

Sensory Motor Processing of Targeted Movements in Motor Cortex

*C. Ghez, D. Vicario, J. H. Martin, and H. Yumiya

Center for Neurobiology and Behavior, Columbia University, College of Physicians and Surgeons, New York, New York 10032

How the brain translates sensation into action represents a central and challenging question for motor physiology. The complex nature of the problem is evident from the multiple demands to be met whenever we rapidly move our limbs to a target. Information about the target controls the contraction of specific muscles among many possible alternatives. Thus, arbitrary components of a virtually infinite array of sensory inputs provide the spatial coordinates of the target- and control-selected elements of a second large array of muscles. Furthermore, accuracy requires not only the control of muscles acting as prime movers, but also of muscles that maintain postural stability. Appropriate sequencing mechanisms assure that commands reach certain muscles before they reach others. Finally, the nervous system must deal with the complex nonlinear properties of muscles and the dynamic changes in input signals arising in the course of movement. Changes in muscle length represent late and indirect consequences of neural signals, and changes in afferent activity can affect intervening control elements.

The major supraspinal structures that control the spinal cord have a discrete

somatotopic organization on which an orderly arrangement of peripheral inputs is mapped. This input-output relation can be characterized as homotopic. Regions controlling a given body part receive sensory information from closely related body parts. For example, in the motor cortex there exists a clear relation between the muscles controlled by local aggregates of neurons and the sites in the periphery which provide sensory input to these neurons (see Asanuma, 1981). A similar input-output plan also applies to the red nucleus (Ghez, 1975; Larsen and Yumiya, 1980). Such homotopic input-output relations are unlikely to be responsible for the initiation of skilled voluntary responses where sensory information from arbitrary targets must be conveyed heterotopically across somatotopic boundaries. How such heterotopic information, arising from different sensory modalities and widely varying peripheral loci, is conveyed to the output representations in motor cortex or red nucleus is a central question for understanding the initiation of the skilled movement. Moreover, since such heterotopic input-output relations are subject to learning, this question is relevant to the more general problems of plasticity and memory which underlie the adaptive control of movement.

We have approached these problems through studies of tracking performance and correlated neural activity. The task re-

*To whom correspondence should be addressed: Center for Neurobiology and Behavior, College of Physicians and Surgeons, 630 West 168th Street, New York, New York 10032.

quires the animals to perform rapid, accurate motor responses with their forelimbs according to information provided by a display. Such a tracking task challenges the animal's ability to translate complex sensory information into appropriate motor commands. Changes in display properties and in the loads opposing the animal's movements have been used to probe the adaptive capacity of the intervening neural processes. This chapter is divided into three sections. The first section (A) examines the features of tracking performance to define general rules governing the processing of sensory inputs related to the target. From these results it appears that, as a first approximation, the behavior conforms to a closed-loop feedback model with continuous sampling of sensory events. The second section (B) examines the properties of neurons in the arm area of motor cortex and suggests that the arm area of motor cortex includes two separate regional subdivisions: one involved in response initiation and another more concerned with the control of ongoing movement. The third section (C) reports anatomical differences in projections to the two regions of motor cortex. We will discuss our observations and their possible implications from a very general perspective to provide a broad, albeit speculative, conceptual framework. We will attempt to define the minimal features of the translational processes between stimulus and response, and to distinguish these translational mechanisms from processes of a more adaptive nature (Houk and Rymer, 1981), which control the translational mechanisms themselves. This distinction is important because, during performance, temporal constraints are crucial for the first, but not for the second. Our data suggests that when learning the task, the animals generate complex internal models of both the display and their peripheral plant as well as a set of correspondence rules relating the two. Contextual cues allow the animal to select the appropriate models for

processing sensory information from the display. We also suggest that neural mechanisms allow decision and response selection to antedate the stimulus.

Methods

Tracking performance and single-cell correlates of behavior were studied in cats, using a versatile and flexible tracking paradigm (Ghez and Vicario, 1978a; Ghez and Martin, 1982). The animal is restrained in a nylon sleeve. Its head and left humerus are rigidly fixed to an external frame which mechanically isolates the forearm from the body. The animal's forearm is strapped in a splint attached to a lever mounted on the axle of a servo-controlled torque motor equipped with a strain gauge, potentiometer, and tachometer (Fig. 1A). The lever can be rigidly fixed to record forces under near isometric conditions. When the lever is free to rotate, the servo-controlled torque motor can simulate inertial, viscous, or spring loads.

The animal faces a display (incorporating a retractable feeder), which can be moved horizontally from side to side by a second servo-operated torque motor. The angular position of the display is a function of a voltage difference (error voltage) between a criterion target level, under experimental control, and the output of one of the transducers in the manipulandum controlled by the animal. The display position can be made to reflect either an error in the force exerted by the animal on the fixed lever, or an error in lever position when it is free to rotate. The servo operates to bring the display in front of the animal when the force or position (produced by the animal's forelimb muscles acting on the lever) matches the criterion target level. The display moves away from the animal's mid-sagittal axis to the right or the left, reflecting the error voltage, when the force or position signal is greater or less than the target level.

Behavioral sessions are subdivided into

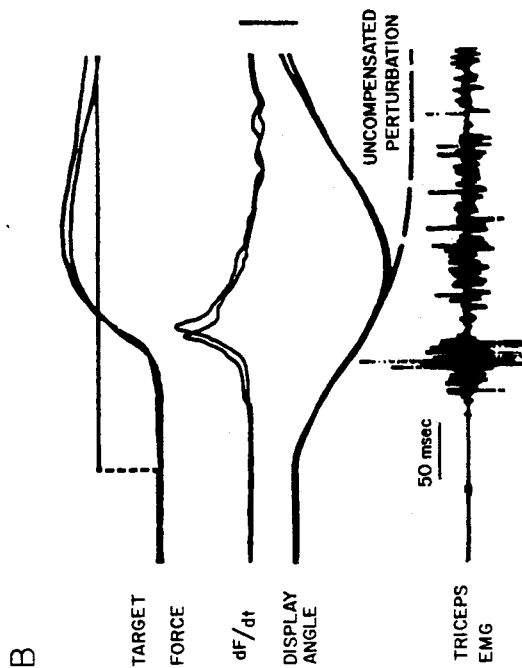
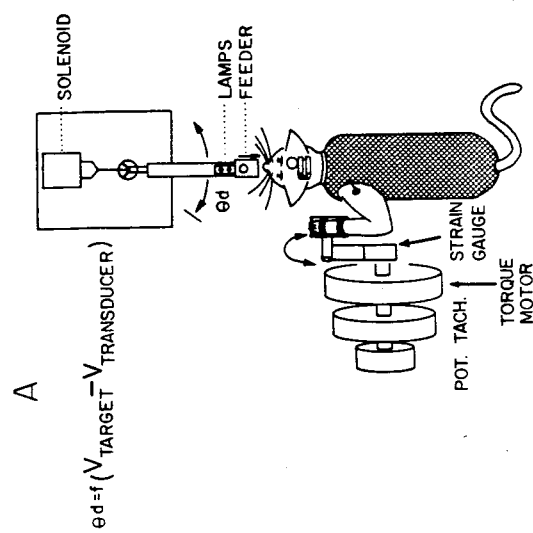


FIG. 1. A: Schematic diagram of experimental arrangement. B: Isometric responses to two equal step changes in target level. *Upper traces:* Target and force levels. *Second traces:* Corresponding changes in dF/dt . *Third traces:* Change in display angle corresponding to change in target level and in subsequent force applied to the lever. The dashed line indicates the shift of the display to the same target step change in target level and in subsequent force applied to the lever (uncompensated perturbation). The bottom trace shows the triceps EMG. The correspondence between the burst of EMG activity and the rising phase of dF/dt should be noted. Vertical calibration: 0.5 Newtons, 17.4 Newtons/sec, 10° (display angle).

discrete trials separated by time-out intervals of a few seconds. At the beginning of each trial, the animal adjusts the force it applies to the fixed lever (or the lever position) so as to align the display with its mid-sagittal axis. Following a randomly varied interval (1 to 2 sec), the target level is abruptly changed. This target step creates an instantaneous error voltage and a display shift to which the animal responds by rapidly adjusting the force it exerts on the lever (or the lever position) to bring the display back to center. After a steady period of realignment, the animal is rewarded with food. Two features should be noted. First, a step change in target level requires about 200 msec to move the display to a new steady-state position. Inertia and internal friction cause the display to act as a low-pass device. Its properties were sufficiently linear that target steps of different sizes produced proportional angular displacements the peak acceleration and peak velocity of which are also proportional to the target step. As a result, information contained in the velocity and other derivatives of the initial display trajectory predict its final position and, therefore, the amplitude of the response required to bring the display back to center. Second, when driven by the target step, the display sweeps by the cat's face and the animal can use either visual cues or vibrissal deflection to sense its motion. Opaque contact lenses are applied to the animal's eyes to make it rely only on cutaneous information from vibrissal deflection. To make the animal rely on vision, the vibrissae are either shaved or retracted with a fitted mask.

Alterations in task conditions can be used to assess the adaptive capacity of processes intervening between stimulus and response. (1) Changes in gain of the display system, made by increasing or decreasing its angular response to a given value of the error signal, require the animal to alter its response strategy since a given amount of dis-

play motion now requires a different magnitude of output. (2) Changes in display polarity can be made. With the standard polarity of displayed error, display shifts to the right require extensor force adjustments, and to the left, flexor force adjustments. Requirements are reversed when the polarity of displayed error is inverted. Animals trained with both display polarities during training can learn both relationships and can be switched from one condition to the other without degrading their performance. In adapting to a sudden polarity change, the animals rely entirely on the effectiveness of their responses, since no additional cues are given. (3) The loads opposing lever movement can be changed to challenge the animal's adaptive capacity under anisometric conditions. (4) The response from the display to the animal's output can be delayed to deny the animal the information it would normally receive about the effectiveness of its response. In order to probe the animal's immediate response strategy, we have made extensive use of surprise or trick trials where behavior or unit activity is assessed when unexpected changes in task conditions are made from one trial to the next.

Single units were recorded with paralene-insulated, etched tungsten electrodes driven by a hydraulic microdrive fitted on an X-Y stage, which allows two-dimensional adjustment of penetration sites in the cortex. Concentric bipolar electrodes were implanted stereotaxically in the cerebral peduncles (where liminal stimuli produced contraction of forelimb muscles) for antidromic identification of cortical projection neurons. Control over the behavioral experiments and data acquisition was carried out with a general purpose computer PDP 11T03. An interactive language developed by P. Oratofsky provided raster displays and histograms of unit activity synchronized with particular events of interest. Data could be selected and sorted to detect

trends and relations between cellular and behavioral events. An algorithm to determine automatically the time of onset of behavioral responses and their initial direction was programmed to exclude experimenter bias. The algorithm identified the peak of the first derivative of the force response to target shift, and the direction of the force change. Then, in a series of backward iterations, the first bin where the rate of change of force exceeded zero was located. The onsets of increase in unitary activity were scored as the middle of the first interspike interval after stimulus, which was less than half as long as the average interspike interval in the prestimulus period.

A. Tracking Performance Reflects the Operation of a Continuous Feedback System

General Features of Motor Responses: Pulse Step Control

During training, the cats learned to match accurately the force they applied to the lever, or the lever position, with the criterion target level according to task conditions. Examples of isometric responses are shown in Fig. 1B. Step changes in the target, shifting the display away from midline, elicited rapid adjustments in force or position which returned the display to midline. The responses accurately compensated for target steps of different sizes and directions. Under isometric conditions the peak force was a linear function of the peaks of the first and second derivatives of force (Ghez and Vicario, 1978b). Similarly, when limb motion was studied, the change in limb position was a linear function of the earlier peaks in velocity and acceleration (Ghez, 1979). The times taken to achieve the peak dF/dt or the peak acceleration, remained constant and were independent of the change in force or position. Similar rules have been found to apply to limb move-

ments in humans (Taylor and Birmingham, 1948; Freund and Budingen, 1978; Lesienne, 1979) and monkeys (Lamarre et al., 1980). An additional feature of the behavior in the present task was that exposure to one size or to a limited range of display shifts was sufficient for the animals to make appropriate responses to a wide range of stimuli. Even for a novel stimulus size, the response derivatives remained scaled. Thus, the animals learned a general response strategy.

These observations suggest that the dynamic phase of the response trajectory is governed by an initial phasic control signal of variable amplitude and limited duration. The final force or position is governed by a tonic command which may be represented as a step (Ghez and Vicario, 1978b). Under constant loading conditions, the ratio of these two components has an approximately constant value. Both components are modulated in amplitude according to the requirements indicated to the animal by display shifts of different sizes.

