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Single Cell Studies of the Primate Putamen

II. Relations to Direction of Movement and Pattern of Muscular Activity*

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Summary. The major goal of this study was to determine whether the activity of single cells in the primate putamen was better related to the direction of limb movement or to the underlying pattern of muscular activity. In addition, the neural responses to load application were studied in order to determine whether the same neurons were also responsive to somatosensory stimuli. Two rhesus monkeys were trained to perform a visuomotor arm tracking task which required elbow flexion/extension movements with assisting and opposing loads in order to dissociate the direction of elbow movement from the pattern of muscular activity required for the movement. Neurons in the putamen were selected for study only if they were related both to the task and to arm movements outside the task. Most (96%) of the cells studied responded to load application: 36% of these showed short-latency (< 50 ms), "sensory" responses. Forty-four percent of neurons had significant relations to the level of static load as the animal held the arm stationary against the steady loads: in general, static load effects were relatively weak. During the elbow flexion/extension movements in the task, 76% of cells had significant relations to the direction of movement, and 52% of neurons had significant dynamic relations to the level of load. Half of all neurons studied were primarily related to the direction of movement independent of the load. Only thirteen percent of cells in the putamen had a pattern of activity similar to that of muscles. These results indicate that neuronal activity in the putamen is predominantly related to the direction of limb movement rather than to the activity of particular muscles and that the basal ganglia may play a role in the specification of parameters of movement independent of the activity of specific muscles. These results also indicate that the basal ganglia receive proprioceptive input which may be used in the control of ongoing movement.

Key words: Single cell activity – Putamen – Behaving primate – Direction of movement

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Introduction

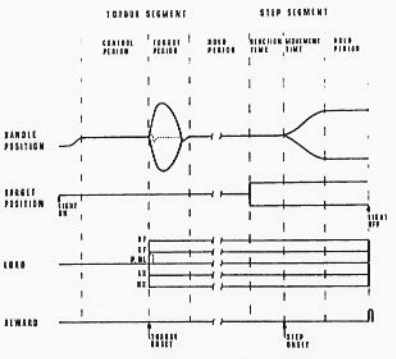
The precise contribution of the basal ganglia to the control of movement remains unclear. A better understanding of the relation of neuronal activity in these nuclei to specific aspects of movement (e.g., the direction, amplitude, velocity, and acceleration of movement and the activation of specific muscles) could provide important clues about the role of the basal ganglia in motor function. Studies in behaving primates have revealed a relation of neuronal activity in various nuclei of the basal ganglia to parameters of movement, including the direction of limb movement (DeLong 1971, 1972; Liles 1978, 1979; Aldridge et al. 1980b; Georgopoulos et al. 1983), the amplitude and velocity of step movements (Georgopoulos et al. 1983), and the magnitude of isometric force (DeLong 1972; Branch et al. 1980; Liles 1981).

The relation of neuronal discharge to direction of movement could be due to one or more factors. It could (1) represent a central correlate of a command signal which specifies the direction or trajectory of movement independent of the activation of specific muscles or external conditions; (2) represent a central correlate of a command signal related to the activation of a particular muscle or muscle synergy; or (3) result from proprioceptive feedback from the evolving movement. The previously demonstrated relation to static force suggests a possible relation of neural discharge to muscles, while the finding of somatosensory inputs to the basal ganglia (Anderson et al. 1976; DeLong and Georgopoulos 1979) makes proprioceptive feedback a definite possibility. However, it is also possible that movement direction may be coded by neurons in the basal ganglia independently of specific muscles.

In order to clarify the basis for the relation of neuronal discharge to direction of movement, we studied the activity of single cells in the putamen of monkeys trained on a paradigm which dissociated the direction of limb movement from the pattern of muscular activity and which allowed us to determine the responsiveness of the same neurons to peripheral inputs. This task enabled us to study the relation of neuronal activity in the basal ganglia to the processing of central commands (for the direction of movement), to muscular activity, and to proprioceptive feedback.

The putamen of the primate was selected for study since it appears to play a major role in the motor functions of the basal ganglia by virtue of its inputs from the premotor, motor and sensory cortices (Künzle 1975, 1977, 1978).

The results of this study have been presented in preliminary form (Crutcher and DeLong 1981, 1982).



BEHAVIORAL PARADIGM

Fig. 1. Schematic diagram of the behavioral paradigm. There were two parts to each trial: the torque segment and the step segment. The random-duration, hold period between these two segments of the task is represented by the interruption of the horizontal lines. In the torque segment of the task one of five loads was applied to the handle: a heavy load opposing flexion (HF), a light load opposing flexion (LF), no load (NL), a light load opposing extension (LX), or a heavy load opposing extension (HX). The dotted line in the position trace represents the movement which resulted from a brief perturbation (P) applied in some cases in the unloaded classes. The task is described in detail in the text

Materials and Methods

Behavioral Apparatus and Paradigm

Two rhesus monkeys were trained to perform a visuomotor tracking task, which required flexion/extension movements of the elbow. The monkey was seated in a primate chair with its arm resting on a low-friction manipulandum, such that the elbow joint was directly above the axis of rotation of the manipulandum. The arm was abducted by 70 deg. The arm was held in place by two rigidly supported velcro straps; one just below the elbow and one at the wrist. The other arm of the monkey was restrained at the animal's side. In front of the monkey was a display panel with two horizontal rows of light-emitting diodes (LEDs). Each row of LEDs was 32 cm long and contained 128 LEDs. The illuminated LED in the upper row indicated the target position. The illuminated LED in the lower row indicated the handle position to the animal.

A schematic diagram of the behavioral paradigm is shown in Fig. 1. During the intertrial interval all LEDs were turned off, and no load was on the handle. At the onset of the trial a LED came on at the center position. The monkey was required to move the handle so that the LED representing the handle position was aligned under the center LED. This starting position corresponded approximately to a 90 deg angle at the elbow. The electronically defined center window was 2 degrees wide. Correct positioning within the window was signaled to the animal by a brightening of the LED. After a control period of random duration (1–3 s), during which the monkey held the arm stationary within the center window, one of four pseudorandomly selected loads (or no load) was abruptly applied to the handle by a brushless DC torque motor and remained on. The four loads were 150 grams (1.47 N) opposing extension, 75 g (0.74 N) opposing extension, 150 g opposing flexion, and 75 g opposing flexion. The loads were sufficient to displace the monkey's arm from the center window. After the monkey had realigned the handle within the center window, a variable (1–2 s) hold period began. During this period the animal held the arm stationary at the center position against the steady load. At the end of this hold period the center light was extinguished and a target light appeared 4 cm either to the right or left, and the monkey had to make the corresponding elbow extension or flexion movement of 7.5 deg amplitude to realign the LEDs at the new target position. After holding 1–2 s at the new position a liquid reward was given. Failure to stay within the center window or target window (3 deg wide) or to reattain the target position within the specified time limit after the load was applied or the target shifted resulted in abortion of the trial. The class was selected using a randomized block design: trials were presented randomly in blocks of ten trials, one trial for each combination of five loads and two directions of elbow movement.

