Sensorimotor Contributions of the Basal Ganglia: Recent Advances

In the last decade, a great deal of research has been aimed at ascertaining the manner in which the basal ganglia (BG) contribute to the control of movement. The formation of workable hypotheses, however, has been limited by the great variety of putative roles reported in the literature. Reported functions have often been in direct conflict. Recent developments, however, provide new perspectives from which to view seemingly discordant functions. Data reviewed in this article suggest a distinct anatomical topography within the BG, allowing for highly specialized subfunctions. In parallel, BG cellular activity has been found primarily in association with specific sensory and task-related dimensions relevant to particular movements. The multiple sensorimotor contributions of the BG therefore are not contradictory, but represent BG contributions within different functional contexts. These multiple roles of the BG offer particular clinical insights. [Connor NP, Abbs JH. Sensorimotor contributions of the basal ganglia: recent advances. Phys Ther. 1990;70:864-872.]

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Basic investigations into the neural processes underlying the control of movement can provide crucial information to movement scientists and clinicians striving to better understand these complex systems. Toward this goal, neural structures presumed to exert an influence on motor control have been the focus of intensive study in the last two decades with regard to anatomical connections, physiology, and biochemistry. Among these structures (Fig. 1), the subcortical nuclei comprising the basal ganglia (BG) have generated a great deal of scientific interest. Although various schemes exist for describing the structure of the BG, for the purpose of this article, the BG will be said to consist of the putamen, the caudate, the globus pallidus, and the substantia nigra. The abbreviation “BG” will refer, in a general manner, to the entire group of nuclei; “striatum” will be used to refer to the caudate and the putamen.

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The large body of research on the BG is testimony to the assumed importance of these structures in normal motor performance and in Parkinson’s disease (PD), Huntington’s disease, hemiballismus, and other movement disorders. Unfortunately, putative functions ascribed to the BG have been varied, conflicting, and often confusing. For example, although some work suggests a role in premovement programming and movement initiation, other research suggests a role in the specification of movement variables such as movement velocity or posture. Thus, the formation of workable hypotheses concerning the actual function of these anatomical structures has been limited by the diversity of supposed functions. Recent developments, however, provide evidence for a high degree of functional partitioning within the BG. When viewed from this perspective, the multiple functions previously reported may not be incorrect.
The need to reassess the role of the BG in motor control arises from findings in three areas of research. First, recent evidence for anatomical differentiation in BG connections provides support for considering specificity of sensorimotor functions within particular regions of the BG. Second, the sensory inputs to the BG suggest a role in processing or receipt of stimuli specifically relevant to motor actions. Third, analyses of single neuronal responses in awake rats, cats, and monkeys have led to the hypothesis that specific patterns of BG activity may be associated with particular motor performance requirements.

The insights provided by these recent developments are due to the use of subtly different BG recording sites in animals, responses being evoked by different sensory stimuli, or different types of movements or tasks being observed. An overgeneralization from observations of BG disorders in human subjects also has contributed to the confusion. The fact that BG disorders result in both movement restriction (e.g., PD) and movement excess (e.g., hemiballismus) has been difficult to reconcile without a consideration of anatomical topography and specialized function.

**Basic Functional Organization**

Important conceptual changes have occurred within the last decade concerning how the BG relate to other neural structures. Old notions of the BG as centers downstream from the primary motor cortex or as sites for the global convergence of multiple inputs have been replaced with models advocating a different role. Data on afferent and efferent connections and physiological data place these nuclei at a point upstream from the primary motor cortex with multiple, parallel circuits segregated for different functions and different body parts. A high degree of anatomical and functional specificity within the BG is suggested by the consistent and selective neuronal responses observed in certain BG nuclei during movement, afferent and efferent projections to specific regions of the cortex, and their well-defined topographical organization.

**Participation of Specific Basal Ganglia Nuclei in Motor Control**

Based on recent anatomical advances, Alexander et al proposed a revised organizational scheme whereby five anatomically segregated, but parallel, neural circuits traverse the BG and subserve different functions. According to this model, specific nuclei within the BG are associated with the "motor circuit." These nuclei include the putamen, the ventrolateral globus pallidus internal segment (GPI), and the substantia nigra pars reticulata.
(SNpr). Several forms of data support this generalization.

The direct motor role of the putamen has been demonstrated in recordings of single neurons during movement in primates in which most neuronal discharge patterns were coupled with active limb movements. In addition, movements of single body parts (primarily contralateral) can be evoked in awake animals by microstimulation of the putamen over a continuous 200- to 1,200-μ region of striatal tissue.

In studies of monkeys, neurons of the globus pallidus (GP) and the SNpr have also been found to respond during active limb movements. Although stimulation of the GP did not evoke movements during rest, it altered arm movement time. In addition, temporarily cooling GP structures resulted in jerky, hypometric arm movements in monkeys along with periods of agonist-antagonist muscle contraction, not dissimilar to what is observed in patients with PD.