The notion of an initial amplitude-modulated phasic command was also supported from electromyographic (EMG) recordings of agonist muscles during rapid responses (characterized by steep relations between the changes in force or displacement and their derivatives). Under conditions where both agonist and antagonist were silent at the initial resting force level, a single burst of activity is seen in the agonist coinciding with the rising phase of either dF/dt or acceleration. Although the integrated EMG activity in the burst correlates with the peak value of dF/dt (and in the anisometric case with the peaks of both acceleration and velocity), the duration of the burst does not, and it remains independent of the size of the response (see Desmedt and Godaux, 1977a, 1978b and Freund and Budingen, 1978 for comparable studies in humans). Similar EMG and kinematic results have recently been reported in both intact and deaffer-

ented monkeys (Lamarre et al., 1980). Those findings indicate that the phasic and tonic components of the motor strategy do not depend on sensory feedback.

Although the amplitude of the initial EMG burst is likely to reflect the magnitude of supraspinal control signals, the termination of this burst is likely to be strongly influenced by segmental mechanisms. Such mechanisms include post-spike hyperpolarization and recurrent inhibition in the motoneurons (MN) and other factors (Burke and Rudomin, 1978) that may contribute to burst termination. Thus, the initial force impulse can result from an excitatory supraspinal signal of limited duration, which is further sculpted by local negative feedback mechanisms. The resultant amplitude-modulated command appears to represent a feed-forward control signal to overcome the low-pass properties of muscle (Partridge, 1965), viscosity of muscle-tendon linkages, and limb inertia (Ghez, 1979; Partridge and Benton, 1981). Responses with these properties can be considered ballistic in that a major portion of the force or position trajectory is determined by an impulsive command limited to the accelerative phase (or the rising phase of dF/dt) (see Desmedt, 1981a).

Under constant loading conditions, the ratio of phasic and tonic components of the descending command appears to be closely regulated. This ratio is, however, adaptively altered (in the absence of any selective reinforcement procedure) when the configuration of opposing loads is changed (Ghez, 1979). When viscous loads which oppose movement are experimentally increased, humans (Taylor and Birmingham, 1948) and cats (Ghez, 1979) adapt by increasing initial phasic torques and thus increase the pulse-step ratio. When elastic loads are changed, the cats adapt by corresponding changes in both phasic and tonic torques (Ghez, 1979).

In experiments where inertial rather than viscous loads were imposed, adaptive increases in the pulse-step ratio are con-

strained because instability or overshoot of final position can result from a strategy which increases phasic torques to maintain high initial velocities. Thus, with a high moment of inertia, the peak velocity remains markedly reduced over controls, even with extensive training (see also Taylor and Birmingham, 1948). The EMG activity may also fail to show a well-formed initial burst in the agonist, and cocontraction of the antagonist becomes conspicuous. These alterations do not result from the added load opposing the initial acceleration but, rather, from changed mechanical requirements associated with accurate termination of movement. Indeed, had the peak velocity remained the same, the animal would have had to actively decelerate the limb. Otherwise, the momentum (mass \times velocity) of the moving limb would have produced overshoot beyond the desired final position. We have verified this by comparing the trajectories of movements opposed by an inertial load (simulated by acceleration feedback) with ones where the forces opposing acceleration were the same but where the need for active deceleration was eliminated. This was achieved by half wave rectifying the acceleration signal used as a feedback controlling the torque motor. With this condition, the subjective feel of the lever resembled that of a bicycle wheel where a ratchet mechanism prevents the foot from being dragged when pedaling stops. Under this latter condition, which effectively eliminates momentum, the animal gradually increased initial acceleration to produce movements that were similar to both unloaded conditions and to those associated with viscous loads. Thus, increasing demands for control of the terminal phase of movement are normally met by decreasing the initial phasic command coupled with cocontraction, rather than by producing a precisely timed phasic burst in antagonist muscles to decelerate the limb. Cocontraction serves to increase the stiffness of the joint at the terminal equilibrium point (Polit

and Bizzi, 1979; Hogan, 1980; Lestienne et al., 1981) and may be controlled by a specific population of cortical neurons (Humphrey and Reed, 1981, *this volume*).

These observations have the following implications: (1) Under isometric or under constant loading conditions, force or limb trajectories are directed and scaled from their inception according to earlier sensory events from the display. (2) The phasic torques which contribute to limb trajectory are under adaptive control to take into account both the magnitude of opposing loads and the mechanical consequences of rapid movement. Therefore, changes in steady-state commands producing rapid or gradual shifts in the mechanical equilibrium points (Feldman, 1967; Polit and Bizzi, 1977; Cooke, 1979) cannot be regarded as the sole determinant of limb trajectories.

The adaptive control of phasic and tonic components of the motor output suggests that performance of the task allows the cats to generate an internal model of the peripheral plant. This model includes the static and dynamic forces opposing movement of their limb as well as late reactive events (Bernstein, 1967) arising as a consequence of movement. This view is also compatible with the recent observations of Bizzi and Abend (*this volume*) on the control of limb trajectories in monkeys. Our results suggest that the pulse-step ratio could represent a principal variable under adaptive control. Additionally, we propose that the level of cocontraction is principally determined by the reliability of the model of the peripheral plant and to be under separate adaptive control. (See Ghez and Martin, 1982 for further discussion of this issue in relation to triphasic EMG patterns occurring in rapid limb movement.)

Factors Affecting Reaction Time: Role of Stimulus Uncertainty

The sudden shift of the display elicited appropriate motor responses with extraordi-

narily brief latencies. Response latency was dependent on the sensory modality and intensity, as well as on the magnitude of the motor output measured as the rate of change of force (Ghez and Vicario, 1978a). These relationships are attributable to modality-specific differences in sensory processing time and to spatial and temporal summation in central and segmental relays (Ghez and Vicario, 1978a). Response latency did not vary with the accuracy of the initial force or position response. However, a systematic decrease in latency occurred as the length of training increased. Cats trained for several months to 2 years have daily mean latencies (measured from target step to first change in dF/dt) of 50 to 70 msec (Ghez and Vicario, 1978a). Cats trained for 2 to 3 years reveal still lower daily mean latencies between 40 and 50 msec. Similar effects of extensive training have been reported in humans (Mowbray and Rhoades, 1959).

In all cats, the response latency was not dependent on uncertainty in the time, direction, or magnitude of the stimulus (Ghez and Vicario, 1978a) (Fig. 2). In Fig. 2A, the open histogram represents latencies of isometric responses of a given size to a stimulus the amplitude of which was maintained constant for over more than 50 trials. The shaded histogram represents the latencies to a stimulus of the same amplitude presented within a series of randomly varied stimulus amplitudes (eliciting responses of different sizes). In Fig. 2B the two histograms illustrate, in a second animal, latencies to target shifts of constant amplitude and direction (open histogram) and of responses under conditions of directional uncertainty (shaded histogram). The responses in the shaded histogram were made to target shifts of the same direction as those in the control series that were embedded as surprise trials (average: 1 in 10 trials) within a series of target shifts in the reverse direction. In both cases, the latency distributions overlap, with no significant differ-

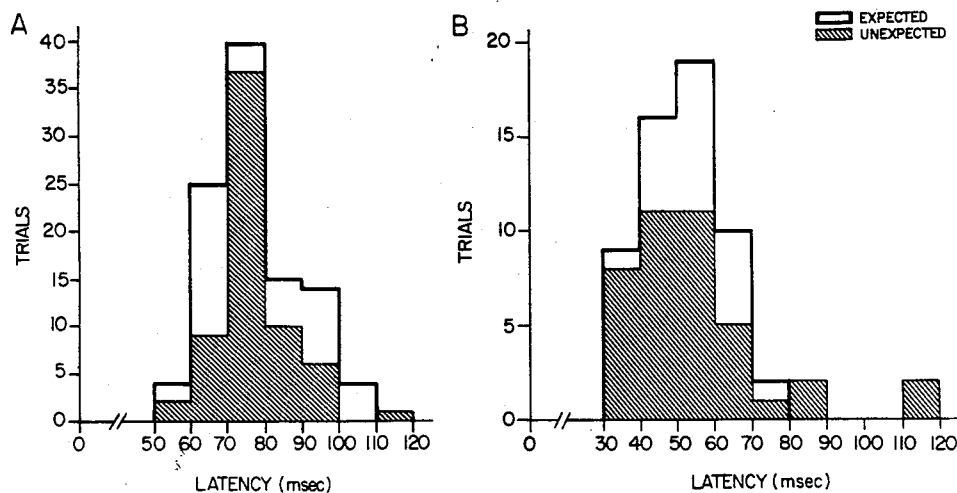


FIG. 2. Influence of uncertainty in amplitude and direction of target shift on response latency. A: *Hatched histogram* illustrates the distribution of response latencies to target shifts of set amplitude presented during a series of trials where perturbation amplitude was varied randomly (mean latency = 77.2 msec, SD = 10.7 msec, SE = 1.3, $N = 65$). *Open histogram* shows the distribution of response latencies measured during control trials where animal was presented target shifts of set amplitude only (mean latency: 77.2 SD = 11.9, SE = 1.2, $N = 102$). B: *Hatched histogram* shows the distribution of response latencies to target shifts eliciting extensor responses presented randomly in a series of trials requiring flexor responses (mean latency = 54.5 msec, SD = 19.1, SE = 3.0 msec, $N = 40$). *Open histogram* shows the distribution of extensor response latencies under conditions where the animal expected only target shifts requiring extensor response (mean latency = 51.4 msec., SD = 10.7, SE = 1.4, $N = 56$).

ences for conditions of either amplitude or direction uncertainty. In conclusion, the need to estimate either the magnitude or the direction of the response required by the stimulus does not add time to the processing of sensory events (see also recent findings in primates by Georgopoulos et al., 1981). Rather, response latency depends only on the sensory modality, stimulus, and response amplitudes, and the level of training. Furthermore, the time of onset of motor responses is not determined by the demands of specific information processing interposed between sensory events and the motor output commands.

Continuous Control of Motor Output by Newly Acquired Sensory Information

Another challenge to the neural processing of targeted movements occurs when a new

stimulus appears before the response to a first target is completed. When human subjects are required to respond to two stimuli delivered in quick succession, the latency of the response to the second stimulus is prolonged (Telford, 1931) and occurs approximately a reaction time after the first response. This suggested intermittency in the processing of serial stimuli (Navas and Stark, 1968), as if stimuli-eliciting responses were processed by a unique channel of limited capacity (Welford, 1980). However, the observed lengthening in reaction time varies in different task conditions (Vince, 1948; Welford, 1952, 1980; Brebner, 1968; Megaw, 1972). This single-channel formulation implies that information about a second stimulus may be stored during the processing associated with the first stimulus.

These issues were addressed by examin-

ing the cat's responses to a second target shift when presented during the first reaction time or during the dynamic phase of the first response. Cats performed isometric force adjustments with their forearm in response to sequences of two-step changes of target levels presented at various interstimulus intervals (ISI) (double stimulation). In addition, the response of one animal to delayed feedback was examined. The double stimulation or delayed feedback was always introduced on surprise trials

presented at random within a much larger series of single stimulus trials.

