Role of basal ganglia in limb movements


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Summary. Recent anatomic and physiologic studies have shed new light on the functional organization of the basal ganglia and their role in movement. The basal ganglia receive topographically organized input from the entire neocortex. Influences from sensorimotor and "association" cortices appear to remain segregated in the basal ganglia. The concept of segregated parallel subcortical loops subserving "motor" and "complex" functions is discussed. Recent neurophysiologic studies in behaving primates suggest that basal ganglia output plays a role in controlling the direction and amplitude of movement but is not primarily involved in the initiation of limb movement or selection of specific muscles. These studies are generally consistent with data from patients with Parkinson's disease, which likewise indicates a deficit in the programming of movement amplitude in step-tracking tasks, with little or no change in reaction-time or pattern of muscular activity.

Key words: Basal ganglia — Anatomical organization — Movement — Motor function — Single cell recording

Numerous clinicopathologic studies have indicated a major role of the basal ganglia in the pathogenesis of movement abnormalities occurring in patients with disorders such as Parkinson's and Huntington's Disease. Yet the role of these structures in normal motor mechanisms remains poorly understood. This review is focused on the functional organization of the basal ganglia and their role in the control of limb movements. Emphasis is placed on recent anatomic and neurophysiologic studies in primates, because of their relevance to human disorders. The contribution of the basal ganglia to the control of limb movements has been evaluated in behaving primates with a variety of techniques, including single cell recording, lesions and electrical stimulation. We have focused here on studies carried out in animals trained on well-controlled arm-movement tasks. For a more detailed review of these and related topics see DeLong and Georgopoulos (1981).

Functional-anatomic considerations

The "basal ganglia" are composed of several anatomically and functionally related nuclei located in the telencephalon, diencephalon, and mesencephalon. These include the striatum, the globus pallidus, the substantia nigra, and the subthalamic nucleus. The striatum of primates is divided by the internal capsule into a dorsomedial portion, the caudate nucleus and a ventrolateral portion, the putamen. The globus pallidus (or pallidum) of primates is a composite structure formed by an external segment (GPe) and an internal segment (GPi), each with distinctive anatomic relations. The substantia nigra is likewise a composite structure formed by a densely cellular dorsomedial portion, the pars compacta (SNpc) and a less dense ventrolateral portion the pars reticulata (SNpr).

The overall anatomic relationships of the basal ganglia are summarized in Figure I. The striatum is generally viewed as the major "receptive" portion of the basal ganglia. It receives inputs from three major sources: (1) the dopaminergic neurons of the SNpc, (2) the intralaminar nuclei of the thalamus, and (3) areas of the neocortex. The projections from the neocortex to the striatum are topographically organized (Goldman and Nauta 1977, Kemp and Powell 1971, Kunzel 1975, 1978, Yeterian and Van Hoesen 1978). Whereas the somatosensory, motor and premotor cortices project largely to the putamen, the "association" cortices project largely to the caudate. These anatomic relations suggest a role of the putamen in more strictly "motor", and of the caudate in more "complex", behavioral functions. Indeed, studies in primates have shown that restricted bilateral lesions of specific areas of the caudate nucleus can produce behavioral impairments which correspond to deficits seen following lesions of those specific areas of prefrontal cortex which project to the lesioned caudate areas (see Divac 1977 for a review). A role of the caudate in complex behavior is also suggested by studies of single cell activity in behaving primates (see DeLong and Georgopoulos 1981; and Rolls 1982 for a review). Lesions of the putamen, on the other hand, are associated with motor disturbances (e.g., Beaubaton et al. 1980, Denny-Brown and Yamanisawa 1976, Hoer and Villis 1980). Neurophysiologic evidence for a predominant role of the putamen in motor functions has come from studies of single cell activity in the putamen of behaving primates (Crutcher and DeLong 1984 and b; DeLong and Strick 1974; Liles 1979) which have revealed a high proportion of cells related to specific movements of the leg, arm and face. These cells are, moreover, somatotopically organized in those portions of the putamen which receive topographically organized projections from the motor cortex (Kunze 1978).
The finding that the somatotopic motor representation in the putamen is preserved in GP, by virtue of topographic projections from the putamen, suggested that there exist segregated pathways through the basal ganglia for the control of different body parts. These findings led us (DeLong and Georgopulos 1981) to re-examine the evidence for the widely held view that the basal ganglia serve as a "funnel" from association areas to the motor cortex (Evarts and Thach 1969; Kemp and Powell 1970). Upon reviewing the relevant anatomic studies, as outlined above, we concluded that the available evidence is most consistent with the view that influences from the sensorimotor and premotor cortices are ultimately directed largely upon premotor areas, whereas influences from the association areas are directed largely upon the prefrontal cortex. We thus proposed the concept of segregated, parallel cortico-subcortical loops subserving "motor" and "complex" functions, as shown schematically in Figure 2. In this scheme, just as the leg, arm and face representations remain segregated throughout the cerebral cortex, basal ganglia and thalamus, so are the influences from the cortical association areas separately routed through the subcortical nuclei by virtue of nonoverlapping, topographically organized projections. According to this scheme there is little or no convergence within the basal ganglia of pathways which originate from the association areas or from the somatotopically organized sensorimotor areas. This view of the functional organization of the basal ganglia provides a framework wherein disturbances not only in motor, but also in more complex behavior, may separately result from damage to different portions of these nuclei.

