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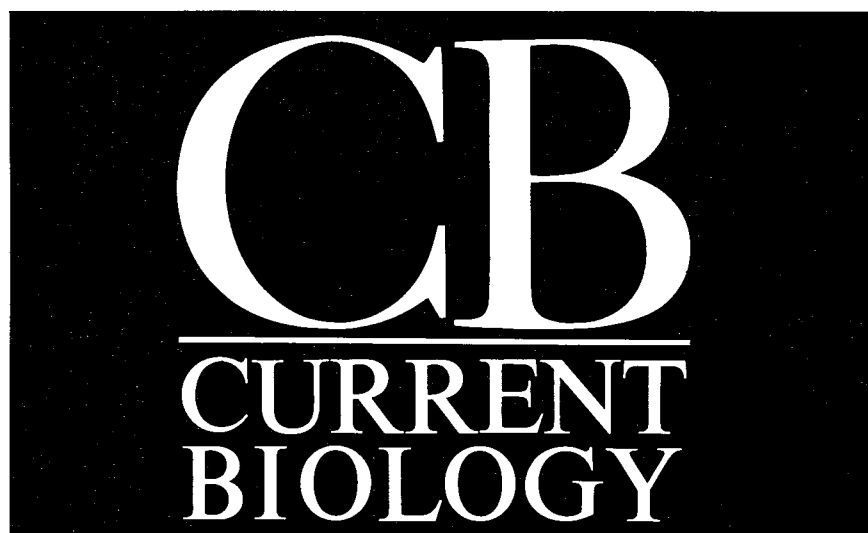
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# Organization of voluntary movement

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There have recently been a number of advances in our knowledge of the organization of complex, multi-joint movements. Promising starts have been made in our understanding of how the motor system translates information about the location of external targets into motor commands encoded in a body-based coordinate system. Two simplifying strategies for trajectory control that are discussed are parallel specification of response features and the programming of equilibrium trajectories. New insights have also been gained into how neural systems process sensory information to plan and assist with task performance. A number of recent papers emphasize the feedforward use of sensory input, which is mediated through models of the external world, the body's physical plant, and the task structure. These models exert their influence at both reflex and higher levels and permit the preparation of predictive default parameters of trajectories as well as strategies for resolving task demands.

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## Introduction

In recent years approaches for investigating the planning and execution of voluntary movement have undergone substantial changes. Emphasis has shifted away from the study of simple behaviors (e.g. button presses, single-joint movements) and limited performance measures (e.g. reaction time, global errors) to analysis of naturalistic motor tasks such as reaching, catching, and manipulation. This shift has been facilitated by the availability of methods for monitoring the kinematics of multi-joint movements and by the introduction of new conceptual frameworks that have been derived in part from the field of robotics.

Selecting from a large number of issues that are currently under investigation, we will focus on two fundamental questions. First, how is information concerning the spatial attributes of a goal or target transformed into information about which joints to move and which muscles to contract? Theoretically, accurate responses require that the intended action, which must unfold in an external reference frame, be converted into motor commands that are coded in a distinct internal reference frame. A central question is whether separate neural processing modules perform the necessary computations in serial stages or whether the components of the sensorimotor transformations are processed in parallel. The second question asks how feedback and feedforward control mechanisms are integrated to achieve accuracy in motor performance. A theme that is emerging is that this integration is based

on the use of internal models or representations of the mechanical characteristics and control properties of the limbs, external objects, and task structure. In reviewing new results that bear on these questions, we will focus on studies of upper limb movement, particularly in reaching tasks. Such tasks require the nervous system to project the hand or fingers, located at the end of the limb, to a target or intended position. Reaching is frequently integrated with touching, grasping, or manipulation of objects.