Connections not included within the motor circuit, however, may also exert significant effects on movement. The dopaminergic nigrostriatal projection from the substantia nigra pars compacta is likely to act on the motor circuit, inasmuch as its destruction with the neurotoxin MPTP (1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine) produces parkinsonian-like motor impairments in monkeys and humans. In addition, the subthalamic nucleus (STN) may also participate in motor operations. Recordings of STN cell activity have revealed modulation in discharges during orofacial, arm, and leg movements. Disruption of excitatory projections from the STN to the motor circuit is thought to result in hemiballismus.

Basal Ganglia Afferent and Efferent Connections

Principles of BG connections proposed in an early experimental report identified the striatum as “independent of the cerebral cortex,” but serving a modulatory function upon the corticospinal system’s influence on lower motoneuron activity. More recent anatomical data, however, indicate that the BG are not separate “extrapyramidal” structures as classically described, but ultimately project to “pyramidal” or corticospinal tracts. As illustrated in Figure 3, corticostriate afferents originate in virtually all cortical areas, often bilaterally, and reciprocal connections with these cortical areas appear to be the rule. Afferents to the BG motor circuit are primarily to the putamen from the motor, premotor, and somatosensory areas in primates.

Regarding efferent projections, thalamic nuclei that project to the primary motor cortex do not receive BG pallidonigral efferent fibers (Fig. 4). Anatomical tracing demonstrated that projections from the thalamic nuclei known to receive BG efferents were directed to the supplementary motor area (SMA). Therefore, BG projections to the primary motor cortex, and then subsequently to motoneurons, apparently are indirect, via the SMA. The BG are thus two steps removed from the primary motor cortex; additional processing of BG efferents could occur within the SMA prior to reaching the primary motor cortex.

This seemingly hierarchical relationship of the BG, the SMA, and the primary motor cortex is only partially reflected in the general timing of neural activity recorded in animals while performing trained movements. That is, the majority of the SMA neurons fire prior to those in the primary motor cortex.
During particular motor actions, only discrete portions of the BG motor circuit nuclei are engaged, depending on which body part is in motion. In particular, the somatotopic organization observed in sensorimotor cortical fields is maintained in the putamen, the GP, and the substantia nigra. The putamen serves as a case in point: a "leg" region is present in the dorsolateral putamen, a "face" region is present in the ventromedial zone, and an "arm" representation is present intermediate.

Somatotopic segregation of BG motor representation may account for much of the disparity within the literature on human disorders. Although no BG disorder presents a perfect model, results from human experiments, especially in patients with PD, are often used to illustrate normal aspects of BG function. If one somatotopic region is more impaired than others, it follows that movements represented in such a region would be impaired to a greater degree than those of other body parts. For example, although arm-movement studies in patients with PD have revealed reduced movement amplitude and velocity and prolonged movement time, multi-articulate facial movements do not manifest similar deficits. Moreover, even within the oromotor system, differential impairment of upper lip, lower lip, and jaw has been manifested in the speech movements and orofacial isometric forces of several PD subjects. Therefore, the practice of examining only a few human subjects in an experimental paradigm, each with idiosyncratic variations of BG neuronal involvement, may have contributed to the wide variety of proposed BG-related movement impairments. The implications for clinical assessment and therapy are likewise clear. Each such patient must be individually examined and broad generalizations avoided.
Figure 4. Diagram of anatomical relationships between cerebellar and basal ganglia efferents and motor and premotor cortical areas illustrating (1) pathway from caudal portions of the deep cerebellar nuclei (DNC) to area X (a thalamic nucleus) and then to the arcuate premotor area (APA); (2) pathways from the substantia nigra pars reticulata (SNpr) and the internal segment of the globus pallidus (GPi) to the ventrolateral nucleus pars medialis (VLM), the ventrolateral nucleus pars oralis (VLO), and then to the supplementary motor area (SMA); (3) the pathway from rostral portions of the deep cerebellar nuclei (DNr) to the ventral-posterior-lateral nucleus pars oralis (VPLo) and then to the motor cortex (MC); and (4) the reciprocal connections between the MC, the APA, and the SMA. (Reprinted with permission 42)

Sensory Processing

The anatomical location and connectivity of the BG certainly allow these nuclei to influence sensorimotor information flow. A recent anatomical tracing study in primates revealed that motor and sensory corticostriate projections overlap extensively in the rostrocaudal putamen. Furthermore, sensory corticostriate projections to the cat striatum appear as highly interdigitated zones responsive to either deep or cutaneous stimulation. Therefore, based purely on anatomical evidence, there is good reason to suspect a high degree of convergence among different sensory modalities or between motor and sensory information in the striatum. A complete explanation of sensorimotor convergence, however, is not forthcoming by simple sensory mapping, inasmuch as patterns of sensory activity may be quite different during actual behavior. For example, areas in the rat striatum that are sensitive to somatosensory stimuli at rest did not show the same sensitivity during unrestrained movement.

