensorimotor transformations [9•,35•,36•]. This discussion emphasises the role of corticocortical projections, but the cerebellum, basal ganglia, and other structures could also contribute. This perspective is consistent with the hypothesis—described earlier for the parietal cortex—that co-ordinate transformations can be produced by merging inputs in different co-ordinates [2,4••].

Another fundamental issue addressed by several recent studies is that of serial order. Reaching models predict a temporal sequence of co-ordinate transformations between representations of different movement attributes. However, the distributions of cell onset times from different areas are often more striking for their degree of temporal overlap than their temporal separation [1,2,8•,30••]. Moreover, onset times are only one possible manifestation of serial order in the brain. Recent studies have found

Figure 3



The effect of arm orientation on the discharge of motor cortical cells during reaching movements from a central start to eight peripheral targets. Movements were performed using similar hand paths but different arm orientations, either **(a)** with the arm in the vertical plane (natural) or **(b)** with the arm oriented largely in the horizontal plane (abducted). Extrinsic variables related to target location or hand path remained similar for the two arm orientations, but intrinsic variables related to arm geometry or motor commands to muscles necessary to execute the reaching movements varied between the two conditions. A majority of cells showed a significant change in their level of discharge prior to, during and/or after movement, and/or a change in their directional preference between arm orientations. The cell in this figure shows both effects. Each raster illustrates the discharge pattern of the cell during five repeated trials to each target. The position of each raster denotes the direction of movement. Arrowheads mark the onset of movement. Thicker bars before and after movement onset denote time of appearance of the target light and end of movement, respectively. Modified from [59].

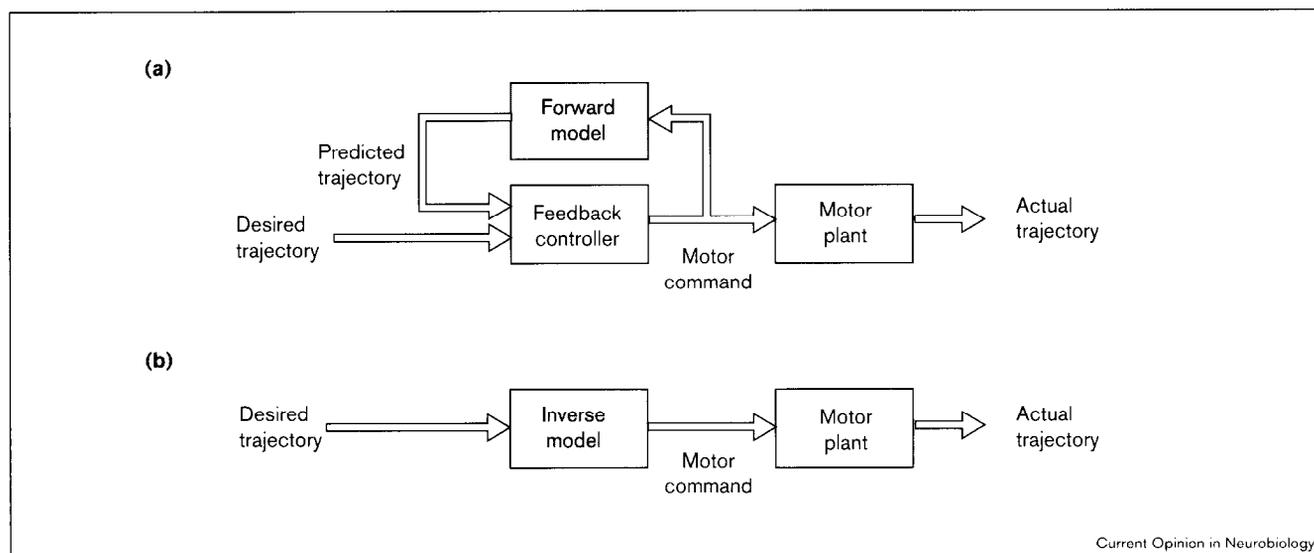
strong evidence of serial temporal order expressed as changes in the task-related information processed by single cells and by cell populations at different times during behavioural tasks. Fu *et al.* [43] reported a progressive change in the kinematic parameters about movement trajectories signalled by MI and PMd cells before and during reaching movements. Other studies [32,33,38,39,41] reported that the earliest activity after presentation of an instructional signal was predominantly related to target location and other extrinsic task attributes. Target-related activity declined in prominence with time as progressively more context-dependent and limb-movement-specific activity became expressed. This serial order was not absolute, however. Neuronal correlates of different putative operations and representations could be found at all times throughout the trial in overlapping populations of cells, but their relative prominence changed gradually with time.

The nature of the MI representation of reaching movements is under continued study. The covariation of MI activity (at the single-cell and population level) with the extrinsic kinematic parameters of hand path is well documented [43–48,49]. This kinematic analysis of the directional signal generated in MI has now been extended to movement sequences [50,51]. It is also well established that MI cell activity varies as a function of output

forces [52]. These studies support a primary role for MI in processing directional information about movement [53]. Modelling studies have examined how an MI signal that specifies hand-centred extrinsic directional attributes of motor output could be converted by other networks into appropriate muscle activity patterns [54,55]. In these models, MI represents the limb as a functional whole, and transformations from extrinsic parameters into intrinsic joint- or muscle-centred representations are realised elsewhere.