Double stimulation

When presented with two successive target steps, the animals always either aborted their responses or increased the force they exerted on the lever according to the direction of the second stimulus (Vicario et al., 1979) (Fig. 3). In Fig. 3A, averaged ($N=12$) control and test trials are shown for surprise stimuli requiring the animal to abort

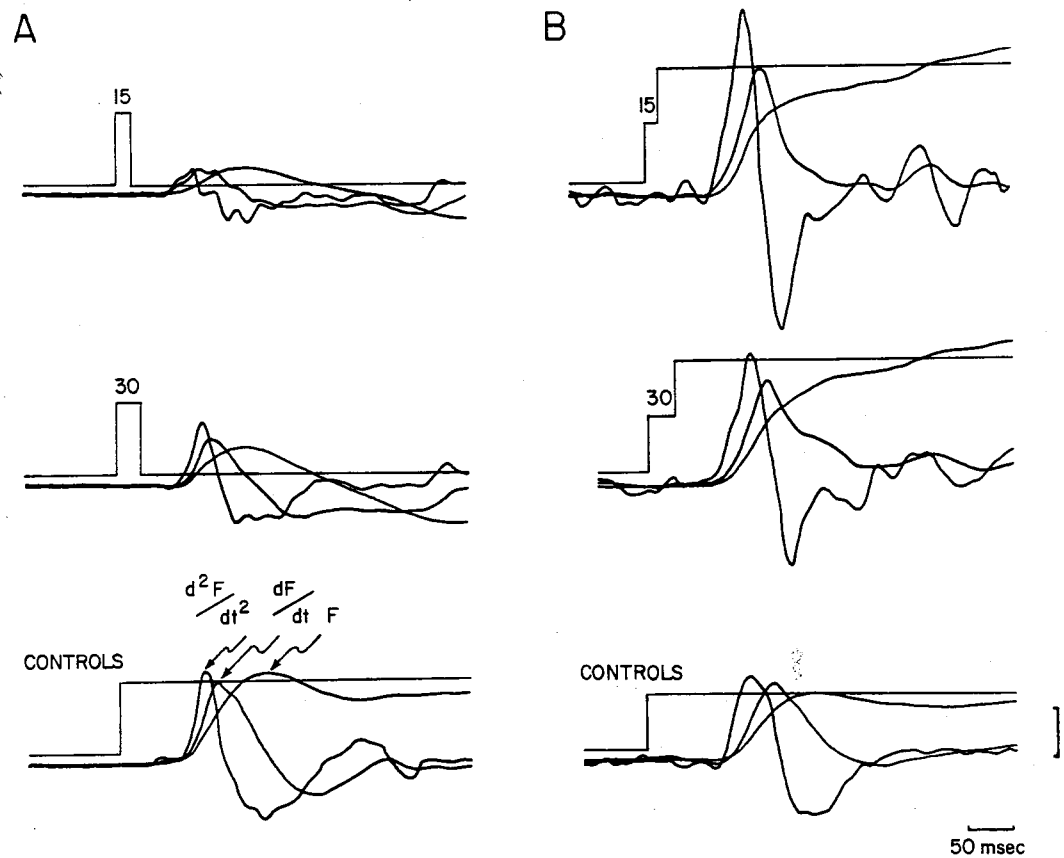


FIG. 3. Average ($N = 12$) responses to double target steps. A: Responses when the second step required the force to return to the baseline level. The animals force trajectory (F) and its first (dF/dt) and second derivatives (d^2F/dt^2) are shown together with the timing of target steps. Top two sets of traces show responses for interstimulus intervals of 15 and 30 msec. The bottom set shows control traces obtained when only one target step was delivered. B: Responses when the second step required an increase in the final force output. All traces as in A. Vertical calibration: 0.5 Newtons, 12.5 Newtons/sec, 500 Newtons sec². Averages synchronized with target steps.

its force response after ISIs of 15 and 30 msec. The first stimulus required extension and the second, a return to baseline. In contrast to what one might have expected had new target information been sampled intermittently or stored while awaiting the programming of the first response, the second stimulus causes the animal to abort the ongoing response immediately. Both the peak force and the first derivative of force are reduced when compared to the control trials (bottom of the figure). In these experiments, where the second stimulus called for termination of the response, both the magnitude and the duration of the initial EMG burst are reduced. In Fig. 3B, the second target step required an increase in the level of force at ISIs of 15 and 30 msec. Here again, the animal effectively updates its response by increasing both the first derivative of force and the final force achieved. The effectiveness of updating is dependent on the ISI. For ISIs of 15 and 30 msec shorter than the time from response onset to the peak dF/dt of the first response (i.e., during the impulsive phase of the response), both the resulting peak value of the second derivative of force, d^2F/dt^2 , the peak dF/dt and the integrated EMG of the initial agonist burst were increased, but burst duration was not lengthened. For ISIs exceeding the time from onset to peak dF/dt , the force derivatives corresponding to the second response were reduced relative to controls. Response returned to control levels for ISIs of ≥ 250 msec. The EMG activity associated with the second response also varied with the ISI, showing a marked depression for values slightly longer than the time to peak dF/dt . Thus, for ISIs of 30 to 50 msec, the integrated EMG burst of the second response was reduced to only 30 to 40% of control values associated with the response to the first stimulus. Thereafter, a slow recovery took place with a return to control values for ISIs of >200 msec.

Cats are thus capable of using sensory

information to update evolving motor responses in the present tracking task. For short ISIs this updating process is accomplished by amplitude modulation of the phasic output associated with the initial response. The effectiveness of such updating is limited by the time remaining within the phasic period. For longer ISIs, transient refractoriness is observed which does not delay the time of onset of the second response, but reduces its amplitude. Such refractoriness may be due to segmental mechanisms associated with the abrupt termination of the initial EMG burst, or to masking phenomena in various sensory nuclei conveying target information to central structures (Judge et al., 1980; Laskin and Spencer, 1980). The finding of continuous and effective response modulation for ISIs within the time to peak dF/dt may be analogous to response grouping (lack of separable responses) sometimes observed at short ISIs in human double-stimulation experiments (Welford, 1980). Such "grouping" is usually discussed in terms of the time course of single-channel loading. In our case this initial period corresponds to the interval during which phasic response initiation signals can gain access to MN pools before being significantly modified by the segmental consequences of MN excitation. In the more common case where positional responses to serial stimuli are studied, mechanical factors introduce significant delays between muscle contraction and a measurable response. Moreover, segmental influences and feedback effects make interpretation of late motor outputs problematic. Nonetheless, using a light-weight manipulandum, trained monkeys can modify their targeted movements with only a small increase in reaction time when a new stimulus is presented (Georgopoulos et al., 1981).

Delayed feedback

When feedback of the force error was delayed on random trials, the animal's initial

force response returned the display to center only after a given delay interval. Feedback delays of 60 to 180 msec were presented at random. If sensory information from the display was sampled or used intermittently, the ensuing response should consist of a series of discrete steps in the form of a staircase. This was, however, never observed; rather, the animal's response showed a continuous increase in force until the display was affected by the initial response at the end of the delay period (Fig. 4). The upper traces of Fig. 4A show ensemble averages of control and test force responses. The lower traces show the associated control and test display trajectories. In Fig. 4B, the first derivatives of the response and of the display illustrate more clearly the method used to determine when divergence in the trajectories takes place. In addition, response and display derivatives are shown for a delayed feedback of 180 msec. Averages collected for trials at a feedback delay of 180 msec were used as control trajectories for determining the late stimulus and response events (S3 and R3). R3, at the turnaround of the force trajectory, occurs after the initial force response at R1 has altered the display trajectory at S3. The updated responses R2 and R3 to the effective stimuli in S2 and S3 had only slightly longer latencies (mean 20 msec) than those of the initial responses. These small differences are predictable from the reduced stimulus and response amplitudes associated with later stimuli (see Ghez and Vicario, 1978a).

In order to obtain the most accurate estimate of the point of divergence of the control and test response trajectories, a special procedure was used to select the responses serving as controls in the absence of delayed feedback. This procedure was based on our previous observation that the early components of the force trajectory (the first and second derivatives of force, in particular) were predictive of the ensuing force profile. The first 50 msec of the first deriva-

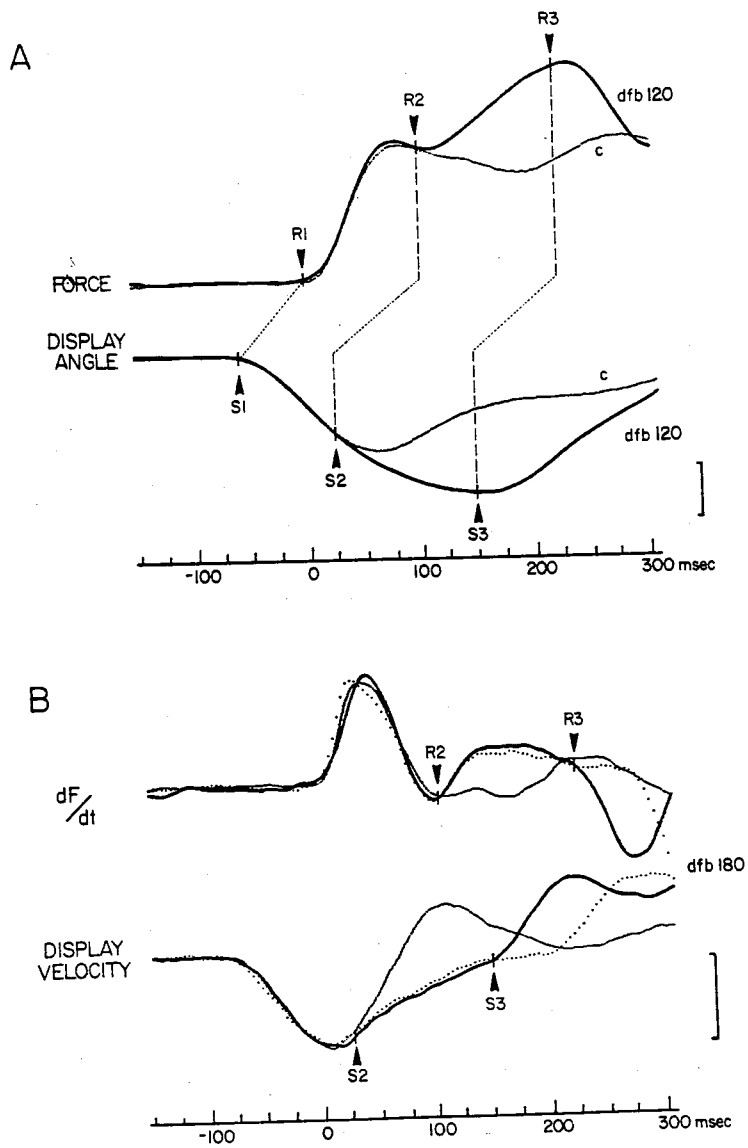
tive of the initial component of the force response in each test trial with delayed feedback was taken as a template to select among control responses the one that most closely approximated it. Using this procedure, the bin where the test and control responses diverged could be computed and the time of onset of the updated response determined.

In conclusion, the results support the concept that the responses are under continuous control by the display, and further indicate that sensory events produced by specific features of display motion cannot simply act to trigger a fixed, predetermined motor response (cf. Houk, 1978). If this were so, delaying feedback should not influence the cat's response, since the effect of the delay is to allow a display trajectory to unfold, which the cat normally experiences when its response latency is prolonged. Since the configuration and accuracy of short- and long-latency responses are identical (Ghez and Vicario, 1978a), the cat must take its response into account to interpret the stimulus. Thus, the effective neural signal determining the response is likely to be derived by the animal on the basis of a comparison between actual stimulus events and those predicted on the basis of its motor response. This implies that when learning the task, neural mechanisms generate an internal model of the display. We assume that parameters of such a model would be governed by an adaptive controller so that subsequently presented stimuli might be processed differently.

Discussion

A striking feature of the behavior elicited in our tracking task is the short, reflex-like latency of motor responses elicited by display shifts. The general rules governing targeted limb movements in cats indicate, however, that this behavior differs from both reflex actions and triggered voluntary

MOTOR CONTROL OF TARGETED MOVEMENTS



responses, described in humans while sharing some of the properties specific to both. As in many reflexes, the direction and intensity of the responses reflect those of particular sensory events. In our targeted response, these sensory events are produced by movement of the display in one or another direction. The tracking responses are altered in a fashion similar to what may be expected of a reflex when the stimulus is either curtailed or increased by double stimulation.

Tracking performance differs, however, from reflex behaviors in several respects. First, the behavior is learned, and adaptive changes in response configuration occur in relation to the achievement of an appetitive goal. Both the topography and gain of the stimulus-response relationship are rapidly changed when display properties (Ghez and Vicario, 1978*b*) or loading conditions are altered (Ghez, 1979). Adaptive changes in direction and gain of the vestibulo-ocular reflex have also been documented (Miles and Fuller, 1974; Gonshor and Melvill Jones, 1976*a,b*; Melvill Jones and Davies, 1976; Robinson, 1981; Melvill Jones and Mandl, *this volume*). In that case, however, the

changes in direction are slow to develop and eventually constitute a new stable property of the system. The adaptive changes in phasic and tonic components of the motor program which regularly and rapidly follow changes in load in our paradigm suggest that response configuration is critically dependent on an internal representation of the complex properties of the peripheral plant. Although the nature of such a representation is at present uncertain (see Saltzman, 1979); it must be stored and regulated by mechanisms that are fundamentally different from those that determine the response. Second, the nature of the responses obtained using delayed feedback suggests that complex comparisons are required in sensory processing as well. We have proposed earlier that the neural signal determining response updating might be derived from a comparison of afferent input with an internal representation of display properties based on recently acquired information. A final difference between tracking performance in our task and reflex action is that the output configuration is not dependent on which sensory modality conveys information about the display. Similar rules ap-

FIG. 4. Responses obtained when force feedback was delayed 120 msec (DFB 120). A: The upper traces show superimposed ensemble averages of control (*light trace*) and test (*heavy trace*) responses obtained on trials when the display was unresponsive to the animal's output for a period of 120 msec following the target stimulus. The *lower traces* show superimposed averages of display trajectories for the control and test trials. Averages of 10 trials in each condition were synchronized by the onset of the force response. Control trials were selected by a matching procedure using the first 50 msec dF/dt of the force response as described in the text. Arrows S1, S2, S3 indicate the times of divergence (from the control trajectory) of the test display trajectory which elicited the three force responses at arrows R1, R2, R3. Vertical calibration: 0.5 Newtons, 10°. B: For the same trials as in A, the traces show superimposed averages of first-force derivative and display velocity of control (*light traces*) and DFB 120 msec delayed trials (*heavy traces*). Dotted traces show averaged responses and display velocity for trials where the feedback delay was increased to 180 msec (DFB 180). These traces are superimposed to illustrate the algorithm used to determine the timing of late stimulus and response events (S2, S3, R2, and R3). S2 was determined by the divergence of control and test display velocities, R2 by the divergence of control and test dF/dt . S3 was determined by the divergence of display velocity of the DFB 120 and DFB 180 trials, since the third effective stimulus is the onset of the resumption of display feedback which begins to return the feeder to the center position. R3 was determined by the divergence of dF/dt for the DFB 120 and DGB 180 trials: i.e., when the animal stopped exerting increasing force because the display had become responsive. Vertical calibration: 15 Newtons/sec, 180 degrees/sec. All traces are averages ($N = 10$) synchronized with force onset (R_1).

ply when responses are elicited by visual, vibrissal, and combined inputs.