In some cases a load of 75 g was applied briefly (20 ms) to the handle during the control period of the unloaded (NL) classes. This load resulted in a small perturbation of the arm but in most cases did not elicit an active response by the animal.

Surgery and Recording

Surgical and recording techniques are described in detail in the companion paper (Crutcher and DeLong 1984). After the animal

was fully trained, a stainless steel recording chamber was stereotaxically positioned over a round opening in the skull such that the axis of the cylinder passed through the center of the putamen. The recording chamber was placed laterally and tilted 50 degrees from the vertical to avoid passage of the electrode through the arm area of the motor cortex and the internal capsule. Glass-coated, platinum-iridium microelectrodes (1–5 MΩ at 1,000 Hz) were used to record extracellular potentials.

Output from a potentiometer coupled to the axis of the manipulandum provided a record of handle position. Velocity signals were obtained by differentiating the position signal with an analog circuit. The velocity signal was sampled at 100 Hz. The times of occurrence of neuronal spikes were recorded as interspike intervals with a resolution of 0.1 ms. The sampled velocity, interspike intervals, and the times of behavioral events were stored on-line using a PDP 11/10 computer.

The monkey was allowed to perform the task as the electrode was slowly advanced through the putamen in search of task-related cells. This was done because neurons in the putamen have very low levels of spontaneous activity (DeLong 1973; Anderson 1977). If a cell was task-related, as judged from an on-line, response-aligned raster display, a full data file was collected for that cell.

Electromyograms

In separate recording sessions electromyographic (EMG) activity was recorded from muscles of the upper torso and arm. Fine, intramuscular wires with 1–2 mm of wire exposed at the tip were used for recording. The EMGs were amplified, rectified, filtered (100–2,000 Hz), and fed into a sample-and-hold integrator (Bak Instruments). The processed EMG signals were sampled at 200 Hz and the sampled data were stored on-line with the PDP-11/10 computer. The muscles sampled included the brachialis, brachioradialis, biceps (long head), triceps (long and lateral heads), pectoralis, infraspinatus, acromiodeltoid, teres major, atlantoscapularis anterior, supraspinatus, trapezius, cervical and thoracic paraspinous, flexor carpi radialis and ulnaris, palmaris longus, extensor digitorum communis, extensor carpi radialis longus, and the deep wrist flexors.

Data Analysis

The activity of each neuron during the step segment of the task was analyzed as follows. First, each trial was divided into several epochs (see Figure 1): namely, the Hold Period (one second prior to the shift of the target light), the Reaction Time (RT, from the stimulus to move to the onset of the behavioral response), the Movement Time (MT, from the beginning to the end of the step movement as determined from the velocity record), and the Step Period (this epoch includes both the RT and the MT). The rationale for studying the Step Period was that the neural response often spanned both the RT and MT, and analysis of either the RT or the MT alone occasionally gave misleading results. Second, the discharge rate of each neuron for each epoch of each trial was determined. Third, a two-way analysis of variance (ANOVA) with replications (Snedecor and Cochran 1967) was performed on each neuron for each epoch. This analysis was used to determine whether there were statistically significant ($p < 0.01$) effects of direction, load, or direction x load interactions for each neuron. Fourth, two separate linear regression analyses of the discharge rate of each neuron for each epoch were performed. These included regressions across all five load conditions for both directions of movement. The slope of the regression line provided a measure of the strength of the neuronal relation to load for those neurons with significant load effects in the two-way ANOVA.

Results

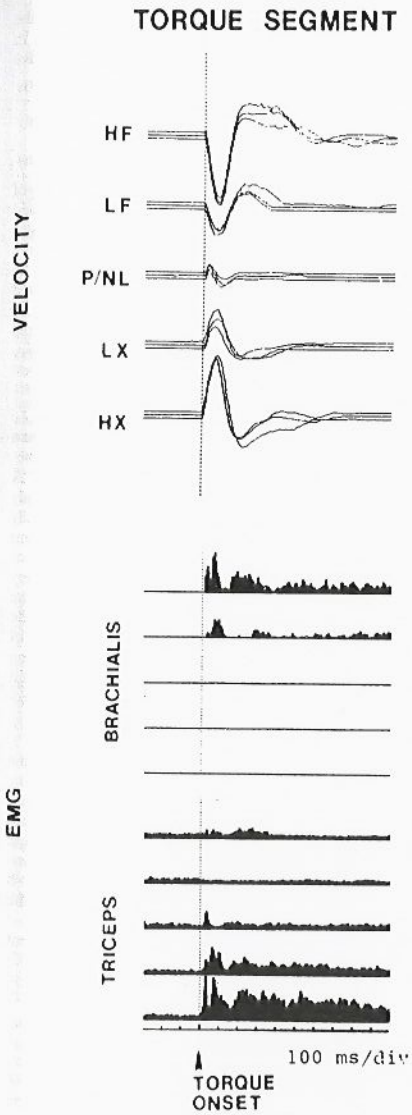
Behavioral and Electromyographic Data

Torque Segment. Figure 2 shows representative trial-by-trial velocity traces and EMGs during the torque segment of the task. The five sets of velocity traces show the behavioral responses to application of each of the five loads. When a load opposing extension (classes LX and HX) was applied to the handle, this resulted in passive flexion of the monkey's arm followed by an active extension to return to the center window. The middle set of traces (P/NL) show the response to a brief (20 ms) perturbation in the direction of flexion. This was occasionally followed by a later, corrective response by the animal (e.g., see the late response at 400–500 ms in the middle trace in the P/NL class). There was little variability in the behavioral responses between the different limbs or monkeys studied.

EMG histograms for the brachialis and the lateral head of triceps during the torque segment are also shown in Fig. 2. These muscles had a characteristic triphasic pattern of response to the torque. Following the return to the center window there were also appropriate levels of graded, tonic EMG activity as the monkey held the arm stationary against the steady loads. The brief perturbations (P/NL) elicited a stretch reflex (e.g., see triceps) but did not, in general, elicit an active response from the animal.

