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Single Cell Studies of the Primate Putamen

I. Functional Organization*

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Summary. In order to clarify the functional organization of the putamen and the nature of sensory inputs to this structure we studied the relation of single cell activity to active movements and somatosensory stimulation in the awake primate. Neurons ($N = 707$) were categorized on the basis of their relation to active movements or responses to sensory stimulation of individual body parts. 38% of neurons studied were related to the arm, 9% to the leg, 11% to the mouth or face, and 3% to axial portions of the body. The remaining neurons exhibited non-specific activation which could not be confidently localized to an individual body part (12%) or did not respond during the examination (26%). The high proportion of arm neurons was due to the focus of this study on cells related to arm movements. A large proportion (41%; $N = 270$) of the "arm" neurons was responsive to somatosensory stimulation. For these neurons the most effective stimulus (82%) was passive joint rotation. Six (5%) of the arm neurons responded to cutaneous stimulation. The putamen was found to be somatotopically organized. Neurons related to different body parts (leg, arm, and face) were segregated, and each body part was represented over a long anteroposterior extent of the nucleus. Clusters of 2-5 neurons with similar relations to active movements or responsive to passive movements of a single joint were often encountered over a 100-500 μ distance. Clusters of neurons with sensory driving were organized by joints. Rather than a single elbow or shoulder area, multiple clusters of neurons related to each joint were widely distributed over a long

anteroposterior extent of the nucleus and were adjacent to clusters of neurons related to other joints of the arm. These clusters of neurons with similar functional properties may correspond to the subunits of the striatum which have been revealed by anatomic and morphologic studies. We propose that these clusters of neurons with similar functional properties represent the basic functional units of the striatum in a manner analogous to the functional columns of the neocortex.

Key words: Single cell activity - Putamen - Awake primate - Somatotopy - Functional organization

Introduction

The striatum receives the bulk of afferents to the basal ganglia. In primates, the striatum is divided by the internal capsule into the caudate and the putamen. Whereas the caudate receives its input primarily from "association" areas of the cortex (Künzle 1978), the putamen receives the entire corticostriate projection from the sensory and motor cortices (Künzle 1975, 1977; Jones et al. 1977) and the bulk of projections from the premotor cortex (Künzle 1978). On anatomical grounds, it thus appears that the putamen plays a major role in the mediation of the motor functions of the basal ganglia. Direct evidence for this motor function has been obtained from single-cell studies in behaving primates (DeLong 1972, 1973; Anderson 1977; Liles 1979, 1981), in which changes in cell activity have been found to be correlated with limb and body movements during performance of motor tasks.

Since the putamen receives a major input from the somatosensory as well as from the motor cortex, it is reasonable to expect that neurons in the putamen would discharge in response to somatosensory stimu-

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lation as well as in relation to active movements. However, there have been no previous studies of the responses of putamen neurons to somatosensory stimuli in the awake primate. In the globus pallidus of the primate, which receives a major projection from the putamen, DeLong and Georgopoulos (1979) found evidence for sensory driving from deep structures, such as muscles and joints. In the cat, several investigators have described changes in neuronal activity in the striatum (Schneider and Lidsky 1981) and the pallidum and entopeduncular nucleus (Lidsky et al. 1975; Neafsey et al. 1978) evoked by sensory stimulation of the face and perioral structures. Recordings in anesthetized and paralyzed animals have indicated that basal ganglia neurons are responsive to somatosensory stimuli, as well as to visual and auditory stimuli, but that these responses are non-specific in nature (see Krauthamer 1979). It is important, therefore, to determine (1) to what extent the activity of neurons in the putamen is modified by somatosensory stimulation in the awake primate and (2) whether these inputs are specific enough to be used by the basal ganglia in the control of ongoing movements.

An important question concerning the functional organization of the putamen is whether this nucleus is somatotopically organized. Anatomically, this is suggested by the fact that projections from the leg, arm, and face areas of the motor and sensory cortices terminate in different regions of the putamen (Künzle 1975, 1977). However, neurophysiological evidence for such an organization is limited (DeLong 1972; Liles 1979).

