Basal Ganglia: Internal Organization

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Introduction

The basal ganglia are a group of subcortical nuclei involved in a variety of processes, including motor, associative, cognitive, and mnemonic functions. The dorsal division of the basal ganglia consists of the striatum (divided into the caudate nucleus and putamen by the internal capsule in primates and other species), the external segment of the globus pallidus (GPe; simply globus pallidus in rodents), the internal segment of the globus pallidus (GPi; entopeduncular nucleus (EP) in several species, including rodents and cats), the subthalamic nucleus (STN), and the substantia nigra (SN). The latter structure is divided into two main parts, the dorsal pars compacta (SNc), in which the dopaminergic nigrostriatal neurons are located, and the more ventral pars reticulata (SNr). In addition to these structures that are associated with motor and associative functions of the basal ganglia, there is a ventral division of the basal ganglia (ventral striatum or nucleus accumbens; ventral pallidum, which is equivalent to GPe and GPi; and the ventral tegmental area, which is a medial continuation of the SNc). The ventral division of the basal ganglia is primarily associated with limbic functions. The nomenclature of divisions of the basal ganglia can be particularly confusing to a reader new to the field. For this reason a table (Table 1) of commonly used terms and their synonyms or homologous structures is included.

The main transmitter used by neurons of the basal ganglia is γ-aminobutyric acid (GABA); as many as 99% of all basal ganglia neurons are GABAergic. The only exceptions are glutamatergic neurons of the STN, dopamine neurons of the SNc, and one population of interneurons in the striatum that utilizes acetylcholine. The major inputs to the basal ganglia are glutamatergic and are derived from the cerebral cortex and the thalamus. The main point of entry of the cortical and thalamic information to the basal ganglia is the striatum, although there are also significant projections to the STN (Figure 1). Virtually the entire cortical mantle projects onto the striatum. The corticostriatal projection is derived from several classes of cortical pyramidal neurons that predominantly innervate the ipsilateral striatum but also the contralateral striatum. The corticosubthalamic projection is derived from more restricted regions of the cortex (see below). The corticostriatal and thalamostriatal projections are highly topographically organized and impart functionality onto the striatum and, consequently, other divisions of the basal ganglia. The main synaptic targets of the cortical and thalamic inputs to the basal ganglia are the medium-sized densely spiny projection neurons of the striatum (Figures 2 and 3).

In what is now considered the classical view of basal ganglia circuitry, the functional organization is such that cortical and thalamic information is processed within the striatum and integrated with the many other inputs that reach the basal ganglia (e.g., from amygdala, hippocampus, and dorsal raphé), which primarily innervate the striatum, and then the 'processed information' is transmitted to the output nuclei of the basal ganglia, that is, the GPi (or EP) and the SNr, by two routes, the so-called direct and indirect pathways. In the direct pathway, cortical and thalamic information is transmitted directly from the striatum to the output nuclei. In the indirect pathway, cortical and thalamic information is transmitted indirectly to the output nuclei via the complex network interconnecting the GPe and STN. The basal ganglia then influence behavior by projecting, via the output nuclei, to the thalamus (mainly the ventral anterior and ventral lateral nuclear complex, mediodorsal nucleus and the intralaminar nuclei) that in turn projects back to the cortex or by projecting to subcortical regions that are involved in movement, including the superior colliculus, the pedunculopontine nucleus (PPN), lateral habenula, and reticular formation (Figure 1).