Step Segment. Figure 3 shows representative trial-by-trial velocity traces and EMG histograms for the step segment of the task. All trials were aligned at the onset of the movement as defined by a threshold change in the velocity record. The reaction times were typically 225 ± 43 ms (mean ± S.D.; average of all trials of one monkey). The durations of the movements were 332 ± 90 ms. It can be seen from Fig. 3 that the durations of movement and the peak velocities were similar for both directions of movement and for all loading conditions. There was a weak tendency for the heavily assisted movements to be the slowest, but this trend was less than the inter-monkey and inter-trial variability in step velocity.

The characteristic pattern of EMG activity of the prime movers of the elbow for the step segment of the task is shown in Figure 3 and is graphically represented in Fig. 4. During the hold period prior to the movement there were graded levels of tonic EMG activity for the appropriate muscles (e.g., activity in the elbow flexors with a flexor load). During the step movement there was a graded increase in activity above the hold period EMG level for the appropriate agonist when the load opposed



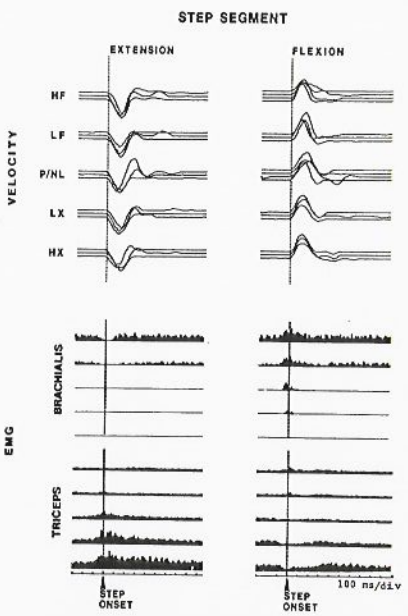


Fig. 3. Movement-aligned velocity traces and EMG histograms of brachialis and lateral head of triceps during extension and flexion movements in the step segment of the task for each of the five load conditions. As in Fig. 2 the loads for the EMG records below are the same as for the velocity records above

the movement in the preferred direction or when there was no load. See, for example, the brachialis during flexion in classes HF, LF and NL. When the load assisted the flexion movement (LX and HX) there was little or no increase in activity in the elbow flexors. Rather, the movement was performed by decreasing the tonic activity in the normal antagonist muscle (i.e., triceps). The force exerted by the handle moved the arm to the new target position. This paradigm thus dissociated the direction of elbow movement from the pattern of muscular activity.

Fig. 2. Representative velocity traces and EMG histograms during the torque segment of the task. An upward deflection of the velocity trace represents movement in the direction of flexion. Abbreviations for the five applied loads are the same as in Fig. 1. The applied loads for the two sets of EMG histograms below are the same as those for the velocity records above

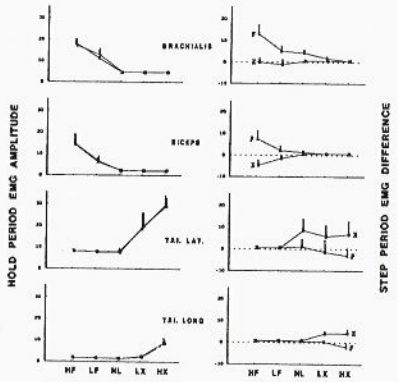


Fig. 4. Average EMG activity of the prime movers of the elbow during the hold period prior to the step period and during the step movement for each of the ten classes. The column of graphs on the left shows the activity of the brachialis, long head of biceps, and the lateral and the long heads of triceps as the monkey holds the arm stationary under each of the five load conditions. The EMG amplitudes are scaled in arbitrary units and the vertical line for each point represents one standard deviation. The column of graphs on the right shows the difference in EMG activity from the hold period for the step period of the task for each muscle for both flexion (F) and extension (X) movements under each load condition (shown on the abscissa). The step period is defined as the time from the target light appearance to the end of the movement

The EMGs of many of the muscles in the upper torso and arm were sampled (see Material and Methods). During multiple EMG recording sessions the brachialis, brachioradialis and lateral head of triceps were consistently well related to the task. The long heads of the triceps and biceps were primarily recruited during the step movement when the load opposed their normal movements; e.g., note their lack of response in the unloaded classes in Fig. 4. The times of onset of activity of the prime movers of the elbow in the unloaded classes of the step segment were 50–70 ms before the onset of movement. Several muscles of the shoulder girdle were active in the task (pectoralis, infraspinatus, acromiodeltoid and teres major). These muscles all had a pattern of activity in the step segment of the task very similar to the long heads of the biceps and triceps, i.e., they were active only when the load opposed movements in their preferred direction. Other muscles of the arm and trunk were either not active in the task or showed tonic activity unrelated to any specific portion of the task. There was little or no evidence of cocontraction of antagonist muscles, and none of the muscles studied showed a consistent increase in activity for one direction of movement under all five load conditions.

Neuronal Activity in the Task

Recordings were obtained from three hemispheres of two rhesus monkeys. Single neurons were recorded in 75 histologically identified electrode penetrations in the putamen. The putamen was studied from stereotaxic coordinates anterior 7 to anterior 20 (Snider and Lee 1961). Of the 707 neurons isolated and studied in the putamen, 120 were selected for study in the behavioral task. Neurons were selected for study only if they were task-related and were related to arm movements outside the behavioral paradigm (see Crutcher and DeLong 1983).

Spontaneous Activity. Most neurons in the putamen of the awake monkey had very low levels of spontaneous activity or were not spontaneously active. A small percentage of neurons, however, was tonically active at about 3–6 imp./s. These latter tonically active neurons were seldom related to any movement which the animal made either outside the task or during task performance and were consequently excluded from our sample. The discharge rate of the remaining neurons during the control period of the task generally reflected the low level of activity of most neurons when the animal was at rest. During the control period 11% of the neurons studied did not discharge. The median firing rate of the remaining task-related neurons was 1.2 imp./s.