## Coordinate transformations and trajectory planning in reaching movements

In order for the brain to move the hand to a point in space, the frame of reference in which the target is perceived in sensory space needs to be transformed into an intrinsic or motor reference system [1–4]. The general rules that underlie such transformations, as well as the coordinates and the origin of the intrinsic coordinate systems, are all crucial issues. Several possible intrinsic coordinate systems could be used to represent the movement for planning hand trajectory. One possibility would be for a joint-based reference system to specify movements of arm segments around their joints (e.g. shoulder, elbow, wrist). The underlying computation that transforms a hand trajectory in extrinsic space into a trajectory in joint space is called inverse kinematics; it begins with the

### Abbreviation

CNV—contingent negative variation.

31. DONOGHUE JP, SANES JN: **Organization of Adult Motor Cortex Representation Following Neonatal Forelimb Nerve Injury in Rats.** *J Neurosci* 1988, 8:3221-3232.

32. SANES JN, SUNER S, DONOGHUE JP: **Dynamic Organization of Primary Motor Cortex Output to Target Muscles in Adult Rats. I. Long Term Patterns of Reorganization Following Motor and Mixed Peripheral Nerve Lesions.** *Exp Brain Res* 1990, 79:479-491.

Motor cortical reorganization can occur following amputation or motor nerve transection in adult rats, establishing the plasticity of the motor cortex in adults. This and [33••] are the first reports on the reorganization of the motor cortex following nerve lesions.

33. DONOGHUE JP, SUNER S, SANES JN: **Dynamic Organization of Primary Motor Cortex Output to Target Muscles in Adult Rats. II. Rapid Reorganization Following Peripheral Nerve Lesions.** *Exp Brain Res* 1990, 79:492-503.

Reorganization of the motor map can occur within hours of nerve transection. This suggests that local changes within the cortex are responsible for the process.

34. JACOBS KM, DONOGHUE JP: **Reshaping the Motor Cortical Maps by Unmasking Latent Intracortical Connections.** *Science* 1991, 251:944-947.

The motor effects of microstimulation of the motor cortex can be changed by injecting bicuculline (a GABA antagonist) locally in the cortex. This suggests that the organization of the motor map is dynamic and depends on intact intracortical GABA-mediated inhibitory mechanisms.

35. NUDO RJ, JENKINS WM, MERZENICH MM: **Repetitive Microstimulation Alters the Cortical Representation of Movements in Adult Rats.** *Somatosens Mot Res* 1990, 7:463-483.

Repeated microstimulation of the motor cortex resulted in a change of the boundaries of the motor map. This indicates that the map is dynamically maintained and is probably activity-dependent.

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movement or path of the hand and produces the corresponding rotations at the joints. The torques required to achieve the desired changes in angles at each joint must then be derived, a procedure known as inverse dynamics. The inverse dynamic computation is particularly complex for multi-joint movements because the active torque required at each joint depends not only on the complex inertial field of the limb, but also on torques produced by motions occurring at all other joints (interaction torques). A final muscle computation is also required, in a quite different intrinsic coordinate system, to select and activate muscles appropriately to achieve the required torques.

### Shoulder-centered motor planning

An important approach to understanding sensorimotor transformations has been undertaken by Soechting and collaborators [5,6]. They have identified and analyzed systematic errors in reaching to the locations of remembered targets in order to make inferences about the types of sensorimotor transformations used by the nervous system. In an initial series of studies [5,6] they demonstrated that subjects make systematic errors in hand movements that are consistently centered around the shoulder rather than the head or eyes. These errors did not occur when subjects used a pointer to reach the remembered location. Thus, errors in hand position did not reflect a general perceptual error but rather a specific error in a sensorimotor transformation. From an analysis of directional errors made when the subjects were required to place their finger-tip midway between the target and either the shoulder or the head, they found that subjects possessed equally accurate head-centered and shoulder-centered representations [7]. This would not be expected if subjects were first to compute shoulder position in terms of head coordinates. The authors have therefore proposed that to generate reaching movements the nervous system transforms the retinocentric coordinates of the target into a polar coordinate system that is successively head-centered and then shoulder-centered. Ultimately, the target is represented in a polar system of coordinates whose dimensions are the distance from the shoulder and the two directions defined by the horizontal and vertical angles (azimuth and elevation), respectively [8••]. The results of these psychophysical studies fit with those of single-cell studies of parietal cortex neurons in primates, which show that the patterns of activation depend on the target position relative to both the eye and the head [4,9]. Both sets of observations suggest that the transformation into a shoulder-centered coordinate system takes place in stages.