The transformation from extrinsic to intrinsic parameter spaces is critical for successful motor performance. For instance, the mechanical action of muscles varies strongly in a systematic manner with arm posture when analysed in either arm- or body-centred reference frames [56], and so must be taken into account to produce the correct movement. If the movement representation in MI incorporates information about intrinsic movement attributes, its cell activity should likewise vary systematically with arm posture. This was first shown by Caminiti *et al.* [57,58], and has now been extended by two studies. In the first study [59], monkeys made reaching movements along similar hand paths to targets in identical spatial locations, but used two different arm orientations (Figure 3). Many MI cells showed changes in the level and directionality of task-related activity between arm orientations [59].

Figure 4



The use of 'forward' and 'inverse' internal models in two control architectures for reaching movements. **(a)** Forward models predict the consequences of motor commands [82,83]. **(b)** In contrast, inverse models calculate the required motor command to produce desired results [68,84]. (A notable example of an inverse model is the sensorimotor transformation presumably used to convert task-space plans into motor actions.) Although they are distinct theoretical constructs, forward and inverse models can be difficult to distinguish empirically. For example, in dealing with complex dynamics of the controlled system, one strategy is to develop an accurate forward model that predicts the sensory consequences of motor commands (a). This can be used to estimate the motor error and effectively create a zero-lag feedback controller. An alternate strategy is to develop an inverse model of the dynamics, which yields the motor command required to produce a given task-space trajectory (b). This effectively lumps the function of the forward model and controller (a) into a single system. Because both architectures will yield the same torque profile during well-practised movements, they may be difficult to distinguish empirically.

Simulations showed that cells encoding specific variables in joint-centred co-ordinate frameworks would undergo similar changes in activity with arm posture. Cells in PMd were statistically less sensitive to changes in arm posture than in MI, consistent with a preferential role for PMd in planning higher-order extrinsic or visuospatial aspects of the task [60*].

In a complementary study [61*], a monkey used its whole arm to exert static isometric forces in constant spatial directions against a force transducer that it held in its hand. The transducer was positioned in nine different spatial locations on a plane. MI cell activity changed as a function of hand location, often showing an arc-like shift in the cell's preferred force direction at different hand locations, even though the extrinsic spatial direction of force output at the hand did not change.

There is new evidence of even more specific muscle-centred information in MI. Scott [62*] recently reported preliminary evidence of parallel trends in the variation of onset times and magnitude of activity as a function of arm movement direction between groups of shoulder and elbow muscles, and functionally corresponding groups of MI cells. Bennett and Lemon [63**] identified corticomotoneuronal cells that made direct monosynaptic connections to spinal motoneurons innervating more than one muscle. They observed parallels between the pattern of facilitation of the corticomotoneuronal cells on their

target muscles and the patterns of changes in activity of the cells and muscles in different task conditions. Both studies indicate that MI can provide fairly specific information about the co-ordinated patterns of muscle activity required for multi-articular movement.

However, these correlations do not mean that MI represents movement exclusively in muscle-centred co-ordinates. The evidence of neuronal correlates of higher-order operations and movement representations in MI suggests that it plays a much larger role in motor control than specifying muscle contractile levels [38**,39**,41*,50*,51*,64,65]. One of these roles, in conjunction with PMd, could be a transformation from extrinsic to intrinsic motor co-ordinates [38**,39**,41*,59*–62*,63**].

Does the nervous system use internal models in controlling reaching movements?

An alternative perspective on MI function is that the covariation of MI activity with arm postures, output forces, and muscle activity may implicate it in an internal model of the peripheral skeletomuscular plant (Figure 4). An internal model could be explicit or implicit, just as the morphology of the body is explicitly represented in the figures of a gross anatomy book but implicitly represented in the genetic code that shapes its development during embryogenesis. Internal models have been attributed to specific neuronal structures and circuits [66,67*], or have been simply operationally defined, such as that

part of the motor system that adapts to changes in movement dynamics [68]. By the broadest definition, any neuronal system whose input–output properties mimic attributes of the kinematics or kinetics of the peripheral skeletomuscular plant or that can adapt to changes in the environment contains an internal model that is implicit within those parameters of the system.

By this broad definition, the motor system almost certainly uses internal models. A recent study [69••,70•] suggests that the stiffness of the human limb during voluntary movement is not sufficient for a control strategy that does not account for movement dynamics. This implies an internal model of limb dynamics that provides anticipatory compensation for dynamic factors such as inertia and interjoint interaction forces (although this compensation might not be complete [71]). The anticipatory adjustments of grip force to the load caused by whole-arm movement [72••] also show that a component of the motor system contains information about the expected dynamic consequences of arm movement.

Further evidence for internal models is the existence of after-effects after adaptation to novel force environments [68,73]. The physical reality of this internal representation is indicated indirectly by the finding that consolidation of the adaptation in long-term motor memory takes several hours [74••], implying slow physiological processes that cause long-term changes in the input–output behaviour of neural circuits. The degree to which adaptation generalises across the workspace outside of the tested region [68,75•] or to nontested task conditions [15•,16•,76,77••] can indicate whether the form of internal models is general or specific to the effector and task conditions. The internal model for limb dynamics may be in joint-centred co-ordinates [68,78,79•], or in the extrinsic parameters of a perceptual planning space [67•,76,80,81].