An additional question concerns the more detailed aspects of the functional organization of the putamen. The apparently homogeneous striatum may, in fact, be a mosaic of subunits. For example, both the corticostriate (Jones et al. 1977; Goldman and Nauta 1977) and thalamostriate (Kalil 1978) projections are characterized by discontinuous patches of terminal labeling. In addition, Graybiel and coworkers (1981, 1982) have described patches of dopamine histochemistry and acetylcholinesterase and enkephalin immunoreactivity in the striatum and Goldman-Rakic (1981, 1982) has found evidence of distinct cellular compartments within the striatum. These findings suggest that functional equivalents of these anatomically identified subunits might be found in the striatum. Some evidence for this has been found by Liles (1979), who observed clustering of neurons in the putamen with similar relations to a limb movement task in the primate.

In order to clarify the functional organization of the putamen and the nature of sensory inputs to this structure we have studied the relation of the activity

of single neurons to active movements and passive manipulations of different body parts. Preliminary results of the present study have been published previously (Crutcher and DeLong 1981, 1982).

Methods

This study was carried out in rhesus monkeys which were trained to perform a visuomotor tracking task which dissociated the direction of arm movement from the pattern of muscular activity. See the companion paper (Crutcher and DeLong 1984) for a complete description of the task.

Surgery

After the animals were fully trained in the behavioral task, surgery was performed under pentobarbital anesthesia. An 18 mm diameter hole was cut in the skull, and a cylindrical stainless steel recording chamber was stereotactically positioned over the hole. The chamber was cemented in place with dental acrylic. The cylinder was tilted 50 degrees from vertical in the coronal plane to avoid passage of the electrode through the arm area of the motor cortex or the internal capsule. A T-bar used for fixation of the head during recording was attached to the skull with dental acrylic.

Recording and Data Collection

During recording sessions the monkey's head was immobilized. A Narishige hydraulic microdrive was used to lower glass-coated, platinum-iridium microelectrodes (1–5 MΩ impedance at 1,000 Hz) through the dura and into the brain. The electrode penetrations were separated by 1 mm. The signal was amplified and filtered at 200–10,000 Hz. The extracellular spike potentials were discriminated with a differential amplitude discriminator. The criteria for recording potentials from cell bodies were (1) initially negative, biphasic potentials, and (2) initial negativity > 0.2 ms in duration.

Because many neurons in the putamen are not spontaneously active, the animal was allowed to perform the arm-movement task as the electrode was slowly advanced in search of task-related cells. In other non-task-related parts of the putamen the animal was periodically examined by the experimenter in an effort to activate otherwise silent cells.

The relation of the activity of each isolated cell to active movements and passive manipulation of different body parts was studied by listening to the neural activity on audio headphones as the monkey made spontaneous movements and during examination by the experimenter. Movements of the arm were also elicited by offering the monkey raisins in various locations. Movements of the lips, tongue and jaw were elicited by offering liquid rewards, and by presenting a cotton-tipped applicator saturated with water which the animal could lick. The monkeys were also trained to permit passive manipulations consisting of gentle, passive joint rotation, tendon and muscle taps, light touch to the hairy and glabrous skin, and gross visual stimuli. Noxious stimuli were not used. Neurons which were related to active and/or passive arm movements were also studied in greater detail in the behavioral paradigm (Crutcher and DeLong 1984).

Histological Reconstruction

At the end of the experiment the animals were deeply anesthetized with pentobarbital and perfused first with isotonic saline and then

with a 10% buffered formalin solution. The brains were frozen, sectioned in the coronal plane at 40 µ intervals, and stained with cresyl violet.

In order to determine accurately the location of each neuron studied the electrode penetrations were carefully reconstructed. This was done by making outline drawings of coronal sections of the brain at 0.5 mm intervals and plotting the location of each of the glial tracks caused by the passage of the electrodes. The histologically reconstructed electrode map was then compared with the cylinder map to identify each penetration. All electrode penetrations were successfully located and identified. The cell locations within each penetration were then plotted on magnified outline drawings of the putamen. During recording sessions the depths of neural landmarks (entry into or exit from the cortex, putamen and globus pallidus) were recorded. Each of these structures has a characteristic spontaneous activity, particularly the putamen and pallidum (DeLong 1971, 1973), which provided reliable electrophysiological landmarks. By using the electrophysiological landmarks and taking shrinkage of the brain into account the location of each recorded cell within the putamen could be accurately plotted.

Results

Data Base

Recordings were obtained from three hemispheres of two juvenile rhesus monkeys. Each animal was studied for 2–3 months. Seven hundred and seven single neurons in the putamen were studied in 75 electrode penetrations. All penetrations were histologically identified as described in the methods. The putamen was studied from stereotaxic coordinates anterior 7 to anterior 20 (Snider and Lee 1961). The majority of the electrode penetrations were in the central half of the nucleus in the dorsoventral plane.