Although the segregation of influences from association and sensorimotor cortices appears to be maintained throughout the basal ganglia, there is abundant evidence that integration of input from different cortical regions takes place within these structures. This was suggested by the studies of Kemp and Powell (1970), who demonstrated overlapping corticostriate projections to the striatum from adjacent brainstem and spinal cord.

![Diagram of basal ganglia connections](image)

**Fig. 1.** Schematic diagram of principal intrinsic and extrinsic connections of basal ganglia. GPe, external pallidal segment; GPi, internal pallidal segment; SNpr, substantia nigra pars reticulata; SNpc, substantia nigra pars compacta; STN, subthalamic nucleus; CM, center median; VL, n. ventralis lateralis; VA, n. ventralis anterior; SC, superior colliculus; RF, reticular formation; VTA, ventral tegmental area; TPC, n. tegmenti pedunculopontinus pars compacta. The dashed lines indicate dopaminergic pathways. Projections from the raphe to the striatum and substantia nigra have been omitted. (From DeLong and Georgopulos 1981 with permission of the American Physiological Society)

The segregation of influences from "association" and sensorimotor cortices in the caudate and putamen, respectively, appears to be maintained at subsequent levels by topographically organized projections from the caudate and putamen (Johnson and Rosvold 1971, Szabo 1967, Szabo 1970) to separate regions of both segments of the GP and the SNpr, the major sources of basal ganglia output. Within both GPe and GPi a somatotopically organized representation of movement related neurons has been found in those portions of each structure which receive their input from the putamen (DeLong and Georgopulos 1979, 1981). The apparent segregation of "motor" and "complex" functions observed throughout the striopallidal system appears to be maintained further at the thalamic level by subsequent topographically organized projections to the thalamus from Gpi and SNpr (e.g. Carpenter et al. 1976, Nauta and Mehler 1966, Kuo and Carpenter 1973, Kim et al. 1976). The bulk of basal ganglia output appears to be directed ultimately (via the thalamus) to the premotor and prefrontal cortices (see DeLong and Georgopulos 1981, Schell and Strick 1983). Projections from Gpi to the brainstem and from the SN to the superior colliculus provide additional output pathways.

![Diagram of thalamus connections](image)