These psychophysical studies reveal some of the properties of the putative internal models used for the planning and control of reaching. The concept of internal models may prove a valuable complement to the concept of sensorimotor co-ordinate transformations for interpreting the response properties of parietal and precentral neuronal activity. For instance, if cells contribute to an internal model that is implicated in adaptation to changing task conditions or constraints, one may predict that their coupling to sensory or motor events will change during adaptation or motor skill acquisition.

Conclusions

Recent results suggest that the control of arm movements involves spatial and temporal gradients of neural activity across interconnected regions of parietal and precentral cortex. Parietal areas appear predominantly involved in representations of the environment and body, and early representations of potential motor actions. Precentral motor areas select the overt motor action and implement

details of its execution. Neuronal events in these areas can be described in terms of sensorimotor transformations or in terms of the control-theory formalism of internal models. Even though the neurophysiological data suggest that the motor system does not literally implement these formalisms [2,3], they nevertheless have heuristic value. In particular, they make predictions about the properties of single cells and neural circuits that can be tested in future neurophysiological experiments.

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- of special interest
- of outstanding interest

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- In this follow-up to his influential review published four years earlier [85], Goodale further elaborates the hypothesis that the visual system is modular, with a fundamental division between systems dedicated to perception and to more cognitive functions and those concerned with visuomotor behaviour. In this scheme, key functions of the parietal cortex are to extract information about the structure of the external world, such as the spatial location, distance, physical dimensions, and spatial orientation of objects, and to perform some of the associated visuomotor transformations that are required to organise successful visually guided movements.
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A PET study of the distribution of activity during visually guided reaching movements in humans, with special attention as to whether the parietal cortex represents reaching movements according to the visuospatial location of the target or in limb motor co-ordinates. Whereas MI represented the behaviour exclusively in limb-centred co-ordinates, most other task-related cortical areas, including the parietal cortex, processed both visuospatial and limb motor information.

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A rigorous quantitative study of the distribution of metabolic activity across the cerebral cortex of monkeys performing a visually guided reaching task with one arm. Of particular note, the arm regions of the primary motor and somatosensory cortex and parts of area 5 are contralaterally activated, suggesting a direct role in controlling the reaching limb. In contrast, parts of the premotor cortex, area 5, and area 7 are bilaterally activated, implicating a role in higher-order integration of visuomotor information during visually guided reaching behaviour.

14. Clower DM, Hoffman JM, Votaw JR, Faber TL, Woods RP, Alexander GE: **Role of the posterior parietal cortex in the recalibration of visually guided reaching.** *Nature* 1996, **383**:618-621.

The authors used PET techniques to localise the cortical regions implicated in adaptation to laterally displacing prisms during visually guided reaching. After subtracting the activity patterns presumed to reflect sensory, motor, and error-correction aspects of the task, the only remaining differential activation was in a small part of the parietal cortex contralateral to the arm used to reach. This region may correspond to the cortex near the fundus of the intraparietal sulcus in macaque monkeys, but interspecies homologies are often problematic. The authors did not find a differential activation of the cerebellum, even though the latter has also been implicated in prism adaptation. They propose that the cerebellum is implicated in other aspects of the adaptation process, but not to the action-specific realignment of limb and visual reference frames.

15. Martin TA, Keating JG, Goodkin HP, Bastian AJ, Thach WT: **Throwing while looking through prisms. II. Specificity and storage of multiple gaze-throw calibrations.** *Brain* 1996, **119**:1199-1211.

It is well documented that the adaptation of reaching movements to displacing prisms does not transfer well from the practised arm to the unpractised arm. This study demonstrated that the adaptation acquired during overhand throwing of balls at a target also does not transfer well to underhand throws to the same targets using the same arm, indicating that the adaptation process may be specific to the biomechanics of the limb motions.

16. Kitazawa S, Kimura T, Uka T: **Prism adaptation of reaching movements: specificity for the velocity of reaching.** *J Neurosci* 1997, **17**:1481-1492.

Human subjects reached from a fixed starting position to different target locations while wearing displacing prisms. When adaptation was completed with one movement velocity, transfer was progressively poorer for test movements at increasingly different velocities. This indicated that adaptation is not just specific to the form of the limb motions, but also to its time-dependent parameters. The authors concluded that the adaptation did not involve a static shift in either the visual or proprioceptive inputs responsible for a body-centred representation of the spatial location of the hand and target.

Instead, the change occurs in a subsequent stage that translates the spatial information into time-dependent parameters describing the kinematics and kinetics of the motor command.

17. Colby CL, Duhamel J-R, Goldberg ME: **Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area.** *J Neurophysiol* 1996, **76**:2841-2852.

The response properties of cells in LIP were characterised in five different task conditions. LIP cells responded in a variety of different circumstances, and did not appear to be involved exclusively in sensory or motor processes. Cognitive factors, such as directed attention and anticipation of predictable events, also strongly modulated cell activity. The authors concluded that LIP cells are primarily involved in the representation of behaviourally relevant spatial locations at which sensory events had occurred or toward which overt or covert actions would soon be directed. Comparison with the studies from Andersen's group [4**,22*,23*,24**] illustrates the difficulties confronted by researchers attempting to understand the neuronal mechanisms and functions of nonprimary cortical areas.

18. Ferraina S, Johnson PB, Garasto MR, Battaglia-Mayer A, Ercolani L, Bianchi L, Lacquaniti F, Caminiti R: **Combination of hand and gaze signals during reaching: activity in parietal area 7m of the monkey.** *J Neurophysiol* 1997, **77**:1034-1038.