Both the short absolute latency and the factors by which it is influenced distinguish our tracking behavior from triggered voluntary responses commonly observed in man. Triggered responses are generally postulated to include a process that selects the category of response appropriate to the behavioral goal. The notion that response selection intervenes during the reaction time interval is derived from observations that the latency of motor responses increases progressively with the number of choices available (see Welford, 1980). Additionally, the translation of sensory information into "motor commands" is also assumed to be subject to a limited information handling capacity (Welford, 1952, 1980). These considerations have suggested that voluntary behaviors involve a more digital process than reflex actions, which more closely resemble analog transformations (Houk, 1978). Neither of these two constraints, however, applies in our paradigm, since correct responses are made to both predictable and unpredictable stimuli appearing singly or in pairs.

Under conditions applying in our task (see below), input-output processing is simplified to eliminate the need for response selection during the reaction time interval and a category of motor response emerges with the automatic (and analog) properties of reflexes and the flexibility of voluntary responses. We propose that the neural mechanisms involved implement a set of spatial rules which determine the topographic correspondences between sensory inputs from the display (target) and elements of the motor output representations. This set of rules, formally analogous to a map, would allow any member of an ordered array of sensory inputs providing direction and magnitude information to access specific output elements without the need for a selection or programming opera-

tion to intervene in the reaction time interval. Thus, prior to the occurrence of the display shift, contextual cues indicate to the animal the processing it will have to perform and thereby determine behavioral set. Then, appropriate elements process incoming and outgoing signals according to the specific expectations embodied in the models. Errors occurring during performance of the task and exposure to changing conditions are considered to act on adaptive control elements which alter internal models and maps.

In human subjects, a decrease in the susceptibility of reaction time to the number of choices available is known to occur with practice for highly compatible stimulus-response conditions. For example, when human subjects must move the finger to which a vibratory stimulus is applied, the increase in latency with increased numbers of possible stimuli is modest (Smith, 1979). In general, however, stimulus-response compatibility is a post hoc explanation given to explain differences in susceptibility to choice effects (Welford, 1980). It implies the existence of a set of rules which may be used to connect ordered sets of stimuli (possibly even of a symbolic nature) and responses (Duncan, 1977). In certain cases, this notion is applied to the spatial demands of the task (Fitts and Deininger, 1954). It is, however, unclear to what extent "compatibility" differences reflect constraints relating to preferential stimulus-response linkages or rather to high levels of practice obtained from every-day experience with demands similar to those of the task. All these considerations may apply to our task and our highly practiced subjects. In addition, several other attributes of our task may simplify input-output requirements and encourage learning of a general response strategy rather than just individual stimulus response pairs. (1) The task itself can be viewed as requiring the transformation of a stimulus amplitude and direction

into a response with similar dimensions and where only the direction and filter parameters need adjustment. (2) The compensatory nature of the tracking task requires the animal to attend only to a single input (rather than to both a target and a cursor, as in pursuit tasks), thus simplifying the spatial demands made on attentional mechanisms (Posner et al., 1980). (3) The lack of temporal and spatial discontinuities of the display and its linear properties allow the information provided by its trajectory to be highly redundant.

B. Roles of the Motor Cortex in the Initiation and Control of Voluntary Motor Responses

The extremely short latency in behavioral task suggested that only a few processing stations need be interposed between the arrival of target information and the generation of motor commands and that, within limits, new response requirements can be fairly directly relayed to motor structures. These considerations and the documented role of the primate motor cortex in movement (Phillips and Porter, 1977; Evarts and Fromm, 1978; 1981) led to the following questions: (1) Can the motor cortex contribute to the initiation of responses with such short reaction times? (2) Do the patterns of discharge of task-related neurons reflect the existence of a preset input-output relationship activated by the arrival of a signal derived from the stimulus? (3) What is the relationship between task-related neural activity and the specific homotopic input-output organization documented in acute physiological studies (Asanuma, 1981). To approach these questions, we recorded the activity of single neurons in the motor cortex of 6 cats trained to perform isometric responses in the compensatory tracking task described above. Differences in peripheral receptive fields and in task-related patterns of single unit activity were

observed between pre- and postcruciate regions of motor cortex (area 4 γ). A parallel series of experiments was conducted to determine the anatomical differences in projections to these two regions. (section C).

Functional Specialization Within Area 4: Regional Differences in Receptive Fields and Task Relations

Penetrations were made in the lateral halves of the anterior and posterior sigmoid gyri. Intracortical microstimulation (ICMS) was applied at 500- μ m intervals and following the recording of each neuron to ascertain its location within the somatotopic representation in motor cortex. Single neurons were sampled in areas where ICMS, using currents of $\leq 20 \mu$ A, produced contraction of forelimb muscles active in the task (Ghez et al., 1982). Approximately 450 neurons were found to show a clear temporal relation between changes in their activity and behavioral events during task. Most neurons could also be driven by somatosensory stimuli to the forelimb while the animal was at rest and not performing the tracking task.

Receptive fields fell into two broad classes which we called simple and complex. Throughout the arm area of the motor cortex (defined by ICMS and by histologic reconstruction), neurons were found with discrete cutaneous or deep receptive fields (simple fields) (cf. Brooks et al., 1961a,b; Buser and Imbert, 1961; Asanuma et al., 1976). In addition, many neurons were observed whose forelimb receptive fields had more complex temporal or spatial characteristics (complex fields). The response of some of these neurons was temporally labile, being brisk at times, then diminishing or disappearing entirely within seconds or minutes, only to reappear a short time later. Such neurons have also been noted by others (Brooks et al., 1961a,b; Brooks and Levitt, 1964; Baker et al., 1971). Other neurons classified as complex were those with

directional receptive fields on the skin, those that received convergent input from superficial and deep receptors, and those showing multiple excitatory and inhibitory foci which could be spatially discontinuous. Neurons with one or more of these complex properties were preferentially located in regions of area 4 γ rostral to the cruciate sulcus, where they represented about 45% of neurons with peripheral receptive fields. In contrast, complex fields were only observed in about 10% of neurons caudal to the cruciate sulcus. Comparable rostro-caudal differences in receptive field properties have been reported in acute preparations (Buser and Imbert, 1961; Brooks et al., 1961a,b; Brooks and Levitt, 1964).

Dramatic differences were also observed between rostral and caudal portions of the arm area of motor cortex in the timing of neuronal discharge during task performance. Only units in rostral regions were modulated in advance of the animal's force response (lead cells), although task-related activity that lagged force production (lag cells) was observed in both rostral and caudal regions. The change in lag cells could often be attributed to stimulation of the neurons' receptive field which accompanied the behavioral response. For example, a neuron which was passively driven by stimuli to the hair on dorsal forearm was also phasically activated during elbow flexion, which produced shearing of the skin around the strap securing the forearm to the lever. However, this close association was not always seen and many neurons with exquisitely sensitive cutaneous or deep receptive fields in the responding limb or muscle, were not modulated during either the phasic or tonic portion of isometric or isotonic responses. The regional differences observed in all animals are schematically illustrated for the rostral (MC_r) and caudal (MC_c) compartments of area 4 (Fig. 5).

Although lead cells constituted only about 10% of all task-related units, they

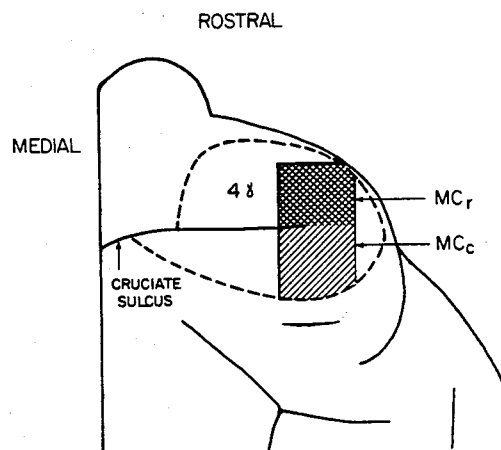


FIG. 5. Functional specialization in feline motor cortex. Motor cortex (area 4) is surrounded by dashed line. The area within the solid line schematically illustrates the regions where microstimulation elicited forearm movements at $\leq 20\mu\text{A}$ in 6 cats. *Hatched area*: Region from which cells with simple receptive fields were recorded and where task-related activity lags force response (includes MC_r and MC_c). *Cross-hatched area*: Approximate location of cells with complex receptive fields and whose task-related activity on average leads force response (MC_r only).

were more extensively evaluated because only this population of neurons could have contributed to response initiation. Approximately 80% of the 45 lead cells examined had receptive fields of the complex type, suggesting that such neurons receive complex convergent patterns of peripheral input. Of the lead cells, 90% showed reciprocal response patterns with increased activity for forearm force in one direction (either flexor or extensor) and decreased or no modulation for force developed in the opposite direction. The modulation in unit activity of lead cells could be characterized as phasic (14%), tonic (22%) or, in the majority of cases, mixed (64%). In 80% of lead cells, the degree of modulation in activity varied with one or more of the following parameters: rate of change of force, steady-state force developed, or integrated EMG in

agonist muscles. These discharge patterns and output properties are comparable to those reported for neurons in monkey motor cortex during conditioned arm movements (Evarts, 1966; 1968; Lamarre et al., 1978; Thach, 1978; Fetz and Cheney, 1980) and isometric responses (Smith et al., 1975; Hepp-Reymond et al., 1978). The differences in properties of single neurons described imply a functional subdivision of the cat motor cortex and may correspond to the dual representation of forelimb muscles documented by Pappas and Strick (1979, 1981a) using ICMS. We have regularly confirmed their finding that low-threshold effects in a given muscle can be obtained from discontinuous sectors within area 4 (see Anderson et al., 1975; Jankowska et al., 1975; Strick and Preston, 1978a; Kwan et al., 1978; for results in monkey). Furthermore, our observations show that neurons recorded in a zone from which low-threshold ICMS effects in a given muscle are obtained need not lead the contraction of that muscle during execution of a learned behavioral response.

Mapping of Target Related Sensory Inputs in Neurons of MCr

The finding that activity of lead cells in rostral motor cortex was not as tightly coupled to events arising in the periphery as traditional input-output mapping had suggested (Asanuma, 1975) raised the possibility that they receive other inputs. To determine whether sensory inputs associated with display motion might be coded in their activity, we first examined, trial-by-trial, the times of onset of changes in unit activity in relation to the stimulus and the force response. Next, to dissociate effects related to the magnitude and direction of stimulus from effects related to ensuing responses, we examined unit activity when the gain or polarity of the error signal controlling the display was changed.