**Fig. 2.** Schematic depiction of the postulated segregation of pathways from the "association" (complex loop) and the sensorimotor areas (motor loop), through the basal ganglia and thalamus. (From DeLong et al. 1983 with permission from Springer-Verlag)
cortical areas, for example the motor and somatosensory areas. Autoradiographic studies (Goldman and Nauta 1977; Jones et al. 1977; Kunzle 1975) further suggested that the overlap may be even more extensive than indicated by the earlier degeneration studies. Studies by Yeterian and Van Hoesen (1978) have indicated, moreover, that convergence of corticoostriate projections is based not simply on proximity of cortical regions, but on whether or not cortical regions are interconnected. A theoretical outcome of the application of this organizing principle to the "arm" representation at cortical and putamen levels is shown in Figure 3. This hypothetical scheme depicts integration within the putamen of cortical inputs from the "arm" areas in cortical areas 6, 4, 3, 1, 2, and 5. Indeed, Jones et al. (1977) demonstrated overlapping projections in the putamen from hand regions in cortical areas 4, 3, 1, 2, and 5. Together, these studies raise the possibility that interactions may arise in the basal ganglia that may not be found at the cortical level (DeLong and Georgopoulos 1981). According to this idea, integration of afferent inputs to the putamen (and more generally the entire striatum) takes place primarily in the rostro-caudal plane. Specifically, motor and sensory inputs to the arm, leg, and face areas within the putamen remain segregated, whereas inputs related to a single body part (e.g. arm) from a variety of cortical areas appear to converge along a rostro-caudal functional (arm) cylinder.

In addition to the projections to GP from the striatum, GP is under the influence of the subthalamic nucleus, which is positioned at the center of an internal loop formed between the two segments of GP. The STN receives its major input from GPe and in turn sends projections back to both pallidal segments and to the SN (Carpenter and Strominger 1967, Nauta and Cole 1978). Although major attention has been directed to the projections from the cortex to the striatum, a topographically organized projection to the STN has also now been demonstrated in primates from the motor and premotor cortices (Hartmann von Monakow et al. 1978). In recent studies of the activity of neurons in STN in relation to movement (DeLong and Georgopoulos 1981) we have observed a somatotopic organization of movement-related neurons similar to that suggested by anatomical studies. Since the STN projects to both segments of the GP and to the SN, it can directly influence the output from the basal ganglia. It is well established that discrete lesions of the STN in man and primates may result in large amplitude involuntary movements of the contralateral limbs, termed hemiballismus (Carpenter et al. 1950, Whittier 1947, Whittier and Mehler 1949). Since these movements can be abolished by subsequent lesions of GPe or its efferent projections, it is postulated that loss of the modulating influences of the STN on GP leads to dyskinesias because of the resulting abnormal output from GP. This could be regarded in a functional sense as a disconnection of GP from the cortico-subthalamic input, which is unique to primates. It is noteworthy in this regard that cortico-subthalamic connections have not been identified in subprimates.

The issue of precisely which portions of the frontal lobe receive basal ganglia output, and the related question of whether integration of basal ganglia and cerebellar output occurs at the thalamocortical level, require consideration, since recent studies necessitate a significant revision of the earlier view that the output from these two systems is integrated in the thalamus and motor cortex (Allen and Tsukahara 1974, Evarts and Thach 1969, Kemp and Powell 1971). Numerous studies have shown that projections from the deep cerebellar nuclei, the globus pallidus, and the substantia nigra to the thalamus terminate in separate parts of the thalamus (e.g. Asanuma et al. 1983, Carpenter et al. 1976, DeVito and Anderson 1982, Kall 1981, Kuo and Carpenter 1973, Mehler 1971). In brief, these studies indicate that cerebellar efferents terminate in regions of the thalamus which project directly to the motor cortex, whereas basal ganglia efferents terminate in regions which project largely to pre-motor and pre-frontal areas. A recent study by Schell and Strick (1983), indicates, however, that whereas cerebellar output is directed to the motor cortex via the pars oralis subdivision of the nucleus ventralis posterior lateralis (VPLo), such output also influences the arcuate premotor area (APA) via area X of the thalamus. According to this study basal ganglia output is directed in large part to the supplemental motor area (SMA) via the pars oralis subdivision of ventralis lateralis (VLO). In addition, basal ganglia must influence more rostral regions of the forebrain via projections from both the parvocellular and pars compacta portion of ventralis anterior (VA). Thus basal ganglia and cerebellar influences appear to take separate, parallel pathways through the thalamus, with the basal ganglia output directed to the SMA and pre-frontal cortex and the cerebellar output to the motor cortex (area 4) and the APA.
Functional organization of movement-related neurons

**Striopallidum**

As mentioned above, in both the putamen and GP, there is a clear correlation between cell discharge and active movements of specific body parts, e.g., leg, arm, and orofacial structures (Crutcher and DeLong 1984a; DeLong 1971; DeLong and Georgopoulos 1979; DeLong et al. 1983). An important finding of these studies was that cells related to movements of particular body parts were grouped together within each structure in a somatotopic manner, as shown for the putamen in Figure 4. An additional result of these studies was the demonstration of the considerable anteroposterior extent of the leg, arm and face motor representation, as also shown for the putamen in Figure 4.

