

# HIGHER ORDER MOTOR CONTROL

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The framework within which motor functions have been studied in the brain has been dominated by a presumed hierarchical organization of the brain mechanisms underlying motor function. Hughlings Jackson (1889) postulated three levels of "motor centres":

(1) The anterior spinal horns and their homologues higher up (nuclei of motor cranial nerves) are the lowest motor centres (both of the cerebral and cerebellar systems). These lowest motor centres, with the corresponding sensory centres, make up the lowest level of evolution of the central nervous system. (2) The convolutions of the Rolandic region are the middle motor centres. With the corresponding sensory centres, they make up the second or middle level of the central nervous system. (3) The prae-frontal lobes are the highest motor centres of the cerebral system. With the corresponding sensory centres, they make up the third or highest level of the central nervous system, that is, the "organ of mind."

He based the distinction among these levels on the degree of combinatorial representation of muscles to form complicated motor acts. He stated (Jackson 1889):

To speak figuratively, the central nervous system knows nothing of muscles, it only knows movements. . . . There are, we shall say, thirty muscles of the hand; these are represented in the nervous centres in thousands of different combinations—that is, as very many movements; it is just as many chords, musical expressions and tunes can be made out of a few notes. I now speak of the representation of the muscles of the hand in the three orders of motor centres just spoken of. (1) In some lowest motor centres . . . these muscles are represented in numerous different combinations, as simple and very general movements. (2) In the middle motor centres . . . the same muscles are represented (re-represented) in still more numerous different combinations, as complex and special

movements. (3) In the highest motor centres . . . the same muscles are represented (re-represented) in innumerable different combinations, as most complex and most special movements.

Therefore, for Jackson, “higher” meant a larger number of degrees of freedom in combinations and re-combinations of motor elements. This view refers to the output stage of processing of the motor command. This stage is preceded by other stages, which include processing of the motor intention from its inception as a self-initiated or stimulus-guided movement to its translation to combinations of motor elements for its implementation. I use the term “higher motor control” in this review in the latter sense, that is in reference to processes that lead to the initiation of a motor response. For motor responses guided by visual signals, a more or less serial model can be considered: Given a relevant stimulus, events in the brain proceed from stimulus-processing areas to movement-producing areas. Although in a general sense this sequence is true, it is clear now from studies in behaving animals that there is activation in parallel of many motor areas and that a clear sequential activation is not observed. The concept then has emerged, based especially on the effects of lesion studies, that different areas might be related to different aspects of motor processing. The almost simultaneous activation of these areas reflects the parallel processing of the motor command from different aspects. This review deals with psychophysical and neural studies of aimed motor responses, e.g. isometric force pulses or movements; other movements (e.g. key presses) are not considered. In particular, I review below three aspects of motor function; namely, the specification of motor parameters, the question of coordinate transformations, and cognitive operations related to the planning of movement.

## SPECIFICATION OF THE DIRECTION AND AMPLITUDE OF AIMED MOTOR RESPONSES

### *Psychophysical Studies*

The idea that the direction and amplitude of a motor response may be subserved by different processes is supported by the results of psychophysical studies (Rosenbaum 1980, Favilla et al 1989, Soechting & Flanders 1989a,b, 1990). Favilla et al (1989) used a paradigm in which subjects were forced to emit a targeted force pulse at regular time intervals irrespective of whether they were ready or not, that is whether their reaction time was completed or not. Visual signals specified the direction (of two possible) and amplitude (of three possible) of the upcoming force and were presented at various times preceding the force-triggering auditory cue. There were three major findings of these studies. First, when the visual

specification signal preceded the force-triggering signal by more than 300 ms, the forces were of the proper direction and amplitude. Second, when the visual specification signal preceded the force-triggering signal by less than 100 ms, the forces were in a random direction (flexion or extension) and of a default amplitude (the middle of the three possible). And third, for intermediate time intervals, the directional errors diminished gradually as the interval increased and the force amplitude became closer to that dictated by the target (see also Hening et al 1988). **These findings indicate that the motor command is completed gradually during the reaction time.**