Neuronal Relations to Individual Body Parts

Neurons were categorized on the basis of their relation to active movements and/or responses to passive stimulation of individual body parts. Table 1 lists the numbers and percentages of neurons related to each body part. The activity of 47% of the neurons examined was related to active movements and/or passive manipulation of the limbs. Eleven percent were related to licking and/or chewing movements or to sensory stimulation of the face or of intra- or perioral structures. One percent of neurons were related to gross visual stimulation or to eye movements and 3% of neurons were related to axial portions of the body. The remaining neurons exhibited non-specific changes in activity during the examination, which could not be confidently attributed to any specific portion of the body (12%) or did not change their activity during the examination

Table 1. Numbers and percentages of neurons related to each body part. Almost all of the leg, arm, and orofacial neurons were related to active movements of that body part. A significant proportion of those neurons also responded to passive manipulations of the same body part. A few of the leg, arm, and orofacial neurons and many of the axial neurons were related primarily to passive manipulations

	N	%
Arm	270	38
Leg	65	9
Orofacial	80	11
Visual	4	1
Axial	21	3
Non-specific	87	12
Non-responsive	180	26
Total	707	100

Table 2. Numbers and percentages of neurons responsive to sensory stimulation of different parts of the arm

	N	%
Hand/fingers	14	13
Wrist	15	13
Elbow	35	31
Shoulder	48	43
Total	112	100

(26%). The high proportion of arm neurons is due in part to the fact that attempts were made to record primarily in those regions of the putamen where neurons related to the arm movement task were located.

Relations to Active Movements

The majority of neurons studied (415/707) showed relations to active movements of the leg, arm, or face. Of the 270 neurons related to the arm, 19% were related to active movements of the distal arm (wrist/fingers), and 40% to movements of the proximal arm (elbow/shoulder). The remaining 41% of arm neurons were related to active movements of the arm, such as reaching or grasping movements, but the source of the activation could not be localized confidently to a specific portion of the arm.

Responses to Passive Manipulations

A significant proportion of neurons related to active movements of specific body parts also responded to