In addition to the somatotopic grouping of neurons, a clustering of neurons with similar functional properties within the leg, arm and face areas has been observed within the putamen (Crutcher and DeLong 1984a; Liles 1979). As illustrated in Figure 5, discrete clusters of 2−5 neurons with similar relations to active movements or responses to somatosensory stimulation were typically encountered over a 100−500 micron distance along a given penetration. Different clusters of leg, arm and orofacial neurons were seen throughout most of the anteroposterior extent of the putamen. Some clusters contained neurons whose activity was related only to active arm movements while others contained neurons related to both passive and active arm movements. Clusters of neurons with sensory driving were organized by joints, i.e., all or most neurons in a cluster responded best to passive movements of the same joint. Within the “arm” area of the putamen there appeared to be multiple clusters of neurons related to each joint. Additional evidence for this type of clustered, somatotopic organization includes the recent demonstration of discrete foci within the putamen.

![Fig. 4. Locations of neurons related to movements of different body parts 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 0.5 mm of that anteroposterior level, ranging from anterior 7 (A7) to anterior 20 (A20). For each section, lateral is to the left. (From Crutcher and DeLong 1984a with permission from Springer-Verlag)](image-url)
Substantia nigra: SNpr and SNpc

In studies which have examined neuronal relations to movements of different body parts, cells in the SNpr have been found to discharge primarily in relation to licking and chewing (DeLong et al. 1983, Mora et al. 1977).

In contrast to the findings in GP, STN and putamen, only a small proportion of cells in the SNpc exhibited significant phasic changes in discharge in relation to active (or passive) movements of the limbs or orofacial structures, and even these neurons did not appear to encode specific information regarding movement parameters (DeLong and Georgopoulos 1979, DeLong et al. 1983). In a recent study, Schultz (1983) observed a modulation of a larger proportion SNpc neurons in relation to vigorous, large amplitude, proximal (but not distal) limb movements. As in our studies there did not, however, appear to be any specific relation between cell discharge and parameters of movement. Steinfels (1981) found no modulation of SNpc neurons during locomotion in the freely moving cat. These findings suggest that the nigrostriatal dopamine system, rather than conveying specific information about movement may exert a general tonic modulatory effect upon the striatum. Several independent lines of evidence are consistent with this view: (1) the relatively small absolute number of nigrostriatal DA neurons and their rather divergent projections to the striatum (Fallon and Moore 1978); (2) the slow conduction velocities of nigrostriatal axons (Guyenet and Aghajanian 1978); (3) the beneficial effects of L-DOPA and direct-acting dopamine receptor agonists (such as apomorphine) on the behavioral disturbances resulting from lesions of the nigrostriatal DA pathways; and (4) the recent observation that intracerebral transplants of embryonic SN neurons, (which lack their normal afferent input) can compensate for behavioral disturbances following nigrostriatal DA pathway lesions (Bjorklund et al. 1981).

It is possible that DA release in the striatum may be modulated by graded changes in the firing rate or by recruitment of additional SNpc neurons. It is also possible that DA release could be phasically regulated by local mechanisms within the striatum, such as presynaptic modulation of DA terminals by thalamic and cortical afferents (see DeLong et al. 1983). Thus, a lack of phasic modulation of SNpc neurons during certain types of movement does not necessarily rule out a phasic action of dopamine within the striatum, although it does suggest that such phasic release may be, in part, independent of impulse flow in the nigrostriatal pathway.