### Modularity in the specification of final arm orientation

Soechting and colleagues have also examined how this shoulder-centered coordinate system can be effectively translated into an intrinsic coordinate system. In psychophysical experiments they have found that subjects are able to match the angles of limb segments in ex-

ternal space (elevation for up-down and yaw for side-to-side orientation) more accurately than they are able to match joint angles [10] (see, however [11•]). On the other hand subjects make systematic errors in computing segment angles. An analysis of these errors suggests that the transformation of target information into segment angles involves a linear approximation [6]. Arm and forearm elevation are each a linear function of both target distance and elevation, while target azimuth specifies arm and forearm yaw angles. The authors have proposed that, to specify target location in shoulder-centered coordinates, target distance, elevation and azimuth are partitioned into two processing channels specifying limb segment elevations and yaw angles, respectively [8••]. They reason that, if processing were partitioned into two channels, subjects should be able to use the channels separately, but would not be able to separate processing occurring within a single channel. They found that subjects could indeed point accurately to a target's azimuth while ignoring its distance, but could not accurately match elevation while ignoring distance. This result is consistent with their hypothesis that information about target elevation and target distance is processed in a confounded manner within the same channel.

These studies have two limitations. First, the investigators did not systematically vary the starting position of the subjects' movements. It is thus not certain that the origin of the proposed shoulder-centered coordinate system is, in fact, independent of starting position, as the theory proposes. Second, as trajectories themselves were not examined, shoulder-centered coordinate systems could perhaps be relevant only to the specification of terminal posture after movement is complete.

### Extent and direction planning in hand space

An alternative to the hypothesis of Soechting and co-workers is that movements are planned in a hand-centered coordinate system. This conclusion is supported by the findings of several groups [12–16], based on neuronal studies in primate cortex, which suggest that the direction and extent of movement are encoded as intended movement vectors whose origin is at the hand. During reaching, the control of hand position is fundamental to the task definition and thus appears likely to be a critical variable in the planning process itself. For example, when subjects reach from one point to another, hand paths are approximately straight and show a unimodal bell-shaped velocity profile. In contrast, the associated joint trajectories are highly variable and may show reversals in direction. These findings are most compatible with a direct, central planning of hand trajectories [2,17].

Two general mechanisms have been proposed to simplify trajectory planning and implementation of hand trajectories: parallel processing and equilibrium point control. In the first, the direction and extent of movement may be planned by independent or 'parallel' neural processes. In the second, joint kinematics (and dynamics) emerge from the specification of a sequence of successive positions, forming an equilibrium trajectory [18,19•].

Evidence in favor of each of these will be discussed below.

### Parallel processing of direction and extent

Evidence in favor of distinct channels for programming the direction and extent of movement was initially obtained from the finding that errors in the amplitude and direction of force impulses are independent (for example, see [20]). Further studies [21•] have shown that the values of these parameters are also computed independently at higher levels of cognitive processing controlling response preparation. For example, increases or decreases in the amplitude probabilities of flexion targets produce corresponding biases in the amplitudes of both flexion and extension responses [21•].

Psychophysical evidence of channel independence is complemented by studies of cognitive evoked potentials (contingent negative variations or CNVs), during motor programming in a precued reaction time task [22•]. By varying the precued information available prior to the go signal, MacKay and Bonnet [22•] found that the programming of movement direction produced CNVs over the contralateral somatosensory areas, while the programming of amplitude was associated with CNVs that were focused over the primary motor areas. This difference in topographic distribution favors separate mechanisms for the programming of direction and magnitude of force, and is compatible with a parallel processing of these features. The authors also found that preparation may be completed before the triggering stimulus, which also points to the existence of an independent channel for triggering responses (see also [23,24]).