Cells in parietal cortex area 7m were studied in a combination of tasks meant to dissociate activity related to eye and arm movements and stable positions. Cells showed a wide range of combinations of properties, but the majority of cells showed complex interactions between oculomotor and limb motor behaviour. This study extends the distribution of arm- and eye-movement related activity in the parietal cortex onto the medial surface of the hemisphere.

19. Ferraina S, Garasto MR, Battaglia-Mayer A, Ferraresi P, Johnson PB, Lacquaniti F, Caminiti R: **Visual control of hand-reaching movement: activity in parietal area 7m.** *Eur J Neurosci* 1997, **9**:1090-1095.

Cells in parietal area 7m were tested in an instructed delay task requiring reaching movements of the arm to visual targets in normal ambient light conditions and in the dark. Many cells showed significant differences in activity between light and dark conditions, and showed complex interactions between eye and arm movements at all times during the task, including the delay period. The authors concluded that the directionally tuned activity prior to and during reaching movements in the dark confirm that these cells contribute to the preparation of motor responses.

20. Salinas E, Abbott LF: **A model of multiplicative neural responses in parietal cortex.** *Proc Natl Acad Sci USA* 1996, **93**:11956-11961.

Gain fields imply a multiplicative interaction between inputs in different co-ordinate systems, but single cells are generally assumed to perform only simple additive operations on their synaptic inputs. This study shows that a multiplicative interaction between inputs will arise within a recurrently connected population of simple neurons with excitatory connections between similarly tuned cells and inhibitory connections between differently tuned cells, even though each single cell sums its synaptic inputs linearly. The multiplicative gain field is expressed at the single-cell level, but the cells do not perform a multiplication – it is an emergent property of the dynamical interactions within the network. Multiplicative interactions could also perform co-ordinate transformations in the limb motor system [21], because the network in the motor cortex may have the same recurrent internal organisation [86].

21. Salinas E, Abbott LF: **Transfer of coded information from sensory to motor networks.** *J Neurosci* 1995, **15**:6461-6474.

22. Bracewell RM, Mazzoni P, Barash S, Andersen RA: **Motor intention activity in the macaque's lateral intraparietal area. II. Changes of motor plan.** *J Neurophysiol* 1996, **76**:1457-1465.

If activity during a delay period is related to intentions to make a saccade, that activity should change as new sensory information requires an update in the motor plan. Monkeys were trained to saccade to the last of a variable-length sequence of potential targets presented during an instructed delay period. Because the monkey could not predict which would be the last target, it had to plan a new saccade as each stimulus appeared. Many LIP cells changed their activity after the appearance of each visual target, as expected as the monkey altered his intended motor response.

23. Mazzoni P, Bracewell RM, Barash S, Andersen RA: **Motor intention activity in the macaque's lateral intraparietal area. I. Dissociation of motor plan from sensory memory.** *J Neurophysiol* 1996, **76**:1439-1457.

Using a double-saccade task with an instructed delay period, the authors dissociated the retinal locations of visual stimuli from the metrics of the instructed saccades. They found that whereas some cells signalled the location of visual cues, the majority were related predominantly to the direction of the next saccade, whether or not the visual stimuli fell in their retinal receptive fields. They concluded that much of the LIP activity is related to the planning of overt eye movements, and less to sensory or cognitive processes.

24. Snyder LH, Batista AP, Andersen RA: **Coding of intention in the posterior parietal cortex.** *Nature* 1997, **386**:167-170.
- Monkeys were instructed by visual cues to make only eye or arm movements to particular target locations. Many cells were selectively active prior to only

eye or only arm movements in specific directions. However, a sizeable minority seemed to be nonspecifically active prior to movements of either the arm or eyes in a particular direction. When tested in a modified task in which the monkeys made simultaneous eye and arm movements in opposite directions, the discharge of most of the 'nonspecific' cells was shown to be correlated to only the eye or arm movements. Without this extra control, those cells might have been interpreted as related to other cognitive operations, such as directed attention.

25. Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R: **Representing spatial information for limb movement: role of area 5 in the monkey.** *Cereb Cortex* 1995, 5:391-409.

26. Caminiti R, Ferraina S, Johnson PB: **The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule.** *Cereb Cortex* 1996, 6:319-328.

This review article proposes a solution to a long-standing conundrum regarding the fact that although PMd is attributed a role in visuomotor planning, there was no obvious source of visual input. The authors propose that the recently identified visuospatial and visuomotor activity in medial parts of the superior parietal cortex (areas MIP, 7m, MDP and PO) is relayed to PMd via corticocortical projections. The resulting distributed network of parietal and precentral populations is a presumed substrate for the transformation of visual target signals into limb-centred motor commands.

27. Crammond DJ, Kalaska JF: **Neuronal activity in primate parietal cortex area 5 varies with intended movement direction during an instructed-delay period.** *Exp Brain Res* 1989, 76:458-462.

28. Ferraina S, Bianchi L: **Posterior parietal cortex: functional properties of neurons in area 5 during an instructed-delay reaching task within different parts of space.** *Exp Brain Res* 1994, 99:175-178.

29. Kalaska JF, Crammond DJ: **Deciding not to go: neuronal correlates of response selection in a go/nogo task in primate premotor and parietal cortex.** *Cereb Cortex* 1995, 5:410-428.