Somatosensory inputs

A significant proportion of the neurons in the putamen and GP which are related to active movements of specific body parts, also respond to natural somatosensory stimulation of the same body part (Crutcher and DeLong 1984a; DeLong and Georgopoulos 1979). For the putamen, 41% of arm movement-related cells responded to somatosensory stimuli. Essentially all parts of each limb were represented in ensembles of putamen neurons with response areas ranging in size from a single to several joints. However, driving from the proximal portions of the arm was more commonly observed than from the distal. Of 112 cells responding to
somatosensory stimulation. 43%, 31%, 13%, and 13% were best related to manipulations of the shoulder, elbow, wrist, and hand respectively. The preponderance of somatosensory responses was from deep rather than superficial structures, and the majority of cells (83%) responded to joint rotation. Only 5% of neurons had cutaneous receptive fields on the glabrous skin of the hand and none responded to light touch of the hairy skin of the arm. The responses of "arm" neurons to controlled passive displacements of the elbow produced by application of a load during a behavioral task were also studied. Of neurons which responded to passive manipulations of the elbow or shoulder, 74% responded to load application at latencies between 25 and 50 ms. Given the neuronal response latencies to perturbations observed in the sensory and motor cortices (Evarts 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. Neurons with short-latency, "sensory" responses typically exhibited highly specific directional and amplitude relations. These findings indicate that the putamen receives somatosensory inputs of a specific and spatially restricted nature. Furthermore, these inputs may be used to control or monitor ongoing movements.

These findings are in contrast to some earlier studies which indicated that striatal neurons have large receptive fields (Anderson et al. 1976; Harper and Lidsky 1977; Sedgwick and Williams 1967), or are responsive to polysensory stimuli (Albe-Fessard et al. 1960; Krauthamer 1979; Sedgwick and Williams 1967). These discrepancies may be due to the fact that most of the studies cited above referred to the caudate nucleus of the cat, which receives major inputs from other areas of the cortex in addition to those from the sensorimotor cortex, whereas our study was carried out in that portion of the striatum which receives its major input from the sensorimotor cortex, i.e., the putamen. Species differences and anesthesia may also be significant factors.

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 (e.g. Fetz et al. 1980; Lemon and Porter 1976) and the thalamus (MacPherson et al. 1980; Strick 1976). 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 prevalent view that the basal ganglia play a major 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 impairment of distal portions of the limbs in diseases such as Parkinsonism, is as great as the proximal impairment. Experimentally, cooling of the basal ganglia in primates in one study resulted in 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.

Initiation of movement

It has been found in reaction-time tasks that most changes in neuronal discharge in the basal ganglia begin before the onset of movement but after the first EMG changes (Anderson and Horak 1981; Crutcher and DeLong 1984a; DeLong and Georgopoulos 1981; Georgopoulos et al. 1983). In these studies changes in discharge in about one-fourth of the cells begin before the first EMG changes. Overall, changes in neuronal discharge seem to occur later in the basal ganglia than in the motor cortex. For example, approximately 50% of the cells in motor cortex changed activity before the earliest EMG changes (approximately 80 ms prior to movement) in reaction time tasks (e.g. Evarts 1974; Thach 1978); this percentage was respectively 24%, 11%, and 29% in GPe, GPi, and STN (Georgopoulos et al. 1983), and 19% in the putamen (Crutcher and DeLong 1984b). These data for the putamen are shown in Figure 6. It appears, from comparing the results of studies in basal ganglia with those in motor cortex, that neuronal activation in the motor cortex may precede activation in the putamen and GP. However, comparisons of timing relations between different brain areas based on studies involving different animals, different paradigms and different laboratories must be made with some reservation. Studies comparing different areas in the same animal preforming on the same task are needed to fully settle this issue.

It is interesting that microstimulation of the GP has been reported to slow limb movements when delivered after the first changes in EMG activity but prior to movement onset (Horak and Anderson 1980). Moreover, lesions (Horak and Anderson 1980) and cooling (Beaubaton et al. 1981, Hore and Villis 1980) of GP resulted in slowing of movements without prolonging reaction times. In fact in the study by Beaubaton et al. reaction times were actually shortened. The one exception to these findings is a report (Beaubaton et al. 1980) of a slight prolongation of reaction times in baboons performing a visuo-motor pointing task during cooling of the putamen. Taken together, these studies are consistent with the view that the putamen and GP, in these tasks, are more involved in the execution of limb movement than in the timing of its initiation (Aldridge et al. 1980; Anderson and Horak 1981; Crutcher and De-
Long 1984b; Georgopoulos et al. 1983; Hallett and Khosibin 1980). It is possible, however, that the small population of neurons that are active early in such reaction-time tasks may play some role in the initiation of movement and that, in other types of paradigms, (e.g., self-initiated movements), or in different portions of the basal ganglia (e.g., the caudate or substantia nigra), neurons may be involved more specifically in movement initiation. It is of interest that Neafsey et al. (1978) found a significant proportion of neurons in GP and entopeduncular nucleus of the cat that responded well before the first charges in EMG activity during self-initiated movements. In these studies, however, early changes occurred in the cortex and thalamus as well.