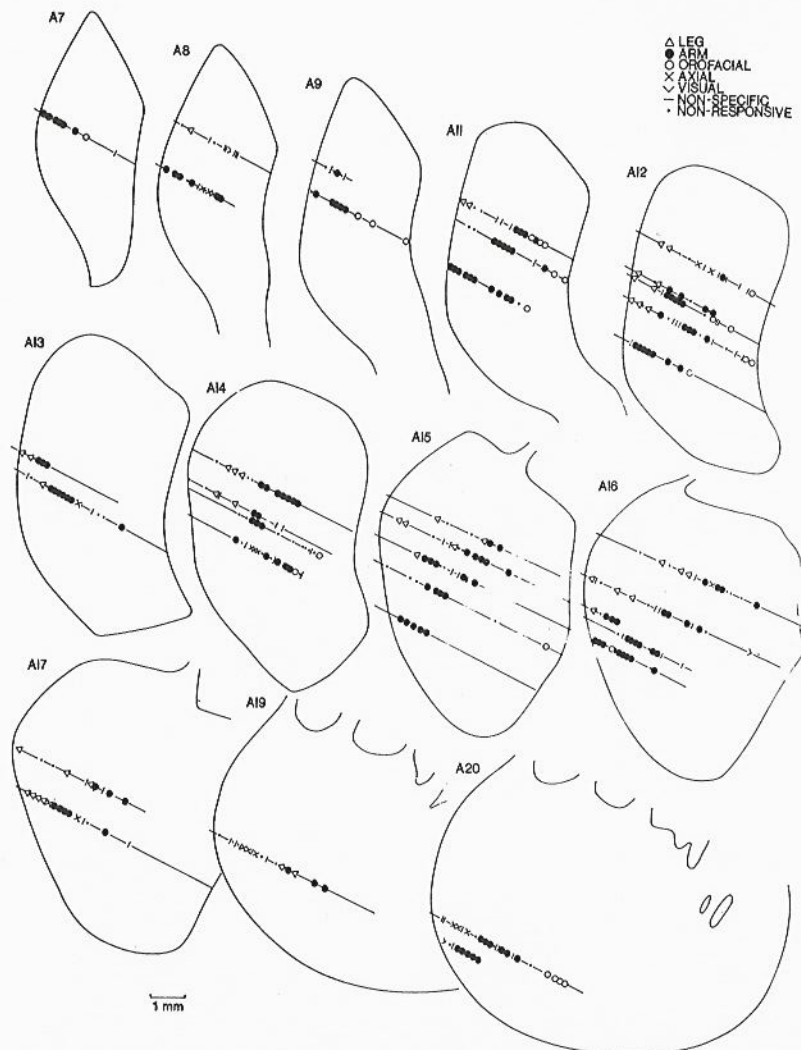


Fig. 1. Locations of neurons studied in the examination in one monkey. Data from both hemispheres are plotted on outline drawings of coronal sections of the left putamen. Each drawing shows the locations of all of the neurons studied within a half mm of that anteroposterior level, ranging from anterior 7 (A7) to anterior 20 (A20). For each section, lateral is to the left

Table 3. Anteroposterior distribution of neurons related to individual body parts. Each column lists the number and percentage of neurons of each type found in each anteroposterior quarter of the nucleus. For example, A 20-17 represents all neurons studied from anterior 20 mm to anterior 17 mm (Snider and Lee 1961). A larger number of neurons were encountered in the central half of the nucleus than in the rostral and caudal poles because there were more electrode penetrations in that region

	A 20-17	A 16-14	A 13-11	A 10-7
	N %	N %	N %	N %
Leg	12 (14)	28 (9)	24 (11)	1 (1)
Arm	26 (30)	124 (41)	75 (36)	45 (42)
Orofacial	4 (5)	18 (6)	41 (20)	17 (16)
Axial	9 (10)	6 (2)	3 (1)	3 (42)
Non-specific	17 (19)	34 (11)	24 (11)	12 (26)
Non-responsive	20 (23)	90 (30)	42 (20)	28 (26)
Total	88 (100)	300 (100)	209 (100)	106 (100)

passive manipulation of the same body part. In general, the neural relations to active movement were stronger than the responses to passive manipulation. 41% of arm, 55% of leg, and all of the axial neurons responded to somatosensory stimuli. The high proportion of sensory responses of axial neurons may be due to the difficulty of identifying neurons related to active movements of the trunk. Table 2 lists the number of neurons with sensory driving from each portion of the arm. Responses to passive manipulations from all parts of the limb were observed. However, the proximal portions of the arm were more heavily represented than were the distal.

The preponderance of somatosensory responses was from deep rather than superficial structures. For example, for the 112 arm neurons which were responsive to sensory stimuli, 92 responded to joint rotation, ten responded to muscle palpation, and four responded to tapping tendons or muscles. Six neurons had cutaneous receptive fields on the glabrous skin of the hand. None of the arm neurons responded to light touch of the hairy skin of the arm. However, one of the 21 axial neurons had a large cutaneous receptive field over the ribs.

For all neurons studied the sensory driving was very specific. For example, 81 of 92 neurons which responded to joint rotation were activated by movements about a single joint (often only in one direction). The remaining 11 neurons responded to movements of two contiguous joints, but most were preferentially related to one of the two joints. The six neurons with receptive fields on the glabrous skin of the hand had small receptive fields, e.g., on the radial half of the palm and ventral thumb.

The responses of 116 "arm" neurons to passive displacements of the elbow produced by application

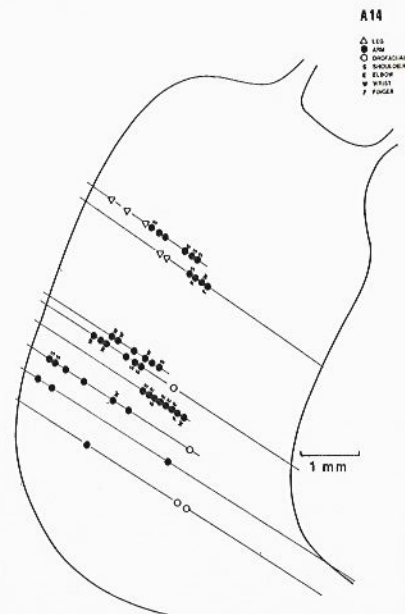


Fig. 2. Locations of neurons related to active movements or passive manipulations of the leg, arm, mouth or face at a single coronal level (anterior 14) from one hemisphere of a different animal from that in Fig. 1. Arm symbols with adjacent letters indicate the locations of neurons responsive to passive manipulations of the shoulder (S), elbow (E), wrist (W), or fingers (F). Arm symbols without adjacent letters show the locations of neurons related to active, but not passive, arm movements. Lateral is to the left

of a load during the behavioral task were also studied. Of the 38 neurons which responded to passive manipulations of the elbow or shoulder in the examination and which were studied in the task, 74% responded to load applications at latencies between 25 and 50 ms. Conversely, of the 47 neurons which did not respond to passive manipulations of the arm only 21% had short-latency torque responses. These short-latency, "sensory" responses were also specific. For example, of the 17 "elbow" neurons with short-latency responses to load application, eleven responded to only one direction of load application and the remaining six neurons all had clearly different magnitudes of response to the two directions of load application. These findings indicate that neurons in