Overlying this feed-forward organization of the basal ganglia are many feedback pathways. The major one of these is the dopaminergic projection from the SNc that predominantly innervates the striatum but also innervates the STN and GPe. This projection modulates the flow of cortical and thalamic information through the basal ganglia. Loss of these dopamine neurons in Parkinson's disease leads to an imbalance of the flow of cortical information through the basal ganglia in favor of the indirect pathway and the motor symptoms associated with this disorder. Other feedback systems include the serotonergic projection from the dorsal raphé and the projection from the GPe to striatum (see later).
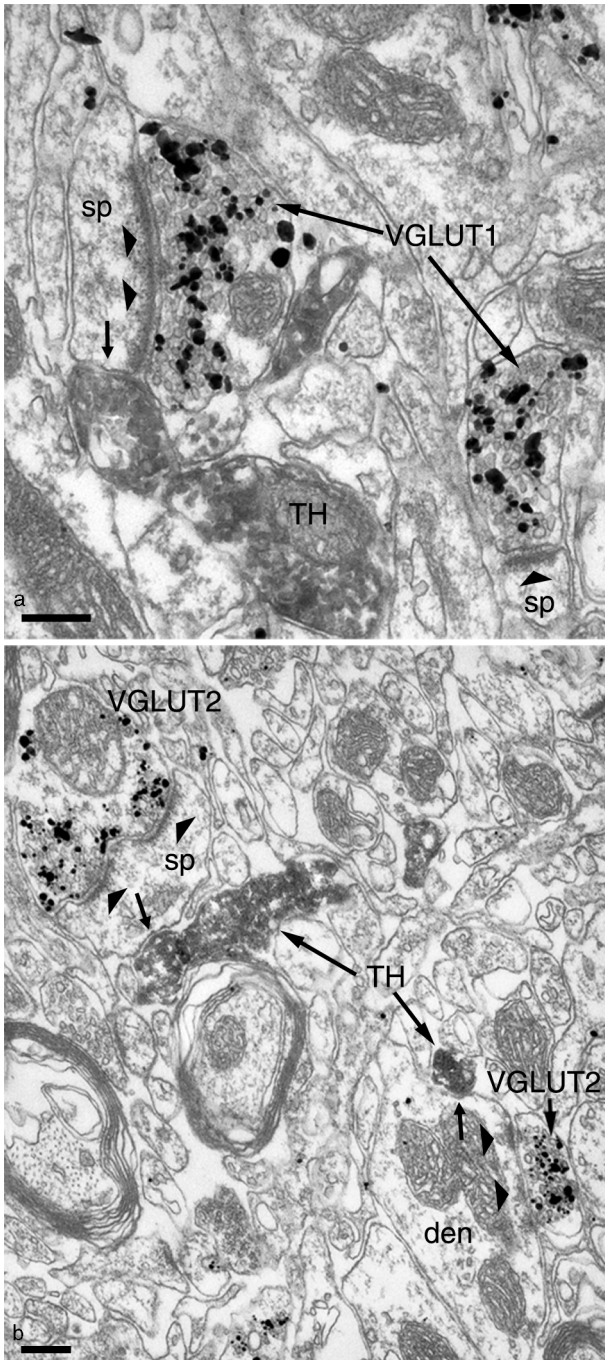
Table 1   Nomenclature

Commonly used name for a particular structure	Homologous structure and/or synonyms
Striatum	Neostriatum, caudate-putamen
Globus pallidus (rat)	External segment of globus pallidus (GPe; primate)
	Lateral globus pallidus (GPl; primate)
Entopeduncular nucleus (rat)	Internal segment of globus pallidus (GPi; primate)
	Medial globus pallidus (GPm; primate)
Ventral striatum	Nucleus accumbens

