

**The Hierarchical Control  
of Skilled Hand Movements**

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## ABSTRACT

This report explores the neurophysiology of *motor schemas* and the neural mechanisms through which concurrent and sequential motor schema activations are interwoven to produce complex, skilled movements. Following Arbib's schema theory [2][3][4], which characterizes motor schemas as the competitive control structures for submovements in a task, motor schemas are hypothesized here as characteristic patterns of sensorimotor neural activity corresponding to simple, prototypical movements and configurations. These elementary "building blocks" of motor behavior combine to generate all skilled movements. The hierarchical and componential aspects of motor control are discussed with respect to grasping movements of the hand, whose "prototypical" kinematic nature is analyzed briefly. We then discuss neural mechanisms which could allow a *coordinated control program* ([2][3][4]) to regulate the flow of sensorimotor information to and among the motor schemas, thereby interweaving their activations in accordance with the current task and sensory environment. Finally, these regulatory mechanisms are incorporated into a simple mathematical model of motor schema competition, in which the excitatory and inhibitory interaction between motor schemas is formalized as a relaxation process, regulated by the currently active coordinated control programs.

## 1 Introduction

All skilled movements, however complex, are composed essentially of various combinations and sequences of a limited number of elementary "building blocks" of motor behavior. These *functional synergies* innervate diverse musculatures across several limbs, treating adjacent limbs as single functional units. Extending Bernstein's [5] view that multilimbed movements pass through "typical" kinematic configurations, this report speculates that each functional synergy could be associated with a "preferred posture", a characteristic configuration which the functional synergy, acting alone, would establish. It is through the superimposition of several concurrently active functional synergies that the unique, complex trajectories of movement we commonly observe are generated.

Arbib [2][3] characterizes the sensorimotor control structure for a functional synergy as a *motor schema*. In terms of its neural representation, a motor schema is thought to correspond to a "characteristic pattern of neural activity" [2]. Each motor schema's degree of participation in a motor act depends on its *activation level*, which reflects the schema's "perceived" suitability to the current sensory environment, given the task circumstances. Motor schemas *compete* for a role in each task, exciting or inhibiting each other according to their compatibility or incompatibility. The relative autonomy of a motor schema accounts for the motor system's flexible adaptability to new or unexpected situations encountered in the course of a skilled action. Unexpected events (eg, a collision) in the course of a movement will give rise to the self-induced activation of precisely those schemas which deem themselves suitable to those unpredicted conditions.

A motor schema's autonomy is not absolute, however, since its response to the environment must somehow account for the current needs and goals of the individual. In this light, Arbib [2] posits that a *coordinated control program* (CCP) imposes a hierarchically-organized temporal structure on the activity of motor schemas, "interweaving" their concurrent and sequential activations to achieve the individual's goals. This report attempts to characterize motor schemas and CCPs, both in terms of their neural correlates, and through a formal treatment of the processes by which sim-

ple and complex movements may be selected in response to the sensory and task environment. Motor schemas and CCPs shall be characterized as the recognition structures for simple and complex movements, respectively. Whereas motor schema activations are sensory-driven, occurring primarily in response to tactile information from the periphery, CCP activations are largely task-driven, reflecting the intention-related goals of the individual and the physical and functional requirements of the task.

The realm of human prehensile behavior is an exciting domain for the schema-theoretic analysis of movement, since hand movements are highly skilled and dextrous, owing to the hands' prominent representation in sensorimotor cortex. Human grasping movements may be analyzed in terms of the temporal phases involved in the reaching and grasping components [4][29], as well as in terms of the actual functional synergies involved, which serve as the essential primitives in any skilled movement sequence. Arbib's CCP for reaching and grasping [2][3] (see figure 1) illustrates the high-level channelling of pertinent sensory information to the control structures responsible for different submovements. Subschemas for finger adjustment and hand rotation, movements which precede the actual grasping of the object, receive visual and proprioceptive information necessary for their respective sensorimotor transformations. A major focus of this report will be the CCP's role in channelling such sensory and task-parametric information to its subordinate schemas, and the CCP's mediation of the competitive process by which motor schemas activate.

We begin in section 2 with a brief review of the neurophysiology of movement, focusing on the functional significance of a few sensorimotor structures in the brain, with emphasis on the roles they may have in supporting motor schema and CCP activity. Section 3 discusses the hierarchical nature of motor control, and the role of the CCP in channelling sensorimotor information to and among its subordinate structures. Section 4 discusses the role of motor schemas and CCPs in human grasping movements. In section 5, a simple mathematical model of motor schema competition is presented, in which the selection of simple movements is viewed as a constraint relaxation process. Finally, in section 6, we review the issues involved in attempts to characterize the process of mapping a set

of grasping task requirements to an appropriate hand configuration.

## 2 The Neurophysiology of Motor Schemas

This section presents an overview of modern motor neurophysiology, with special emphasis on the functional roles played by certain brain structures in the support of schema activity. Although this review involves some speculative claims as to the schema-theoretic functions of some structures, we must avoid assuming that motor schema or CCP activity can be strictly localized to any restricted site in the brain. Rather, the neural activity associated with a single schema is probably distributed across many regions and layers in the brain, and this has contributed to the difficulty in experimentally establishing the existence of motor schemas. Moreover, any two schemas' characteristic patterns of activity may overlap topographically, so we must take care not to invoke a strictly spatial framework when envisioning conceptually the excitatory and inhibitory interactions among an assemblage of motor schemas.

### 2.1 Primary motor cortex and the pyramidal tract

The principle site of output from the cerebral cortex to the motoneurons of the spinal cord is the *primary motor cortex* (MI), located in the precentral gyrus, or area 4 of Brodmann (see figure 2). MI, like other cortical areas, consists of six layers of neurons. Each layer has a distinctive neuronal population, and the layers can be classified according to the efferents and afferents to and from specific subcortical structures, as well as other regions of cortex.

*Pyramidal tract neurons* (PTNs), neurons whose axons pass through the medullary pyramids, arise in layer V of MI and synapse on the alpha and gamma motoneurons, and on some interneurons, in the spinal cord. PTN spinal projections diverge, so a single PTN may innervate more than a single muscle [16]. Some PTNs in MI project to alpha motoneurons, which innervate extrafusal muscle fibers, the main source of muscle power.

Figure 1. Arbib's CCP for reaching and grasping (from [2])

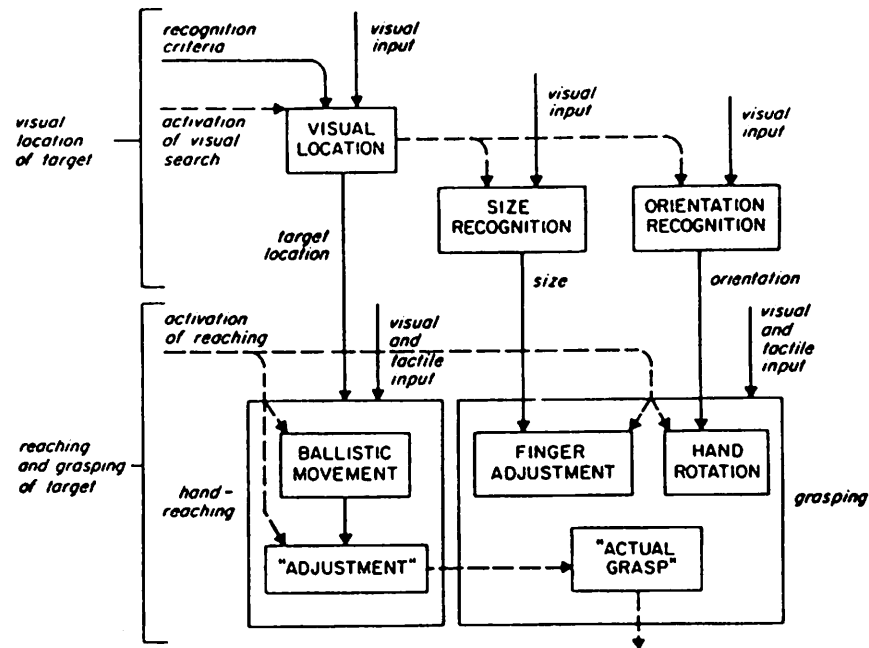
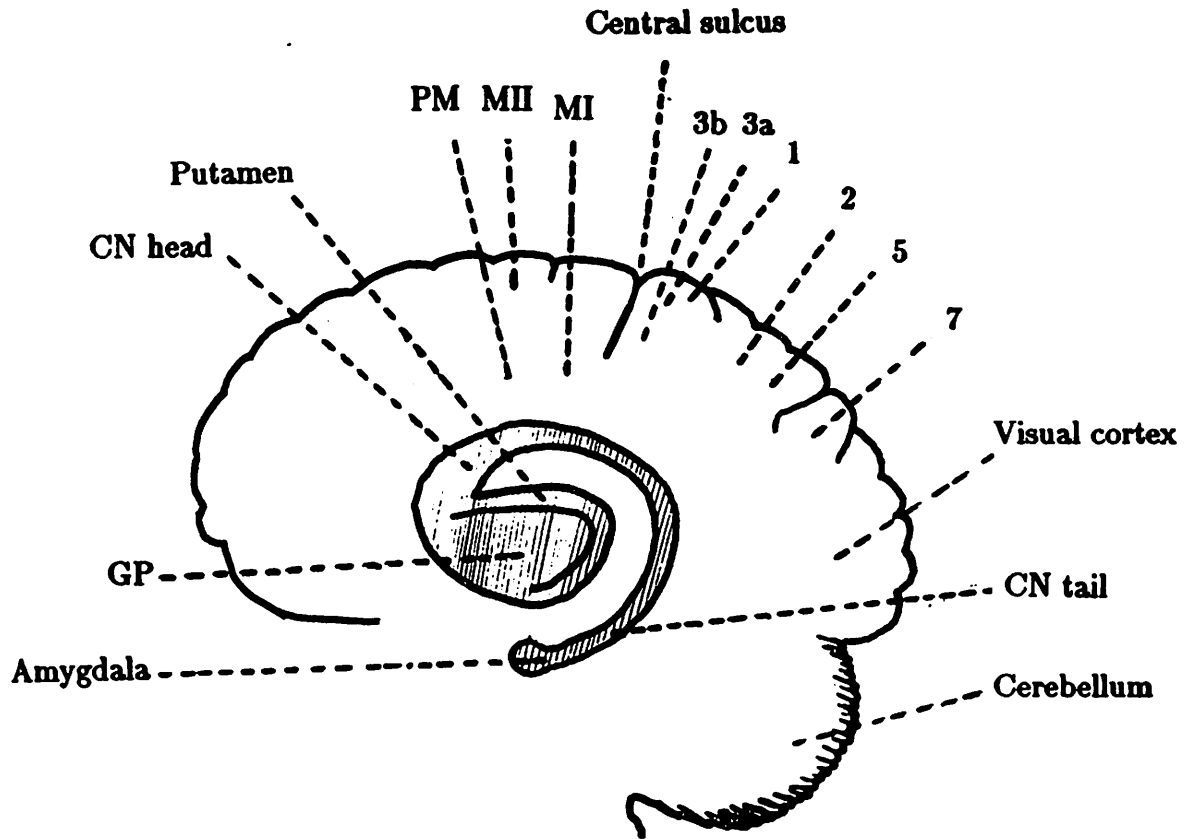


Figure 2. The sensorimotor brain



Other PTNs synapse on gamma motoneurons, which innervate intra-fusal muscle fibers, which contribute to a feedback system, whereby a movement can be corrected "on line" if unexpected resistance hinders the limb's trajectory.