Neuronal Responses to Load Application. Of the neurons studied during the torque segment of the task, 96% (111 of 116) responded to load application. Only increases in activity were observed, perhaps because of the low spontaneous activity of these neurons. An example of a neuron with a short-latency response to application of flexor loads is shown in Fig. 5. The latency histogram for the neurons studied is shown in Fig. 6. The earliest response observed was at 25 msec. Thirty-six percent of the neurons studied responded at latencies earlier than 50 ms. Nineteen percent of the neurons responsive to load application had a short-latency response to one direction of load application and a long-latency response to the other direction of load application. For these neurons only the short-latency responses are included in Fig. 6. It is likely that the majority of early torque responses (< 50 ms) were

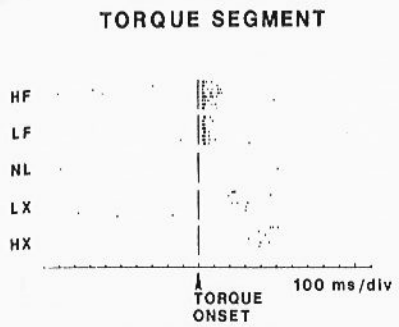


Fig. 5. Raster display of the activity of a neuron with short-latency, sensory response to load application. The load applied for each of the five classes of trials is shown on the left. The dark vertical lines represent the time of load application (torque onset). Each horizontal row of dots represents the action potentials of this neuron during a single trial. This cell had a short-latency response to the application of flexor loads only and showed a greater response to application of the heavy flexor load than the light flexor load

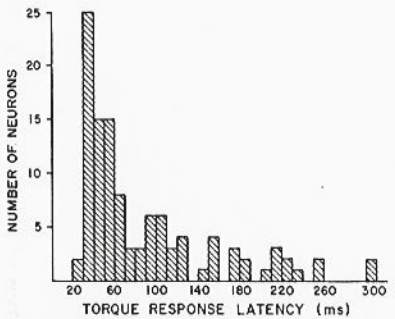


Fig. 6. Distribution of neuronal response latencies to load application. The onset of the response was defined as the first bin (10 ms bins) of the stimulus-aligned histogram showing a subsequently sustained increase in activity above the prestimulus level

sensory in nature and that most of the later neuronal responses were related to the animal's active return movement to the center position (see Discussion).

The responses of 34 neurons to perturbations, which briefly displaced the arm but which did not elicit an active response from the animal (see Fig. 2), were also studied. Of these neurons, 44% had short-latency responses to the perturbation. The remaining

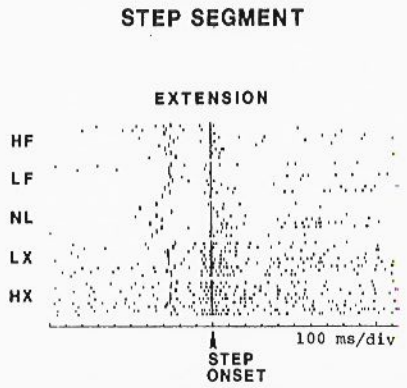


Fig. 7. Example of a neuron with a static load effect in the hold period of the task and a dynamic load effect during the step movement. The dark vertical lines indicate the time of the onset of movement as determined from the first change in velocity. The dark vertical marks 200–300 ms prior to the onset of the step movement indicate the time of the stimulus to move for each trial. The time prior to these marks is the hold period

19 neurons tested either had no response to the perturbation (N = 11), or had late responses associated with small-amplitude, corrective movements the animal made on some trials (N = 8).

The responses to load application were very specific. For example, for 91% (105/116) of neurons tested the response was directional. That is, the intensity or the latency of response was appreciably different for the two polarities of load applied. Moreover, 29% (34/116) of the neurons tested showed different magnitudes of response to the two different amplitudes of load of the preferred direction. For the 42 neurons with short-latency (< 50 ms) responses to load application, 88% of these short-latency responses were directional and 48% were amplitude-related. An example of a neuron with short-latency direction and amplitude effects is shown in Fig. 5. In general, the direction effects were stronger than the amplitude effects.

Static Load Effects. Forty-four percent (53/120) of neurons studied showed a statistically significant relation to the level of static load during the hold period (ANOVA, $p < 0.01$). An example of the discharge of a neuron with a static load effect is shown in Fig. 7. This neuron was tonically active during the hold period as the monkey held the arm stationary against extensor, but not flexor, loads.

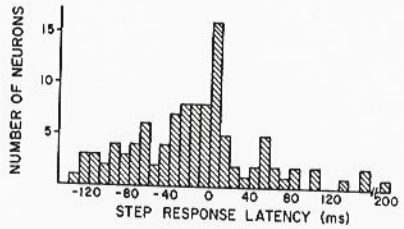


Fig. 8. Distribution of neuronal response onset times for the step movement for the unloaded class. The onset of the neural response was defined as the time at which the first sustained increase in activity above the hold period level occurred, as judged from the movement-aligned rasters and histograms of cell activity. The onset of the movement is at time 0 and negative numbers represent times prior to movement onset

In order to quantify the relation to load, a linear regression analysis was done on the activity of neurons with static load effects. For 29 (55%) of these neurons, the frequency of discharge varied linearly with the magnitude of the load ($p < 0.01$). The median slope of the relation to load was 1.13 imp./s/N (range 0.15–6.43 imp./s/N). This corresponds to an increment in tonic firing rate of 1.67 imp./s for a 150 g increment in load. The remaining 24 neurons had a significant load effect in the two-way ANOVA, but did not have significant linear regressions. This was due primarily to the fact that the two-way ANOVA detected nonlinear and nonmonotonic load effects as well as linear relations to load.

Neuronal Relations to the Step Movement. Eighty eight percent of the neurons studied (N = 120) showed a change in activity during the step segment of the task. For the vast majority of cells the changes were increases in activity. The response onset histogram is shown in Fig. 8. The peak of the histogram is at the onset of the movement. The median time of response onset is 10–20 ms prior to the beginning of movement. Only 19% of these neurons became active before the earliest change in EMG activity (–70 ms). Increases in neuronal activity often extended throughout much of the duration of the movement. An example is shown in Fig. 9. This neuron became active approximately 80 ms before the beginning of flexion movements in the step segment and remained active throughout much of the duration of the movement. Some neurons became active early in the step segment and had more phasic responses. An example is shown in Fig. 10.

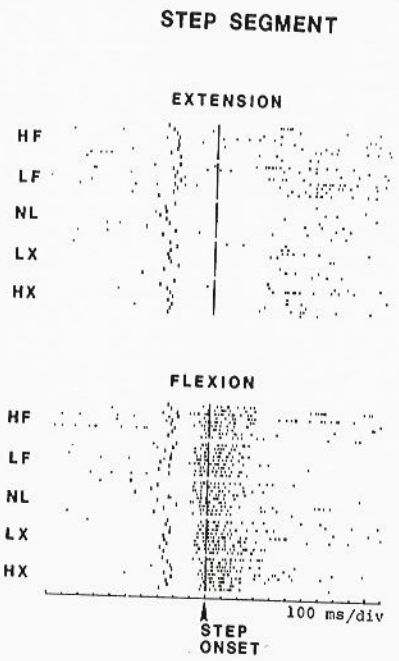


Fig. 9. Example of a neuron with a long lasting increase in activity during flexion, but not extension, movements in the step segment of the task. Conventions are the same as in Fig. 7

In order to quantify both the direction and load effects in the step segment of the task the activity of all neurons was analyzed using a two-way ANOVA and a linear regression analysis (see Material and Methods). The results are presented in Table 1. Most neurons (76%) had a significant relation to the direction of arm movement during the step period of the task (RT + MT). The majority (57%) of neurons which were active during the step segment of the task were active only during one direction of arm movement (see e.g., Figs. 9 and 10). The remainder of neurons with significant direction effects increased their activity during both directions of arm movement, but the response was significantly greater for one of the two directions. A small number of neurons were equally active during both directions of movement (n = 18).