Striatum

The principal neurons of the striatum, the medium-size densely spiny neurons (MSN; Figure 3), give rise to the direct and indirect pathways. The MSNs have a perikaryon about 15 μm in diameter and give rise to several dendrites that are initially spine free but then become densely laden with spines after the first bifurcation. They account for up to 97% of striatal neurons in rodents but a smaller proportion in primates. They utilize GABA as their major neurotransmitter and are subdivided into two major subpopulations on the basis of their projection region, pattern of axonal collateralization, and neurochemical content. One subpopulation gives rise to the direct pathway, they preferentially project to the output nuclei of the basal ganglia (but also send a collateral to the GPe), and selectively express the neuropeptides, substance P and dynorphin, and D1 dopamine receptors. The other subpopulation gives rise to the indirect pathway, they exclusively project to the GPe and express enkephalin and D2 dopamine receptors. Both populations also give rise to local axon collaterals, the principal target of which are other MSNs. Axon terminals derived from MSNs form symmetric synapses (Gray's type 2) and their morphological features are similar in all their target regions (Figure 4(a)). Their spines are the main target of corticostriatal afferents and at least part of the thalamostriatal projection; both projections form asymmetric synapses (Gray's type 1; Figure 2). An individual cortical axon gives rise to only very few synapses with an individual MSN; since MSNs possess in the region of 10 000–15 000 spines, the implication is that there is a massive convergence of cortical axons (and possibly thalamic axons) on an individual MSN. The MSNs are also the principal target of the dopaminergic feedback from the SNc (spine necks, dendrites, and perikarya; Figure 2).
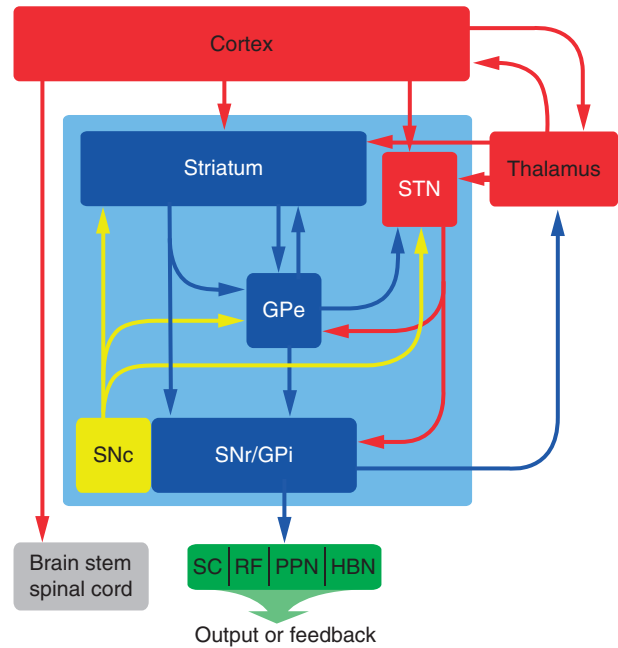
Figure 1   Simplified block diagram of the basal ganglia and their principal connections. The nuclei of the basal ganglia are included in the light blue box and consist of the striatum, the external segment of the globus pallidus (GPe), the subthalamic nucleus (STN), the substantia nigra pars reticulata and the internal segment of the globus pallidus (SNr/GPi), and the substantia nigra pars compacta (SNc). The two major inputs to the basal ganglia are from the cortex and the thalamus (mainly the intralaminar nuclei). The SNr and GPi constitute the output nuclei of the basal ganglia. The basal ganglia influence behavior by the output nuclei (SNr/GPi) projecting to the thalamus and thence back to the cortex, and projections to the superior colliculus (SC), the reticular formation (RF), the pedunculopontine nucleus (PPN), and the lateral habenula (HBN). Dopamine neurons of the SNc provide a massive feedback projection to the striatum and to the GPe and STN, which modulates the flow of cortical and thalamic information through the basal ganglia. In the now classical description of the organization of the basal ganglia, the output from the striatum to the output nuclei is referred to as the 'direct pathway' of information flow through the basal ganglia. This pathway leads to a disinhibition of basal ganglia targets and is considered to be associated with basal ganglia behavior. The 'indirect pathway' consists of the projection from the striatum to the GPe and the projection of the GPe to the STN and thence to the output nuclei. However, recent evidence suggests that the indirect pathway is much more complicated, involving a complex network interconnecting the GPe and the STN and the output nuclei. Furthermore, the STN receives input from both the thalamus and cortex. Activity in the indirect pathway is believed to underlie, at least in part, the resting inhibitory output from the GPi/SNr, and activation of the indirect pathway leads to a greater inhibition of basal ganglia targets and is considered to be associated with the attenuation of basal ganglia behavior. Dark blue indicates structures that are principally GABAergic, red indicates structures that are principally glutamatergic, yellow indicates structures that are dopaminergic, and green indicates structures with variable neurochemistry.