30. Johnson PB, Ferraina S, Bianchi L, Caminiti R: **Cortical networks for visual reaching: physiological and anatomical organization of frontal and parietal lobe arm regions.** *Cereb Cortex* 1996, 6:102-119.

A combined neurophysiological-neuroanatomical study of the distribution of response properties of cells in the precentral gyrus and the superior parietal lobule in instructed-delay tasks, and of the corticocortical interconnections between these two regions. The authors found a gradual rostrocaudal change in the relative frequency of so-called 'signal' and 'set' versus 'movement' and 'position' activity across the proximal-arm representation in PMd-MI, with the former more prominent in PMd and the latter stronger in MI. They also found corresponding response patterns and gradients in the medial bank of the intraparietal sulcus, but the orientation of the gradient was opposite, with the 'signal' and 'set' activity more prominent ventrally (caudally) in the sulcus (i.e. MIP). Parts of PMd-MI and the superior parietal lobule displaying similar functional properties tended to be interconnected via corticocortical projections. A superb study.

31. Jackson SR, Husain M: **Visuomotor functions of the lateral premotor cortex.** *Curr Opin Neurobiol* 1996, 6:788-795.

A concise review of evidence supporting the hypothesis that PMd and PMv fulfil different roles in the planning of visually guided movements, and for the existence of homologues of these areas in the human.

32. Wise SP, Di Pellegrino G, Boussaoud D: **The premotor cortex and nonstandard sensorimotor mapping.** *Can J Physiol Pharmacol* 1996, 74:469-482.

The authors review many lines of evidence that PMd is critically important when motor behaviour requires nonstandard sensorimotor transformations. Nonstandard mappings involve situations in which the relationship between a stimulus and the response it instructs is arbitrary, or in which the visual stimulus guiding an action does not also serve as the target of the signalled response, or in which gaze, attention, and action are not all directed towards the same spatial location. The ability to form nonstandard mappings endows the organism with rich behavioural flexibility. Of particular note is an elegant 'population-vector' analysis of the effect of dissociating the spatial locus of attention from that of the intended movement target on the directional signal generated by a population of PMd cells in an instructed-delay task with nonstandard mapping.

33. Wise SP, Boussaoud D, Johnson PB, Caminiti R: **Premotor and parietal cortex: corticocortical connectivity and combinatorial computations.** *Annu Rev Neurosci* 1997, 20:25-42.

A review of the pathways of visual input into PMd, and of the response properties of PMd cells. The authors also consider the role of PMd within the context of several different computational models that perform visuomotor transformations from the spatial co-ordinates of target location to the motor co-ordinates of arm movement.

34. Tanné J, Boussaoud D, Boyer-Zeller N, Rouiller EM: **Direct visual pathways for reaching movements in the macaque monkey.** *Neuroreport* 1995, 7:267-272.

35. Fogassi L, Gallese V, Fadiga L, Luppino G, Matelli M, Rizzolatti G: **Coding of peripersonal space in inferior premotor cortex (area F4).** *J Neurophysiol* 1996, 76:141-157.

This study reported that many PMv cells possess both a somatic receptive field (RF) and a visual RF that is usually located in the peripersonal space immediately adjacent to the somatic RF. The visual RF shifts its spatial location with the somatic RF during body movements, and is independent of the retinal location of visual stimuli. Most cell responses were independent of eye position. The authors concluded that this body-centred hybrid somatic/visual co-ordinate system is useful for organising visually guided arm and head movements. In an interesting discussion, the authors contrasted these properties with the co-ordinate systems for spatial localization in oculomotor areas and concluded that the differences reflect the differing sensorimotor co-ordinate transformations required in the two motor systems.

36. Graziano MS, Hu XT, Gross CG: **Visuospatial properties of ventral premotor cortex.** *J Neurophysiol* 1997, 77:2268-2292.

Extending the results of [35*], the authors used a range of controlled stimuli and statistical analyses to confirm that many PMv cells have contiguous bimodal somatic/visual receptive fields (RFs) that move as a unit during body movements. Like Fogassi *et al.* [35*], they concluded that the visual RFs are body-centred and nonretinotopic. However, they emphasised that the activity level of the majority of cells is modulated by eye, head, or arm position. They proposed that this modulation may reflect a polymodal interaction, similar to that reported for oculomotor cells in parietal cortex, by which a sensory co-ordinate transformation is realised to produce body-fixed visual RFs.

37. Boussaoud D: **Primate premotor cortex: modulation of preparatory neuronal activity by gaze angle.** *J Neurophysiol* 1995, 73:886-890.

38. Shen L, Alexander GE: **Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex.** *J Neurophysiol* 1997, 77:1171-1194.

Monkeys made limb movements to displace a cursor towards a target location on a computer monitor. In one condition, cursor and limb movement were collinear. In the other, cursor motion was rotated 90° counterclockwise from limb movement. Using ANOVA analysis, the authors reported evidence in MI of neuronal representations of target location, of limb movement output, and of cell activity reflecting the complex interactions between the two levels of representation. Although there was extensive temporal overlap, there was also a clear serial order in the expression of these different aspects of the task, with a strong trend for early target-related activity, gradually replaced by more limb-centred activity. The complete dissociation between the motion of the cursor and of the limb in the rotated condition provides some of the strongest evidence to date of the existence in MI of higher-order representations of task objectives and constraints independent of peripheral motor output.