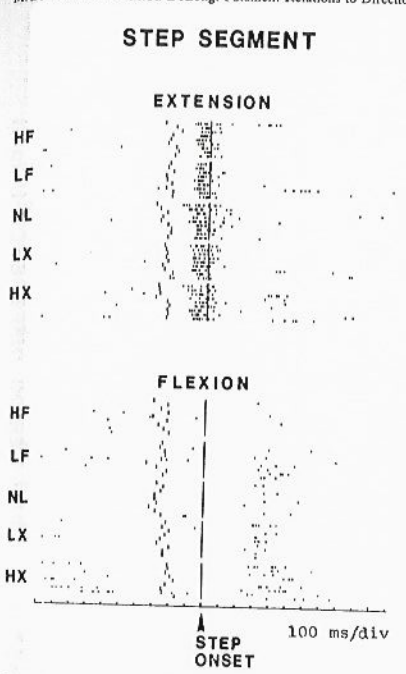


Fig. 10. Example of a neuron which was phasically related to active extension movements for each of the five load conditions. This neuron was inactive during elbow flexion movements

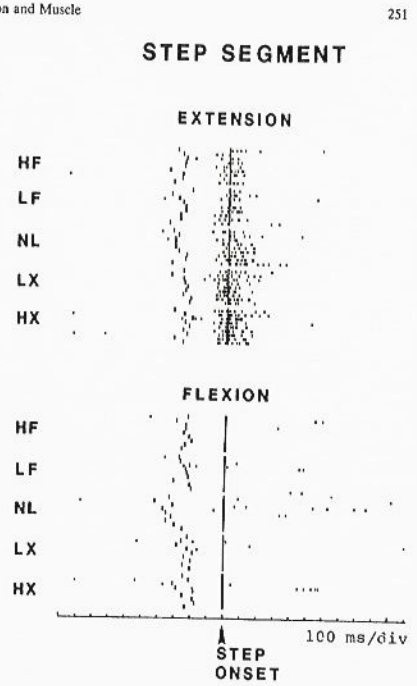


Fig. 11. Example of a neuron related to active extension movements with a weak dynamic load effect

Table 1. Numbers and percentages (N = 120) of neurons with statistically significant direction effects, load effects, linear relations to the load, and direction x load interactions (F-test, $p < 0.01$) in each of the three epochs of the step segment of the task

	Reaction time	Movement time	Step period
	N %	N %	N %
Direction	51 (42)	93 (77)	91 (76)
Load	43 (36)	49 (41)	62 (52)
Regression on the load	26 (22)	32 (27)	38 (32)
Dir x load	21 (17)	40 (33)	42 (35)

Many neurons had dynamic load effects, i.e., statistically significant (two-way ANOVA, $p<0.01$) relations to the level of load during the step period of the task (see Table 1). Figure 7 shows an example of a neuron with a clear dynamic load effect during the extension step movements. This neuron was most active during the step movement when the load opposed the movement (HX and LX), and almost inactive when the load assisted the movement (HF and LF). Many of the neurons with dynamic load effects were active during one direction of movement under all loading conditions, but were more active when the load opposed the movement. In these cases the load effect was often weak. An example of this is shown in Fig. 11. Figure 11 shows an example of the activity of a neuron with a direction x load interaction.

A third of the neurons studied had significant linear relations to the load during the step period of the task (see Table 1). The average slope of regression line for the step period discharge rate was 3.22 ± 1.53 imp./s/N. The slope of the regression line during

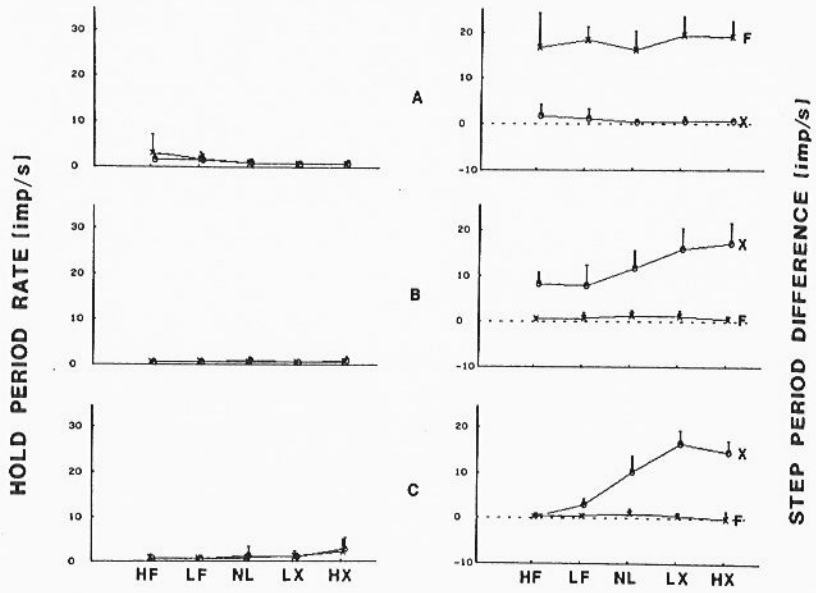


Fig. 12. Examples of the pattern of activity of three neurons (A, B, and C) in the step segment of the task. This figure is analogous to Fig. 4. The graphs on the left show the average firing rates of each neuron during the hold period for each of the five load conditions. The graphs on the right show the average change in activity from the hold period for each neuron for both directions of movement under each of the five loads

the movement time alone was 4.73 ± 2.06 imp./s/N. A smaller percentage of neurons had significant linear relations to the load than had significant dynamic load effects in the two-way ANOVA. As with the static load effects, this was because the two-way ANOVA detected nonmonotonic and nonlinear relations to the load.

Patterns of Activity in the Task. A major question of the present study was whether the activity of neurons in the putamen would be related primarily to the direction of movement or to the pattern of muscular activity needed to produce that movement. The muscles that were active in the task had a characteristic pattern of activity (e.g., see Figs. 3 and 4). Neurons were classified as having a pattern of activity similar to the muscle pattern if (1) they had a significant static load effect, (2) they had a strong dynamic load effect in the step period, and (3) the dynamic load effect was in the appropriate direction, i.e., greater activity with loads which opposed movement in the preferred direction. Thirteen percent of the neurons studied met these criteria (e.g., see Fig. 7). Only three of the 16 "muscle pattern" neurons became active in the step period prior to the first change in EMG activity.