The striatum also contains at least three populations of GABA interneurons: (1) fast-spiking, parvalbumin (PV)-positive interneurons; (2) those that express nitric oxide synthase (NOS); and (3) those that express calretinin. The PV-positive neurons receive major inputs from the cortex, thalamus, and neurons of the GPe (see the next section) and provide an inhibitory input to the MSNs. The striatum also contains a population of large cholinergic interneurons that receive input from the cortex, thalamus and MSNs, and in turn innervate MSNs. The interneurons are also targets of the dopaminergic input from the SNc. The interneurons account for only a small proportion of striatal neurons (∼3–10%, depending on species). In addition to its functional division into the direct and indirect pathways, the striatum possesses subcompartments, the striosomes (or patches), matrix, and matrisomes, which possess different neurochemical markers and have different input/output characteristics.

GPe

The main extrinsic synaptic target of MSNs that give rise to the indirect pathway are the neurons of the GPe. All GPe neurons are GABAergic and differentially express the calcium-binding proteins PV or calbindin. They are arranged in such a way as to expose

Figure 2 Synaptic connections of cortical, thalamic, and dopamine terminals in the striatum. (a) Electron micrograph of a section immunolabeled to reveal the vesicular glutamate transporter 1 (VGLUT1) as a marker of glutamatergic corticostriatal terminals and tyrosine hydroxylase (the rate-limiting enzyme in the synthesis of catecholamines; TH) as a marker of dopaminergic nigrostriatal axons and terminals. The VGLUT1 immunoreactivity was revealed by means of an immunogold method (electron-dense particles, which appear as dense black blobs), and the TH was revealed by an immunoperoxidase method (amorphous, electron-dense reaction product giving the labeled structure an overall dark appearance). The majority of cortical terminals typically form asymmetric synapses (Gray's type 1; arrowheads) with