Table 4. Anteroposterior distribution of neurons responsive to passive shoulder, elbow, wrist, or finger movements or related only to active arm movements. The numbers in parentheses indicate the percentages of neurons of each type in each anteroposterior quarter of the nucleus

	A 20-17		A 16-14		A 13-11		A 10-7		Total
	N	%	N	%	N	%	N	%	N
Shoulder	4	(15)	28	(23)	10	(13)	6	(13)	48
Elbow	6	(23)	17	(14)	8	(11)	4	(9)	35
Wrist	0	(0)	9	(7)	5	(7)	1	(2)	15
Finger	1	(4)	5	(4)	3	(4)	5	(11)	14
Active arm	15	(58)	65	(52)	49	(65)	29	(64)	158
Total	26	(100)	124	(100)	75	(100)	45	(100)	270

the putamen do receive somatosensory inputs of a specific nature.

Somatotopic Organization

The location of each neuron studied in the examination was plotted on outline drawings of the putamen.

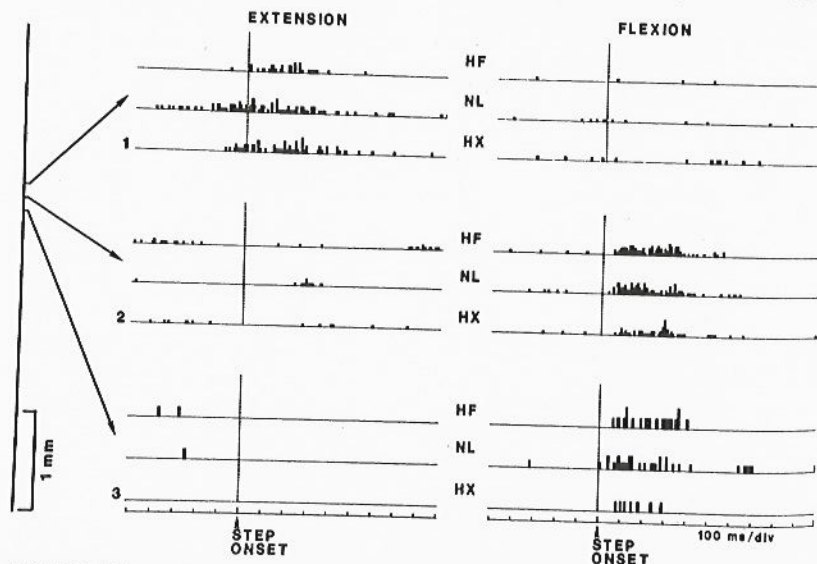


Fig. 3. Activity in the step portion of the behavioral task of three neurons encountered in a single microelectrode penetration. The vertical line on the left represents the mediolateral width of the putamen, and shows the relative locations of each of the three neurons. The two columns show movement-aligned histograms of activity for each neuron during the extension and flexion step movements under three different loading conditions: a heavy (150 g) load opposing flexion (HF), no load (NL), or a heavy load opposing extension (HX).

Data obtained from both hemispheres of one monkey are shown in Fig. 1. Neurons related to different body parts were somatotopically organized. Neurons related to the leg were located in the dorsolateral putamen, orofacial neurons were ventromedial, and arm neurons lay between the leg and orofacial areas. There was only slight intermingling of arm neurons with leg and orofacial neurons. Non-specific (NS) and non-responsive (NR) neurons were located throughout the region studied. Although the leg, arm, and orofacial neurons were found throughout the anteroposterior (AP) extent of the putamen which was studied (see Table 3), leg neurons were less common in the caudal putamen, and there were fewer orofacial neurons in the rostral putamen. This is seen both in Fig. 1 and in Table 3.