Important insights were also gained by an analysis of errors in pointing. When aimed movements are made in 3-D space in the dark, the errors in direction are smaller than the errors in distance, and, accordingly, the information transmitted by the movement about the location of the target is higher for the direction than for the amplitude of the movement (Soechting & Flanders 1989a). Additional support for a separate specification of the direction and amplitude of the movement comes from studies in which the direction and amplitude of an upcoming movement are precued separately (Rosenbaum 1980). When the set of possible movements contains movements of different directions and amplitudes, prior information to the subject ("precueing"), before the trigger signal, concerning the direction (or amplitude) of the upcoming movement results in a significant reduction of the reaction time. The reduction is highest when both movement direction and amplitude are prespecified, but the reaction time savings for known direction are greater than those for known amplitude. Similar findings are obtained in monkeys (Riehle & Requin 1989) and indicate that the direction and amplitude of movement are subserved by separate processes.

### *Neural Studies*

Several studies in behaving monkeys have been devoted to the relations between direction and amplitude of movement and single cell discharge in various brain areas. Most studies have found differences in cell activity for movements in different directions, but the relations to movement amplitude are less obvious. I summarize the results of these studies below separately for single and multi-joint arm movements.

**SINGLE JOINT MOVEMENTS: RELATIONS OF NEURAL ACTIVITY TO DIRECTION OF MOTION ABOUT A JOINT** The results of several studies have documented the fact that cell activity differs for movements in opposite directions about a joint; for example, this has been found in the motor cortex (Evarts 1968, Schmidt et al 1975, Tanji & Evarts 1976, Thach 1978, Kubota & Funahashi 1982, Flament & Hore 1988, Crutcher & Alexander 1990), the

premotor cortex (Weinrich & Wise 1982), the supplementary motor area (SMA) (Crutcher & Alexander 1990), the basal ganglia (Crutcher & DeLong 1984, Liles 1985, Mitchell et al 1987, Crutcher & Alexander 1990), the red nucleus (Gibson et al 1985), and the cerebellum (Thach 1978). **Because motion about a joint is brought about by the action of muscles (which is inherently directional), it is important to determine whether cell activity relates to the direction of joint movement or the muscle activity because, under most conditions, the two are closely related.** Indeed, this dissociation can be achieved by applying external loads such that movement in the same direction is performed with different muscle activations. It has been an important finding that whenever such a dissociation was tried, a good proportion of cells was found to relate to the direction of the movement *irrespective of the muscle pattern used to implement the movement*. This has been observed in the motor cortex (Thach 1978, Alexander & Crutcher 1990a, Crutcher & Alexander 1990), the SMA (Alexander & Crutcher 1990a, Crutcher & Alexander 1990), the putamen (Crutcher & DeLong 1984, Alexander & Crutcher 1990a, Crutcher & Alexander 1990), the globus pallidus (Mitchell et al 1987), and the dentate and interpositus nuclei (Thach 1978). The same dissociation has been observed during preparation for movement. In the experiments of Alexander & Crutcher (1990a), the monkey first moved the forearm in the direction (flexion/extension) indicated by a visual stimulus (right/left). Then, the forearm moved to the initial position and a preparatory period ensued at the end of which the stimuli at both positions (right and left) were turned on. The monkey was required to move the forearm in the direction of the previous movement. Now, static loads opposing flexion or extension could be applied to the manipulandum that the monkey moved, and this task was performed under a variety of such load conditions. Thus the effect of the intended direction of movement on the neural activity was dissociated from the effect of the muscle pattern that was dictated by the loads applied. It was found (a) that many cells in the motor cortex (37%,  $n = 202$ ), the SMA (55%,  $n = 222$ ), and the putamen (33%,  $n = 317$ ) showed changes in activity during the preparatory period, (b) that these changes were selective in anticipation of elbow movements in a particular direction (87% in motor cortex, 86% in SMA, and 78% in putamen), and (c) that these changes were independent of the loading conditions (83% in motor cortex, 80% in SMA, and 84% in putamen). These workers concluded (Alexander & Crutcher 1990a):

The near absence of "loading effects" that could be considered preparatory suggests that directional preparatory activity, at least in these three motor areas, may not play a significant role in coding for either the dynamics or the muscle activation patterns of pre-planned movements. **Instead, such activity may be coding for the intended direction**

of movement at a more abstract level of processing (e.g. trajectory and/or kinematics), independent of the forces that the movement will require.