dendritic spines (sp) of the principal neuron of the striatum, the medium-size densely spiny neuron (MSN; see **Figure 3**). Note that cortical terminals make synaptic contact with the dendritic shafts of MSNs to a much lesser extent and also make synaptic contact with the dendritic shafts of interneurons. The TH-immunoreactive axon makes symmetric synaptic contact (Gray's type 2; small arrows) with the neck of the spine that receives the input from the cortical terminal. This spatial relationship between cortical terminals and nigrostriatal terminals has been considered the principal site of interaction between dopamine and glutamate in the striatum and, indeed, the basal ganglia as a whole. Note that dopaminergic terminals also contact the dendritic shafts and perikarya of MSNs and of interneurons. (b) Electron micrograph of a section of striatum immunolabeled in a manner similar to (a) except that the vesicular glutamate transporter 2 (VGLUT2) was used as a marker of thalamostriatal terminals. Axon terminals derived from the thalamus make synaptic contact with a higher proportion of dendritic shafts than do corticostriatal terminals, although the relative proportions of spines and shafts varies with the thalamic nucleus of origin. In this micrograph, one VGLUT2-positive terminal forms an asymmetric synapse (arrowheads) with a spine (sp; top left). A second VGLUT2-positive terminal forms asymmetric synaptic contact (arrowheads) with a dendritic shaft (den; lower right). Both the postsynaptic spine and the postsynaptic dendritic shaft receive synaptic input (small arrows) from TH-positive terminals, indicating that, at least in qualitative terms, the spatial relationship between glutamatergic thalamostriatal terminals and dopaminergic terminals is similar to the relationship between corticostriatal and dopaminergic terminals. Scale bar = 200 nm (a, b). From Moss J and Bolam JP (unpublished).
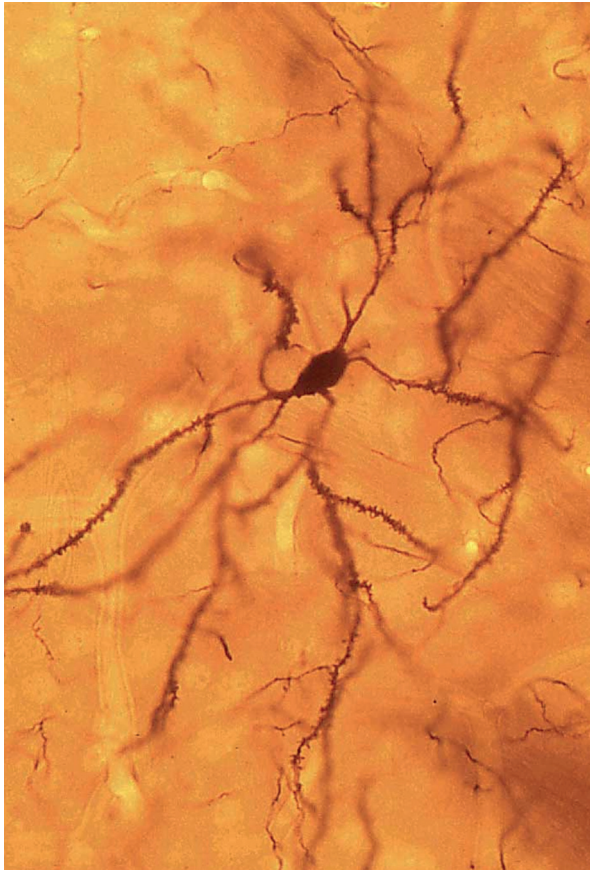
Figure 3 Golgi-impregnated medium-size densely spiny neuron (MSN) in the rat striatum. This is the principal neuron of the striatum, accounting for up to 97% of all striatal neurons. They are GABAergic, give rise to the output from the striatum, and give rise to local axon collaterals. The cell body is approximately 15 μm and in this focal plane gives rise to four primary dendrites. The dendrites are initially spine free and then become densely laden with spines, usually after the first bifurcation. An individual MSN possesses 10 000–15 000 spines, each of which receives a glutamatergic input at its head (see **Figure 2**). The axon is not visible in this micrograph, but segments of Golgi-impregnated axons (much finer structures), presumably derived from other neurons, are present in the field. At this anatomical level, the MSNs giving rise to the direct and indirect pathways are indistinguishable, as are MSNs from different species.

the maximum extent of their dendritic arbor to the incoming striatal afferents. Thus their principal input is from the striatum; pallidal neurons are ensheathed by striatal terminals in a manner similar to neurons of the GPi (**Figure 4(a)** and see below). However, GPe neurons also receive prominent inputs from the STN (**Figures 4(e) and 4(f)**) and from the local axon collaterals of other pallidal neurons. Individual GPe neurons in turn give rise to projections to functionally related territories of the STN, the output nuclei of the basal ganglia, and the SNc (**Figure 5**), where they form symmetric synapses predominantly with the cell bodies and proximal dendrites of their target neurons (**Figures 4(b), 4(c), and 6**). In addition, all GPe neurons give rise to local axon collaterals that underlie a complex and structured microcircuitry within the GPe (**Figure 5**). About a quarter of GPe neurons give rise to collaterals that innervate the striatum in addition to the projections described above (**Figure 5**). Their principal synaptic targets within the striatum are the proximal regions of the PV-positive and NOS-positive GABAergic interneurons. Because the main synaptic targets of the PV-positive GABAergic interneurons are the MSNs, and an individual interneuron can innervate several hundred MSNs, GPe neurons can theoretically control the activity of every neuron in the striatum. Thus, by virtue of their extensive axon collaterals, GPe neurons are in a position to influence the activity of neurons at every level of the basal ganglia. The strategically important placement of their synapses on the proximal regions of their target neurons (**Figure 6**), their GABAergic nature, and their high resting discharge imply a critical role in the modulation of the flow of information through the basal ganglia.