MI is topographically organized, with respect to the musculature it innervates. In the early 1950s, Penfield [49] and his associates mapped MI in terms of the locations of muscles activated by stimulating different zones of cortex. The "motor homunculus" of figure 3 illustrates MI's topography. In addition to the laminar and topographical organization of MI, the cells of MI and other cortical areas are arranged in *columns*, which pass vertically through the six cortical layers. Due to abundant vertical projections interconnecting the cells of a column, the firing rates of neurons in a column are fairly interdependent. The column, therefore, is considered the basic functional unit in cortical processing. Axonal projections from the ventrolateral (VL) thalamus synapse on neurons in layers II, III and IV of MI (see [17] for a review). These thalamic afferents convey information from the cerebellum, a brainstem structure concerned with the execution of rapid, ballistic movements. Thalamic modulation of MI is "sharpened" by interneuronal inhibition among cortical columns.

Georgopoulos *et al* [22][23] observed in 1982 that many movement-related PTNs in MI have a "preferred direction" of limb displacement. According to their *vector hypothesis*, each PTN "casts a vote" for the direction of movement, weighted by the cell's firing rate. If each PTN is represented as a vector with a direction the same as the PTN's preferred direction and a magnitude equivalent to the PTN's departure (plus or minus) from its resting firing rate, the direction of limb displacement is indicated by the weighted sum of the PTNs' preferred directions. This directional organization of MI, superimposed on the topographical organization, points to the distributed nature of motor control: cutaneous, proprioceptive, visual, and motor afferents from various sensory and motor structures converge on MI, where their "votes" are tallied to yield the resulting movement. We might consider MI to be a site of mediation between different factions in the sensorimotor apparatus.

It follows from the observations by Penfield and Georgopoulos that the

type of movement executed is determined largely by the topographical pattern of neural activity in MI. If, as discussed in the introduction, all movements can be described as combinations of a finite number of discrete, simple movements called "functional synergies", then perhaps the neural activity in MI, if examined closely enough, will display characteristic neural activity patterns, each corresponding to a distinct functional synergy. Such prototype patterns, if they exist, would represent MI's portion of the "characteristic patterns of neural activity" which Arbib posited were the neural correlates of motor schemas. The cohesiveness and regularity of each pattern might be maintained by excitatory interneuronal communication, and inhibitory interneuronal communication would help to maintain a topographical pattern's distinct boundaries.

In addition, interneuronal inhibition would serve as the messenger of suppression between patterns which overlap topographically, ensuring the emergence of the distinct, unambiguous patterns in MI's neural activity. Regulation of such interneuronal communication by the higher motor centers could enable the motor system to relax the degree of mutual exclusion among overlapping or nonoverlapping patterns, making possible the blending, when desired, of several functional synergies. Didday [14] demonstrated how such a suppressive mechanism could account for the mutual exclusion of neuronal activity in different topographical regions of a frog's superior colliculus, allowing the frog to select (usually) one fly, from among many in its visual field, at which to snap. MI, which has topographical characteristics somewhat similar to the superior colliculus' retinotopy, could also be the site of such a lateral-suppressive mechanism, albeit involving fixed, *prototypical* patterns of neural activity corresponding to motor schemas for the basic movement primitives.

## 2.2 Motor set in MI

As argued above, MI could be one site of competitive motor schema interactions. The activation of a motor schema, i.e., the emergence of its characteristic, topographical activity pattern in MI, would give rise to the immediate execution of the corresponding functional synergy. Arbib [2][3]



has suggested that CCPs interweave the concurrent and sequential activations of motor schemas to bring about the required combination of sub-movements in a skilled motor act. The coordinated interweaving of motor schema activations might be enforced through the neural mechanism of *motor set*, which we now examine.

In 1976, Evarts and Tanji [17][18] monitored premovement neural activity in the primary motor cortex of monkeys. They found evidence that sensory information is selectively gated to pyramidal tract neurons (PTNs), depending on the premovement signals from *set cells*, which relay the current intention of the animal to primary motor cortex. The set cells, located perhaps in area 6, a high-level motor center, are able to facilitate or block, depending on the desired movement, sensory input to primary motor cortex regions concerned with specific movements. An example of this neural gating mechanism is illustrated in figure 4: when set cell A is highly active, it stimulates an inhibitory neuron which mediates the flow of tactile information (from somatosensory cortex) to the arm flexor PTN. Since sensory input to the arm extensor PTN remains unchecked, a tactile stimulus will produce an arm extension. On the other hand, if set cell A is dormant and set cell B is active, the arm extensor PTN's access to the sensory input will be blocked, leaving the arm flexor PTN's input open, and a tactile signal will trigger an arm flexion.

As one might imagine, the higher motor centers' ability to regulate the flow of various sources of sensory information to different regions in primary motor cortex is a powerful means by which to effect a desired movement. The contention of the present report is that the higher motor centers mediate the activity of motor schemas through the regulation of sensory information to each motor schema's neural representation. Through the same neural gating mechanism, the higher motor centers might also regulate the excitatory or inhibitory communication flow *among* motor schemas. This would make mutual exclusivity among various motor schemas' activations possible, to any desired degree (for instance, if the simultaneous activity of two given motor schemas is undesirable, the higher motor centers can establish lines of inhibitory communication between the two schemas' activity patterns, so that if one schema activates, the other will be suppressed).

Therefore, the higher motor centers may "implement" a CCP simply by imposing the correct motor set on intermediate motor structures such as MI, through the mechanism of neural gating.

To illustrate various aspects of administrative control which would be afforded to the higher motor centers by their ability to establish arbitrary motor sets in MI, let us consider four facilitations that the utilization of neural gating would provide as a means of enforcing an orderly sequence of submovement executions:

(1) The selective denial of topographically-relevant PTNs' access to different sources of sensory input (recall figure 4) could enable the higher motor centers to establish loops between sensory trigger stimuli and arbitrary functional synergies, as in the *long latency reflex* [15][40][41] and the intention-related *grasping reflex* [64]. Hence, the higher motor centers can "program" reflexes, as needed.

(2) The mutual exclusion of any given pair of motor schema activations could be "implemented" by setting up, via neural gating, symmetric lines of communication between the sites of the schemas' topographical patterns of activity. Conversely, schemas can be made to "cooperate" by establishing lines of excitatory communication (or by blocking lines of inhibitory communication) between their patterns. If the motor schemas' characteristic patterns overlap, this cooperation would lead to a blending of the sites of two patterns, to form a composite pattern and movement. In this case, the blending of the two prototypical movements would take place in MI. If, on the other hand, two schemas' patterns are topographically distinct, the blending of movements will take place at the periphery.

(3) If asymmetric, one-way lines of inhibitory communication are set up between two motor schemas' patterns of activity, the recipient schema will be inhibited whenever the other is activated. Thus, the higher motor centers could enforce the sequential ordering of any pair of submovements by priming their schemas for activate and by establishing an asymmetric channel of inhibitory communication between them.

Figure 3. The motor homunculus (from [7])