A salient feature of the functional organization of the putamen was the pronounced clustering of neurons with similar functional properties. Typically, along a given penetration discrete clusters of 2-5 neurons with similar relations to active movements or responses to somatosensory stimulation were

encountered over a 100-500 μ distance. This is illustrated in Figs. 1 and 2. Clusters of leg, arm and orofacial neurons were seen throughout most of the AP extent of the putamen. Three separate clusters of axial neurons at widely-spaced intervals (A8, A14, and A20) are also seen in Fig. 1. Because of the relative locations of the leg, arm and orofacial areas (i.e., the leg area dorsolateral and orofacial area ventromedial) and the angle of approach, it was common to record first from a cluster of leg neurons, then from one or more distinct clusters of arm neurons and, finally, from clusters of orofacial neurons.

Within the arm area some clusters of neurons were related only to active arm movements while others were related to both passive and active movements. A few clusters contained neurons which were primarily related to passive rather than to active movements. Clusters of neurons with sensory driving were organized by joints, i.e., all or most neurons in a cluster were related to passive movements of the same joint. An illustration of this is shown in Fig. 2. This figure shows the location of all the leg, arm, and orofacial neurons recorded in eight electrode penetrations. Clusters of neurons responsive to passive shoulder, elbow, wrist, or finger movements are evident. In none of the penetrations surrounding the penetration with five elbow neurons in either the coronal or sagittal plane were additional elbow neurons encountered. This suggests that these clusters are rather circumscribed in extent.

Rather than a single elbow or shoulder area within the arm area, there were multiple small clusters of neurons related to each joint. These clusters were found over a long AP extent of the putamen. Table 4 shows the AP distribution of neurons responsive to passive movements of the shoulder, elbow, wrist, or fingers, or related only to active arm movements. Shoulder, elbow and finger neurons were found throughout the AP extent of the nucleus. There was a uniform distribution of neurons related to active (and passive) arm movements. Wrist neurons however, were found primarily in the central portions of the nucleus. It is unclear whether this represents a restricted distribution of wrist neurons or is due to sampling bias. There was little suggestion of any internal organization of the arm area other than a weak tendency for neurons related to the distal arm to be found medial to proximal arm neurons.

Within a single cluster all or most of the neurons were usually related to similar movements of a single joint, whether active or passive or both. Figures 3 and 4 show examples of the similarities and dissimilarities of the activity of adjacent neurons in the behavioral task. Figure 3 shows the activity of three

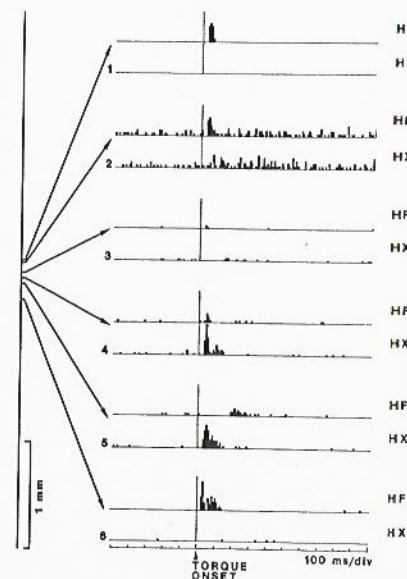


Fig. 4. Task-related activity of six, closely-spaced neurons in a single electrode penetration. As in Fig. 3, the vertical line on the left represents the mediolateral width of the putamen and shows the relative locations of each neuron. The six pairs of histograms show the responses of the six neurons to sudden application of either the heavy extensor (HX) or the heavy flexor (HF) load.

neurons which were studied in a single electrode penetration over a distance of 240 μ . Neurons 2 and 3 were related to both passive and active shoulder movements in the examination, and had virtually identical patterns of activity in the task. Both discharged during the active flexion movements for all loading conditions. The other neuron in that cluster (1) had the reciprocal pattern of activity. Figure 4 shows the activity of six neurons recorded over a 370 μ distance. The striking thing about this cluster of neurons was that five of the six neurons (1, 2, 4, 5, and 6) were responsive to passive elbow movements in the examination, and all five neurons responded to load application at short-latency. Neurons 1, 2, and 6 in the cluster responded to passive extension, as shown by the short-latency torque response in the HF class. The fourth and fifth neurons in the cluster had the opposite pattern; they responded at short-latency to passive flexion in class HX. Only one of these five

neurons was related to active arm movements during the step portion of the task. The third neuron in the cluster was related to shoulder movements in the examination, and was not responsive to load application. These two penetrations demonstrate two characteristics of intracolumnar organization. (1) Usually, all or most of the neurons in a cluster were related to active movements of the same body part (e.g., the shoulder) or responded to passive movements of the same joint in the examination. (2) The neurons in a cluster generally had either the same or reciprocal patterns of activity in the behavioral task.