Indeed, an even higher order relation of neural activity to visual signals was observed when the visually defined direction was dissociated from the direction of the upcoming joint movement (Alexander & Crutcher 1990b). In the usual task, the visual instruction (target), the monkey's cursor and the monkey's forearm all moved in the same direction, whereas in the dissociation task the forearm moved in the opposite direction from that of the cursor (and target). It was found that the activity of a good proportion of cells in the motor cortex (40%), the SMA (36%), and the putamen (38%) showed selective discharge prior to all pre-planned movements of the cursor toward one or the other direction (right or left in the visual display), *irrespective of whether the limb movement involved extension or flexion of the elbow*.

The findings summarized above show conclusively that the changes in activity observed in central motor structures in tasks with visually guided movements do not relate exclusively to upcoming peripheral motor events (e.g. muscle contractions) but instead reflect higher order processing of visuomotor information. Of course, the fact that central motor structures relate to upcoming motor events is well documented (Evarts 1981, DeLong & Georgopoulos 1981, Brooks & Thach 1981). Unfortunately, however, this has led to the commonly held belief that central motor structures relate to *nothing but* peripheral motor events, and this narrow view is untenable. For example, it has been commonly believed that the major, *if not the only*, function of the motor cortex is to control the force exerted by the limb, or just the muscular activity to be developed. Unfortunately, such a simplistic and one-sided view of the motor cortex as nothing but a muscle controller has permeated theoretical accounts of motor cortical function as well (Mussa-Ivaldi 1988). The truth is that only a fraction of motor cortical cells relates to muscular activity. For example, in the sample of Fetz & Cheney (1980), only 18% of the cells tested showed postspike facilitation suggesting monosynaptic connections to motoneurons. When more general criteria of resemblance of cell activity to muscular activity were used under conditions that dissociated muscular pattern from other variables (e.g. the direction of joint movement), the proportion of muscle-like cells in the motor cortex was found to be approximately one third (Thach 1978, Crutcher & Alexander 1990). Even for cells that are predominantly active during the movement itself, the proportion of muscle-like cells was 36% in the motor cortex, 41% in the SMA, and 24% in the putamen (Crutcher & Alexander 1990). In contrast, the majority of cells in these structures reflect truly directional (i.e. load-independent) effects and/or effects of visual signals guiding the movement.

It is interesting that when the movement is a simple key press, the complexity of neural responses is more evident in the SMA than in the motor cortex (Tanji & Kurata 1985). It seems that the motor cortex is more involved in planning or preparatory stages of the motor command when the upcoming movement possesses spatial characteristics (e.g. direction) specified by visuospatial information.

**SINGLE JOINT MOVEMENTS: AMPLITUDE** Attempts to document relations between single cell activity and the amplitude of movement have not been very successful. In the motor cortex, Hamada & Kubota (1979) did not find significant relations between frequency of discharge of identified pyramidal tract neurons during the reaction time and movement amplitude.

**MULTIJOINT MOVEMENTS: DIRECTION OF MOVEMENT IN SPACE** Significant relations of single cell activity to the direction of movement in space have been found in the motor cortex (Georgopoulos et al 1982, 1986, Schwartz et al 1988, Kalaska et al 1989, Caminiti et al 1990), premotor cortex (Weinrich & Wise 1982, Godschalk et al 1985, Park et al 1987, 1988, Karluk & Ebner 1989, A. P. Georgopoulos, J. F. Kalaska, M. D. Crutcher, R. Caminiti, unpublished observations), basal ganglia (Georgopoulos et al 1983b), and cerebellum (Fortier et al 1989). The importance of the motor cortex for reaching movements was demonstrated recently by the disturbed reaching following reversible inactivation of this area by local injection of lidocaine or muscimol (Cooper et al 1989).