STN

The STN is a small nucleus located below the thalamus; it consists of a relatively homogeneous population of neurons that extend their dendrites in the principal plane of the nucleus. The most distinguishing characteristic of this nucleus is that, unlike the majority of neurons in the basal ganglia (99%), neurons of the STN use glutamate as a neurotransmitter and thus exert excitatory influences on their targets. Traditionally, the principal inputs of STN neurons have been considered to be derived from the GPe, and indeed these neurons provide the major inhibitory input to the STN (**Figure 4(c)**). In fact, the STN is reciprocally connected to functionally related regions of the GPe. Two other major inputs to the STN are derived from the cortex and intralaminar thalamic nuclei. The glutamatergic corticosubthalamic input is mainly derived from the motor, premotor, and prefrontal cortices and is exclusively ipsilateral and, at least in part, is derived from collaterals of cortical neurons innervating the striatum. The corticosubthalamic axon terminals form asymmetric synapses principally with small-diameter dendrites, and this pathway is the fastest route by which the cortex can influence the STN and, through the projections of STN neurons, the output neurons of the basal ganglia. The thalamic input to the STN is also glutamatergic, gives rise to asymmetric synapses with small-diameter dendrites, and is derived from those thalamic nuclei that also innervate the striatum. The STN also receives input from
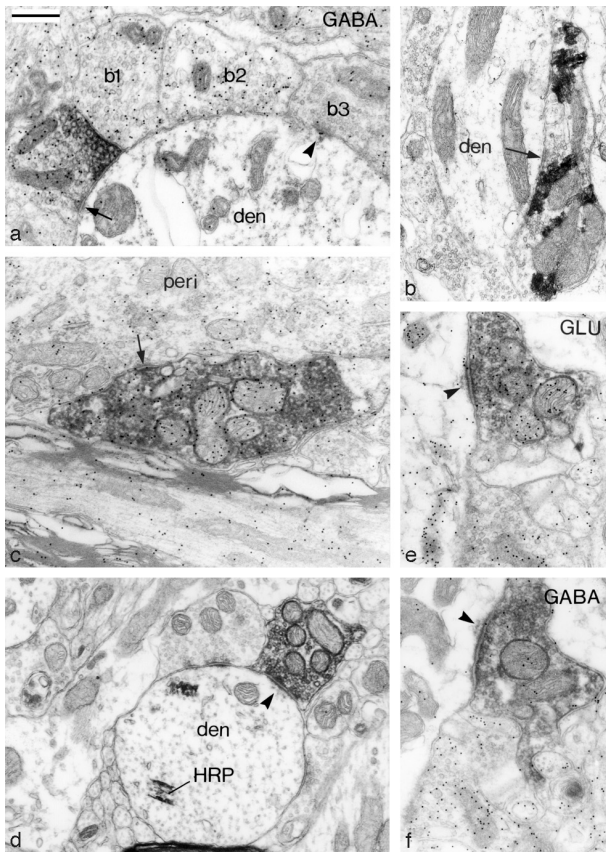
Figure 4 Characteristic features of synaptic terminals of neurons of the basal ganglia. A series of electron micrographs illustrating typical ultrastructural features, synaptic specializations, and neurochemistry of synaptic terminals derived from the striatum (a), the external segment of the globus pallidus (GPe) (b,c), and the subthalamic nucleus (STN; (d–f)). The sections illustrated in (a), (c), and (f) were labeled by the postembedding immunogold method to reveal γ-aminobutyric acid (GABA) immunoreactivity, and the section illustrated in (e) was processed to reveal glutamate (GLU) immunoreactivity. (a) A striatal terminal (farthest to the left) in the internal segment of the globus pallidus (GPi) labeled following an injection of the anterograde tracer biotinylated dextran amine (BDA) in the putamen of a squirrel monkey. The terminal is identified by the electron-dense reaction product formed by the histochemical reaction to reveal the BDA. It is in symmetric synaptic contact (arrow) with a dendrite (den) and is immunoreactive for GABA (as indicated by the high density of immunogold particles overlying it). Two neighboring boutons (b1 and b2), which also possess the morphological features of striatal terminals, are also immunoreactive for GABA. These terminals are derived from the striatal medium-size densely spiny neurons. Contrast these with bouton b3, which forms an asymmetric synapse (arrowhead) and does not display GABA immunoreactivity. This bouton possesses morphological features of a terminal derived from the STN. (b, c) Terminals derived from the GPe forming symmetric synaptic contacts (arrows) with a dendritic shaft (den) in (b) and a perikaryon (peri) in (c). The terminal in (b) is in the rat entopeduncular nucleus (equivalent to GPi) and was labeled after an injection of the anterograde tracer *Phaseolus vulgaris* leucoagglutinin in the GP of the rat. The bouton in (c) is in the STN and was labeled after an injection of BDA in the GPe of the squirrel monkey. This section was incubated to reveal GABA immunoreactivity, and the labeled bouton displays a high concentration of immunogold particles overlying it, indicating that it is enriched in GABA. Note the