Control of movement parameters and muscle pattern

In order to quantitatively the finding (DeLong 1971) of a relation of neural activity in basal ganglia neurons to the direction of arm movements and a possible relation of neural activity to the speed of movement (DeLong and Strick 1974), the relation of neuronal discharge to movement parameters was studied in animals trained to perform a step tracking task in which the amplitude, speed and direction of movement were varied (DeLong and Georgopoulos 1979; DeLong et al. 1983; Georgopoulos et al. 1983). Significant neuronal relations to both the direction and amplitude of movement were observed in GPe, GPI and STN during both the movement time (MT) and the initial premovement time (IPT the 100 ms prior to the onset of movement), i.e. the period during which most of the changes in EMG began to occur. In general, the frequency of cell discharge was a linear function of the movement amplitude. The incidence of significant amplitude effects was highest in the MT, but the effects were also present in the IPT. The effects of movement amplitude became most apparent when a wide range of amplitudes was used. The relations between cell discharge and peak velocity of movement in the step tracking task were similar to those described above for the amplitude of movement. This is not surprising since amplitude and peak velocity were highly correlated.

The finding of significant directional effects in GP can be explained by the fact that neurons in the putamen (Crutcher and DeLong 1984b) and the STN (Georgopoulos et al. 1983), which both project to GP, show a strong relationship to the direction of movement. The directional relations in the putamen and STN can, in turn, be accounted for by the inputs to these structures from the cerebral cortex, since both precentral and parietal cortical cells show significant relations to the direction of movement (Evarts 1966; Georgopoulos et al. 1982; Kalaska et al. 1983; Schmidt et al. 1975).

Relations to muscles or movement

In order to determine whether the activity of neurons in the basal ganglia is related to the direction of movement, per se, or to the underlying pattern of muscular activity, monkeys were trained in a separate study (Crutcher and DeLong 1984b) to perform a visuomotor tracking task which required elbow flexion/extension movements with assisting and opposing loads. This task dissociated the direction of arm movement from the pattern of muscular activity. Of 120 arm-movement related neurons in the putamen 58% were related to the direction of arm movement whereas only 13% showed a pattern of activity "like muscle". A putamen neuron whose activity was related to movement direction is shown in Figure 7. These results indicate that neurons in the putamen are predominantly related to the direction of movement, rather than to the activity of individual muscles. In an ongoing study in our laboratory similar relations to direction of movement have been found in GP (Mitchell et al. 1983). These results, together with those related to amplitude of movement (Georgopoulos et al. 1983), suggest that the basal ganglia may be involved in the control (or monitoring) of movement parameters rather than the selection of specific muscles. The significance of these directional effects is unclear, but it is of interest in this regard that Beabaton et al. (1981), in a reaction time task found inaccuracies in movement produced by either reversible cooling or coagulation of GP. In fact, these workers suggested that movements were slowed because of these inaccuracies. This finding might be due to the loss of directional or amplitude effects on movement.

A recent study of the effects of cooling of the GP on reaching movements in a reaction time task, Horak and Anderson (1980) indicated that the slowness of movement during cooling might be due to a generalized change in the amplitude and rate of rise of EMG activity in the muscles of the contralateral arm. In addition, microstimulation at different sites in GP produced either a speeding up or slowing of the agonist burst in step tracking movements.