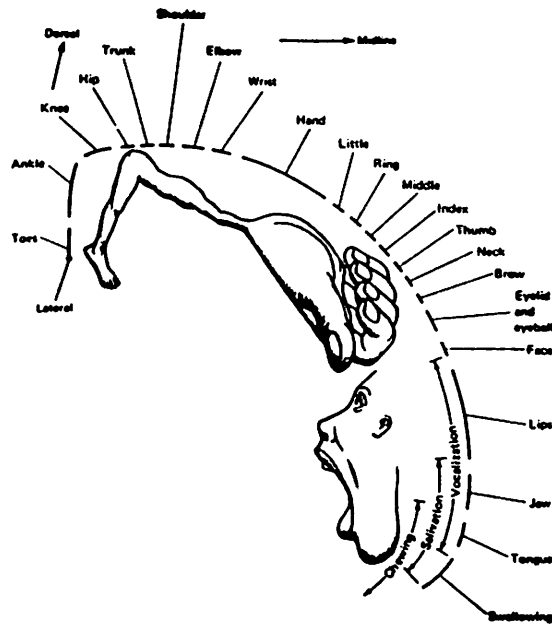
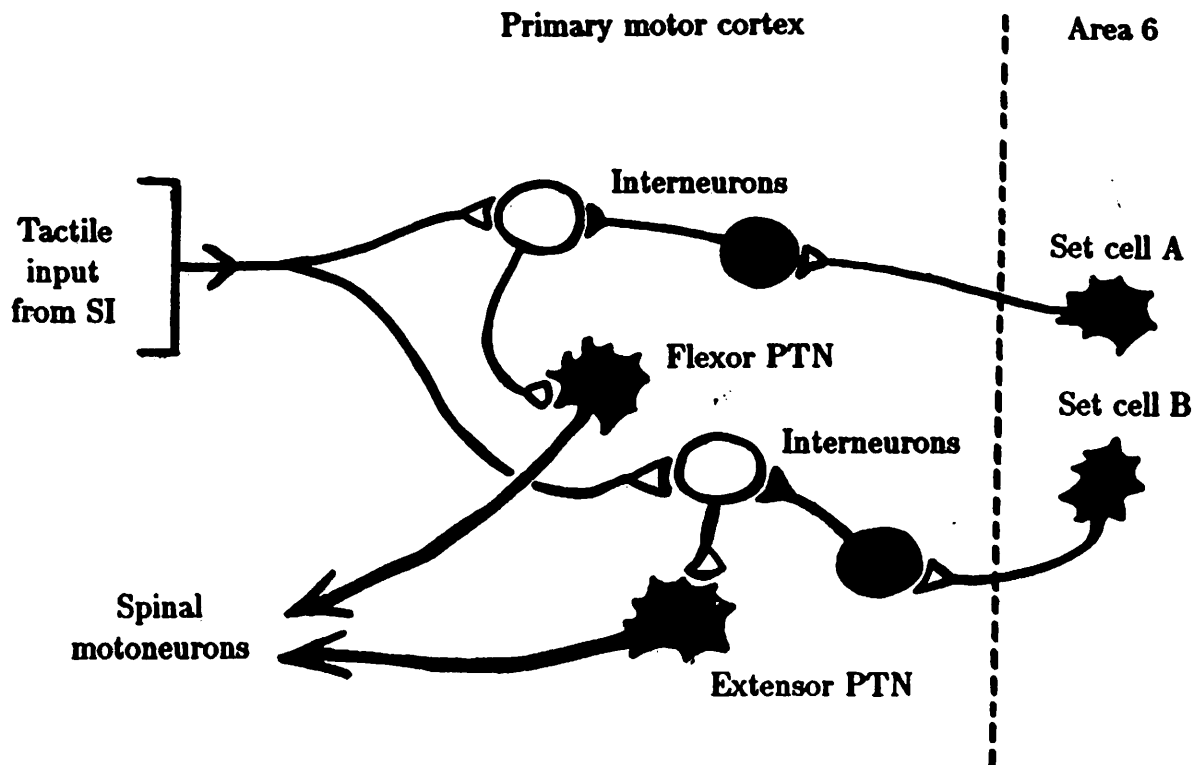


Figure 4. Neural gating in motor cortex



(4) The higher motor centers will be in a position to leave much of the decision making regarding movement selection to the intermediate motor structures, such as MI, effectively easing the planning burden of the former: The priming of a chosen set of motor schemas, either through direct neural excitation of PTNs or by the gating of sensory stimuli to PTNs, coupled with the establishment of inhibitory lines of communication among those motor schemas (to ensure that only one schema activates, as in (2), above), the higher motor centers may initiate competition between a set of "favored" motor schemas, leaving the final decision to the intermediate motor level. This scheme effectively distributes the processing of sensorimotor information through the motor hierarchy, allowing efficient use of resources, through parallelism.

It should now be apparent that the interweaving of motor schema activations can be accomplished through various neural gating tactics involving the temporary establishment of excitatory or inhibitory communication channels to and among the topographical patterns of neural activity corresponding to different motor schemas. In section 5, we will present a simple mathematical model of the competitive process of motor schema interaction that takes place in the communication flow "environment" of a given motor set, and show how complex movement sequences can evolve out of that competitive framework.

### 2.3 Area 6 and the basal ganglia

Area 6 of cortex is a higher motor center, whose activity is associated with the execution of complex movement sequences. Comprised in part of the *premotor area* (PM) and the *supplementary motor area* (SMA or MII), area 6 may contain the set cells responsible for the motor set of MI [15][67]. MII occupies the medial part of area 6, and PM is situated more laterally, just in front of MI (see figure 2). Both areas are topographically organized, but with less clarity than in MI [50]. For example, the arm and hand areas of area 6 overlap, so some cells activate the musculature of both the arm and the hand. Stimulation of area 6 evokes complex movements and movement sequences [6][9][48][50].

Since area 6 is viewed as a higher motor center, its influence over the motor set of MI, to which it sends numerous axonal projections, could empower area 6 to interweave the activations of motor schemas, via the four facilitations outlined above. We might therefore relate area 6 activity to the recall and execution of CCPs for skilled movement sequences. Prior to a movement sequence, area 6 set cells would establish the excitatory and inhibitory lines of communication in MI, and other intermediate motor structures, necessary to effect this interweaving of submovements. Premovement neural activity has indeed been observed in area 6 [24][53][62][63]. Such activity could represent the activation of CCPs that will take part in the task. Such CCP activity would include the increased activity of area 6 set cells whose axons convey to MI the establishment of the correct motor set for interweaving the activations of motor schemas, as prescribed by the skills which the CCPs represent. Moreover, area 6 may support the competitive environment in which CCPs vie for participation in a task, similar to the motor schema competition taking place in MI.

Roland *et al* [53] support the position that area 6 is a site at which learned skills are selected and recalled from long-term motor memory. The process of selecting a learned skill (a practiced sequence of simple or complex movements) to meet the demands of a task requires task-descriptive, musculature-independent information. A prehensile task, for example, might consist of an object description, including physical and functional characteristics which will aid in the selection of a grasp, plus a manipulation component (what to do with the grasped object). This task description will lead to the selection of a manipulative skill, as well as influence the original choice of grasp [43]. It appears that area 6 is supplied with such task-related information by the *basal ganglia*, motor structures located beneath the limbic cortex.

The basal ganglia include the *caudate nucleus* (CN), the *putamen*, and the *globus pallidus* (GP), among other structures (see figure 2). The basal ganglia participate in the high-level planning of motor acts [47]. With motivational drive and priorities supplied by the limbic system and hypothalamus, the basal ganglia formulate goals and choose strategies for achieving those goals. Committing the organism to a mode of behavior, such as

feeding, the basal ganglia communicate the task-related goals (orient to, approach, and consume some sighted food) and parameters (location of the food) to the motor systems which, in turn, select the appropriate motor programs and musculatures.

CN, in particular, appears to play a role in switching modes of behavior, given external, environmental stimuli and internal, motivational stimuli. Long and tubular in shape, CN receives afferents from diverse areas of association cortex. The anterior part of CN, the *head*, receives sensory information from the orbitofrontal cortex, where visual stimuli are evaluated in terms of reward and punishment experienced previously [31]. For example, food is distinguished from non-food, in this area. The head of CN also receives afferents from the dorsolateral frontal system, which is an area of cortex concerned with the spatial parameters of motor response [31]. Thus, the orbitofrontal system signals *when* to respond, and the dorsolateral frontal system indicates *where* to respond. The *tail* of CN receives projections from the inferior temporal lobe, which communicates the perception of novel stimuli, such as changes in the environment [56]. Neurons in that visual association area respond to particular colors and orientations and adapt rapidly, so that only new stimuli are passed to CN. Lesions in the CN of cats cause *obstinate progression*, whereby the cat displays excessive orientation to visual and auditory stimuli and compulsively approaches the stimuli. The tail of CN may therefore have a role in orienting the animal to, and initiating action towards, new visual stimuli. In sum, CN's general function may be to initiate interaction of the animal with its environment.

Arbib's CCP for reaching and grasping, shown in figure 1, includes perceptual schemas for visually determining the location and orientation of the object to be grasped. In light of the CN head's concern with object location, and the tail's response to orientation information, we might therefore suggest that these CN structures partially comprise the neural substrates for those perceptual schemas.

The *substantia nigra* (SN), a structure in the tegmentum, which neighbors the basal ganglia, has an intimate functional relationship with the basal ganglia. The *pars compacta* (SNC) modulates CN and the putamen with diffuse, dopaminergic input, which presynaptically inhibits cholinergic

activity in those basal ganglia structures [44]. Another division of SN, *pars reticula* (SNR), serves as an output structure for the basal ganglia, together with GP. SNR and GP both send task-related information, input from CN and the putamen, to area 6 and prefrontal cortex, via VA- and VL-thalamic relay. As Rolls [55][56] recently suggested, SNC might modulate CN to respond to food-like stimuli according to the hunger state of the animal. More generally, SNC may input internal priorities (eg, hunger, thirst, aggression) from the hypothalamus and limbic system and diffusely modulate selective regions of CN accordingly, to influence CN's decision to switch behavioral modes. CN therefore appears to "judge" whether or not the motor systems should respond to cortically-conveyed, environmental events, given the animal's internal, motivational inclinations, communicated via SNC.

The putamen and GP appear to have a role in specifying or adjusting task parameters. The putamen receives input from SI, MI, MII, PM and area 5. Projections from corresponding topographical regions in different areas of sensorimotor cortex converge in the putamen, leaving the topography intact. For instance, the arm regions in each sensorimotor area project to the same zone in the putamen [12]. DeLong *et al* [12] recently monitored discharge rates of basal ganglial neurons in active monkeys. They observed that cells in the putamen and the part of GP to which the putamen projects tend to discharge in relation to the direction of movement, per se, irrespective of the musculature used. Putamen cells have also been found whose activity relates linearly to the static force of a grip [10]. Some GP cells' discharge rates are also related to the amplitude of a movement [12]. DeLong *et al* [12] suggest that Parkinsonian patients fall short of a target during a reaching movement because of inappropriate amplitude specifications by GP.

The basal ganglia, in consort with the intermediate cerebellum [37], regulate joint stiffness, through the cocontraction of agonist/antagonist muscle pairs. The ancient stiffness mechanisms of the basal ganglia and extrapyramidal tracts enable us to temporarily "freeze out" unneeded degrees of freedom [5]. Finger and wrist movements, for example, are often facilitated by freezing out movements of the arm and shoulder. Parkinsonian patients sometimes experience unchecked stiffness, due to inadequate dopaminergic

regulation of the basal ganglia by SCN.

Taken together, the above considerations suggest that the putamen and GP supply and monitor some of the parameters of movement (direction, force, amplitude, stiffness) and issue corrections to the motor systems, based on feedback from sensorimotor cortex. The basal ganglia send their task-related information to area 6 (among other destinations), via VA- and VL-thalamic relay. This task information, together with sensory input from the parietal lobe, could serve as criteria for the selection and recall of skilled movements, as accomplished through CCP competition.