When the direction of movement varies in the whole range of 2-D or 3-D space, the directional relations are formally the same: Cell activity is broadly tuned to the direction of movement. Thus (a) individual cells discharge at highest rates with movements in a particular direction ("preferred direction"), (b) cell activity decreases progressively with movements in directions farther away from the preferred direction, (c) the tuning curve ranges throughout the whole directional continuum, and (d) the preferred directions of a large population of cells are distributed throughout the directional continuum. These relations have been studied thoroughly in the motor cortex (Georgopoulos et al 1982, 1986, Schwartz et al 1988, Kalaska et al 1989, Caminiti et al 1990), cerebellar cortex, dentate and interpositus nuclei (Fortier et al 1989), and areas 2 and 5 of the parietal cortex (Kalaska et al 1983, Kalaska 1988). From the tuning properties of single cells summarized above, it follows that (a) single cells do not provide unambiguous information about the direction of the movement, except at the peak of the tuning curve, and (b) for a particular movement direction, a whole population of cells will be engaged. Therefore, it is reasonable to suppose that unique, unambiguous information about the direction of the movement resides in the neuronal population. Indeed, a weighted vector

sum of individual vectorial contributions by single cells in the population provides a good prediction of movement direction in motor cortex (Georgopoulos et al 1983a, 1986, 1988), cerebellar cortex, dentate and interpositus nuclei (Fortier et al 1989), and area 5 of the parietal cortex (Kalaska et al 1983). This population directional signal is present during the reaction time (Georgopoulos et al 1984, 1988), during an evolving movement trajectory (Schwartz & Anderson 1989), and during an instructed delay period (Georgopoulos et al 1989a). That the population vector points in the direction of the upcoming movement during the reaction time or an instructed delay period has important implications and potentially significant applications for tasks that require spatial transformations because it provides an accurate and robust monitor of the directional motor intention of a neuronal ensemble as this tendency evolves and changes in time. This feature was utilized to gain an insight into the brain correlates of a mental transformation (Georgopoulos et al 1989b, see below).

The changes in preferred direction when movements are made in different parts of the workspace were studied by Caminiti et al (1990). They found that when monkeys make reaching movements in 3-D space starting from three different points located in sufficient distances on the horizontal plane so as to cover the whole immediate extrapersonal space in front of the animal, the preferred directions shift predominantly in the horizontal plane by an amount approximately equal to the change in the shoulder angle in the same plane. Nevertheless, the population vector calculated within each part of the workspace still provides an accurate prediction of the direction of the movement.

The relations between steady-state cell activity in the motor cortex and the direction of a static load were studied by Kalaska et al (1989) in 2-D space. Significant relations were found in 64% (147/229) of cells between the direction of the load and the steady-state cell activity; in some cells, a relation between cell activity and the magnitude of the load was also observed (Kalaska 1990). The changes in cell activity observed during movements made under different load conditions were, on the whole, additively superimposed. Moreover, load effects were observed much less frequently in cells that were phasically activated; however, those cells did show directional relations to movement.

The fundamental dissociations among load, direction of movement, and direction of the visuospatial signal that were carried out for single joint movements (Alexander & Crutcher 1990a,b, Crutcher & Alexander 1990) remain to be performed for multijoint movements both under reaction time conditions and when a preparatory period is imposed. There is no *a priori* reason to assume, however, that the extension of the dissociation studies (Alexander & Crutcher 1990a,b, Crutcher & Alexander 1990) from

elbow movements to movements involving the shoulder and the elbow would yield qualitatively different results. In fact, the results of Crutcher & Alexander (1990) and of Alexander & Crutcher (1990a,b) were obtained in motor cortical sites from which, in certain cases, shoulder movements could be evoked by microstimulation. It seems that the cortical signals relating to the direction of the intended movement and/or the visual signals guiding the movement, independently of the muscle pattern involved in the movement itself, refer to higher order processing of the visuomotor command, and therefore would still be present when the movement involved motion of more than one joint.

The relations described above have been obtained in reference to the direction of movement in space. The movement is implemented by changes in joint angles brought about by the contraction of muscles acting on those joints. Therefore, it is possible that the relations observed may further relate to one or a combination of these variables, from the visually defined direction to the totality of muscles implementing the movement. For example, it has been proposed that the broad directional tuning and population coding discovered in the motor cortex (Georgopoulos et al 1982, 1983a, 1986) need not relate to the direction of the movement but to the ensemble of muscles by which this direction is implemented (Mussa-Ivaldi 1988). This is certainly *theoretically* possible but it would be true *in reality* if the cell activity in motor cortex would relate *exclusively* to muscles; and this is not so, as discussed above. Such explanations based on motor cortical cells as pure muscle controllers might hold for approximately one third of motor cortical cells that seem to relate to the muscle pattern (Thach 1978, Crutcher & Alexander 1990) but are inadequate to explain the changes in activity of the rest of the cells that relate to the direction of movement (Thach 1978, Alexander & Crutcher 1990a) or to the visuospatial signal (Alexander & Crutcher 1990b) *irrespective of the particular muscles being used*. For these cells, reference to the direction of movement or the visuospatial signals is appropriate. In fact, the finding that these different kinds of cells (i.e. directional, visuospatial, and muscle-like) coexist in the motor cortex, and other central motor structures, may not be accidental: It may form the background for requisite transformations of the motor command.