The shape of the spatial distribution of errors made during multi-joint reaching movements without the benefit of visual feedback also supports a parallel programming of movement direction and extent [25••]. Variability in movement endpoints shows a characteristic elliptical distribution such that extent errors are typically two to three times greater than direction errors. The independence of variable direction and extent errors implies that separate processes are used to specify these parameters. The greater accuracy of movement direction may be due to a preponderant motor cortical representation of direction [15] and the high rate of information transmission for direction in force trajectories [26•,27•]. It should also be noted that the elliptical error distributions remain oriented in the direction of movement, independent of the initial position of the hand in the workspace. This suggests that the origin of the coordinate system used for trajectory planning is at the hand, for if a shoulder-centered coordinate system were used, errors would be oriented in relation to the shoulder.

An advantage of independent specification of direction and extent, based on a hand-centered coordinate system, would be a simplification in computing trajectories. The

programming of direction, which involves the selection of a set of relative joint angle changes (the kinematic plan), could be reflected in a spatial pattern of muscle activation distributed throughout the limb. The programming of extent, on the other hand, could represent the setting of a scaling factor, acting in space and time on the activation profile appropriate for the intended direction [28]. Indeed, monkeys [29•] as well as humans are highly adept at rescaling the velocity profiles and extents of multi-joint movements when display conditions are altered.

### Equilibrium trajectories

A different view of trajectory planning, the virtual trajectory hypothesis [2,19•,30••,31–33], suggests that joint kinematics and dynamics need not be programmed explicitly. Under this hypothesis movement is programmed as a series of successive endpoints of the hand. The joint kinematics and dynamics would emerge from the specification of a succession of equilibrium points [19•]. Restoring forces produced by the elastic properties of muscles and low level neural feedback mechanisms would then provide corrections when perturbations move the limb away from the intended trajectory. The specification of an equilibrium trajectory would thus simplify the effective resolution of the inverse dynamic problem without an explicit representation of inertial, viscous and gravitational opposing forces.

The central computational problem in this formulation is the transformation of hand coordinates into an appropriate pattern of muscle activation for production of joint kinematics. A provocative study by Bizzi and coworkers [30••] in the frog, suggests that this transformation may take place in the spinal cord. Their findings indicate that local spinal networks contain representations of equilibrium points. The authors stimulated the frog spinal cord electrically and recorded the forces produced at the foot in different parts of the workspace. Stimuli applied to particular sites in the lateral gray matter induced convergent force fields that defined unique equilibrium points, whereas direct stimulation of motor neuron areas or motor nerves gave either divergent or parallel fields. A topographic organization of force fields could be identified in the grey matter. In addition, concurrent stimulation at different sites gave rise to an additive force field equal to the sum of the fields obtained from stimulation delivered at the individual points. These observations led Bizzi and coworkers to suggest that networks of spinal interneurons might perform the transformation of a central command in 'foot space' to the muscle contractions executed in joint space. They have further suggested that the observed superposition features could explain, *rana ex machina*, how the spinal cord generates an infinite number of equilibrium positions from a limited number of elementary convergent force fields. It remains to be seen whether such findings also apply to mammalian systems and how feedback and feedforward controls might be distributed in such segmental centers.

## Feedback and feedforward contributions to the accuracy of simple movements

It is well established that muscle and joint proprioceptors contribute to accurate movement by providing input to feedback and reflex mechanisms controlling joint position [34]. Recent studies, however, have also proposed that proprioceptive information can function in the following more complex ways: first, by providing information about initial conditions; second, by updating internal 'models' of the limb; and third, by contributing to the control of interjoint coordination.

### Roles of proprioception in motor planning

Soechting and co-workers [35] have hypothesized that proprioceptive input plays a crucial role in the sensorimotor transformations of reaching by providing information about the initial position of the limb. They envisage limb kinematics to be specified on the basis of a motor error signal derived by comparison of the intended final segment angles with kinesthetically derived information about the initial angles. They found, however, that subjects are unable to synthesize a precise representation of the position of the finger from kinesthetic information [36], but that segment angles are more accurately matched [10]. Nevertheless, there is still no direct evidence that a distinct motor error signal is computed online to drive trajectory control mechanisms.