Discussion

Neural Relations to Active Movement and Sensory Stimulation

The results of the present study and those in the companion paper (Crutcher and DeLong 1983) indicate that the activity of many neurons in the putamen is phasically related to active movements of individual body parts. For most neurons the relations to active movement are highly specific. The specificity of the relations of putamen neurons to movement of individual body parts is similar to that found in pallidal neurons (DeLong 1971; DeLong and Georgopoulos 1979; Georgopoulos et al. 1983), which receive direct projections from the putamen.

This study indicates that a significant proportion of neurons in the putamen respond to somatosensory stimulation. The somatosensory driving was almost always very specific, e.g., cells most often responded to passive movements of only a single joint in one direction or had small cutaneous receptive fields. This is in contrast to some earlier studies which indicated that striatal neurons have large receptive fields (Sedgwick and Williams 1967; Anderson et al. 1976; Harper and Lidsky 1977) or are responsive to polysensory stimuli (Albe-Fessard et al. 1960; Sedgwick and Williams 1967; and see Krauthamer 1979). There are several possible explanations for this discrepancy. For one, the present study was carried out in that portion of the striatum which receives its major input from the sensorimotor cortex, i.e., the putamen (Künzle 1975, 1977; Jones et al. 1977). However, most studies cited above were in the caudate nucleus of the cat, which receives major inputs from other areas of the cortex in addition to those from the sensorimotor cortex. Species differences may also be a factor. For example, studies in the motor cortex have found that in primates, cells have small, fixed receptive fields whereas in cats cells have wide and labile fields (see Rosén and

Asanuma 1972). Another possible factor is that most of the studies which have found large receptive fields and polysensory inputs to striatal neurons were carried out in animals anesthetized with alpha-chloralose. Neurons of the motor cortex have small stable receptive fields in awake monkeys but have wide receptive fields, labile responses and polysensory responses in monkeys anesthetized with alpha-chloralose (see Asanuma 1975; Lemon and Porter 1976).

Reported failures to find neurons responsive to sensory stimulation in the putamen and pallidum in awake monkeys (Matsunami and Cohen 1975; Anderson 1977) are more difficult to reconcile with the present study. However, characterization of the responses of basal ganglia neurons to somatosensory stimuli was not the major focus of either of those studies. Other studies, both in anesthetized (Albe-Fessard et al. 1960) and awake (Lidsky et al. 1975; Anderson et al. 1976; DeLong and Georgopoulos 1979; Schneider and Lidsky 1981) preparations, have reported that striatal and pallidal neurons are responsive to somatosensory stimuli. In the present study, responses to somatosensory stimulation were usually very clear and consistent and did not appear to result from active movements of the animal. In addition, many of these neurons that responded to passive manipulations also responded at short latencies (25–50 ms) to load application in the behavioral task (see Crutcher and DeLong 1984). Given the neuronal response latencies to perturbations observed in the sensory and motor cortices (Evars 1973) and the slow conduction velocity of corticostriatal axons (Liles 1974), these short-latency responses are consistent with a sensory input to the putamen from the cortex.

The finding that somatosensory responses were obtained primarily from stimulation of deep rather than superficial structures, is consistent with the results of similar studies in the motor cortex (see below) and thalamus (Strick 1976; MacPherson et al. 1980) and recent studies in the pallidum and subthalamic nucleus (DeLong and Georgopoulos 1979). These inputs from deep structures may provide necessary proprioceptive feedback which can be used by the basal ganglia in the control of ongoing movement.

The observation that more cells were related to the proximal than the distal arm is consistent with the view that the basal ganglia play a primary role in the control of proximal musculature and posture (see Martin 1967). However, it should be emphasized that many neurons were clearly related to active movements and/or passive stimulation of the distal arm or leg. And clinically, it is well recognized that impair-

ment of distal portions of the limbs in such diseases as Parkinsonism is as great as the proximal impairment. It is noteworthy that cooling of the basal ganglia in primates results in a predominant wrist flexion (Hore and Villis 1980). Together, these findings indicate that the basal ganglia are concerned with the control of distal, as well as proximal limb musculature.