## 2.4 Other sensorimotor structures

Although this report's neurophysiological arguments focus on the roles of MI, area 6 and the basal ganglia, it must not be inferred that the other sensorimotor structures are of any less importance in the organization and control of movement. We shall review their functions, briefly.

Located in the anterior parietal lobe, *somatosensory cortex* (SI) is the primary cortical center for the processing of tactile information. SI consists of Brodmann areas 1, 2, and 3 (see figure 2). Each area of SI is characterized by its own sensory mode and/or perceptual processing capacity. Area 3a, the most anterior area of SI, processes proprioceptive information from the joints and muscle spindles. This area projects to the non-cutaneous region of MI, providing feedback necessary for the precise positioning of the joints. Area 3b neurons respond exclusively to cutaneous stimuli and project to area 1, where further processing yields information concerning object texture [52]. Texture analysis in area 1 entails the monitoring of skin vibration induced by rubbing the glabrous skin, especially that of the fingertips, over the surface of an object. The frequency of vibration, detected by Pacinian and Meissner's corpuscles in and beneath the skin, depends on the fineness of texture and the speed of the exploratory movement [11]. Area 1 apparently compares the vibratory frequency, supplied by area 3b, with the speed of movement, provided by area 3a, to compute the fineness of texture.



The highest level of processing in SI takes place in area 2. Projections from other areas of SI converge there, resulting in large receptive fields, spanning several fingers, for many area 2 neurons. Some neurons respond selectively to the direction of a stimulus during exploratory touch [11]. Other cells respond to specific surface orientations. Roughness, another aspect of texture, is also analyzed in area 2 [11], as analysis of roughness involves the measurement of surface orientations. In 1978, Iwamura and Tanaka [28] found evidence of edge-detecting neurons in area 2 of monkeys' cortex. These cells responded to stimulation of sufficiently narrow and properly oriented regions in their receptive fields. Area 2 apparently participates in the lower levels of object classification by extracting such features as size and shape. Object classification continues in association areas.

SI projects to area 5 (see figure 1), where the spatial relationship of the hand relative to object surfaces is analyzed. Such analysis is important for the tactile guidance of hand movements. Area 7 performs the visual analog to area 5's function, assisting in the visual guidance of the hand and fingers, relative to an object's surface. Roland *et al* [54] suggest that areas 5 and 7 translate proprioceptively- and retinotopically-referenced hand-object relationships, respectively, into extrapersonal space coordinates, in order to allow the motor apparatus of MI and area 6 to make corrective use of that information. Referring again to the CCP in figure 1, the visual analysis of a graspable object's size probably involves area 7 activity, where the retinotopically-coded spatial relationship between hand and object might be translated into the motor signals for finger adjustment.

The *cerebellum*, or "little brain", plays an important role in the control of movement. Located in the dorsal brainstem (see figure 2), the cerebellum consists of the *cerebellar hemispheres*, or *neocerebellum*, the *pars intermedia*, or *paleocerebellum*, and the *archicerebellum*. We shall discuss only the *neocerebellum* here.

The *neocerebellum* receives afferents from most of sensorimotor cortex, but especially from area 6. The *neocerebellum* outputs to the dentate nucleus (DE) which, in turn, modulates MI via ventrolateral (VL) thalamic relay. In 1970, Kornhuber [34] proposed that the *neocerebellum* acts as

a “ballistic clock”, which converts spatial information (where to move the arm) into temporal quantities indicating the length of each muscle burst. Area 7, discussed earlier, provides the visual information, translated from retinotopic coordinates to extrapersonal coordinates, that describes the spatial relationship of the the upper limb relative to external objects. In Kornhuber’s view, this spatial description of the movement is converted to a specification of synergies by the neocerebellum, which then disinhibits the topographically relevant regions of DE to activate the desired synergies via VL modulation of MI. This disinhibition of DE lasts for a precisely-timed instant, yielding a muscle burst of the correct duration which ends when the neocerebellum, like a speedy hourglass, returns to its resting state and resumes its inhibition of DE. Many mathematical models have been proposed regarding the neocerebellum’s mysterious role in facilitating the kinetic control of movement (see [61] for a review).

### 3 Schema Hierarchies

Based on the view that all motor behavior consists ultimately of a limited set of functional synergies [5], and on Arbib’s schema theory [2][3][4], this report posits that motor schemas for simple, prototypical movements serve as the elementary building blocks in the motor system’s organization of motor acts in general. These essential building blocks are combined, through the organizational facilities of motor set, to form the sequences of simple or complex movements which comprise learned skills. Complex movements, in turn, may be combined to form actions of ever-increasing complexity. We might envision the motor hierarchy as a directed graph structure, with CCPs for complex skills parenting low-level CCPs and motor schemas (a tree structure would be an imprecise characterization, since each motor schema (leaf) may have several parents (CCPs)). Each CCP has a characteristic pattern of neural activity which involves the imposition of motor set on the neural structures subordinate to the CCP, effectively interweaving the activations of “child” CCPs, and ultimately, motor schemas.

The present report’s suggestion that motor schemas are the control structures for the simplest, *indivisible* units of movement (functional syn-

ergies), from which all motor behavior is "pieced together" through the organizational framework of a CCP hierarchy, is reminiscent of the scheme by which humans are believed to organize categories of objects. Innate primitives, such as parts of the body and generic shapes, are treated as object primitives which are combined conceptually to form complex object categories. Arguments by Fetz [19] that the motor system operates in a very similar manner to the perceptual system lend credibility to the above analogy.

An important distinction between the hierarchical organization of motor activity and the perceptual organization of complex object categories, of course, is the temporal-sequential nature of a skilled action, as opposed to the comparatively (!) static nature of hierarchical object recognition. A skill's motor hierarchy unfolds in the course of its submovements, instead of "all at once", during the preparatory phase. Indeed, during the execution of movement sequences, the motor hierarchy is in a constant state of flux. MSs in the hierarchy do not activate until necessary, and each MS remains active only as long as necessary. There is now evidence, in fact, that neural activity corresponding to the upper echelons of the motor hierarchy subsides while lower structures remain active and carry out the actual movements:

In 1985, Tanji and Kurata [62] trained monkeys to perform key presses in response to different stimuli. In the *tactile mode*, an *instruction stimulus* (IS) warned the animal to perform a key press in response to a tactile *trigger stimulus* (TS) and to ignore an audio signal. In the *audio mode*, a different IS warned the animal to respond instead to an audio TS and to ignore a tactile signal. The experimenters recorded the activity of neurons in MI and area 6 during the trials. 128 neurons in area 6 responded to the IS, and of these, 44 responded with greater magnitude to one IS than the other (i.e., some neurons responded to the tactile IS but not the auditory IS, and vice-versa). All area 6 neurons that responded to an IS resumed normal activity when the TS that triggered the key press arrived. Thus the activity of neuronal populations associated with the high-level establishment of MI's motor set dissipated at the start of the movement's execution, their influence being no longer required. Neurons in primary motor cortex responded to the IS without preference to one IS or the other.

Figure 5 illustrates the schema hierarchy for a schema-theoretic interpretation of these results. In the trial situation, a TRIAL CCP activates (following Arbib's notion that motor schemas and CCPs can activate in response to the organism's goals and/or the environmental "situation") and opens channels of communication from the source of the anticipated tactile IS to the TACTILE CCP, and from the source of anticipated auditory IS to the AUDITORY CCP. In figure 5, arcs A and B represent the axons of set cells whose activity establishes the sensory communication pathways to the TACTILE and AUDITORY CCPs, respectively, via neural gating. Note that at this point, the active motor hierarchy for the task we are considering consists of only the TRIAL CCP, the other components not yet having been activated. If a tactile IS now occurs, the tactile input to the TACTILE CCP raises that CCP's activation level above its activation threshold, allowing the TACTILE CCP to open (via arc C) a pathway of communication from the source of the tactile TS to the KEY PRESS motor schemas. The latter schemas, upon receipt of the tactile TS, finally activate, producing the key press movement. The event of an auditory TS, in this case, would not evoke any movement, since the sensory source of the auditory TS has not been channelled to the motor schemas.

Alternatively, the event of an auditory IS activates the AUDITORY CCP, which establishes (via arc D) a pathway of communication from the auditory TS source to the KEY PRESS motor schemas. Now, the event of an auditory TS, but not a tactile TS, will lead to the activation of the KEY PRESS motor schemas, eliciting a key press response.

Continuing our schema-theoretic analysis of the Tanji-Kurata experimental data, the preferential responses of the area 6 neurons to one IS or the other are interpreted here as having been due to the separate CCPs (TACTILE and AUDITORY) that activated in response to the respective ISs. The nonpreferential nature of the primary motor cortex neurons to the different ISs follows from the fact that whichever CCP activated (TACTILE or AUDITORY), the anticipated TS was channelled to the same motor schemas.

Finally, we consider the evidence that CCPs deactivate in the course of movement execution. Recall that 128 area 6 neurons resumed normal

activity upon the arrival of the TS. Referring again to figure 5, this may be interpreted as follows: once the TS arrives and the motor schemas activate, the motor schemas suppress the parent CCP through inhibition (arc E), deactivating the CCP, which has fulfilled its role. This seemingly premature dissolution of the upper levels in the motor hierarchy, prior the completion of movement, corresponds to a phenomenon which many of the absent-minded individuals among us have experienced. When we approach a cluttered table with the intention to fetch one of the items, but forget at the last minute what object we were seeking, our hands might grope around the tabletop until they gravitate toward the "forgotten" object. Although the higher, more conscious levels in the motor hierarchy have moved on to other concerns (eg, planning future activities), the lower, more purely sensory-driven components of the hierarchy have remained active and succeed in responding to the sight of the object, as originally planned.

## 4 Human Grasping Movements

This report speculated earlier that the functional synergies which ultimately comprise all motor behavior exhibit characteristic movement trajectories to prototypical kinematic configurations. When the motor schema, the control structure for a functional synergy activates, the purity of the prototypical movement that follows is, of course, subject to the "distortive" effects caused by any other, concurrently executing functional synergy, so the prototypical nature of these basic components of movement may not be altogether obvious.