Inferences about the contributions of proprioception to motor planning can, however, be drawn from the reaching errors observed in patients with large-fiber sensory neuropathy, who do not receive proprioceptive information from their limbs [25••]. In addition to persistently large variable errors, these patients show remarkable systematic errors in the extent and direction of rapid targeted movements when they cannot see their arm. The extent errors, which vary systematically with the direction of movement, can be explained [25••] by a failure in the patients to compensate for the normal anisotropy in the inertial field of the arm [37]. Insight into how proprioceptive information functions in movement planning has been obtained by allowing patients to view their performing limb on alternate trials; inertial errors were dramatically improved both on trials with and without vision of the arm. This improvement must therefore have occurred through feedforward, and not through feedback mechanisms. The authors propose that both vision and proprioception function indirectly by updating an internal representation of the limb used to program the movement [25••]. Interestingly, the prominent directional errors (with resulting 'motor scotomas') of deafferented patients were only modestly improved by vision, suggesting additional roles for proprioceptive input in the regulation of multi-joint trajectories (see below).

### Feedforward control of reflex action during movement

The perspective on the role of reflex feedback in the regulation of movement is also undergoing considerable

change. Until recently, responses to proprioceptive inputs were thought to be fundamentally organized as reciprocal reflexes, principally focused on those muscles acting at the joint where the perturbing stimulus was applied. Recent work, however, reveals a much richer picture [38], indicating that even low level responses depend on behavioral context and may also be organized according to internal models of the limb. Lacquaniti and co-workers [39••] have studied stretch reflexes evoked in elbow muscles while subjects prepare for and catch a falling ball. Instead of the usual reciprocal activation of stretched muscles and inhibition of shortened muscles, perturbing stimuli applied during the 60 ms prior to ball impact evoked muscle coactivation [39••]. This change in reflex organization increases the mechanical impedance (stiffness and viscosity) of the limb. Interestingly, as this change in reflex pattern is timed with high precision to occur just before impact with the ball, it reflects a feedforward process that requires accurate models of both the ball's trajectory and the state of the limb.

A fundamental problem in controlling movement of a multi-segment limb derives from interaction torques produced at each joint by movement at all other joints [40]. Recent work indicates that a key aspect of motor planning is to take account of these torques. Thus, for example, wrist movements produce torques at the elbow that, if the forearm is to remain steady, must be counteracted by prior contraction of elbow muscles. As shown by Aoki [41•], the organization of muscle synergies depends on the direction of motion of the limb segment and not on the activation of specific muscles that act as prime movers. For example, when the wrist is supinated, voluntary wrist extension (downward motion of the hand) is preceded by contraction of elbow extensors. When the wrist is pronated, the same elbow extensor activation is programmed to occur in advance of wrist flexion (also producing downward motion of the hand).

The response to a perturbation also extends beyond the joint or segment where it is applied to produce contraction of muscles that are not themselves stretched. Interestingly, Koshland *et al.* [42••] have shown that the organization of this remote evoked activity closely mimics the pattern of activation associated with contraction of the same prime agonists during voluntary movements. Thus, with voluntary flexion of the elbow, there is prior activation of wrist flexors that counteracts the tendency for the wrist to extend because of movement of the forearm segment. Similarly, when the elbow flexors are reflexively activated by a perturbation there is also contraction of wrist flexors. This occurs even though the wrist muscles are not stretched by the stimulus. The coupling of elbow and wrist flexors is thus used to counter inertial effects that occur during unrestricted voluntary movement. In accord with this suggestion, studies of joint kinematics during cyclical arm gestures indicate that, in a patient rendered proprioceptively deafferented by large-fiber sensory neuropathy, there are prominent, uncontrolled inertial interactions at distal joints (RL Sainburg, HCG Poizner and C Ghez, *Soc Neurosci Abstr* 1991, 17:1386).







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