Cells were classified as "directional" if (1) they had a clear relation to the direction of movement during the step period and (2) the dynamic load effect in the step period was weak or absent. Of the neurons studied (N = 120), 50% were classified as "directional". While some of these cells were activated to different degrees with movements in opposite directions, 71% of "directional" neurons were active only during one direction of movement. Examples of neurons related to active movements in one direction were shown in Figs. 9, 10 and 11.

Of the "directional" neurons, 22% had a significant linear relation to the load during the step period. Figure 11 shows the response of a neuron that was

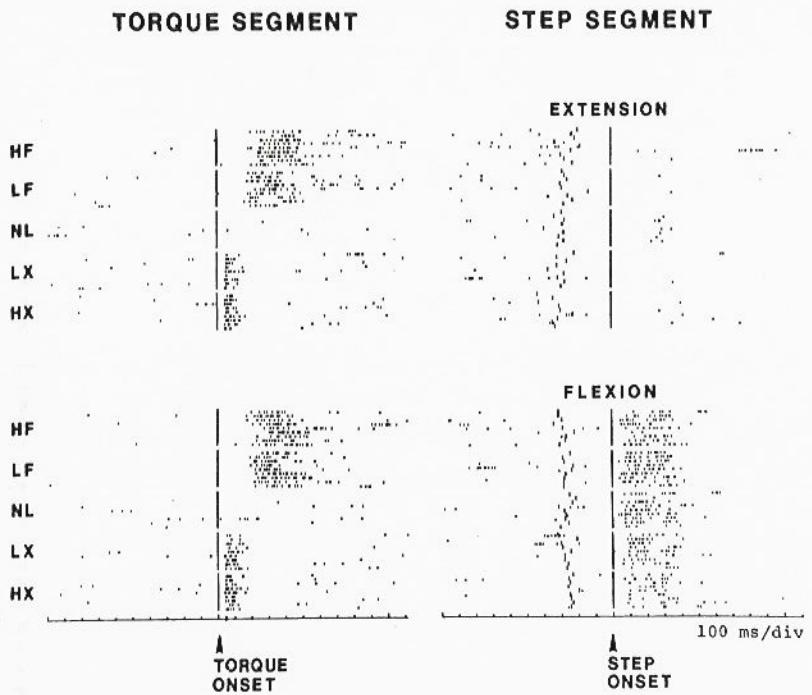


Fig. 13. Example of a neuron related to both active and passive flexion movements in the task. This neuron had a short-latency response to passive flexion (HX and LX classes in the torque segment) and was also related to active flexion (late response to HF and LF torques and during flexion steps)

related to active extension, but was most active when the load opposed the step movement. The reason that neurons like this were classified as "directional" rather than as "muscle pattern" is illustrated in Fig. 12. The upper graphs (12A) show the activity of a "directional" neuron during the hold and step periods. This neuron was active only during flexion movements with no load effect. The bottom graphs (12C) show the activity in the task of a "muscle pattern" neuron. This neuron was active during extension steps primarily when the load opposed the movement or there was no load, but was inactive during the heavily assisted extensions; much like the lateral head of triceps shown in Figs. 3 and 4. The center graphs (Fig. 12B) show the activity of the same neuron illustrated in Fig. 11. It is clear that this neuron was active during all active extensions, including class HF in which the elbow extensor muscles were completely inactive. Unlike the muscles and "muscle pattern" neurons, all of the neurons with dynamic load effects that were classified as "directional" were active for all movements in the preferred direction, including the heavily assisted movements.

The "directional" neurons were subdivided into those with and those without short-latency (50 ms or less) responses to load application. The purpose of this was to try to determine whether the directional responses during the step movement might be due to sensory feedback. Of the "directional" neurons, one third had short-latency torque responses. Figure 13 shows the activity of a neuron that was related to

active flexion movements in the step period but which also responded at short-latency to the passive flexion induced by application of the extensor loads in the torque segment of the task. Nineteen of the 20 "directional" neurons with short-latency responses to the torque were related to passive and active movements in the same direction in the task. The separation of the "directional" neurons into those with and without "sensory" inputs on the basis of the short-latency torque responses was supported by the results obtained by examination of the animal outside the task (see Discussion). Few (4%) of the "directional" neurons with short-latency, "sensory" responses to the torque became active in the step segment of the task prior to the first change in EMG activity (70 ms prior to movement onset), whereas 32% of the "directional" neurons without short-latency torque responses did so. These findings suggest the possibility that the directional responses during the step movement of the neurons with short-latency torque responses may have resulted from proprioceptive feedback generated during movements in one direction.

Discussion

Neural Relations to Direction of Movement or Pattern of Muscular Activity

A major finding of this study was that a large percentage of neurons were related primarily to the direction of arm movement. Previous single-cell studies in the basal ganglia (DeLong 1971, 1972; Liles 1979; Aldridge et al. 1980b; Georgopoulos et al. 1983), motor cortex (Schmidt et al. 1975; Fetz et al. 1980; Georgopoulos et al. 1982; Kubota and Funahashi 1982; Murphy et al. 1982), and thalamus (Strick 1976; MacPherson et al. 1980) also have found that the direction of movement is an important determinant of cell discharge. The high correlation of neuronal activity with the direction of movement observed in the present study, in which the direction of movement was dissociated from the pattern of muscular activity, strongly suggests that many putamen neurons were not primarily related to the level or direction of force exerted by the animal or to the activity of particular muscles, but rather to the direction of movement, per se.

Several investigators have studied the relation of neural activity in the motor cortex or cerebellum to movements with either assisting or opposing loads (Evarts 1967, 1968; Conrad et al. 1977; Thach 1978). It is difficult to compare the results of the present study with theirs because of differences in paradigms and in methods of analysis, presentation, and interpretation of data, but the results of those studies suggest that a larger proportion of neurons both in the motor cortex and in the dentate are "like muscle" than is true for the putamen.