Timing of lead cell activity: Stimulus Synchronization

Surprisingly, 85% of lead cells showed a consistent temporal relationship to the stimulus, a relationship that was largely independent of reaction time. To illustrate this, raster displays of unit activity recorded during single trials were sorted according to reaction time and aligned with the onset of the force change (Fig. 6). The trials with the shortest reaction time are at the top of the rasters. The small plus signs mark the time of occurrence of the stimulus and the zero on the abscissa is the onset of force change. In part A, unit activity is increased with extensor responses elicited by display movement in one direction, and in B, the activity of the same unit is suppressed with flexor responses elicited by display movement in the other direction. These rasters show the reciprocal character of the changes in unit activity. Both increased and decreased unit activity occurred with a consistent latency from stimulus rather than remaining aligned with the onset of the response. The amount of lead of unit activity relative to the onset of the force response varied as a function of reaction time. In Fig. 7, the time by which the change in unit activity leads onset of force response is plotted against the response latency for each trial (see legend). Note in part C that this relationship also applies when the range of reaction times is large. These figures also show that when reaction time is unusually short a unit's activity may actually lag the response. On these axes, a unit, the activity of which was exactly timed to the occurrence of the stimulus would be represented by a regression line with a slope of 1.0. The line for a unit timed to response onset would have a slope near zero. In 38 of 45 lead cells examined, the relationship between lead and reaction time showed a significant correlation coefficient. The slopes of corresponding lead-reaction time regression lines were distributed around a

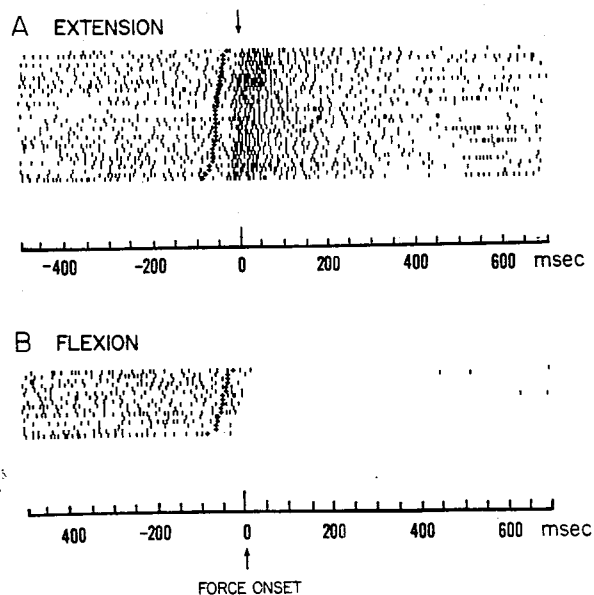


FIG. 6. Modulation of lead cell activity is time-locked to stimulus. A and B: Spike rasters synchronized by the onset of extensor and flexor force, respectively. Rasters are sorted by reaction time with shortest RT shown on top and longest on bottom. + signs mark the time of occurrence of the shift in display position (i.e., stimulus).

mean value of 0.92 (Fig. 8). Thus, the timing of onset of lead activity in rostral motor cortex is better correlated with the stimulus than with the ensuing response. Neurons discharging after the onset of the response (lag cells) typically exhibited lead-reaction time regression slopes which were close to zero (correlation coefficients not significant). In 10 of 13 such units, the variance in latency from stimulus to unit onset was greater than that from force onset to unit onset. This is compatible with lag cells being driven by stimulation of their receptive fields during the behavioral response.

Task-related units in forelimb motor cortex could not be driven passively outside of the context of task by visual, vibrissal, or other stimuli of the type associated with display movement. They were, however, often observed to fire during spontaneous movements of the forelimb. The task-related activity of both lead and lag cells was contingent on the occurrence of behavioral responses (Fig. 9). When reinforcement was withheld, behavioral responses extin-

guished and changes in unit activity no longer followed shifts in the display (B). In trials with incomplete or aborted responses (C), the perireponse time histograms show intermediate amounts of modulation. Thus target-related sensory information is conveyed to neurons in the rostral portion of the arm area of motor cortex in a contingent fashion, and confirms the relation between unit modulation and response magnitude. In addition, for this unit and 5 others that were fully analyzed, unit activity showed a relationship to the amplitude of the stimulus. Since, for a constant stimulus, these cells also exhibited a relation to the amplitude of the response, only a display gain manipulation could fully dissociate stimulus and response amplitudes. When the display gain was changed, the force required remained the same, but the amplitude of the stimulus was different. Fig. 9D shows perireponse time histograms of unit activity in trials following adaptation to a reduction in display gain to one half that of controls in A. For averaged force responses which are

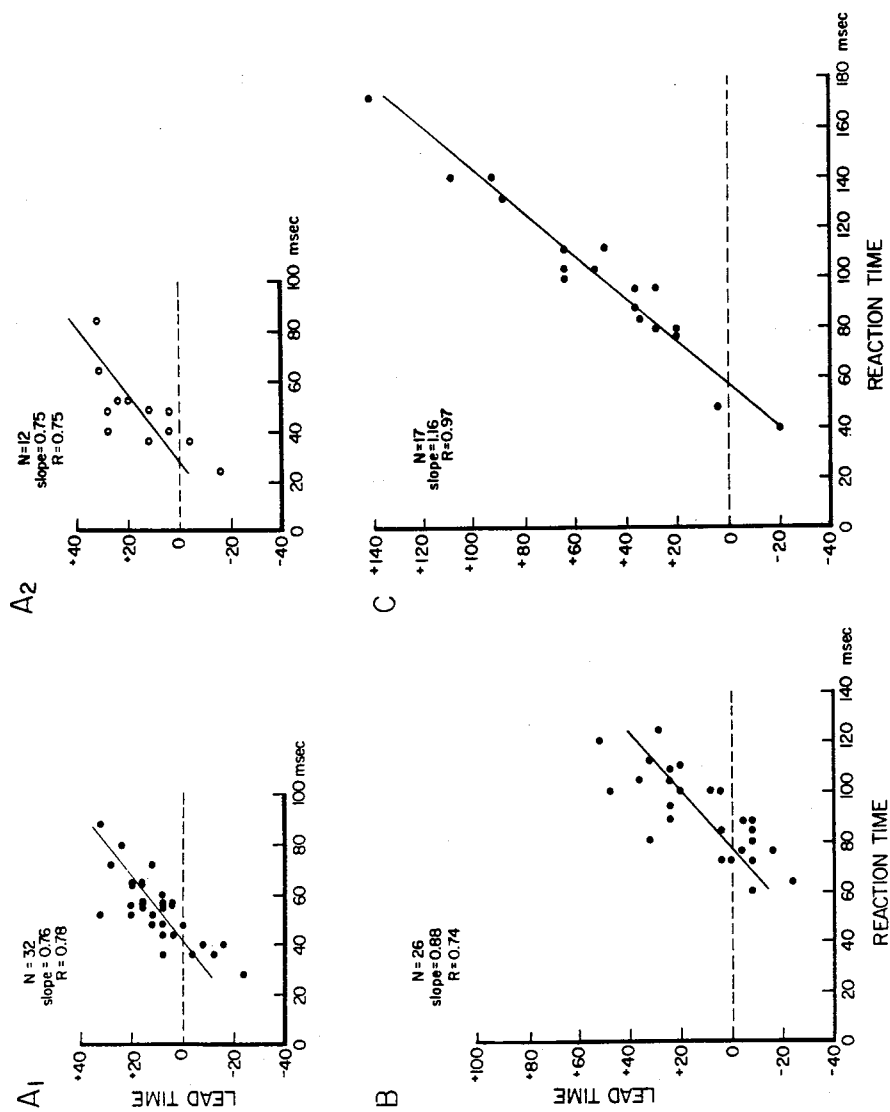


FIG. 7. Relationship between unit lead time and reaction time. Scatter plots for lead time (time from change in unit activity to force change) as a function of reaction time (time from shift in display position to onset of force change). Negative values on ordinate signify lag. A: Scatter plots for unit shown in Fig. 6. A₁: relationship for excitatory responses (*filled circles*) to display shift eliciting extensor responses (i.e., Fig. 6A); A₂: inhibitory responses (*open circles*) to display shifts eliciting flexor responses (i.e., Fig. 6B). B and C: As in A, except for the excitatory responses of 2 different units to display shifts eliciting flexor responses.

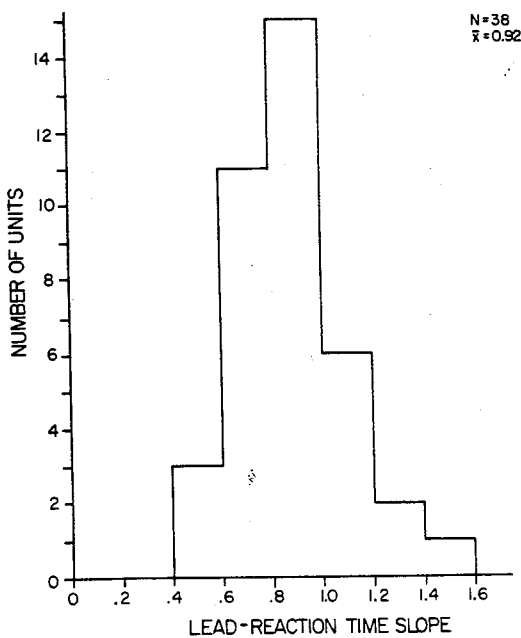


FIG. 8. Histogram of linear regression slope for lead-reaction time relationship. All units included in this histogram exhibited significant lead-reaction time relationships.

comparable to those illustrated in A, the unit activity is markedly reduced.

Changes in stimulus-response relations in lead cells

These observations suggest that the activity of lead cells reflects sensory information related to display movement, but is also contingent on a specific behavioral set. Two possible mechanisms may be envisaged to account for this phenomenon. First, as shown for neurons in monkey posterior parietal cortex and frontal eye fields, the behavioral set associated with task performance could uncover a receptive field in a fixed location which was not, however, detectable when the animal was examined under passive conditions (Wurtz and Mohler, 1976; Yin and Mountcastle, 1977; Robinson et al., 1978; Bushnell et al., 1981; Goldberg and Bushnell, 1981; Mohler et al., 1973; Motter and Mountcastle, 1981). Alternatively, the stimulus site producing excita-

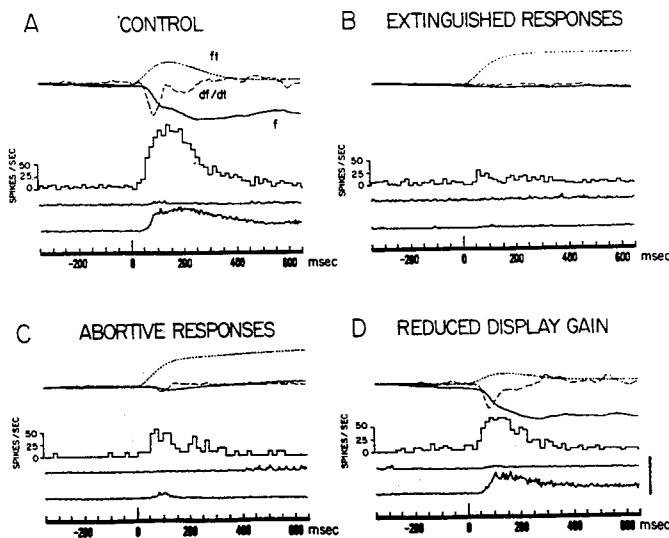


FIG. 9. Lead-cell activity is contingent on behavioral response. A: Control trials, averages ($N = 47$) synchronized by the onset of display movement; from top to bottom, display position (ft), df/dt , force, periresponse time histogram of unit activity, triceps EMG, and biceps EMG. B: Extinguished responses as in A, except for trials where reward was withheld and animal no longer responded ($N = 21$). C: Abortive responses, as in A, except for trials selected for incomplete responses ($N = 10$). D: Reduced display gain as in A, except for half control target display movement elicits comparable force response ($N = 22$). Vertical calibration: 1 Newton, 15 Newtons sec; 20°.

tion or inhibition in the neuron could vary according to the direction of the response required by the stimulus.

We could distinguish between these possibilities by dissociating the coding of the direction of display movement (i.e., stimulus) from coding of the response in task-related unit activity. Units were recorded in 3 animals trained to respond appropriately when the polarity of the displayed error was inverted (Martin et al., 1981) to examine neuronal activity associated with flexor and extensor responses elicited by display movements to right or left.