Comparison of the results of this study with similar studies in the motor cortex of the primate reveals considerable similarities. As in the present study, neurons in the motor cortex were better related to active than passive movements (Fetz et al. 1980), and joint movement was the most effective sensory stimulus (Lemon and Porter 1976; Fetz et al. 1980). Usually, neurons were responsive to movements of only one joint, and usually only for one direction of joint movement (Rosén and Asanuma 1972; Lemon and Porter 1976; Wong et al. 1978; Fetz et al. 1980). There was relatively little cutaneous as compared to joint driving (Lemon and Porter 1976; Wong et al. 1978; Fetz et al. 1980). Cutaneous fields were usually small and stable and usually on the glabrous skin of the hand (Rosén and Asanuma 1972; Lemon and Porter 1976), although Wong et al. (1978) found that neurons responsive to cutaneous stimulation of the proximal arm had larger receptive fields than those with distal receptive fields. The similarity of our results with those of motor cortical studies most likely is due to the fact that the portion of the putamen studied in the present experiment receives a major projection from the precentral motor fields.

Somatotopic Organization

This study reveals a clear somatotopic organization of movement-related neurons within the putamen. Neurons related to leg movements were located in the dorsolateral putamen, orofacial neurons were in the ventromedial putamen, and arm neurons lay between them. These results agree with those of Liles (1979) who found that neurons related to an arm movement task were located in deep or intermediate regions of the putamen, and that neurons related to licking and sucking movements were medial to the arm neurons. Very little intermingling of neurons related to leg, arm, and orofacial movements was observed in the present study and the leg, arm, and orofacial areas occupied a very long anteroposterior extent of the putamen. These findings are in accord with the known topography of the projections from somatotopically organized areas of the sensorimotor cortex (Künzle 1975, 1977). In addition, the location of leg, arm, and face areas in the globus pallidus

(DeLong and Georgopoulos 1979, 1981) is consistent with the present results based on the topography of the projections from the putamen to the globus pallidus (Szabo 1967).

Clustering. A striking finding of this study was the clustering of neurons with similar functional properties. Clusters of movement-related neurons in the putamen were also observed by Liles (1979). Clusters were small (100–500 μ) and corresponded in size (1) with the dimensions of the patches of terminal label characteristic of the corticostriate and thalamostriate projections (Jones et al. 1977; Goldman and Nauta 1977; Kalil 1978), (2) with the cellular islands in the striatum (Goldman-Rakic 1981, 1982) and (3) with the patches of dopamine histochemistry, acetylcholinesterase activity, and enkephalin immunoreactivity (Graybiel et al. 1981; Graybiel and Hickey 1982) which have been reported. The present results support the view that there is a functional correlate to these anatomically defined patches, as previously suggested by Goldman and Nauta (1977). It is possible that the functional clusters of neurons observed in the present study represent the basic functional units of the striatum and might be analogous to the functional columns of the neocortex. This conclusion is supported by the finding that single, small injections of labelled amino acids in the cortex sometimes result in only one patch of terminal labelling in the putamen (Jones et al. 1977).

An important question raised by these studies is whether a given cluster in the putamen receives its input exclusively from one or from several areas of cortex and from one or more columns in a given cortical area. The finding that the neurons in some of clusters were solely related to active movement and a few clusters were primarily related to sensory stimulation rather than to active movement suggests (but does not prove) a lack of convergence of sensory and motor inputs onto a single functional cluster. Although evidence of overlapping projections from different areas of cortex (e.g., the hand representation of areas 4, 3, 1, 2 and 5) to a given region of putamen has been reported (Jones et al. 1977), this does not answer the question of whether projections from each cortical area converge on a single functional cluster. To our knowledge, there have been no studies of the response of individual putamen neurons to stimulation of different cortical areas.

The finding of multiple, widely-distributed representations of each joint in the arm area suggests that there is not a single region of the putamen devoted exclusively to a particular joint. This is similar to the neocortex where representations for each joint are found in premotor, motor and sensory cortical areas.

Even within the motor cortex itself there is not a single circumscribed representation of each joint. Lemon and Porter (1976) found that adjacent neurons in the motor cortex often received afferent input "from strikingly similar zones, but there were many exceptions, in which neighboring neurones had inputs from entirely different parts of the arm". And Fetz et al. (1980) found that cells responsive to passive movements at the wrist, elbow and shoulder were extensively intermingled in a 10 mm diameter circular area in one monkey. These findings in the motor cortex are remarkably similar to those obtained in the putamen in the present study. Thus, it appears that in both the motor cortex and the putamen, clusters of neurons involved in the control of the movements of a single joint are widely distributed and interleaved with clusters of neurons unrelated to that joint.

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