The fact that static and dynamic neuronal relations to force have been well established for the motor cortex and a high proportion of neurons with patterns of activity "like muscle" has been observed does not mean, however, that precentral neurons are unrelated to the direction of limb movement. Many studies have described correlations of neural activity in the motor cortex with the direction of movement (e.g., Fetz et al. 1980; Georgopoulos et al. 1982; Kubota and Funahashi 1982; Murphy et al. 1982). And in the few studies that attempted to dissociate the direction of movement from the pattern of muscular activity there is also evidence of neuronal relations to the direction of movement. For example, Evarts (1967) found that in a wrist movement task 5 of 31 PTNs were better related to the direction of movement than to force, and that other neurons fell between a primary relation to force and a primary relation to displacement. In addition, in a postural fixation task Evarts (1969) found that some cells were active over the entire range of loads (from 400 g opposing flexion to 400 g opposing extension), being related to the rate of change of force (dF/dt) regardless of the level of the steady load. However, since that was not an isometric task, fluctuations in force (e.g., positive dF/dt) were associated with wrist movements in a single direction. Therefore, an alternative interpretation is that there were increase in discharge prior to one direction of wrist movement and decreases prior to the other direction of movement, regardless of the level of static load or the pattern of muscular activity. Therefore, the differences between the results of previous studies in the motor cortex and the present study may be more apparent than real: the activity of neurons in the motor cortex may be quite "directional".

An interesting subset of the "directional" neurons were those with weak dynamic load effects. It is difficult to account for this pattern of activity in the task. If they were related solely to the direction of movement, there should have been no load effect. If their activity was tightly coupled to that of muscles, then they should not have been active during the heavily assisted elbow movements, since none of the muscles studied increased their activity during these movements. There are two ready explanations: (1) There were some muscles which were active during the heavily assisted movements. We believe that this is unlikely because a large number of muscles in the arm and torso were studied, and this pattern of activity was never observed. (2) These neurons were receiving central inputs both from neurons related to muscles and from neurons related to the direction of movement. A slight variation on this theme is that these neurons could have been receiving central inputs related to commands for both force (rather than muscles) and direction. The reason for suggesting this is that this subset of "directional" neurons generally had a smoothly graded load effect across all five load conditions for one direction of movement. This suggests a relation to force rather than muscles because none of the muscles were active for all five load conditions. The reason for suggesting that the "force" input to these neurons might be combined with a "directional" input, is that the dynamic load effects in these neurons were only seen for one direction of movement. For the other direction of movement, the neurons were generally inactive. It is likely that some integration of two or more such signals is occurring either within the basal ganglia or in neurons which project to the basal ganglia.

Static and Dynamic Load Effects

A significant proportion of putamen neurons showed a relation between the activity in the hold period of the task and the level of static load. Several previous studies in the basal ganglia have found similar relations of neuronal activity to steady force (DeLong 1972; Branch et al. 1980; Liles 1981). However, in similar studies in the motor cortex (Evarts 1969; Smith et al. 1975; Hepp-Reymond et al. 1978; Cheney and Fetz 1980) the magnitudes of the static load effect observed were greater than that obtained in the present study, and the studies which examined PTNs, or especially corticomotoneuronal cells, also found higher proportions of neurons with static load effects. This suggests that although there are a significant proportion of neurons in the putamen whose activity is correlated with static force, those neurons which are more directly linked to the segmental motor apparatus are more likely to play a role in the generation of static force.

A significant proportion of neurons in the putamen had significant dynamic load effects (present results and Liles 1981). Several studies have found dynamic relations to load for neurons in the motor cortex (Evarts 1968; Conrad et al. 1977; Cheney and Fetz 1980). Comparison of our results with those obtained in the motor cortex is somewhat difficult, but it seems that dynamic load effects may be less frequent and weaker in the putamen than in the motor cortex. However, the load effects observed in the present study were frequent and strong enough to suggest that the basal ganglia do indeed play a role in the generation of force or receive information about force levels.

Responses to Load Application

The responses to load application were essentially of two types; short-latency responses and long-latency responses. The distinction between them was usually quite clear. We believe that the short-latency responses were "sensory" in nature and the long-latency responses were, in general, "motor" responses related to the active return movement of the arm. Consistent with this distinction was the finding in many neurons of a short-latency response to one polarity of applied load and long-latency response to the opposite polarity of load. Most neurons (86%) classified as being responsive to somatosensory stimulation during examination of the animal outside the task (Crutcher and DeLong 1984) also had short-latency, "sensory" responses to load application. The brief perturbations, which did not evoke an early active response by the animal, did elicit short-latency responses from those neurons with sensory driving in the examination, but not from those neurons unresponsive to somatosensory stimulation. The earliest torque latencies observed in this study (25 ms) were later than those observed in similar studies of sensory and motor cortical neurons (Evarts 1973). However, given the slow conduction velocity of corticostriatal neurons (Liles 1974), these latencies were within the expected range. It should be noted that Strick (1978, 1979) found neurons in the dentate nucleus that responded at similar latencies (30–50 ms) to load application. These cells were related to the "motor set" of the animal rather than to the afferent input produced by the perturbation. Although "reflex" and "intended" responses were not dissociated in the present study, it is unlikely that the short-latency responses observed in the precent study correspond to an "intended" response of the monkey since Evarts and Tanji (1976) found that the "reflex" and "intended" responses of motor cortical neurons to applied loads occurred at 20–25 ms and 40–50 ms, respectively. These results, together with the results of the companion study (Crutcher and DeLong 1984), indicate that a significant percentage of neurons in the putamen are responsive to proprioceptive stimuli.

Timing of Neural Responses During the Step Period

Only 19% of neurons changed their activity prior to the earliest changes in EMG activity. Similar results

have been obtained for other nuclei of the basal ganglia (DeLong 1972; Aldridge et al. 1980a; DeLong and Georgopoulos 1981; Georgopoulos et al. 1983). Comparison of the results of basal ganglia studies with similar studies in the motor cortex (Evarts 1973; Meyer-Lohmann et al. 1977; Georgopoulos et al. 1982; Thach 1978) suggests that the distributions of neuronal response onset times in the motor cortex are earlier than those obtained in the basal ganglia. This is consistent with the fact that a major input to the basal ganglia comes from the motor cortex. These results suggest that the putamen does not play a major role in the generation of the earliest EMG changes in stimulus-triggered movements. This conclusion is supported by the results of studies that found no change in reaction times following cooling (Hore and Villis 1980), kainic acid lesions, or microstimulation (Horak and Anderson 1980) of the GP in trained rhesus monkeys. Taken together, the lesion, microstimulation and single-cell studies are consistent with the view that the basal ganglia are more involved in the execution or facilitation of movement than in the timing of its initiation, as suggested by others (Anderson and Horak 1981; Aldridge et al. 1980b; Hallett and Khoshbin 1980). However, Neafsey et al. (1978) found a significant proportion of neurons in the pallidum and entopeduncular nucleus of the cat that responded well before the first change in EMG activity during self-initiated movements. Therefore, it is possible that the small population of neurons that were active early do play some role in the initiation of movement and that, in other types of paradigms (e.g., self-initiated movements) or in other portions of the basal ganglia (e.g., the caudate), neurons may be involved more specifically in movement initiation.