39. Shen L, Alexander GE: **Preferential representation of instructed target location versus limb trajectory in dorsal premotor area.** *J Neurophysiol* 1997, 77:1195-1212.

The authors studied the activity of PMd cells in the same task as in their companion paper [38**]. They found considerable overlap in the response properties of PMd and MI cells. However, target-centred representations of the task predominated in PMd, unlike in MI, up until the time that movement began. Overall, PMd activity appeared to represent mainly the global extrinsic demands of the task (trajectory of the cursor, not of the limb) and of the behavioural context (rotation condition) in which motions were performed, with a more modest context-independent representation of limb motor output than in MI. This article and its companion both present a clear and focused discussion of the issue of sensorimotor transformations, and are a case study of solid task design and data analysis that should be obligatory reading for all graduate students.

40. Crammond DJ, Kalaska JF: **Differential relation of discharge in primary motor cortex and premotor cortex to movements versus actively maintained postures during a reaching task.** *Exp Brain Res* 1996, 108:45-61.

A comparison of the cell activity in PMd and MI during a reaction-time task. Of particular note, the authors compared the strength and directionality of activity prior to and during movement to visual targets, with the activity associated with actively maintained postures over the targets after the movements. Many cells in MI were strongly related to both movement and posture, and the directionality of activity during the two phases of the task was generally similar, as was also observed for most muscle activity. In contrast, PMd cells were generally most active before and during movement and less active than MI cells during stable postures, with greater variation in directionality of activity in the two phases of the task. This evidence is consistent with the hypothesis that MI was more strongly implicated in the moment-to-moment control of motor output during both dynamic and static phases of the task, whereas PMd was more conditionally related to movement planning.

41. Zhang J, Riehle A, Requin J, Kornblum S: **Dynamics of single neuron activity in monkey primary motor cortex related to sensorimotor transformation.** *J Neurosci* 1997, 17:2227-2246.

Monkeys made wrist movements in two opposite directions by moving either towards or away from visual stimuli (as indicated by the colour of the cue),

in a reaction-time task without delay period. Using a novel analytic method, LOCUS analysis, the authors attempted to identify the nature of the information being processed in the time-varying discharge of MI cells at different times during the behavioural reaction time. They reported neuronal correlates in MI of three putative processing stages required to perform the task (stimulus encoding, response selection according to current stimulus-response association rule and response encoding independent of association rule). Single cells could show correlates of more than one stage at different times. Although there was overlap, there was also a clear serial order across the population of cells, with activity predominantly related to stimulus location first, followed by activity representing the general mapping rule (e.g. move towards or away from the stimulus) and specific stimulus-response pairings, and, finally, the appropriate direction of response. They also observed that cells in the same vertical penetration (i.e. possibly the same cortical column) tended to show the same task relationship. The implication is that the entire stimulus-response transformation is not expressed within a column, but across ensembles of columns.

42. Lurito JT, Georgakopoulos T, Georgopoulos AP: **Cognitive spatial-motor processes. 7. The making of movements at an angle from a stimulus direction: studies of motor cortical activity at the single cell and population levels.** *Exp Brain Res* 1991, **87**:562-580.
43. Fu QG, Flament D, Coltz JD, Ebner TJ: **Temporal encoding of movement kinematics in the discharge of primate primary motor and premotor neurons.** *J Neurophysiol* 1995, **73**:836-854.
44. Ashe J, Georgopoulos AP: **Movement parameters and neural activity in motor cortex and area 5.** *Cereb Cortex* 1994, **4**:590-600.
45. Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT: **On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex.** *J Neurosci* 1982, **2**:1527-1537.
46. Schwartz AB, Kettner RE, Georgopoulos AP: **Primate motor cortex and free arm movements to visual targets in three-dimensional space. I. Relations between single cell discharge and direction of movement.** *J Neurosci* 1988, **8**:2913-2927.
47. Georgopoulos AP, Kettner RE, Schwartz AB: **Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population.** *J Neurosci* 1988, **8**:2928-2937.
48. Kalaska JF, Cohen DA, Hyde ML, Prud'Homme M: **A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task.** *J Neurosci* 1989, **9**:2080-2102.
49. Sanger TD: **Probability density estimation for the interpretation of neural population codes.** *J Neurophysiol* 1996, **76**:2790-2793.

Using probability theory, the author outlines an interesting alternative to the population vector method for estimating population signals. Cell activity is expressed as a probability density function that is proportional to the cell's tuning curve for movements in different spatial directions. The population signal is then defined as the product of the tuning curves for all cells active for a given movement.

50. Kettner RE, Marcario JK, Clark-Phelps MC: **Control of remembered reaching sequences in monkey. I. Activity during movement in motor and premotor cortex.** *Exp Brain Res* 1996, **112**:335-346.

Monkeys performed 12 different sequences of three movements in different directions. The three target locations for each sequence were presented during an initial instruction period, followed by a delay before the monkeys made the movements. Cells in MI and PMd were directionally tuned and tended to retain the same tuning throughout the sequence. Using a single set of tuning parameters for each cell derived from its activity across all sequences, the authors generated population vectors that pointed close to the direction of movement for each movement in each sequence. This implicated MI and PMd in the moment-to-moment control of the directionality of movement as the sequences unfolded.