Two classes of lead cells were observed in rostral motor cortex. The first class showed reciprocal changes in activity (i.e., increases or decreases) depending on the di-

rection of force production, but independent of the direction of display movement (Fig. 10). In parts A and B, average extensor and flexor responses are elicited, respectively, by display movement to the right or to the left. Rasters sorted by reaction time and synchronized by force onset, illustrate the tendency of this unit to modulate its activity with the onset of the stimulus rather than with the onset of the response. In part C, display polarity was inverted. Unit activity increases with the same response as in A, but is temporally related to the stimulus which in part B produced flexion. Part D shows the relation between lead time and reaction time under the two conditions in A and C, and demonstrates that stimulus onset determines tim-

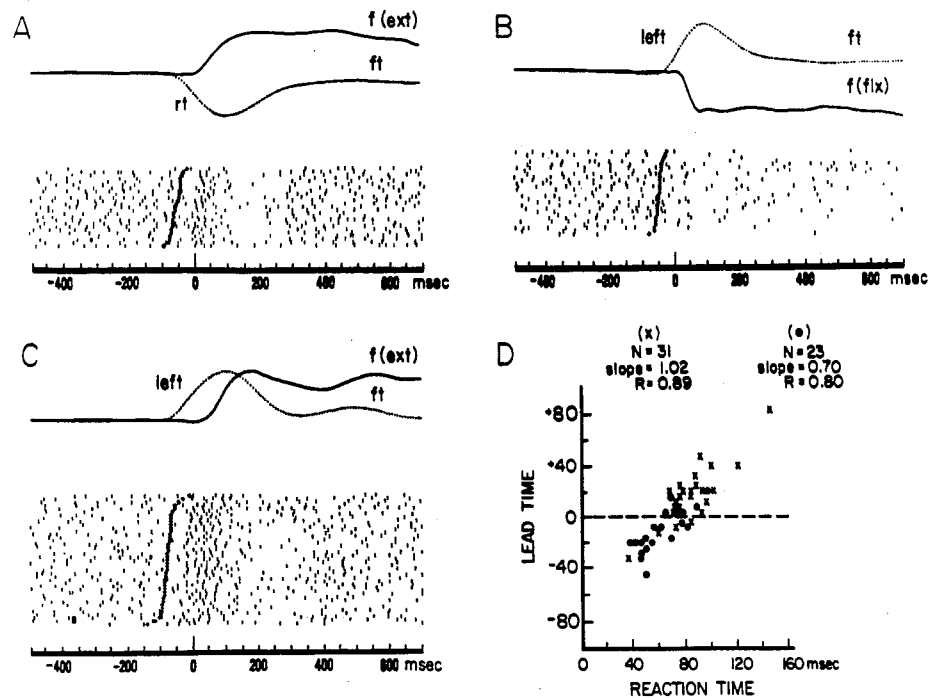


FIG. 10. Response characteristics of a unit, the activity of which is contingent on a single direction of force production. A: Extensor responses elicited by display movement to the right; top: average force and display position synchronized by force onset; bottom: spike raster, aligned with force onset and sorted in order of progressively increasing Rt (top to bottom). B: Flexor responses elicited by display movement to the left, otherwise similar to A. C: As in A, but extensor responses elicited by display movement to the left. D: Relationship between lead time (negative values indicate lag) and reaction time for control trials (filled circles, A) and trials with inverted polarity of displayed error (Xs, C).

ing of changes in unit activity. Thus, display-related afferent input to these neurons can be selected according to behavioral set, possibly by gating mechanisms acting on neurons presynaptic to them.

A second class of lead cells (Fig. 11) showed changes in activity with a single direction of display movement and did not vary with the direction of force production by forelimb muscles. Modulation of activity in these cells, while timed to the stimulus, was contingent on an overt behavioral response as in other lead cells. This class of lead cells may be important in processing target-related stimulus information associated with a fixed effective stimulus site. Cells with similar properties have been observed in monkey posterior parietal cortex (Wurtz and Mohler, 1976; Yin and Mountcastle, 1977; Robinson et al., 1978; Bushnell et al., 1981) and frontal eye fields (Mohler et al., 1973; Goldberg and Bushnell,

1981), but these cells are also responsive to visual stimulation in the absence of a motor response. Alternatively, this group of cells may control one or more behavioral responses which follow the display shift in our paradigm. Two such associated responses were attempts at head rotation and eye movements toward the moving display. The direction of these responses was correlated with the direction of display movement, but was independent of both polarity of displayed error and direction of force produced by the forelimb muscles. Cells whose activity modulates with a single direction of display movement may be important in controlling proximal muscle synergies associated with postural adjustment and joint stabilization which precede the actions of muscles acting on more distal joints (El'ner, 1973). This is consistent with evidence of Asanuma et al. (1981) in pyramidectomized cats suggesting that efferent

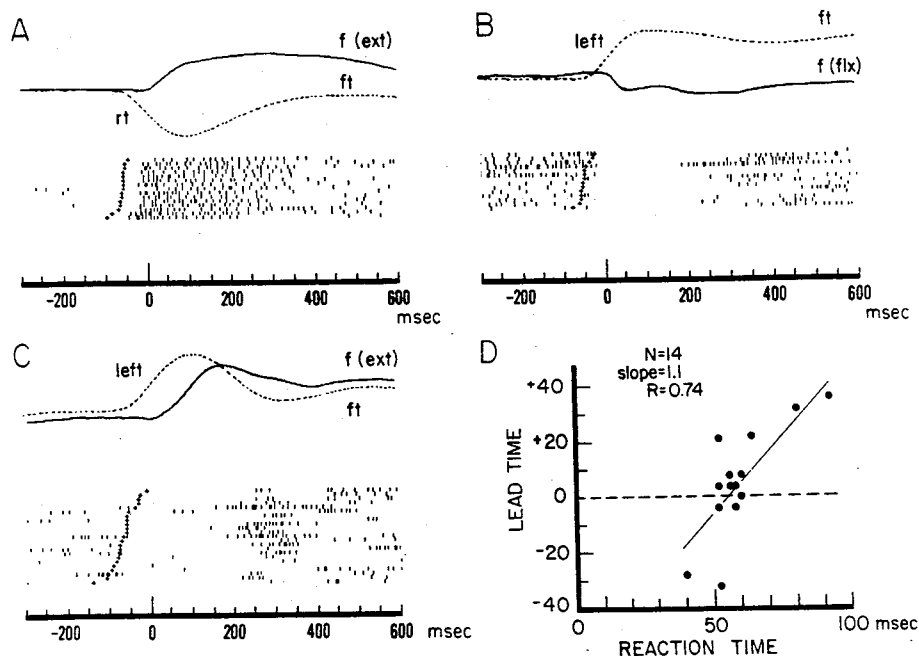


FIG. 11. Response characteristics of a unit, the activity of which is contingent on a single direction of display movement. A-C: As in Fig. 6. D: Scatter plot of the relationship between lead time and reaction time for trials illustrated in A.

zones controlling distal forelimb muscles also send impulses to proximal muscles.

Discussion

The striking conclusion emerging from these observations is that neuronal activity in rostral motor cortex encodes sensory events specifically related to target stimuli as well as the direction and magnitude of the ensuing behavioral response. The topographic features of stimulus representation (i.e., direction and magnitude of display movement encoded in the cell's response) was in many cells specific to the particular transformation required to produce the forelimb response. Our observations suggest that the conclusions of Evarts and Tanji (1974) for intended responses to proprioceptive stimuli may have more general applicability. Thus, in a task requiring spatially accurate responses to stimuli moving in one direction or another, we propose that central programs implement an isomorphic relation or map relating target and response dimensions. The resulting constraints to the flow of sensory information would provide for efficient transfer of a range of stimuli to the elements of motor cortex appropriate for controlling the required muscles. Such a map established through learning and implemented prior to the stimulus could account for the reflexlike properties of tracking behavior we have documented. Related concepts have been employed in models of prey-catching behavior in the frog and toad (Didday, 1976; Arbib, 1981) in which a visual sensory sheet is mapped directly onto a motor sheet in the optic tectum (Ingle, 1976; Ewert, 1976). Although the cat's behavior is the result of associative learning of an arbitrary, rather than a hardwired set of correspondences, once established, such a mapping process can reduce translational delay and output variability. To account for the animal's ability to adapt to a display polarity switch, it is also necessary to invoke

a higher-order process capable of modifying or replacing one map with another. The neural mechanisms for the selective implementation of a specific map may be formally analogous to one's thought to control the reflex action of cutaneous inputs as a function of phase in the step cycle during locomotion (Pearson and Duysens, 1976; Forssberg et al., 1977; Rossignol and Gauthier, 1980).

Although aggregate lead activity in motor cortex could contribute to both the configuration of the response and its time of onset, cortical activity could also act as a gating signal applied to a lower-order station. However, reanalysis of the activity of red nucleus neurons, recorded under identical task conditions (Ghez and Kubota, 1977; Ghez and Vicario, 1978c), revealed that lead activity in this subcortical structure is also better timed to the stimulus and reflects its magnitude (Ghez and Martin, *unpublished observation*). These findings indicate that the variance in reaction time cannot be accounted for by the variance in timing of supraspinal signals originating in either motor cortex or red nucleus. Although this conclusion seems counterintuitive at first, our behavioral data also suggest that response latency is not under explicit control by the processing of target-related inputs. The variance in response latency thus appears as an emergent property of the system as a whole, probably resulting from the participation in varying degrees of several nonsynchronized descending pathways activated in parallel. Their signals must be integrated with afferent inputs by interneurons and/or MNs whose threshold properties introduce new variability. The timing of the commands ultimately delivered to individual muscles may thus be influenced by segmental mechanisms integrating phasic descending commands with changing peripheral signals. This peripheral input could provide information concerning initial conditions including limb position and body

posture (El'ner, 1973; Ghez, 1979; Nashner, 1980; Soechting et al., 1981). The propriospinal system at C₃-C₄, which receives convergent descending and afferent inputs, may provide a critical link in the elaboration of the motor command and its integration with peripheral information (Alstermark et al., 1981; Lundberg, 1979).

Whereas our data suggest that presetting mechanisms acting on, or presynaptic to, neurons in motor cortex can control stimulus-response topography, the encoding of output magnitude remains uncertain. First, although the summed neural activity of both lead and lag cells was, in most cases, significantly related to one or another parameter of the ensuing force response, this finding must be interpreted with caution. Many lead and lag cells exhibited peripheral receptive fields in the responding limb which were likely to be stimulated after onset of muscle contraction. The activation of these homotopic inputs by early response events may have contributed to observed relations between unit activity and motor output. Such feedback might in fact be under central control (Ghez and Lenzi, 1971; Ghez and Pisa, 1972; Evarts and Fromm, 1978) and could be important in the control of tonic force. Second, our limited sample of lead cells subjected to changes in display gain reveals paradoxical features of task-related neuronal responses. For example, on a trial-by-trial basis, using a stimulus of constant size at a given display gain, unit activity of phasic cells covaried with the ensuing peak dF/dt of the response. However, when similar force responses were elicited with a different display gain, the relationship between unit activity and dF/dt changed to reflect the larger or smaller stimulus. This raises the possibility that the gain of the stimulus-response relation might be controlled by mechanisms separate from those controlling response topography. It also suggests that adaptation to changes in display gain (Ghez and Vicario, 1978b) does

not involve the control of the transmission in sensory pathways afferent to motor cortex.

Our findings of stimulus-related properties in neurons of the cat motor cortex contrast with observations made in primates during arm movement. In the monkey, neurons of motor cortex have been reported to modulate their activity with a consistent lead over the motor response (Evarts, 1966; Porter and Lewis, 1975; Lemon and Porter, 1976; Meyer-Lohmann et al., 1977; Cheney and Fetz, 1980; cf., however, Lamarre et al., 1980). Recent work, however, indicates a functional subdivision of even the primate motor cortex into rostral region (M_{Cr}) and caudal regions (M_{Cc}). Neurons in rostral portions appear to discharge earlier than ones caudal in area 4, when monkeys perform a motor task (Lamour et al., 1980; Humphrey, *personal communication*). Moreover, during a visual tracking task, neurons in posterior arcuate cortex (situated rostral to M_{Cc}) show responses which are time-locked to the visual stimulus (Jennings et al., 1980). This suggests that the expansion of frontal cortex in primates relative to carnivores further subdivides sensory and motor properties possessed by single neurons in the cat rostral motor cortex.

C. Differential Cortical and Thalamic Projections to Rostral and Caudal Motor Cortex

The different properties of neurons in the rostral and caudal portions of the arm area of the cat motor cortex raise several questions. The first concerns the pathways relaying target information to the lead cells in motor cortex and simple homotopic input to lag cells. The second question concerns whether duplicate representations of other body parts may exist in separate regions of motor cortex. Finally, could the differences in projections to different subregions of

motor cortex account for the functional differences observed. To address these issues, we have determined the topography of thalamocortical and corticocortical projections to area 4 γ (Hassler and Muhs Clement, 1964) in the cat, using retrograde and anterograde tracer techniques. In a retrograde series, intracortical pressure injections of horseradish peroxidase (80 nl, 30% HRP, Sigma Type VI) were made in a different site area 4 γ in each of 10 cats. These sites were distributed throughout the pericruciate region. After a survival period of 30 h, the animals were perfused through the heart with 0.9% saline followed by a mixture of 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) for 30 min, and subsequently perfused with cold sucrose-buffer (Rosene and Mesulam, 1978). Then the brains were blocked and cut into 50- μ m thick frozen sections. Every third section was processed with tetramethyl benzidine (TMB) and counterstained with neutral red (Mesulam, 1978). The distribution of retrogradely labeled neurons was determined by examining sections under bright-field illumination. An X-Y plotter, electronically coupled to the microscope stage, was used to record locations of labeled neurons. Injections were restricted to cortical gray matter proper and did not extend into white matter.