The results of recent neurophysiological studies suggest that basal ganglia activity is probably not essential for the overall bradykinesia of Parkinson's disease, which may be due to the uncontrolled movements of patients with this disease, and that such movements are not related to the direction of movement and that other aspects of movement such as the timing of agonist and antagonist muscle activity. A role for the putamen is a correction on other aspects of movement such as the timing of agonist and antagonist muscle activity. A role for the putamen is a correction on other aspects of movement such as the timing of agonist and antagonist muscle activity.
slowing of movement. The sequential activation of different muscles in both the lesion and microstimulation experiments was similar to that of controls. These findings are consistent with the data from single cell studies indicating a primary role of GP in modulating the amplitude of movement without effects on movement initiation or the pattern of muscular activity. It should be noted, however, that Hore and Villis (1980) reported increased co-contraction of agonist and antagonist muscles following cooling of the GP and putamen, and suggested that the basal ganglia might play a role in the balance between agonists and antagonists for a particular motor act. Clearly, there is a need for further quantitative studies of the effects of manipulations of basal ganglia output on motor performance.

In addition to the neuronal relations to movement amplitude and direction, several studies have shown a relation between the neuronal activity and force levels. In the putamen (Crutcher and DeLong 1984b), 44% of arm-movement related neurons had significant relations to the level of static load. Several previous studies in the basal ganglia have found relations of neuronal activity to steady force (Allum et al. 1983; Branch et al. 1980; DeLong 1972; Liles 1981). However, in similar studies in the motor cortex (Cheney and Fetz 1980; Evarts 1969; Hepp-Reymond et al. 1978; Smith et al. 1975) the magnitudes of the observed static load effects were greater than in the putamen, and the studies which examined corticomotor-neuronal cells, also found higher proportions of neurons with static load effects.

A significant proportion of neurons in the putamen (52%) showed significant dynamic load effects (Crutcher, DeLong 1983; and Liles 1981), similar to those for neurons in the motor cortex (Cheney and Fetz 1980; Conrad et al. 1977; Evarts 1968). Comparison 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 putamen 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.

The neuronal responses to movement may be regarded as the net result of various factors, including the direction and amplitude of movement. It is possible that a step change in cell discharge is related to movement direction, and that this step change is further modulated according to the amplitude of movement, as shown in Figure 8: Direction and amplitude of movement may be separately controlled, since many neurons showed significant directional effects without amplitude effects, and others showed amplitude-related changes for only one direction of movement. These results may have implications for the broader issue of cerebral control of movement, since the observed neuronal relations in the putamen may largely reflect the nature of the inputs to this structure from the motor, pre-motor, and somatosensory cortices. It is, therefore, possible that similar neural relations to parameters of movement, independent of muscular activity, may also be found in these areas of cortex. In fact, a dissociation between muscular pattern and direction of intended movement was observed by Thach (1978) in the motor cortex. The basal ganglia may, therefore, function as a component of a distributed system controlling parameters of movement.

Patients with Parkinson's disease frequently have difficulty in controlling the amplitude of their limb movements. Single-step large amplitude movements are impaired: these movements fall short of the target (Flowers 1978), which is ultimately reached by a series of small-amplitude movements (Draper and Johns 1964; Flowers 1978). The mechanism of this phenomenon was partially elucidated recently by Hallett and Khoshbin (1980) who observed that Parkinsonian patients were unable to increase the amplitude of the agonist burst in step-tracking movements. Thus, large amplitude movements were achieved by several small amplitude steps. However, the duration of the EMG bursts were normal, as well as the pattern of agonist and antagonist muscular activity. It is possible that loss of pallidal output may account for the overall bradykinesia of Parkinsonian patients, whereas abnormal modulation with excessive output may lead to the uncontrolled movements of patients with involuntary movements, such as chorea and hemiballismus.

In summary, the results of recent neurophysiologic studies in trained primates suggest that basal ganglia output may play a role in scaling the amplitude of movement, by its effects on the magnitude of EMG activity, but that it is not primarily involved in the initiation of limb movement or selection of specific muscles. These studies are generally consistent with the available data on limb movements in patients with Parkinson's disease, which likewise indicates a major deficit in the control of movement amplitude in step-tracking tasks, with little or no impairment of reaction-time (see DeLong and Georgopoulos 1981; Evarts et al. 1981 for reviews) or disruption of the pattern of muscular activity. A role of the basal ganglia in other aspects of movement, such as motor programming (see DeLong and Georgopoulos 1981; and Marsden 1982) and "cognitive" behavior (e.g. Divac 1977; Oberg and Divac 1979) is by no means excluded by these findings.

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