In the realm of grasping movements, an example of a functional synergy commonly observed is the extension of the wrist to the *position of function* (see figure 8), which normally accompanies a powerful grasping movement. The position of function, consisting of a 40-45 degree wrist extension together with a 20 degree ulnar deviation [20], is the wrist pose at which the extrinsic muscles of the hand are able to exert the most force. This functional synergy is presumably effected by establishing the proper balance between the extensor and flexor muscles of the wrist [33], and such a balance should be reflected in the characteristic pattern of neural activity

corresponding to the motor schema for this prototypical movement.

Another indivisible functional synergy associated with prehensile behavior is the *grasp reflex*, an innate, undifferentiated flexion of the thumb and fingers (excluding the thumb, in early infants). This reflex is often elicited in infants by applying tactile pressure to the palm [38][39]. As a baby's motor system develops, the grasping reflex is suppressed, and its release requires conscious intention, thereafter (as in the "sherry glass response" described in [64]). The supplementary motor area, in area 6, has been identified as the suppressor of this reflex [50]. The neural mechanism for executing an undifferentiated flexion of the fingers has been shown to be located in the *extrapyramidal system* [42], which, like MI, is subject to modulation by area 6 [13][26][35]. In terms of the schema-theoretic views presented in this paper, we must therefore allow that CCPs, associated with area 6 activity, interweave the activations of motor schemas represented not only in the pyramidal system (MI), but also in the extrapyramidal system. Moreover, evidence that differentiated finger movements are controlled by way of both the pyramidal and extrapyramidal motor systems [42] suggests that patterns of neural activity for such movements' motor schemas are distributed across those two motor systems.

Other functional synergies could include differentiated finger or thumb extension, in which the pair of interosseus muscles on either side of a digit's metacarpus act synergistically to extend the digits interphalangeal joints [66], and thumb flexion, involving an orderly sequence of thenar muscle contractions, from the lateral to the medial side [32].

Although hypothetical, these are the sort of simple, prototypical movements which could have distinct, characteristic patterns of neural activity in the intermediate motor structures controlling them. As brain scanning technology advances, such topographical patterns, if they exist, could be identified and matched to coincident movements by human subjects. Meanwhile, however, detailed single unit recordings of PTNs in the cortices of laboratory animals could be analyzed to isolate any recurring, topographical patterns showing characteristics related to specific, simple movements.

Figure 5. Schema hierarchy for the Tanji-Kurata Experiment

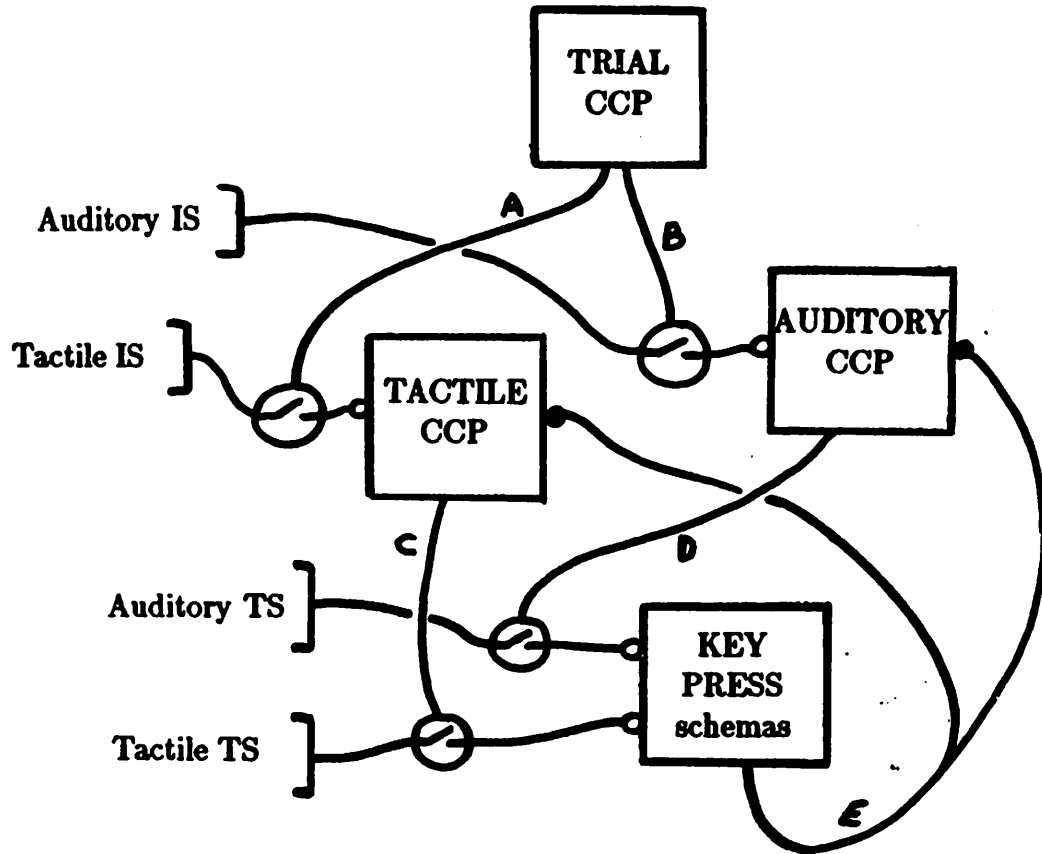
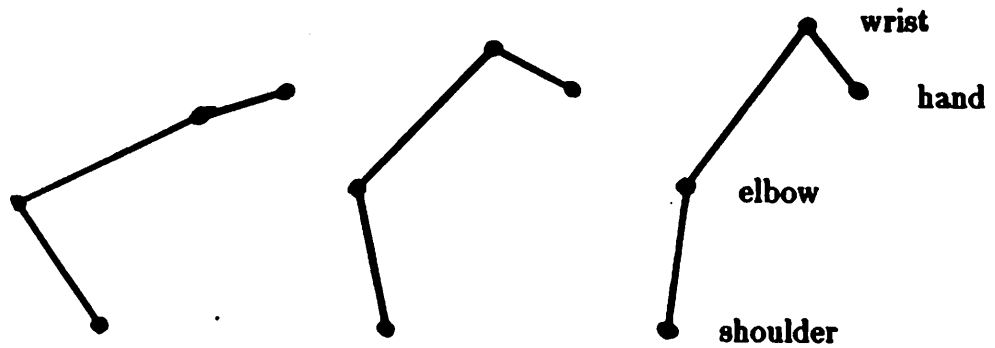


Figure 6. Kinematic indeterminacy of the upper limb



## 4.1 The pad grip: 2-D kinematics

Skilled movements, as well as simple, unskilled movements, often exhibit characteristic trajectories and relatively predictable final configurations. For example, when bringing a coffee cup toward the lips, we pass through a restricted sequence of kinematic configurations, relative to those which are possible. As shown in figure 6, the three degrees of freedom (in 2-D) that the wrist, elbow and shoulder provide allow for infinitely many choices of kinematic configurations through which the upper limb might pass, each yielding the same cup trajectory. Only a limited range within this kinematic space is chosen, however.

A similar phenomenon is observable in grasping movements. To illustrate the regularity in grasps, let us consider the 2-D kinematics of the *pad grip*, a special *precision grip* in which only the pads of one or more fingers and the thumb grip the object (see figure 16).

Borrowing the kinematic framework of Iberall [27] (see figure 7), we first fix the palm in its own coordinate system in the 2-D plane, with axes  $\mathbf{V}_p$  and  $\mathbf{V}_q$ , and discuss the configurations of the digits relative to the palm's frame. When considering points  $P_1$  and  $P_2$  on the thumb and index' pads, we need not consider separately the joint angles of the thumb and index (it turns out that, despite the three degrees of freedom apparently provided by a digit's three joints, the ligamentous and tendinous systems in fact reduce the degrees of freedom to two [60], and these degrees of freedom follow, in turn, directly from the given positions of  $P_1$  and  $P_2$ ). Let *centroid vector*  $\mathbf{V}_c$  define the centroid of a cylinder's cross-section, held in a pad grip. The *separation vector*  $\mathbf{V}_s$  passes from the thumb pad  $P_1$  through the centroid to the index pad  $p_2$ . Note that the magnitude of  $\mathbf{V}_s$  is just the cylinder's diameter, in this somewhat restricted pad grip.



Figure 7. 2-D kinematics of the pad grip (adapted from [27])

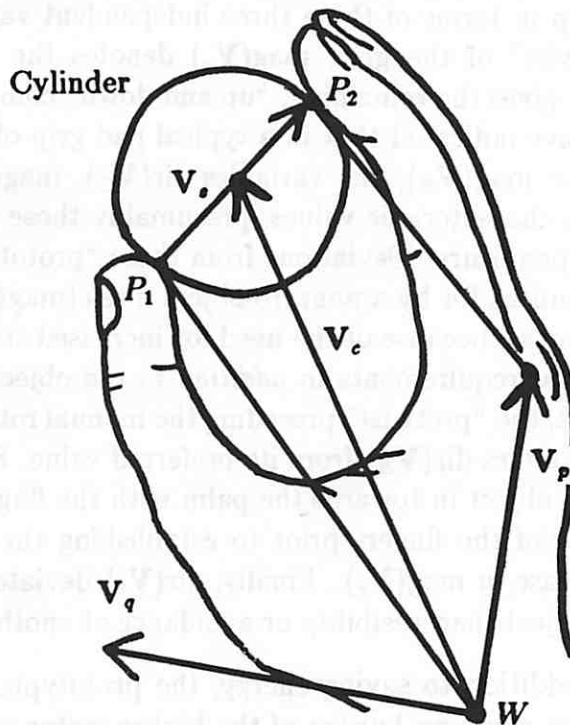
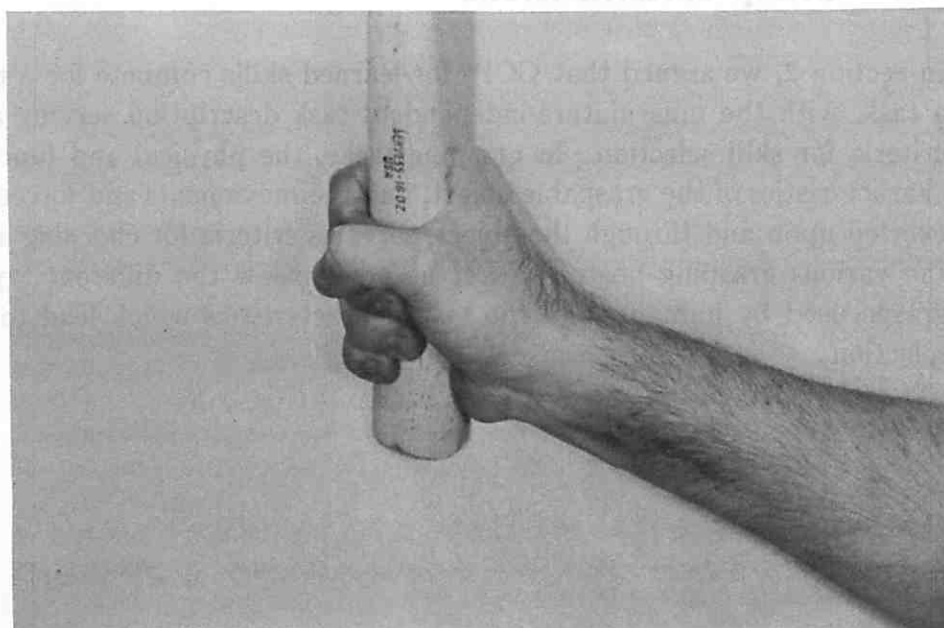