Cortico-cortical Connections

Taken together, the HRP injections in pericruciate cortex retrogradely labeled neurons in areas 6, 3a, 1-2, 5a, 5b, and 2pri as well as in portions of area 4 surrounding the injection site. Scattered labeling was present in other areas including the banks of orbital and suprasylvian sulci and areas 4 δ , 4sfu, 4fu, 3b, and 7. Systematic differences were seen in the locations of cells labeled after pre- and postcruciate injections (Fig. 12). Injection sites were targeted to regions where task-related units had been recorded

in trained animals. Precruciate injections of HRP produced retrograde labeling mainly within irregular and sometimes patchy areas of 4 γ surrounding the injection site (A). Labeling in other cortical areas was sparse. In contrast, the postcruciate injection (B) produced dense labeling in regions to cells labeled within area 4 γ itself.

A comparison of different injection sites revealed a topographic arrangement of projections from somatic sensory cortex to postcruciate area 4. Figure 13 summarizes results from 6 injections. Thus, injections in the medial portion of postcruciate area 4, thought to control hindlimb muscles (Thompson and Fernandez, 1975; Nieoullon and Rispal-Adel, 1976; Larsen and Yumiya, 1979), received projections from portions of areas 1-2, 3a, and 2pri considered to receive sensory input from hindlimb (Woolsey, 1958; Levitt and Levitt, 1968; Landgren and Silfvenius, 1969; Haight, 1972; McKenna et al., 1981). More lateral regions of area 4 γ thought to control forelimb muscles (Asanuma et al., 1968; Nieoullon and Rispal-Adel, 1976), received inputs from sensory forelimb areas (Oscarsson and Rosen, 1963; Haight, 1972; Iwamura and Tanaka, 1978; McKenna et al., 1981). The scattered labeling in area 2 and 5 which appeared after precruciate injections did not show apparent topographic organization. Whereas the projections of primary and secondary somatic sensory cortices dominate in postcruciate regions, the projection from somatic association cortex (areas 5a and 5b) was different. Both MCr and MCC injections labeled equal numbers of cells in this region. A series of anterograde experiments was carried out in 6 cats to confirm the preferential projection of areas 2 and 2pri to the posterior portions of area 4. Multiple injections of either HRP or tritiated amino acids (Lasek et al., 1968; Cowan et al., 1972; Jones et al., 1979; Mesulam and Mufson, 1980) were placed in areas 2 or 2pri in separate experiments (Fig.

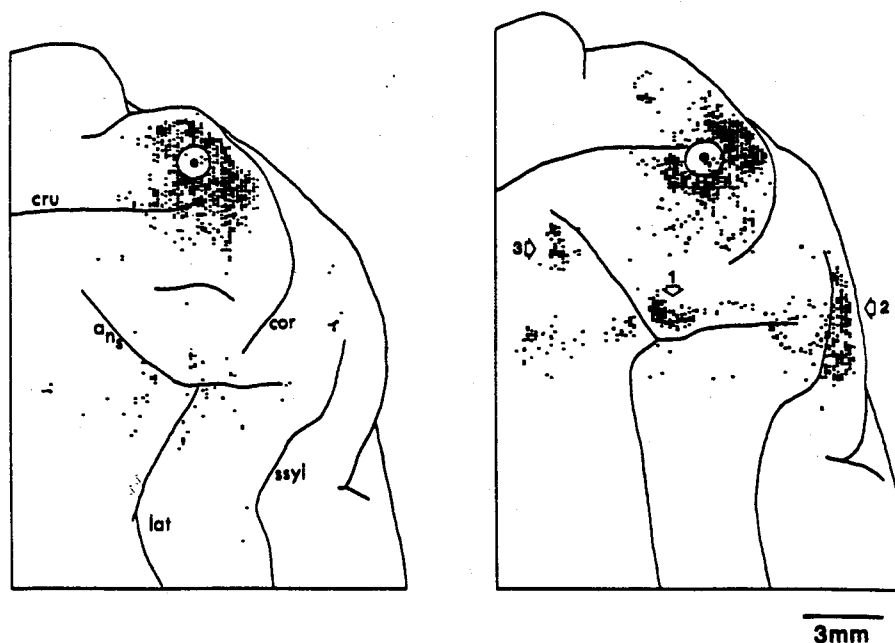


FIG. 12. Distribution of retrogradely labeled cortical neurons following single HRP injections. Surface reconstructions made from sagittal sections. **Left and Right:** Injections in the lateral part of precruciate and the lateral part of postcruciate area 4, respectively. Each *short bar* represents one labeled neuron. *Filled black circle and surrounding line* indicate sites of penetration of HRP-filled micropipette and extent of the reaction product at injection site, respectively. *Arrows 1 and 2* point, respectively, to clusters of retrogradely labeled cells in area 2 and in area 2pri. *Arrow 3* points to a cluster of labeled neurons in area 4δ in the depths of the cruciate sulcus. Cru, ans, cor, ssyl, and lat indicate cruciate, ansate, coronal, suprasylvian, and lateral sulci, respectively.

14). The terminal labeling is most dense in the postcruciate portion of area 4γ. Similar results were obtained with injections in area 2.

Thalamocortical Projections to Area 4γ

In the thalamus, retrogradely labeled cells were found in the ventrolateral (VL) nucleus, the shell zone at the ventrobasal complex (VB) border and in the central lateral (CL) nucleus. Within VL, clusters of labeled neurons formed lamellae in roughly parasagittal planes extending rostrocaudally which were topographically related to the cortical injection site. Medial parts of VL project to medial precruciate, lateral VL to medial postcruciate, and intermedi-

ate regions of VL to portions of precruciate cortex in between. In addition to neurons within VL proper, postcruciate injections labeled clusters of neurons in the shell zone at the VB border. The latter accounted for approximately 30% of labeled neurons in the thalamus following postcruciate injections, whereas only 5% of labeled neurons were in this region following precruciate injections. The strip of labeled neurons in VL lies in a more medial position following the precruciate injection in Fig. 15A than following the postcruciate injection in Fig. 15B. Also to be noted are the clusters of labeled neurons in the shell zone at the VB border following the postcruciate injection. The finding of labeled neurons in the shell zone at the VB border confirms earlier ob-

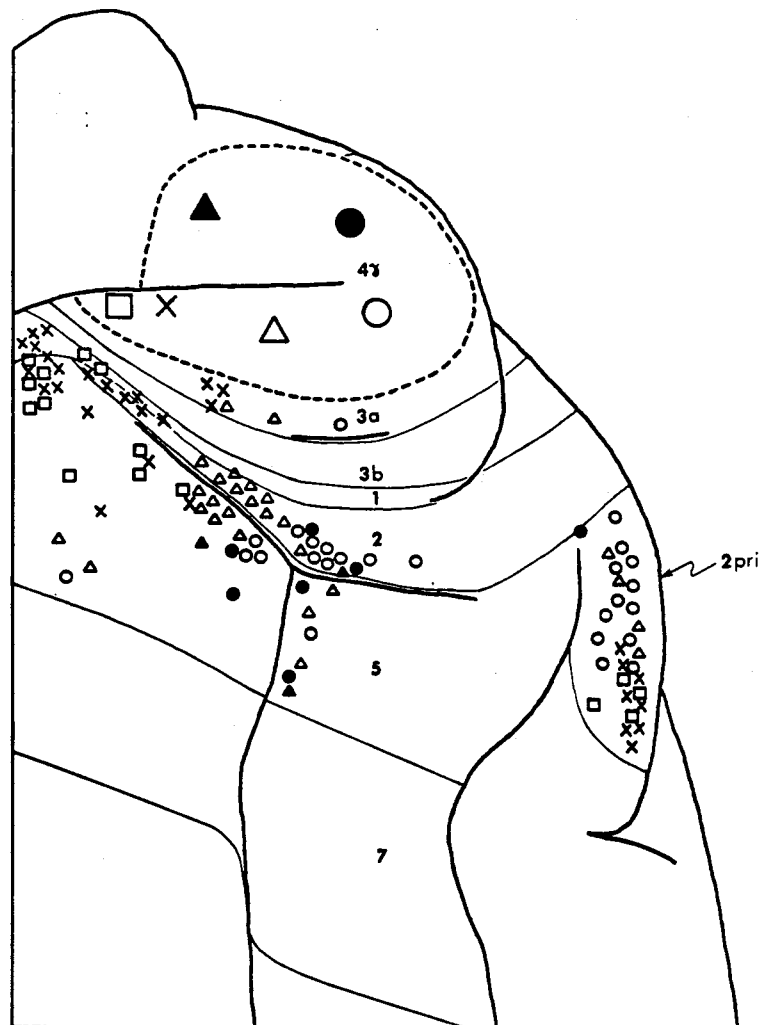


FIG. 13. Schematic illustrations of topographical relations between injection sites in area 4 and locations of labeled neurons in anterior part of ipsilateral cortex. The *large symbols* indicate the locations of single injection sites in different experiments. The corresponding *small symbols* indicate the locations of labeled neurons. Labeled neurons within area 4, area 6, and in the banks of orbital, coronal, and suprasylvian sulci are omitted for clarity.

servations (Larsen and Asanuma, 1979; Asanuma et al., 1979; Hendry et al., 1979). Our current data do not allow us to state that this group of neurons are functionally distinct from the other labeled cells in VL. Retrograde labeling of neurons in CL as reported by Strick (1975) was seen in the caudal portion of CL following each cortical injection; however, no obvious topographic

arrangement of these labeled neurons was seen.

Discussion

These anatomical findings indicate clear differences in both corticocortical and thalamocortical projections reaching MCC and MCr. Projections from somatic sensory

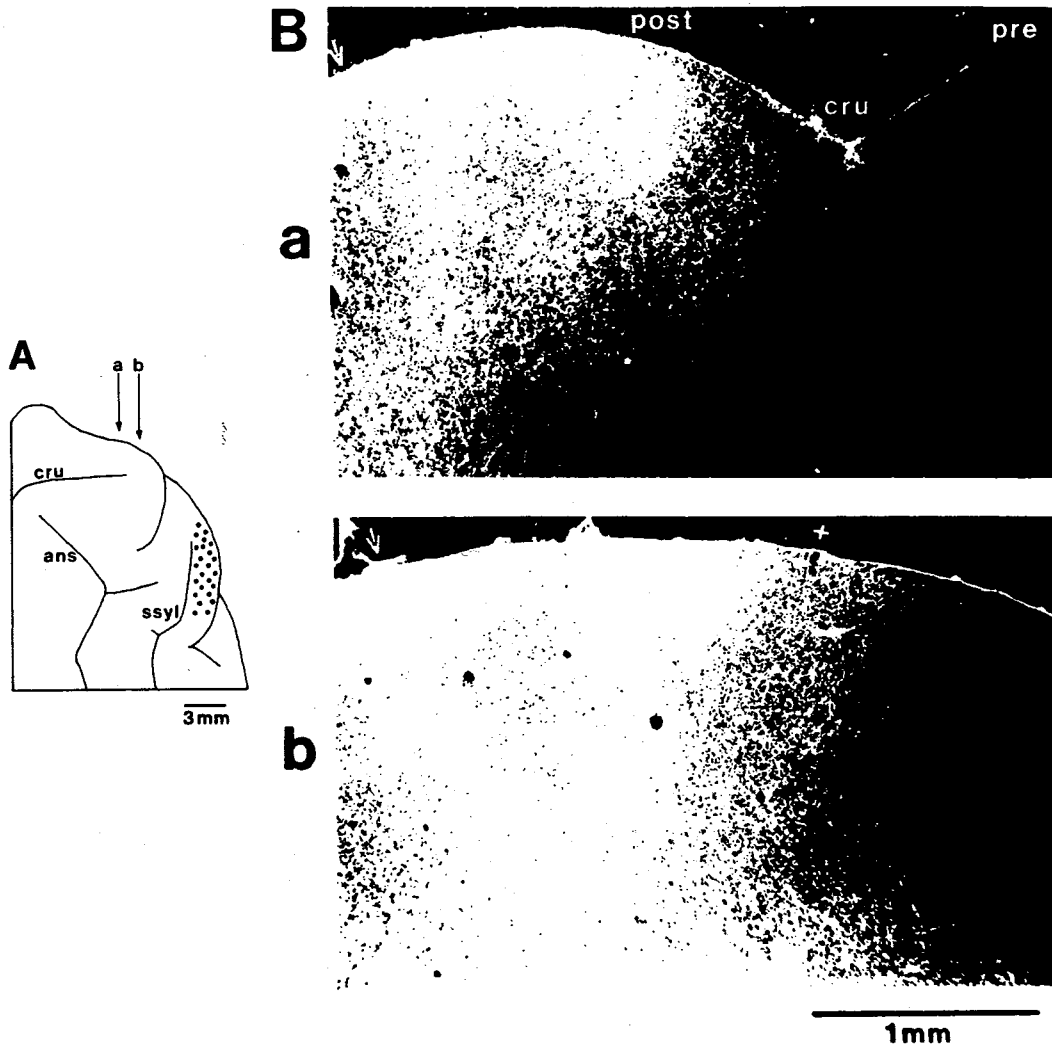


FIG. 14. Differential terminal labeling between MCC and MCr demonstrated by autoradiography after injections of tritiated amino acids into area 2pri. A: Drawing of cortex showing multiple injection sites (*dots*) in area 2pri and locations of the parasagittal sections (a,b) shown in B. B: Dark-field photomicrographs of parasagittal section through area 4. *Arrows* in B indicate the border between area 4 and area 3a. *Plus sign* indicates the anteroposterior level of the lateral extension of the cruciate sulcus.

cortex and from the shell zone at the VB border are preferentially distributed to MCC. Since neurons in both the shell zone (Asanuma et al., 1979) and somatic sensory cortex (McKenna et al., 1981) may exhibit simple receptive fields in the limbs, either of these inputs could account for the preferential distribution of simple fields in MCC

(see Asanuma, 1981; Jones, *this volume*). In contrast, the major projection to MCr appears to arise in the VL nucleus itself.