Nature of Sensory Input

Several studies have indicated that neurons in the striatum, the GP, and the SNpr are selectively responsive to sensory stimuli depending on several functional factors. In cats and rats, cutaneous stimulation produces alterations in striatal neuronal activity, although such alterations are rarely associated with BG cellular activity in primates. Instead, deep stimulation of muscles, tendons, and joints is the most effective somatosensory stimulus in primates. Responses to visual and auditory stimuli in the primate and the human striatum and GP are uncommon whereas striking responses to these stimuli are evoked in monkey SNpr neurons. These observations indicate the potential sensory processing role of the BG and also reflect the limitation of earlier concepts, which based functional conclusions primarily on certain species (ie, cats).

Other indications of sensory processing, such as cellular responses to passive limb manipulation and to load perturbations, in the absence of muscle activity, also suggest the BG may serve in a “proprioceptive” capacity. The GPi is representative; in a primate study conducted by DeLong et al, 22% of the GPi neurons responded to joint rotation and to loads with latencies in the 40-millisecond range, which is compatible with a response driven by sensory input.

In summary, neurons within certain BG nuclei respond to particular forms of sensory input. In humans, a breakdown of sensory systems may contribute to the motor abnormalities observed in patients with PD. For example, numerous researchers have reported losses in visual and tactile discrimination and in visual orientation, delayed auditory brainstem potentials, delayed tactile sensation, and abnormal olfaction. These findings have profound implications clinically and offer direct encouragement for sensory enhancement as a form of treatment.

Sensory Gating in Basal Ganglia

Sensory stimuli that are relevant for a motor action evoke particularly consistent responses within BG nerve cells, but these responses seem to diminish when their relevance decreases. For example, although primate striatal responses to
Because the BG are remote from sites of peripheral sensory transduction, it is not possible to establish their exact role in sensory gating. It appears, however, that sensory stimuli processed in the BG may be "gated out" at some level when not relevant for a motor action or when overly familiar.7,69,79,91 Kimura et al.6,10 found that tonically active neurons in the monkey putamen, which rarely responded to movement, clearly changed discharge patterns after an auditory click, but only when that stimulus triggered licking movements for the consumption of a juice reward. In the expected no-reward condition, the click was not followed by a change in response frequency. Related results were also found in the GP. Similarly, Hikosaka and Wurtz16 found that SNpr responses to visual stimuli were enhanced when those stimuli served as targets for an impending saccade away from the visual target are inhibitory; therefore, a saccade toward a target results in a response enhancement, as observed by Hikosaka and Wurtz.16

Data from patients and the results of lesion experiments in animals help to localize sensorimotor gating to the BG-SMA pathway. For example, although GP neuron responses to passive movements are often confined to manipulation of a single joint,13,26 such selectivity is reduced by MPTP-induced reductions in dopamine levels. In Filion et al.'s study of monkeys with PD,25 the ratio of effective joints per neuron rose from 1.1 to 3.2. In addition, electrolytic lesions in rat GP resulted in paw-reaching disturbances only in experimental conditions requiring reliance on somatosensory or proprioceptive cues as compared with those allowing visual information.93,94 Similar results have been reported for human parkinsonian patients.95,96 Thus, sensory stimuli may not be effectively gated in circumstances of dopamine depletion or BG motor circuit lesion.

Given BG connections, it is not surprising to find that similar gating phenomena have been observed in SMA neurons. In a similar manner to neurons in the BG, neurons active in the SMA prior to and during limb movements were modified by sensory stimuli.51,87 For instance, in Tanji and Kurata's study of primates,97 numerous SMA neurons (31%) responded with differential magnitude when visual, auditory, or tactile stimuli triggered the onset of limb movement. Therefore, neurons in both the BG and the SMA were seen to modify responses to sensory stimuli relative to the requirements of the impending motor task.

**Influence of Motor Performance Factors**

In addition to the role of BG pathways in sensorimotor functions, several other issues must be considered, including motor preparedness ("set"), the type of movement (eg, flexion versus extension), and the task performed. Each factor has been associated with variations in BG neuronal properties.