**MULTIJOINT MOVEMENTS: AMPLITUDE** The relations of cell activity to the amplitude of multijoint arm movements have not been studied as systematically as those to direction. Significant positive and negative linear relations to movement amplitude were observed in the external and internal segments of the globus pallidus and the subthalamic nucleus (Georgopoulos et al 1983b) for push-pull and side-to-side movements. These



results are in accord with a postulated role of basal ganglia in providing signals for the proper amplitude of movement, as suggested by the inability of Parkinsonian patients to produce movements of large amplitudes (see DeLong & Georgopoulos 1981 for a review).

Relations to movement amplitude have been described in the premotor cortex, including amplitude tuning (Park et al 1987, 1988, Karluk & Ebner 1989) and possibly spatial segregation of amplitude-related cells (Karluk & Ebner 1989). The effects of movement amplitude on cell activity in the motor cortex are not as clear as those of movement direction. Although cells were found that exhibited monotonic increases in activity with movement amplitude (Schwartz & Georgopoulos 1987, see also Georgopoulos 1990), the changes were not very strong. However, a signal for movement amplitude may reside in the intensity of the activation of the total population. Interestingly, cells exhibiting relations to movement amplitude were also directionally tuned (Schwartz & Georgopoulos 1987); although approximately 10% of the cells in the motor cortex are activated in a nondirectional fashion, those cells did not provide an amplitude signal. However, detailed investigation for the possible presence of amplitude tuning in the motor cortex remains to be carried out. The relations of single cell activity to movement amplitude in the SMA will also be interesting to study given that this area receives a major projection, via the thalamus, from the basal ganglia (Schell & Strick 1984) in which significant relations to movement amplitude are found (Georgopoulos et al 1983b). Possibly, the amplitude of movement is subserved by the basal ganglia-SMA system. Given that the SMA possesses direct projections to the spinal cord that are as dense as those from motor cortex (Dum & Strick 1989), the ultimate effect could be on spinal circuitry that would have been preshaped for the appropriate movement direction by motor cortical influences.

## THE QUESTION OF COORDINATE TRANSFORMATIONS

### *Joints*

Assuming that at certain levels of processing, the motor command is composed of distributed direction and amplitude components, how are these components ultimately being translated to muscle activation? The hand is attached at the end of a linked arm and is moved from point to point in space by a coordinated motion at the shoulder and elbow joints (Soechting & Lacquaniti 1981). Convincing evidence now indicates that in unconstrained pointing movements in 3-D space, a stage involving translation of the direction and amplitude motor command to joint coordinates is used (Soechting et al 1986, Soechting & Flanders 1989a,b, 1990).

These transformations seem to involve two joint angles that have been shown to be used by the subjects for perceptual estimation of the static orientation of the arm (Soechting & Ross 1984); namely, the elevation from the horizontal plane (elevation angle) and the angular deviation from the sagittal plane (yaw angle). Four such angles (two for the arm and two for the forearm) are sufficient to define the position of the wrist in 3-D space. When the errors in blind pointing were analyzed within this framework, it was found that they are the result of operating linearly within the coordinate frame of these angles. In contrast, when subjects were asked to be very accurate, the relations in the joint angle space were nonlinear. **These results indicate that "natural" pointing movements are carried out within a joint coordinate framework that requires only linear transformations, which, however, result in characteristic errors of pointing.**

A joint coordinate stage in the translation of a direction and amplitude motor command is also supported by the results of experiments in which the trajectories of free drawing movements were investigated. When subjects draw circles or ellipses in 3-D space, there are characteristic distortions in certain planes. These distortions can be traced to and be explained by the hypothesis that motor commands for spatial trajectories are translated to movements through a stage involving the joint angles mentioned above. Moreover, Soechting & Terzuolo (1986) predicted that because of this obligatory translation stage, it will not be possible for a movement trajectory to change direction continuously in 3-D space. This prediction was indeed confirmed (Soechting & Terzuolo 1987).