Active and Passive Directional Neurons

Perhaps the most interesting neurons identified in the present study were the "directional" neurons that did not have a short-latency, sensory response to the torque. Presumably, the pattern of activity of these neurons in the task is not due to directional feedback from the periphery, because joint afferents and muscle spindles would have responded at short-latency to the torque and Golgi tendon organs would be expected to behave "like muscle" in the task. Consequently, it is possible that these neurons may be generating or receiving a command signal for the direction of movement. The precise role that a directional command signal in the putamen might play is uncertain. Such a command signal might be conveyed to other parts of the brain (e.g., motor and premotor cortices), which would then select and activate the appropriate muscles. However, most of these "directional" neurons became active after the first change in EMG activity prior to the step movements. It is, therefore, more likely that neurons in the putamen are receiving a corollary discharge of a directional command signal from the neocortex.

An interesting finding of this study was that a large number of neurons were related to passive and active movements in the same direction. This was true of 19 of the 20 "directional" neurons related to both passive displacements and active movements in the task. Most studies of the motor cortex have obtained quite different results, with passive-active-opposite neurons predominating (Lemon and Porter 1976; Evarts and Fromm 1978; Fetz et al. 1980). However, Lemon et al. (1976) found that 75% (N= 60) of "joint neurons" and 47% (N = 17) of "muscle neurons" responded to passive and active movements in the same direction. It is also interesting that Rosen and Asanuma (1972) found that, for all cells activated by wrist joint receptors, the passive direction and the intracortical microstimulation (ICMS) effects were in the same direction and, for all cells activated from muscle receptors, the passive direction and the ICMS effects were in opposite directions. This suggests the possibility that the basal ganglia preferentially receive afferent input from joint rather than muscle receptors. This conclusion is supported by the findings that many more putamen neurons are responsive to joint rotation than to muscle or tendon taps (Crutcher and DeLong 1984) and that there is a paucity of inputs to striatal neurons from muscle afferents in anesthetized animals (Albe-Fessard et al. 1960). In any case, this predominant input-output relationship indicates that the activity of a significant percentage of putamen neurons is facilitated by passive movements in the same direction as the preferred direction of active movement of that neuron. This specific facilitation of movements in a given direction supports the hypothesis, proposed by others (Denny-Brown and Yanagisawa 1976; Hallett and Khoshbin 1980), that the basal ganglia play a role in the facilitation of movement. However, it should be noted that for some, if not all, of the passive-active-same neurons one cannot rule out the possibility that the "active" response during the step movement resulted from directional proprioceptive inputs occurring during the evolving movement.

Conclusion

The primary goal of the present study was to determine whether neural activity in the putamen would be primarily related to (1) the direction of movement per se, (2) the activation of muscles, or (3) proprioceptive feedback. The results strongly suggest that a parameter of movement (direction) can be encoded in the activity of neurons in the putamen independent of effectors and afferent feedback. It is interesting in this regard that significant relations to the amplitude/peak velocity of step movements have recently been reported for neurons in the globus pallidus and subthalamic nucleus (Georgopoulos et al. 1983). Taken together, these results indicate that the basal ganglia may be involved in the control (or monitoring) of parameters of movement independent of muscles. These results also may have more general implications. Since the primary input to the basal ganglia is from the neocortex, these results also suggest the possibility that neural relations to command signals for parameters of movement independent of muscular activity may also be found in the cerebral cortex. The basal ganglia may thus be viewed as a component of a more distributed system controlling parameters of movement.

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Specialized Subregions in the Cat Motor Cortex: Anatomical Demonstration of Differential Projections to Rostral and Caudal Sectors

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Summary. (1) Ipsilateral cortico-cortical and thalamo-cortical projections to the cat motor cortex were determined from the locations of retrogradely labeled neurons following single small intracortical injections of HRP in area 4γ. These projections were also examined by studying the distribution of anterogradely transported axonal label following multiple injections of HRP or of tritiated amino acids in areas 1–2 of SI and in area 2pri (SII). (2) The number of retrogradely labeled cells in areas 1–2 and in area 2pri differed markedly between HRP injection sites located in the precruciate (anterior sigmoid gyrus) and postcruciate (posterior sigmoid gyrus) subregions of area 4γ. These associational projections from primary and secondary somatosensory cortices were dense to postcruciate subregions but weak to the precruciate subregions. (3) The associational projections from areas 1–2 and from area 2pri to the postcruciate subregion of area 4γ were topographically organized, but no clear topographic organization could be demonstrated for the precruciate projection. (4) Anterograde terminal labeling following injection of either HRP or tritiated amino acids into areas 1–2 and area 2pri confirmed the preferential projection of somatosensory cortex to the postcruciate subregion of motor cortex. The projection from somatosensory areas 1–2 was uniform over its terminal field, but that from area 2pri was more patchy and complex. (5) HRP injections in area 4γ gave rise to lamellae of labeled neurons in the ventrolateral nucleus of thalamus (VL). A topographic relationship was found between the site of injection and the location of the lamella of labeled neurons. (6) The percentage of retrogradely labeled neurons in the shell zone surrounding the border of the ventrolateral nucleus and the ventrobasal complex (VB) was greater following postcruciate than precruciate injections, whereas fewer retrogradely labeled neurons were found in central lateral nucleus (CL) after postcruciate injections than after precruciate injections. (7) These observations support the hypothesis that differential cortical and thalamic projections to different subregions of area 4γ may give rise to the different physiological properties of neurons observed in these subregions (Vicario et al. 1983; Martin et al. 1981).

Key words: Motor cortex – Thalamocortical – Corticocortical – HRP – Cat

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Introduction

Until recently, the primary somatosensory (SI) and motor (MI) cortices of higher mammals have been considered to be organized as unique representations of the body. This simple view was first challenged by the observations of Merzenich and his co-workers (Paul et al. 1972; Merzenich et al. 1978), who found separate representations of the body in cytoarchitectonic areas 3b, 1 and 2 of SI in the monkey. These separate representations receive input from slowly adapting cutaneous mechanoreceptors, rapidly adapting cutaneous mechanoreceptors and joint afferents, respectively. In addition, area 3a has been found to be specifically influenced by muscle afferents (Oscarsson and Rosen 1966; see Jones and Porter 1980 for review). Paralleling these physiological observations are anatomical demonstrations of differences in thalmo-cortical and cortico-cortical connections to the same sensory subregions of monkey cortex (Vogt and Pandya 1978; Jones et al. 1978). Studies of the functional organization of the motor cortex in both the monkey (Strick and Preston 1978a, b; Kwan et al. 1978) and the cat (Pappas and