Our observations unfortunately do not resolve the question of whether duplicate motor representations exist. Taken together, the following considerations tend, however, to support such a view. First, our

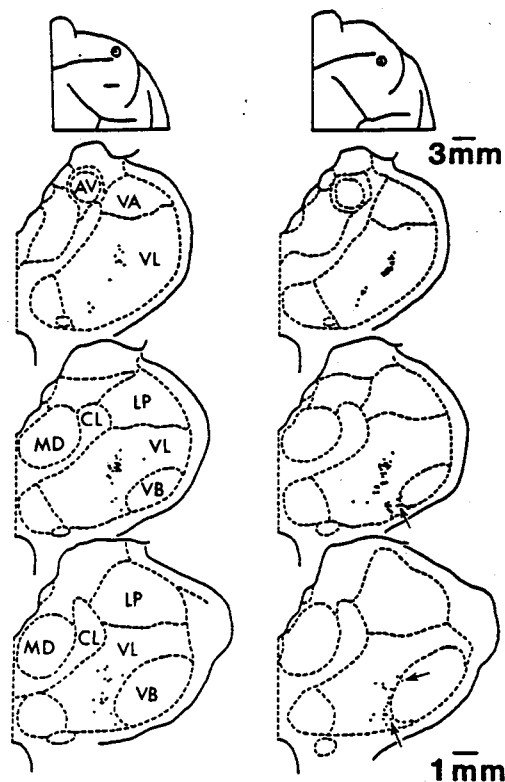


FIG. 15. Distribution of retrogradely labeled neurons in the thalamus following HRP injections into the lateral part of precruciate (Left), and the lateral part of posterocruciate area 4 (Right). Top row: Injection sites. Lower 3 rows: Thalamic frontal sections. Each dot represents one labeled neuron. Tracings of thalamus from top to bottom represent, successively, more caudal sections. Arrows indicate the labeled neurons in the shell zone at the VB border.

anterograde and retrograde studies suggest that the posterocruciate gyrus is somatotopically organized to receive input from the forelimb and hindlimb representations of area 2 and 2pri. Second, physiological observations (Sasaki et al., 1973; Y. Shinoda, *personal communication*) indicate that, in the cat, both fore- and hindlimb representations in the deep cerebellar nuclei focus their outputs (via VL) preferentially on regions rostral to cruciate sulcus. The presence of duplicate cortical representations may imply a similar duplication within VL

proper since the entire projection from VL to MCr and MCc is topographically organized. Such a dual representation in VL has not, however, been documented. Alternatively, MCr might be specialized to accomplish synergic associations between head and forelimb movement which would be in line with convergent projections to MCr by forelimb and face regions of somatic sensory cortex. Preliminary experiments in progress, however, do not favor this hypothesis.

A second unresolved question concerns the pathways which convey target-related heterotopic information to lead cells in MCr. Two possibilities may be entertained. On the one hand it is possible that display-related sensory inputs are processed by cortical sensory mechanisms before giving rise to signals conveyed to the motor cortex and then to spinal levels. A more attractive alternative is that under the highly practiced conditions, input information may be processed by subcortical structures. The cerebellum may provide the proximate input signal determining lead activity in MCr via the VL nucleus of the thalamus. The latter is supported by observations showing both increased reaction time and a concomitant retardation of lead activity in motor cortex neurons in primates, following cooling or ablation of deep cerebellar nuclei (Brooks et al., 1973; Meyer-Lohmann et al., 1977; Lamarre et al., 1978; Conrad, 1978; Brooks, 1979). Increases in reaction time to exteroceptive stimuli in the cat have been reported to follow cooling of the ventrolateral nucleus of the thalamus (Benita et al., 1979).

AN OVERVIEW: TOWARDS A SYNTHESIS

We have examined a learned and highly skilled behavior of the cat under well-controlled conditions. The dominant feature of the behavior is the short latency with which accurate responses are made to a range of

stimuli which vary unexpectedly in direction and amplitude. Extra time does not appear to be required for selection of specific response parameters during the reaction time. We have argued that the apparent simplification of processing demands during the reaction time could result from use of internalized models of target and peripheral plant and of a map of correspondences evoked by contextual cues prior to the stimulus. The behavioral data and correlated patterns of neuronal activity in motor cortex support our hypothesis that central motor programs determining response topographies may be represented as a map which relates target and response dimensions to each other. We have proposed that the behavioral set associated with preparation to respond in specific ways to a range of stimuli provides preferential pathways for the efficient transfer of behaviorally relevant information to the sectors of supraspinal systems controlling components of the motor synergy. Our data do not shed light on the role played by pyramidal neurons with simple receptive fields in the efferent zones of the caudal motor cortex; these were active only late during force development or during tonic force production. However, it seems likely that their output contributes to the composite descending signal ultimately reaching MNs. Whether they function in a feedback role, possibly dependent on changes associated with behavioral set, remains to be clarified. In any case, the specific input-output relations of different sectors of MCC provide for the parallel processing of inputs which could concurrently bias the MN pools of many different muscles.

The simple block diagram of Fig. 16 proposes that two processing networks underlie the stimulus-response transformations (S-R processors) in targeted movement. Each of these processors is assumed to comprise several functional components which perform specific operations on input information. Parameters of these operations

are under adaptive control in order to optimally achieve higher order behavioral goals. The target S-R processor deals with stimuli specifically related to a target of interest, in our case, error signals arriving through visual or vibrissal channels. At an initial stage of this processor, incoming signals are compared with the ones predicted from a learned model of the display (delayed feedback experiments). The resultant error is used to modify ongoing input to constitute a derived forcing function. This derived input is then processed through a network which, perhaps by elements acting as neural gates, constrains the spatial flow of information according to a preset map. The signals derived from this spatial transform would be processed by a network producing phasic and tonic outputs. Both the ratio between phasic and tonic components and the overall gain of the input-output relation are governed by adaptive control elements which take into account an internal model of the peripheral plant. Rostral components of motor cortex are a component of this target S-R processor. The anatomical results suggest that spatially processed inputs initiating movement may reach this spatially processed inputs initiating movement may reach this region from the ventrolateral nucleus and thus possibly take origin in the cerebellum.

The parallel S-R processor receives input signals from the moving limb and body parts affected by motor commands and may, perhaps within a predicted range, act to compensate for deviations between the actual and the intended or reference trajectory. The parallel processor is assumed to include stretch reflexes and other spinal components of the motor servo (Houk and Rymer, 1981) as well as supraspinal elements, such as MCC. This parallel processor would be governed by adaptive controllers that modulate the gain of multiple input output channels with stable topographic relations.

The subdivision of function into signal

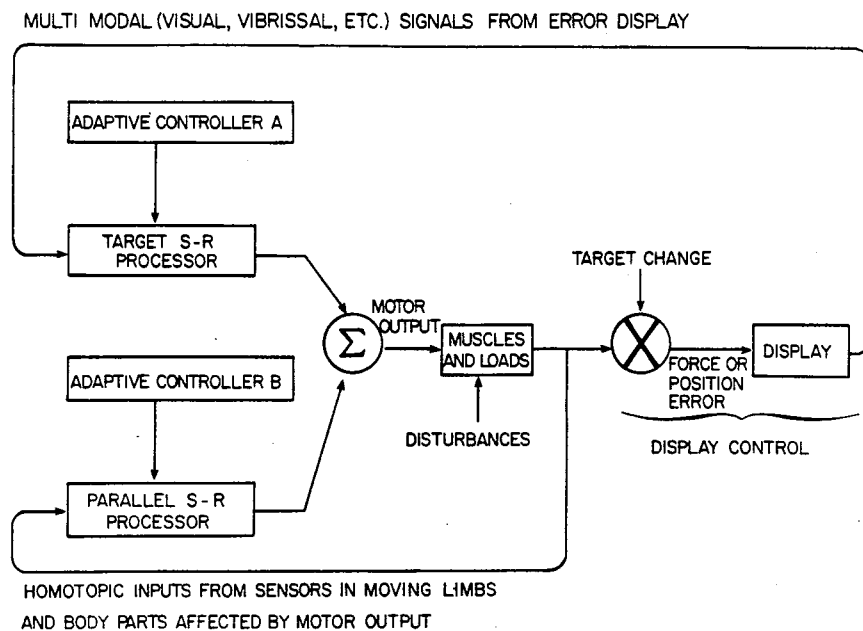


FIG. 16. Dual process model of targeted movement. Motor output signals are assumed to be generated by two processing networks. The Target S-R Processor is devoted exclusively to the processing of stimuli related to the target and operates as a feedback to minimize the displayed error. Output signals from the Target S-R Processor are summed with those from the Parallel S-R Processor to produce the final motor output. This parallel processor is assumed to be capable of processing inputs from somatic and other receptors acting in parallel through hardwired connections on a more spatially complex array of muscular elements than processor A. The Adaptive Controller B is assumed to modulate only the gain of the elements of the parallel processor. The simplified diagram as shown is not intended to exclude influences of the Target S-R Processor or the Parallel S-R Processor. (This diagram has been modified from Houk and Rymer, 1981. with permission.)

transformations carried out by multiple parallel pathways is a general organizational principle of the nervous system. Our results underscore that unified motor output emerges from multiple antecedent elements. This may mirror sensory processes which decompose a unitary event along several parallel channels. One resultant property is that the timing of behavioral events is not under the control of any single system. We thus propose that the temporal details of the overall synergy (i.e., the onset of contraction in different muscle groups) reflects the property of the total system rather than a variable controlled by a particular process. Similar ideas have emerged for neural circuits involved in locomotion (cf., Grillner, 1981).

The acquisition of skill, or motor learning, may thus be a process which simplifies the complexity of input-output requirements of targeted movements in the form of internalized maps of correspondence. To the extent that both input and output domains can be ordered or parameterized (cf. stimulus-response compatibility), all specific pairings may be equivalent and decision time effectively controlled. Such simplifications undoubtedly lead to a degree of stereotyping in motor behavior which is justified by the gains in time and reliability.

The present tracking task embeds the subject in a continuous loop of action and reaction and provides a clear window into the simplest form of sensory-motor association, that between a subject's action and its

immediate consequences. Therefore, such tasks may provide an opportunity to study both the translational mechanisms which allow arbitrary target information to engage motor elements, and also adaptive modifications of these mechanisms when new circumstances require learning.

Our results emphasize that the classic distinctions drawn between the sensory or motor nature of particular brain regions, while of heuristic value, should not obscure the close interrelations between sensory and motor processing. Sensory input can provide cues to enable widespread changes in the processing of subsequent information and the adjustment of transformational programs. Additionally, sensory input provides ongoing information about the trajectory of

targets of interest as well as signals used in local neural servo mechanisms. Similarly, in the context of a highly automatized task such as the one studied here, the concept of command does not seem readily applicable. In fact, once the nervous system is ready to respond to the stimulus and the changes in state alluded to above are implemented, the proximate "command" is the occurrence of the expected stimulus.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the invaluable assistance of Paul Oratofsky for developing computer software, Kathrin Hilten for the illustrations, and Ruth Sharton for her devotion in typing multiple versions of this manuscript.