The findings summarized above impose constraints on theoretical investigations of how a motor command specified in external space coordinates is ultimately implemented by the contraction of various muscles. Attempts at direct links (Mussa-Ivaldi 1988) may be simplistic and may underestimate the intervening transformations. Such hypothetical direct translations (Mussa-Ivaldi 1988) could be feasible in theory but they may not be the route that the motor system uses. Indeed, an important task for neurophysiology is to elucidate the intervening transformations of the target location from spatial coordinates to shoulder-based coordinates, then to arm and forearm elevation and yaw angles, and finally to relative movement vector coordinates. To date, no studies of this problem have been carried out. A scheme for the sequence of these transformations has been proposed (Soechting et al 1989, Soechting & Flanders 1990).

It is clear from the discussion above that the joint coordinate space through which the motor command is transformed does not involve just any arbitrary joint angles but is confined to specific joint angles that are also meaningful psychophysically for the perception of the orientation of the arm (Soechting & Ross 1984). This concept is different from the

view that multijoint movements are “strung” together from single-joint movements. For example, it could be supposed that neural elements in the motor system specify motion about single joints and that multijoint movements come about by stringing together such single joint-neurons. This view may not be true. For example, microstimulation in the motor cortex seems to elicit movements not about a single joint but in a weighted combination of joints (Humphrey & Mitz 1989) and/or muscles (Donoghue et al 1989). The particular joint angles that are meaningful for psychophysical perceptual performance (Soechting & Ross 1984) and for processing of the motor command (Soechting & Flanders 1989a,b) are specific (elevation and yaw), not just any, joint angles. In fact, it could be that the process of combining appropriate components of motions about single joints to form the joint coordinate representation of the motor command is subserved by specific brain areas. One of these areas could be the cerebellum, as suggested by the results of temporary inactivation of the dentate nucleus by local injection of muscimol or its permanent lesion by injection of kainic acid; this inactivation resulted in severely disturbed reaching movements but almost normal wrist movements (Kane et al 1989), a result that led to the conclusion that “the dentate mediates a type of control concerned primarily with multiple rather than single joints” (Kane et al 1989). This finding is in keeping with the disturbed reaching observed following reversible inactivation of the motor cortex by local injection of lidocaine or muscimol (Cooper et al 1989) and the known connectivity between the cerebellum and motor cortex (Asanuma et al 1983).

### *Muscles*

The final stage in the initiation of movement is to implement it in terms of muscle contractions. Free, multijoint arm movements in 3-D space involve a number of muscles acting on separate joints. Even single axons of pyramidal tract neurons (Shinoda et al 1981) or of neurons in the C3-C4 propriospinal system (Alstermark et al 1987) impinge on several motoneuronal pools. Conversely, there is an appreciable convergence on single motoneurons from a large motor cortical territory (Landgren et al 1962). The existence of such divergence/convergence is important by itself but it does not provide much information concerning the generation of appropriate spatiotemporal patterns of muscle contractions. Nonetheless, some insights can be gained into these processes. Consider, for example, a pointing movement with a particular pattern of electromyographic (EMG) activation of several muscles. Given the significant convergence on each motoneuron from central nervous system (CNS) structures, it follows that the particular spatiotemporal EMG pattern of a single muscle is

the outcome of weighted contributions from several central sources. Moreover, since the EMGs of several muscles have to be such that the appropriate movement will be initiated, there has to be a link between the central commands addressing those motoneuronal pools. Apparently, it is not important *how* the appropriate motoneuronal pool activation will be achieved, i.e. what the exact convergent pattern will be, so long as (a) the sum of the converging inputs to the pools are of the correct level, and (b) the relative ratios between the total activation of the proper tools are the appropriate ones. The level of activity in a pool, however, depends on external load conditions, in addition to the movement itself. If such loads are static, it is reasonable to suppose that the appropriate levels in the pool activation will be set and that the changes from these preset levels will reflect the central commands to move. A different problem arises when the configuration of the joint changes from the "natural" posture to an unusual one. In that case it would seem to be necessary that the relation of the desired movement direction and amplitude be redefined in terms of the new joint coordinates. Visual guidance of the movement may play a role in this case. We know that movement trajectories are not really affected under different loads (Lacquaniti et al 1982), but we do not know how movement trajectories performed in the absence of vision are affected when joint configurations are drastically altered.

