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. 36% 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-
lalation 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 histofluorescence 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 stereotaxically 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 manipulations 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 perform 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...