**Motor Set**

Preparation for the performance of an action or motor set is of considerable functional importance, and it appears that BG activity may be part of such preparatory states. For example, single neurons in the monkey putamen respond differentially to information regarding upcoming movements.98 In about 20% of cells, sustained alternation in discharge was observed in trials in which the monkey was given information regarding whether to flex or extend its forearm. Similar, set-dependent firing of SMA neurons has also been reported.51 Monkeys were cued by a light to either push or pull a cast attached to the forearm when a load was delivered to the cast. Altered neuronal discharge frequency was observed after the light and before onset of the load or subsequent movement. In approximately half of these neurons, the response was instruction-dependent. Therefore, it is plausible that the BG and the SMA aid in programming movements based not only on available sensory information but also on instructional set. The inability of patients with PD to initiate movements could be related to diminished or impaired motor preparedness.98

**Movement Types**

It has also been suggested that certain neurons within the BG are active only during particular types of movement. Neurons in the primate putamen and GP have been reported to discharge preferentially for movements made in certain directions.11,14,15,45,89 For example, Alexander95 found 79% of monkey putamen neurons were selective for either flexion or extension.

Similar to principles of organization found in other regions of the motor system,90-96 neurons in the primate putamen and GP appear to be organized in multiple, functional clusters.50,98 Particular types of movements (eg, flexion) related to each joint appear to be represented in these clusters (groups of 2-5 neurons) across multiple sites over a long anterior-posterior extent of the putamen.8 In addition, these small functional neuron clusters corresponded to somatotopically organized microexcitable zones.6,10 The presence of these small functional neuron clusters...
could represent a more finely-grained breakdown of function within the BG, in which individual neurons or neuron clusters are involved in coding specific movement types of particular body parts. As Crutch and DeLong suggested previously, these neuronal clusters may "represent the basic functional units of the striatum."56

**Tasks**

It has been hypothesized for many years that BG neurons respond in a task-specific manner. For instance, Kornhuber97 postulated that the BG were preferentially involved during slow-ramp versus ballistic movements. This hypothesis was partially based on clinical observations that patients with PD do not have difficulty with rapid, ballistic movements involved in saccades. DeLong and Strick98 showed that a large percentage of neurons in the putamen (45%) and a smaller percentage in the GP (17%) fired preferentially under the former condition. This hypothesis, however, has not been consistently supported by more recent studies that also show putamen and GP activity during fast movements.71,99 In addition, recent electro-oculographic data from patients with PD have revealed abnormalities in speed of saccadic eye movements.100

A striking finding related to task-dependent firing of BG neurons also concerns eye movements. In studies of primates,10,17,101-103 caudate and SNpr neurons, which have efferents to the superior colliculus, discharged preferentially prior to saccadic eye movements performed toward visual targets, neuron responses were absent in the dark or in light when a visual target was not present. In addition, some neurons appeared to have "memory-contingent" responses, in which greater alterations in discharge rates were evidenced when the animal was required to remember a target location and move to it following a delay. This result has been interpreted as evidence for gating within single BG neurons such that "sensory or motor activities of the cells are specialized for the different contexts in which behavior occurs."101(p440)

In humans, the notion of task influences via the BG is reinforced by the results of a study65 examining task-dependent motor impairments in patients with PD. When subjects with PD were compared with "normal" (healthy) subjects on tasks requiring either natural speech movements or novel, visually-guided movements of the jaw, subjects with PD manifested slowness of movement only under visual guidance.65 It is possible that such differential, task-dependent PD motor impairments may be a reflection of task-dependent neuronal activity in the BG. Given findings of differential impairment among body parts presented earlier, it would be of interest to examine task-dependencies associated with various somatotopic regions in lesioned animals or humans with BG disorders.

**Conclusions**

Historically, it has been difficult to find a unified theme among the many sensorimotor functions ascribed to the BG and likewise to interpret, evaluate, or treat disorders associated with BG deficits. Recent data reviewed in this article offer several useful perspectives in this respect. Of particular interest is the argument that the function of the BG is not uniform, even within subnuclei, but rather BG functions are variegated with neural activity in a given region selectively related to sensory and task-related dimensions in the performance of particular motor actions. Indeed, the seemingly discordant functions previously ascribed to the BG do not reflect contrasting theoretical positions; rather, each of the claimed functions represents BG contributions within a limited context. As such, multiple findings, whether based on neural activity in waking animals, patient movement limitations in the clinical laboratory, or symptoms in clinical practice, must be viewed as potentially part of the overall picture.

Regarding relations among brain structures for motor control, the functional correlates to the anatomical hierarchy among the BG, the SMA, and the primary motor cortex are quite important. Although pyramidal tract neurons presumably function to implement output patterns for execution of muscle contraction and movement, regions upstream (eg, BG, SMA) appear to be more involved in determining and specifying the nature of those patterns as necessary for achievement of particular movement goals. In everyday life, changing sensory cues and task requirements demand such specification. Importantly, an inability to alter aspects of movement to accommodate changing task demands is commonly observed in patients with BG disorders. In patients with PD, for example, these deficits include inability to adjust speech volume normally, loss of normal adjustments of velocity for movements of different amplitudes, and limitations in executing two movement patterns simultaneously. Such general observations suggest the need for clinical evaluation and treatment that are both behavioral and physical.

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