## COGNITIVE OPERATIONS ON MOVEMENT PARAMETERS

### *Prior Knowledge*

Rosenbaum (1980) showed that when information concerning the parameters (arm, direction, and amplitude) of an upcoming movement was given to subjects, the reaction time decreased by a certain amount. Moreover, the savings in the reaction time were more substantial for direction than for amplitude, a finding that has also been observed in monkeys by Riehle & Requin (1989), who investigated the neural correlates of these savings in reaction time due to prior knowledge of movement parameters. The activity of many cells in the motor and premotor cortex was influenced by prior information concerning movement direction, whereas very few (4/207) neurons showed changes related to prior information about movement amplitude. Two types of directionally selective cells were distinguished on the basis of changes in their activity observed in a preparatory period during which prior information about the direction of the upcoming movement was given. Riehle & Requin (1989) proposed that one cell type may reflect a "presetting" mechanism that would facilitate the programming of the direction of movement to be triggered later by

another signal; the second cell type may be involved in a “preprocessing” mechanism underlying the actual programming of movement direction during the preparatory period. The paucity of neurons related to prior information concerning movement amplitude is in accord with the notion that this parameter may be specified by the basal ganglia/SMA system (see above); therefore, it would be interesting to record in these structures and assess differences in cell activity when information about movement amplitude is manipulated.

### *Transformations of Visuomotor Direction*

In a “natural” situation, a visually guided movement of the arm is towards the target. In specific experiments, however, instructions can be given to the subject such that the movement is the result of a transformation of visually given information. In one study, the direction of movement in 2-D space was required to be at an angle from a visually defined reference direction, which changed from trial to trial. Under these conditions, the reaction time of human subjects increases in a linear fashion with the angle (Georgopoulos & Massey 1987), thus suggesting that a mental rotation from the stimulus direction to the movement direction might underlie performance in this task. This hypothesis is testable because the directional motor intention can be visualized as the neuronal population vector. Indeed, recordings in the motor cortex revealed that the neuronal population vector pointed first in the direction of the stimulus and then rotated gradually and counterclockwise to point in the direction of the movement (Georgopoulos et al 1989b). These findings provide evidence for the mental rotation hypothesis above and underscore the usefulness of the population approach in general and the population vector in particular as a meaningful tool for analysis and interpretation of brain events related to mental transformations. The important idea behind these studies is that brain activity can be interpreted meaningfully and then used as a probe to gain insight into brain correlates of cognitive functions.

## CONCLUDING REMARKS

Hughlings Jackson’s concept of “higher” motor centers as those in which the representation of movement is most versatile, that is in which muscles and their combinations are re-represented, still holds as such on the output side (Donoghue et al 1989, Humphrey et al 1989). In addition, however, these “higher,” pre-Rolandic motor areas, that is the motor and premotor cortices, have now been shown to participate almost in parallel in “higher” processing of the motor command, that is during the stages of its specification and planning before it is being converted to motor output. The

findings reviewed above have laid to rest all simplistic notions that view central motor structures as *nothing but* muscle controllers. Instead, these recent studies have revealed the rich complexity of CNS processing of higher order visuomotor information. This is not surprising, for central motor structures receive convergent inputs from other areas. For example, the proximal arm area of the motor cortex receives input from area 5 of the superior parietal lobule (Strick & Kim 1978, Caminiti et al 1985), area 2 (Jones & Powell 1969), and several premotor areas (Muakkassa & Strick 1979), including the postarcuate area, which is, in turn, reciprocally connected to area 7 of the posterior parietal cortex (Godschalk et al 1984). These cortico-cortical inputs may in fact be more extensive (Darian-Smith et al 1988) and are in addition to thalamic inputs. Therefore, the potential complexity of changes in cell activity with regard to behavioral events was only to be expected (see also Muir & Lemon 1983). The challenge now is not to "pigeon-hole" the function of central motor structures but to accept and respect the complexity of the responses of their cells and to delineate the interactions and contributions of these various structures to the initial planning, intermediate transformations, and execution and ongoing control of limb movements.

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