Figure 8. The power grip and the position of function



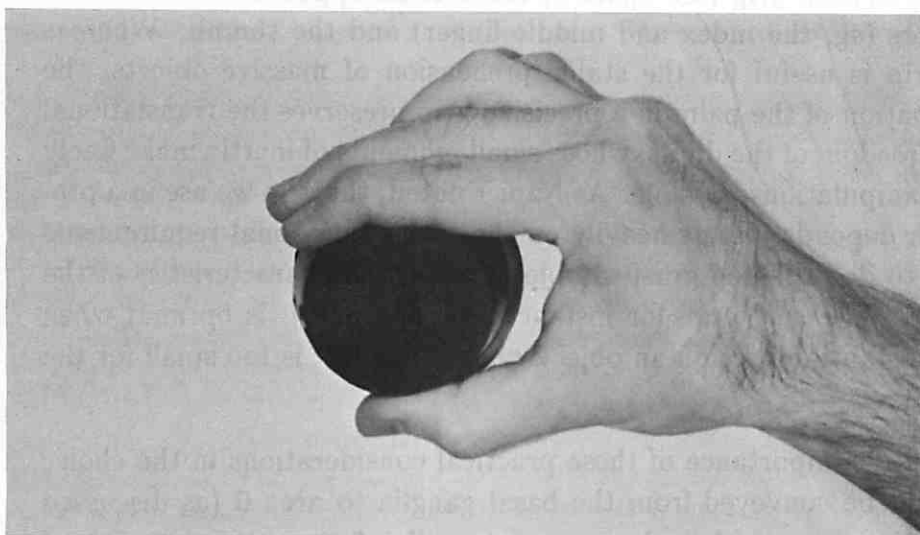
For a given cylinder diameter  $\text{mag}(\mathbf{V}_S)$ , we may now describe any such pad grip in terms of these three independent variables:  $\text{dir}(\mathbf{V}_S)$  describes the “twist” of the grip,  $\text{mag}(\mathbf{V}_c)$  denotes the “reach” of the grip, and  $\text{dir}(\mathbf{V}_c)$  gives the remaining, “up and down” component. Informal observations have indicated that in a typical pad grip of a massless cylinder, with diameter  $\text{mag}(\mathbf{V}_S)$ , the variables  $\text{dir}(\mathbf{V}_S)$ ,  $\text{mag}(\mathbf{V}_c)$  and  $\text{dir}(\mathbf{V}_c)$  tend to take on characteristic values, presumably those which entail the least energy expenditure. Deviations from these “prototypical” values can usually be accounted for by a nonzero object mass ( $\text{mag}(\mathbf{V}_c)$  will increase with the object mass, because of the need for increased stiffness of the digits), or by functional requirements *in addition* to the object’s stable prehension. For instance, the “pretwist” preceding the manual rotation of a cylinder (see figure 14) alters  $\text{dir}(\mathbf{V}_S)$  from its preferred value. Similarly, a preparation to pull the object in towards the palm with the fingers involves a preliminary reaching of the fingers prior to establishing the grip. Hence, we observe an increase in  $\text{mag}(\mathbf{V}_c)$ . Finally,  $\text{dir}(\mathbf{V}_c)$  deviates from its prototype only when object inaccessibility or avoidance of another object demands it.

In addition to saving energy, the prototypical nature of the pad grip eases the planning burden of the higher motor centers, since its kinematic regularity affords a predictable outcome.

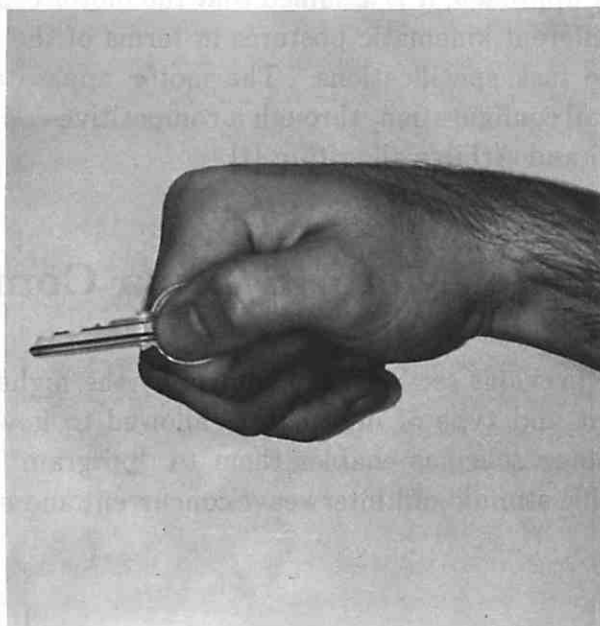
## 4.2 Grasp classifications

In section 2, we argued that CCPs for learned skills compete for a role in a task, with the musculature-independent task description serving as the criteria for skill selection. In grasping tasks, the physical and functional characteristics of the graspable object, and the movements and forces to be exerted upon and through the object, serve as criteria for choosing among the various grasping postures. Let us now review the different types of grasps used by humans, and the task characteristics which lead to their selection.

**Figure 9. A precision grip**



**Figure 10. A side grip**



In 1956, Napier [43] classified human grasps according to the characteristic hand-object relationship of the resulting grip. A *power grip* (see figure 8) is characterized by participation of the palm, which opposes the four fingers. A *precision grip* (see figure 9) involves an opposition between the radial fingers (eg, the index and middle finger) and the thumb. Whereas a power grip is useful for the stable prehension of massive objects, the nonparticipation of the palm in a precision grip preserves the translational degrees of freedom of the digits, whose small moments of inertia make finely accurate manipulations possible. As Napier noted, the grip we use in a prehensile task depends just as heavily on the task's functional requirements (i.e., what to do with the grasped object) as on the characteristics of the object itself. The *side grip*, for instance (see figure 10), is optimal when exerting substantial force on an object whose "handle" is too small for the power grip.

The relative importance of these practical considerations in the choice of grip could be conveyed from the basal ganglia to area 6 (as discussed in section 2), where such task constraints will influence the outcome of the competitive process in which CCPs for different grasp types might vie for participation in the task. The general problem of mapping a set of task requirements to an appropriate grip has been addressed by Iberall [27], whose *opposition space* analysis evaluates kinematic configurations of the hand in terms of the functional attributes they afford, for purposes of gripping. In her approach, it is assumed that the motor centers are capable of evaluating different kinematic postures in terms of the degree to which they satisfy the task specifications. The motor apparatus then chooses the "best" overall configuration, through a competitive-cooperative process based on Amari and Arbib's algorithm [1].

## 5 A Model of Motor Schema Competition

As discussed in previous sections, the control by the higher motor centers over the amount and type of information allowed to flow to and among the different motor schemas enables them to "program" the desired responses to specific stimuli and interweave concurrent and sequential motor

schema activations. A CCP influences the outcome of the interactive process of motor schema competition by specifying the strength of excitatory or inhibitory channels of communication between sensory centers and motor schemas, and between each pair of motor schemas. Since, in a sense, the CCP's role amounts to specifying each motor schema's *compatibility* with each sensory source and each individual motor schema, we may view the competitive process of schema competition as one of constraint relaxation: A motor schema's activation level will be the result of summing the strengths of all sensory signals and the other motor schemas' activation levels, each weighted by the current schema's compatibility with those sensory sources and motor schemas. At a given moment, a motor schema's activation level will depend on all other schemas' activation levels, plus the sensory environment of the moment (hence, the need for an ongoing relaxation process).

Following Arbib [2], we shall assume that if and whenever a schema's activation level exceeds its *threshold of activation*, its corresponding, simple movement will execute. The compatibilities, representing the motor set of the intermediate motor structures, such as MI, will dictate the sequence of schema activations, for a given sequence of sensory signals. A CCP for a learned skill specifies the compatibilities (channels of excitatory and inhibitory communication to each motor schema), thereby dictating the intermediate motor apparatus' response to any possible sensory event (refer to the four facilitations of administrative power that a CCP affords through the capacity to set up the communication environment for each motor schema, as described in section 2).

In an attempt to formalize the process of motor schema competition and activation, let us first define sensory input vector  $\mathbf{s} = (s_1, \dots, s_n)$ , with  $s_i \in [-1, 1] \subset \mathbf{R}$  for  $i = 1, \dots, n$ . Each  $s_i$  represents a fragment of sensory data, for example, a joint angle, the pressure on a finger's pulp, or the retinotopic disparity of the hand's image from the fovea, in the visual field. Now define *sensory compatibility coefficient*  $c_{ij} \in [-1, 1] \subset \mathbf{R}$  as the compatibility of motor schema  $S_i$  with respect to (positive) sensory input  $s_j$ . Similarly, define *cooperative compatibility coefficient*  $c'_{ij} \in [-1, 1] \subset \mathbf{R}$  as the compatibility of motor schema  $S_i$  with respect to motor schema  $S_j$ .