51. Kettner RE, Marcario JK, Port NL: **Control of remembered reaching sequences in monkey. II. Storage and preparation before movement in motor and premotor cortex.** *Exp Brain Res* 1996, **112**:347-358.

The task in this study required memorisation of a sequence of three movements, followed by the recall of each movement in the appropriate order. Whereas many MI and PMd cells were related to the performance of each movement in the sequence, subsets of cells appeared to be more specifically related to the storage and/or recall of particular movements at specific locations in the sequence. This implicates PMd and MI in higher-order cognitive aspects of the motor sequence task, as well as in the execution of each movement in turn.

52. Taira M, Bolino J, Smyrnis N, Georgopoulos AP, Ashe J: **On the relations between single cell activity in the motor cortex and the direction and magnitude of three-dimensional static isometric force.** *Exp Brain Res* 1996, **109**:367-376.

Using a regression model with separate terms for the direction and magnitude of output force, the authors reported that most MI cells (78.6%) showed a significant relation to force direction only, 7.1% to force magnitude independent of direction, and 14.3% to both direction and magnitude of force. They concluded that MI activity is preferentially related to the directional aspect of static force output, with a weaker relation to force magnitude.

53. Georgopoulos AP: **Current issues in directional motor control.** *Trends Neurosci* 1995, **18**:506-510.
54. Georgopoulos AP: **On the translation of directional motor cortical commands to activation of muscles via spinal interneuronal systems.** *Cogn Brain Res* 1996, **3**:151-155.

Based on studies on the motor cortex of monkeys and the spinal cord of frogs, this report describes how directional motor commands could be translated into the co-ordinated patterns of muscle activity required to produce appropriately directed motor output by the limb. This theory suggests that motor cortex regards the limb as a functional whole and that co-ordinated motor patterns are generated only at the spinal level.

55. Lukashin AV, Amirkian BG, Georgopoulos AP: **A simulated actuator driven by motor cortical signals.** *Neuroreport* 1996, **7**:2597-2601.

A neural network is used to control isometric end-point output forces of a two-segment planar model of the human arm. Motor cortical cell activity patterns recorded during an isometric multi-joint task in monkeys are used as input signals for the network, which converts them into a set of muscle 'rest lengths' that generate the desired output force. Only a few cells are necessary to reliably control the limb output forces.

56. Buneo CA, Soechting JF, Flanders M: **Postural dependence of muscle actions: implications for neural control.** *J Neurosci* 1997, **17**:2128-2142.

The effect of arm posture on the mechanical actions of muscles was studied by measuring the changes in direction and magnitude of forces and torques generated by electrical stimulation of muscle bellies while the arm was in a wide range of different postures. With the analytic thoroughness and sophistication characteristic of this team, they showed that force and torque output varied in a systematic and relatively simple manner with arm posture, and also that both arm- and body-fixed reference frames captured this dependence equally well. This study makes readily testable predictions about the response properties of MI cells.

57. Caminiti R, Johnson PB, Urbano A: **Making arm movements within different parts of space: dynamic aspects in the primate motor cortex.** *J Neurosci* 1990, **10**:2039-2058.
58. Caminiti R, Johnson PB, Gali C, Ferraina S, Burnod Y: **Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets.** *J Neurosci* 1991, **11**:1182-1197.
59. Scott SH, Kalaska JF: **Reaching movements with similar hand paths but different arm orientations: I. Activity of individual cells in motor cortex.** *J Neurophysiol* 1997, **77**:826-852.

Monkeys were trained to make reaching movements using similar hand trajectories but with two different arm orientations, in the natural parasagittal plane and abducted in the horizontal plane. This paradigm dissociated extrinsic variables related to the goal of the task such as target location and hand trajectory, which remained relatively constant, from intrinsic variables related to arm geometry and limb dynamics, which varied across the two conditions. The level of discharge prior to, during and/or after movement changed in a majority of MI cells. Many cells showed a significant change in their relationship to movement direction, reflecting a change in the sharpness of their tuning and/or a change in their directional preference. Mathematical models illustrated that cells encoding intrinsic variables of the task would undergo similar changes when reaching movements were performed in the different arm orientations.

60. Scott SH, Sergio LE, Kalaska JF: **Reaching movements with similar hand paths but different arm orientations. II. Activity of individual cells in dorsal premotor cortex and parietal area 5.** *J Neurophysiol* 1997, **78**:2413-2426

An extension of [59] to two other cortical regions that are implicated in the planning and control of limb movements. Many cells in PMd and area 5 showed a significant change in their relationship to movement direction and/or a change in the level of activity prior to, during and/or after movement when reaching using the different arm orientations. In general, the effect of arm orientation on cell activity was greater in MI than in PMd.

61. Sergio LE, Kalaska JF: **Systematic changes in directional tuning of motor cortex cell activity with hand location while generating static isometric forces in constant spatial directions.** *J Neurophysiol* 1997, **78**:1170-1174.

Monkeys generated static isometric forces at the hand in constant spatial directions, while holding the hand at nine different locations in a horizontal

planar workspace. Many MI cells generated tonic activity that varied as a function of the direction of static output forces at a given hand location. The level of activity and its directional tuning also varied with hand location, often showing an arc-like change in directionality across the workspace, even though the spatial direction of output forces at the hand did not vary. The sensitivity of cell activity to arm posture in this isometric task suggests that MI possesses information about the intrinsic posture-dependent mechanical properties of the peripheral skeletomuscular system.