(assume  $c_{ii} = 0$ ). Using a simple constraint relaxation device, similar to the Gauss-Seidel method for solving numerical systems, we may now construct the following operator, to compute  $S_i$ 's activation level  $a_i$  at time  $t$ , with  $i \in 1, \dots, m$ , and given sensory input vector  $\mathbf{s}$ :

$$a_i^{(t)} = \left( \sum_{j=1}^n c_{ij} s_j^{(t-1)} \right) / n + \left( \sum_{j=1}^m c'_{ij} a_j^{(t-1)} \right) / m \quad (1)$$

The left-hand summation of sensory input signals, weighted by schema  $S_i$ 's compatability with respect to each signal, represents the schema's perceived suitability to the current sensory environment (comprising  $S_i$ 's "embedded perceptual schema", in [2][4]), before applying the contextual constraints of other motor schemas' activity. The right-hand summation of all the other motor schemas' activation levels, weighted by  $S_i$ 's compatability with respect to each schema, constrains  $S_i$ 's activation level in the context of those schemas' activations. The compatability coefficients  $c_{ij}$  and  $c'_{ij}$ , together representing the current motor set in primary motor cortex, are provided by the currently active CCPs, which, as discussed previously, effect their respective movement sequences by supplying those compatabilities, through neural gating mechanisms. A simple computer implementation of this relaxation model has shown the formula of equation 1 to be at least feasible: given appropriate, fixed compatabilities  $c_{ij}$ , motor schemas were made to activate (attain activation levels exceeding a threshold) in coordinated sequences, in response to varying sensory signals  $s_i$  and each other's changing activation levels. The following example illustrates how a complex movement sequence may be organized, simply by choosing the appropriate compatabilities.

Figures 11 through 14 illustrate the sequence of hand configurations in a *precision twist*, a cyclical action we commonly perform when turning a small knob or dial. A precision twist entails two basic, concurrent maneuvers: (1) opening and closing the hand in a *pad grip* configuration, and (2) preparing for and executing the twist. (1) may be divided functionally into three phases: the PRESHAPE (figure 15), the CLOSE and the (static) PAD GRIP (figure 16); (2) may be described as a PRETWIST (figure 17) and an ACTUAL TWIST (figure 18). When the grasping maneuvers of

figures 15 and 16 are executed concurrently with the twisting maneuvers of figures 17 and 18, we observe the sequence of postures that comprise a precision twist. Although an oversimplification, let us for simplicity assume that each of these separate submovement phases corresponds to a single motor schema, whose activation results in the corresponding phase's execution. That is, we shall assume the existence of five motor schemas: PRETWIST, ACTUAL TWIST, PRESHAPE, CLOSE and PAD GRIP. Now let us consider the compatibilities a PRECISION TWIST CCP might impose on these five motor schemas, in order to effect an interweaving of their respective movements that will produce the coherent, skilled twisting movement depicted in figures 11 through 14.

First, let us note that each phase has one or more preconditions, i.e., the completion of the previous phase or phases. For example, the PRETWIST's preconditions are the completion of the ACTUAL TWIST and the completion of the PAD GRIP. We shall impose these preconditions by declaring the PRETWIST schema incompatible with the latter two schemas:

$$C(\text{PRETWIST}, \text{ACTUAL TWIST}) < 0 \quad (2)$$

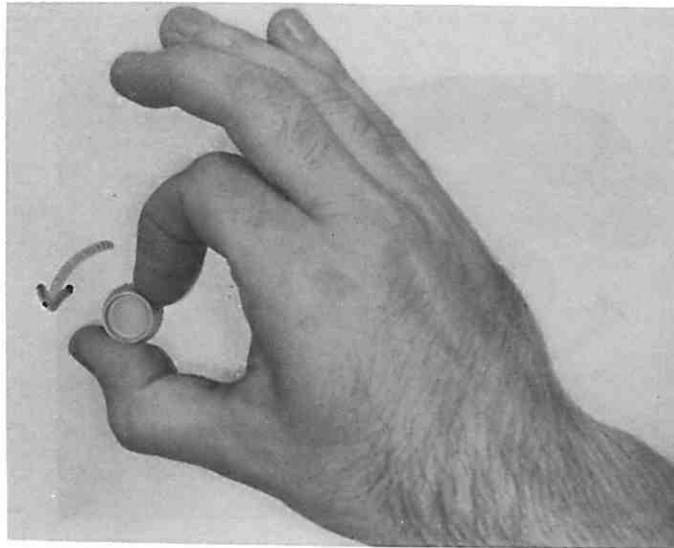
$$C(\text{PRETWIST}, \text{PAD GRIP}) < 0 \quad (3)$$

Recalling Equation 1, whenever the ACTUAL TWIST and PAD GRIP schemas are active, PRETWIST's activation level will receive an inhibitory influence from those motor schemas, ensuring its suppression until the grip is released. Some of the motor schemas, on the other hand, should only execute concurrently. For instance, the ACTUAL TWIST schema should not execute without the PAD GRIP in effect. This may be guaranteed by the following:

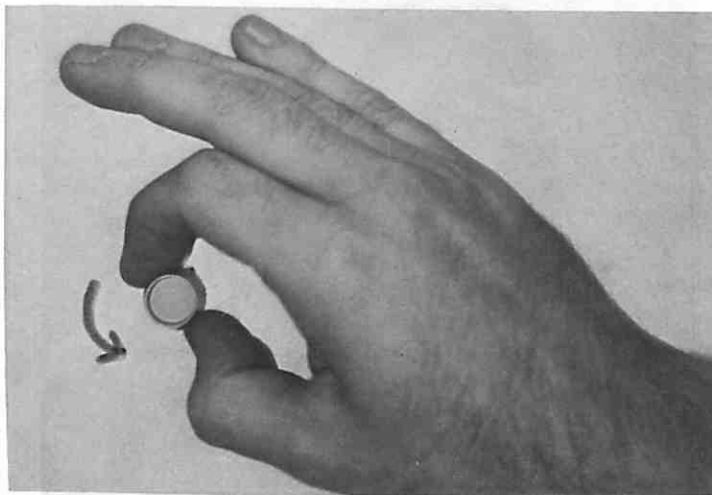
$$C(\text{ACTUAL TWIST}, \text{PAD GRIP}) > 0 \quad (4)$$

$$C(\text{PAD GRIP}, \text{ACTUAL TWIST}) > 0 \quad (5)$$

**Figure 11. Precision twist: start of the actual twist**

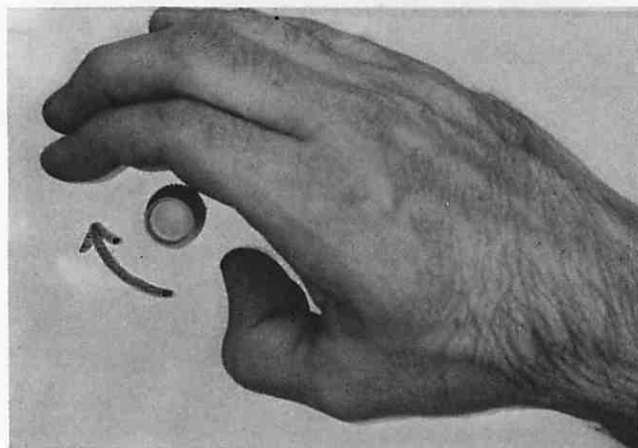


**Figure 12. Precision twist: completion of the actual twist**

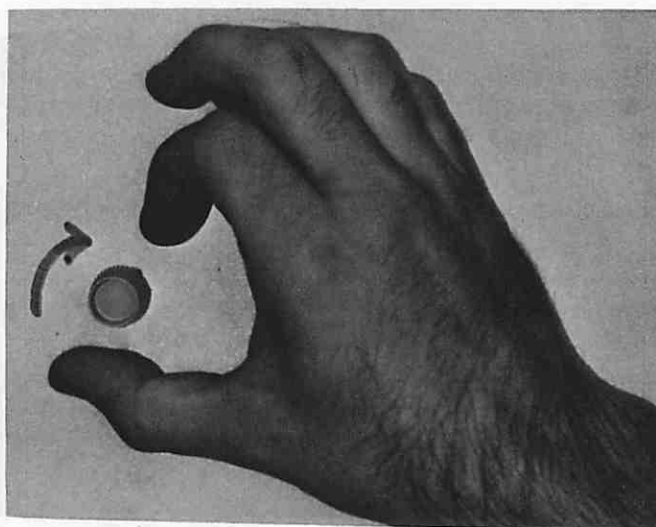




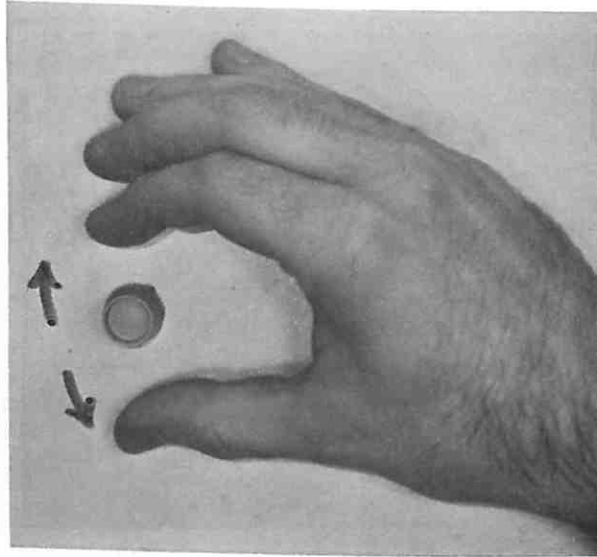
**Figure 13. Precision twist: start of the pretwist**