62. Scott SH: **Comparison of onset time and magnitude of activity for proximal arm muscles and motor cortical cells prior to reaching movements.** *J Neurophysiol* 1997, **77**:1016-1022.

This study found that variations in the onset time and magnitude of shoulder and elbow muscle activity to initiate reaching movements in different directions were similar to those for functionally corresponding groups of MI cells. These results suggest an important role for motor cortex in coordinating motor patterns at the shoulder and elbow during reaching movements.

63. Bennett KM, Lemon RN: **Corticomotoneuronal contribution to the fractionation of muscle activity during precision grip in the monkey.** *J Neurophysiol* 1996, **75**:1826-1842.

This study looked at how the activity of corticomotoneuronal (CM) cells in monkeys may contribute to the coordinated motor patterns of their target muscles during a precision grip task. The activity of CM cells that produced postspike facilitation (PSF) of EMG in two hand muscles were examined during different periods of the motor task. They found that when the muscle with the largest PSF was more active than the other target muscle, the CM cell discharged at a higher rate than when the reverse was true. This suggests that the task-related activity of CM cells often parallels their pattern of facilitation on their target muscles, supporting a role in the fractionation of multi-muscle contractile patterns.

64. Georgopoulos AP, Pellizzer G: **The mental and the neural: psychological and neural studies of mental rotation and memory scanning.** *Neuropsychologia* 1995, **33**:1531-1547.

65. Pellizzer G, Sargent P, Georgopoulos AP: **Motor cortical activity in a context-recall task.** *Science* 1995, **269**:702-705.

66. Kawato M, Furukawa K, Suzuki R: **A hierarchical neural-network model for control and learning of voluntary movement.** *Biol Cybern* 1987, **57**:169-185.

67. Miall RC, Wolpert DM: **Forward models for physiological motor control.** *Neural Networks* 1996, **9**:1265-1279.

A clear review of the uses of and evidence for internal forward models. The authors suggest that the cerebellum acts as a 'Smith predictor' – a system for estimating the current state of the motor system to effectively create a zero-lag feedback controller.

68. Shadmehr R, Mussa-Ivaldi FA: **Adaptive representation of dynamics during learning of a motor task.** *J Neurosci* 1994, **14**:3208-3224.

69. Gomi H, Kawato M: **Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement.** *Science* 1996, **272**:117-120.

Using a high-performance manipulandum, these authors show that the stiffness of the human limb during movement is not sufficient for pure kinematic 'equilibrium-point' control. A mathematical estimation of the equilibrium-point trajectory revealed it to be much more complex than the monotonic endpoint trajectory.

70. Gomi H, Kawato M: **Human arm stiffness and equilibrium-point trajectory during multi-joint movement.** *Biol Cybern* 1997, **76**:163-171.

This article provides a more in-depth presentation of the analysis described by [69**].

71. Gordon J, Ghilardi MF, Cooper SE, Ghez C: **Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy.** *Exp Brain Res* 1994, **99**:112-130.

72. Flanagan JR, Wing AM: **The role of internal models in motion planning and control: evidence from grip force adjustments during movements of hand-held loads.** *J Neurosci* 1997, **17**:1519-1528.

An ingenious method for assessing the motor system's ability to predict movement dynamics is to measure the grip force with which objects are held in the hand during arm movements. These authors showed that humans adjust their grip force in parallel with movement-induced fluctuations in the inertial force, even under various external load conditions. This demonstrates that the subjects can predict the inertial force, and thus, strongly suggests that they have learned an internal forward model of their motor apparatus and the external load conditions.

73. Lackner JR, Dizio P: **Rapid adaptation to coriolis force perturbations of arm trajectory.** *J Neurophysiol* 1994, **72**:299-313.

74. Shadmehr R, Brashers-Krug T: **Functional stages in the formation of human long-term motor memory.** *J Neurosci* 1997, **17**:409-419.

These authors studied the consolidation process for 'procedural' memory during pointing tasks performed in a force-field. They demonstrated that subjects can learn to adapt to two conflicting force-fields only if the training sessions with the different force-fields are separated by at least 5 hours. With shorter temporal distance, the learned 'internal model' of the first field interferes with the learning of the second. This suggests that after initial acquisition, motor adaptation progresses through a second consolidation stage.

75. Pine ZM, Krakauer JW, Gordon J, Ghez C: **Learning of scaling factors and reference axes for reaching movements.** *Neuroreport* 1996, **7**:2357-2361.

Humans controlled the movement of a cursor on a screen by moving a stylus on a digitising tablet. The gain or rotation of the function relating hand and cursor movement were varied. Adaptation to gain changes resulted in accurate reaching and generalised across different targets. Adaptation to rotation was less complete and generalised poorly, arguing against the hypothesis that adaptation involves a re-alignment of reference frames.

76. Dizio P, Lackner JR: **Motor adaptation to Coriolis force perturbations of reaching movements. Endpoint but not trajectory adaptation transfers to the nonexposed arm.** *J Neurophysiol* 1995, **74**:1787-1792.

77. Gandolfo F, Mussa-Ivaldi FA, Bizzi E: **Motor learning by field approximation.** *Proc Natl Acad Sci USA* 1996, **93**:3843-3846.

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