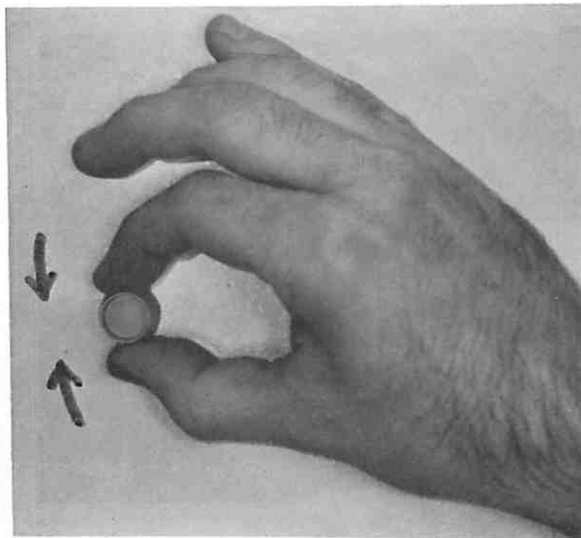
**Figure 14. Precision twist: completion of the pretwist**



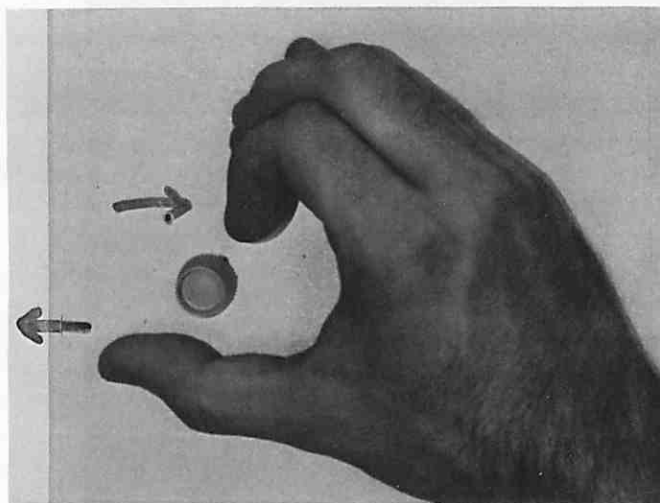
**Figure 15. Precision twist: preshape component**



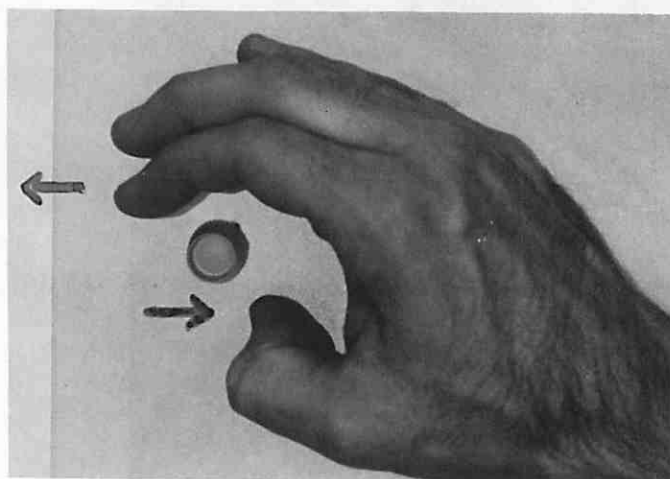
**Figure 16. Precision twist: pad grip component**



**Figure 17. Precision twist: pretwist component**



**Figure 18. Precision twist: actual twist component**



These mutually compatible motor schemas will now support each others' activations, activating and deactivating more-or-less at the same time. Turning now to sensory considerations, the PRECISION TWIST CCP must gate pertinent sensory input to the five motor schemas. The ACTUAL TWIST schema should not activate without assurance that the PAD GRIP is in effect. Therefore, cutaneous information  $S_0$  from the pulp, corresponding to grip force, should trigger the activation of the ACTUAL TWIST schema. Let us impose this condition by declaring the ACTUAL TWIST schema to be compatible with respect to cutaneous input  $S_0$ :

$$C'(ACTUAL\ TWIST, S_0) > 0 \quad (6)$$

In terms of equation 1, the sensory input  $S_0$ , weighted by positive compatibility  $C'(ACTUAL\ TWIST, S_0)$ , will sum with other contributing influences and raise the ACTUAL TWIST schema's activation level by an amount related to  $S_0$ . A great enough pressure exerted on the pulp will therefore serve as a trigger condition for the schema's activation.

These brief examples should make clear the power a CCP can exert over the activities of motor schemas, simply by regulating the flow of information to and among them, which may be achieved through establishing the appropriate motor set in the intermediate motor structures.

## 6 The Mapping from Task to Grasp

So far, we have examined the process by which more-or-less sensory-driven motor schemas interact in a sensorimotor information environment established by the CCPs which are currently active. The CCP for a skilled movement specifies the freedom of excitatory and inhibitory information flow between the motor schemas, and from sensory sources to the motor schemas. This *motor set* dictates the sequence of sensory-driven motor schema activations and their associated prototypical movements. How, then, do the task-driven CCPs themselves activate, in response to the physical and functional requirements of the task?

Let us briefly confront this problem as it pertains to grasping movements: how might a grasping task description (object characteristics and required forces, translations and rotations) map to an appropriate grip type? Recall the different grip types' suitabilities to various task requirements: the power grip is powerful but lacks precision; the precision grip permits finely-graded object translations but lacks the stability of the power grip. Can we suppose that a POWER GRASP CCP, a PRECISION GRASP CCP and a SIDE GRASP CCP compete in area 6 to establish their respective motor sets in primary motor cortex, to bring about their respective grasping movements? Such a simplistic scheme is illustrated in figure 19. Task descriptors activate grasp CCPs suited to the task description, and the CCPs inhibit each other to ensure mutually exclusive activations. The CCP "best-suited" to the task activates and imposes its own compatibility coefficients on the motor schemas, setting the stage for the execution of the CCP's movement sequence (as described in section 4).

The latter scheme is too simplistic, however, in that it does not account for composite grips. A composite of the power and precision grips, for example (see figure 20), is a commonly-observed grip used for handling tools. Note that the power grip component involves only three fingers, instead of the usual four. The thumb and index, wrested from the power grip's control by the precision grip, add a measure of precision to the powerful, but otherwise imprecise, power grip. Either grip, in its "pure" form, would not provide the same blend of power and precision offered by this composite grip.

In general, the five digits are often divided up and "claimed" by more than one control structure. Arbib, Iberall and Lyons [4] have demonstrated that a task's functional requirements map to *virtual fingers*, each comprising a set of physical fingers that share a common control structure. Apparently, CCPs do not compete *per se* to satisfy a task's physical and functional requirements, as in figure 19, but rather, compete for the *allocation* of digits *with which* to satisfy the task requirements.

Perhaps these observations indicate that we should model the mechanism underlying the selection of grasp in terms of a labeling process (using, for instance, the nonlinear relaxation algorithm of Rosenfeld *et al* [59]),

whereby each digit receives a label denoting the CCP that will control its movements. The CCPs would compete to control a digit, i.e., attempt to establish their respective motor sets in the topographical, neural zones corresponding to the digit. A CCP's level of control over a digit would ultimately reflect the degree to which the digit's allocation to that CCP facilitates satisfaction of the task requirements. The mechanism by which the motor apparatus maps a task description to an optimal grasp configuration is explored in greater depth in [27].

Figure 19. A simplistic model of grip selection

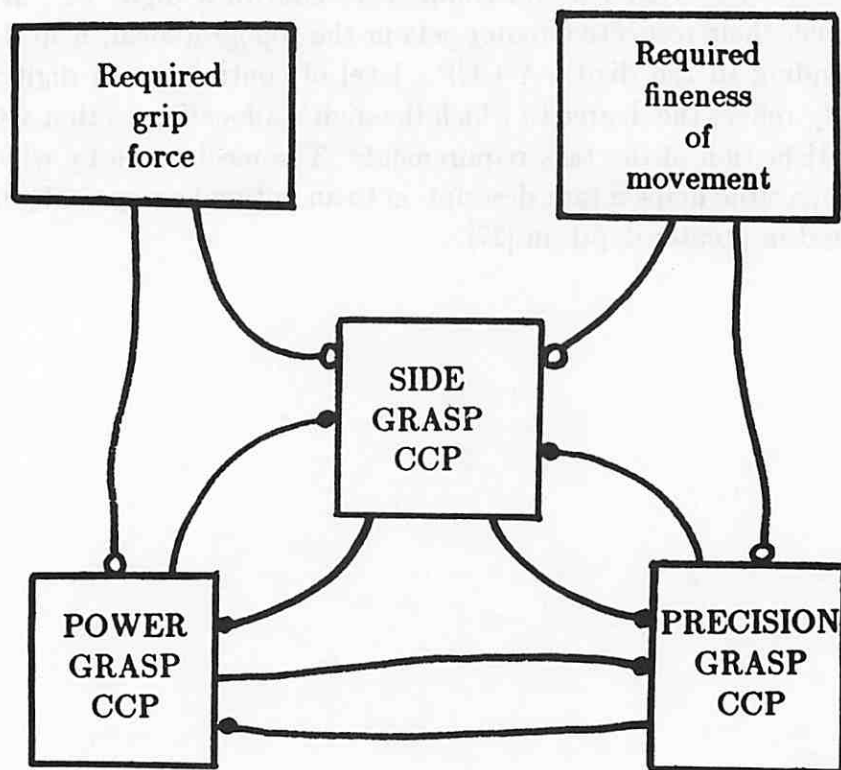
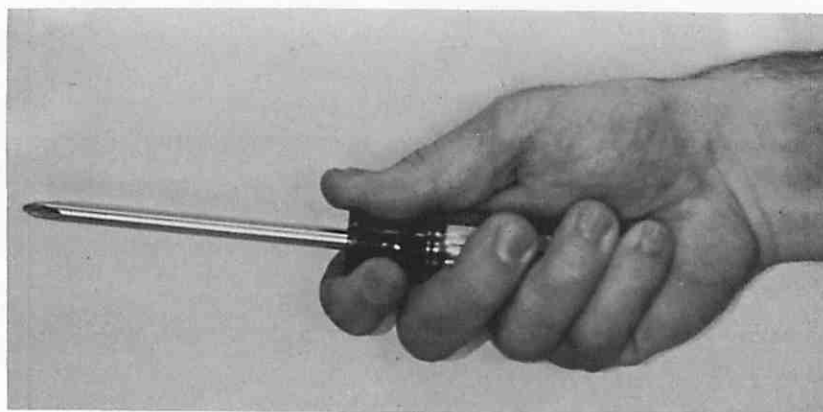


Figure 20. A composite grip



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