dopamine neurons of the SNc, serotonergic neurons from the dorsal raphé, and cholinergic inputs of the PPN.

The main outputs of the STN are to functionally related regions of the output nuclei of the basal ganglia, that is, the SNr (**Figure 4(d)**) and GPi (or EP). Individual STN neurons also innervate the GPe (**Figures 4(e) and 4(f)**), the PPN, and the dopamine neurons of the SNc. In each target, the terminals of STN neurons form asymmetric synapses, and at least some have been shown to be enriched in glutamate (**Figure 4(e)**). The placement of STN terminals is mainly on the proximal regions of their targets. The glutamatergic nature of STN neurons, their relatively high resting discharge rate, and their responsiveness to excitatory inputs from the cortex and thalamus underlie a critical role in setting the level of activity in basal ganglia output neurons.

SNr and GPi

The SNr and the GPi (or EP in rodents) represent the major output nuclei of the basal ganglia, sending their axons to the thalamus and thence back to the cortex or to subcortical structures involved in the control of behavior, including the superior colliculus, parvicellular reticular formation, lateral habenula, and the PPN (**Figure 1**). The relative importance of the two output nuclei in the control of behavior varies among species of different orders. Thus, output to thalamus from the GPi in primates is probably more important than the output from the SNr whereas in rodents, the output from the SNr is probably more important than that from the EP.

Basal ganglia output neurons are large GABAergic neurons with long, infrequently branching, aspiny

similarity in the morphological characteristics of the pallidal boutons despite the fact that they are from different species and in different nuclei. (d) A terminal derived from the STN. This terminal is in the rat substantia nigra pars reticulata and was anterogradely labeled following the injection of the anterograde tracer biocytin in the STN. It forms an asymmetric synapse (arrowhead) with a dendrite (den) that contains retrogradely transported horseradish peroxidase (HRP) from the ventromedial thalamic nucleus, thus identifying it as a dendrite of a basal ganglia output neuron. (e,f) Adjacent sections of the same anterogradely labeled STN bouton in the GPe of squirrel monkey that forms an asymmetric synapse (arrowheads). The bouton is enriched in glutamate immunoreactivity (in (e)) but is not immunoreactive for GABA (in (f)). Note the similarity in the morphological features of the subthalamic terminals in different species and in different nuclei. Scale bar = 0.5 μm (a–f). From Smith Y, Bevan MD, Shink E, and Bolam JP (1998) Commentary: Microcircuitry of the direct and indirect pathways of the basal ganglia. *Neuroscience* 86: 353–387.
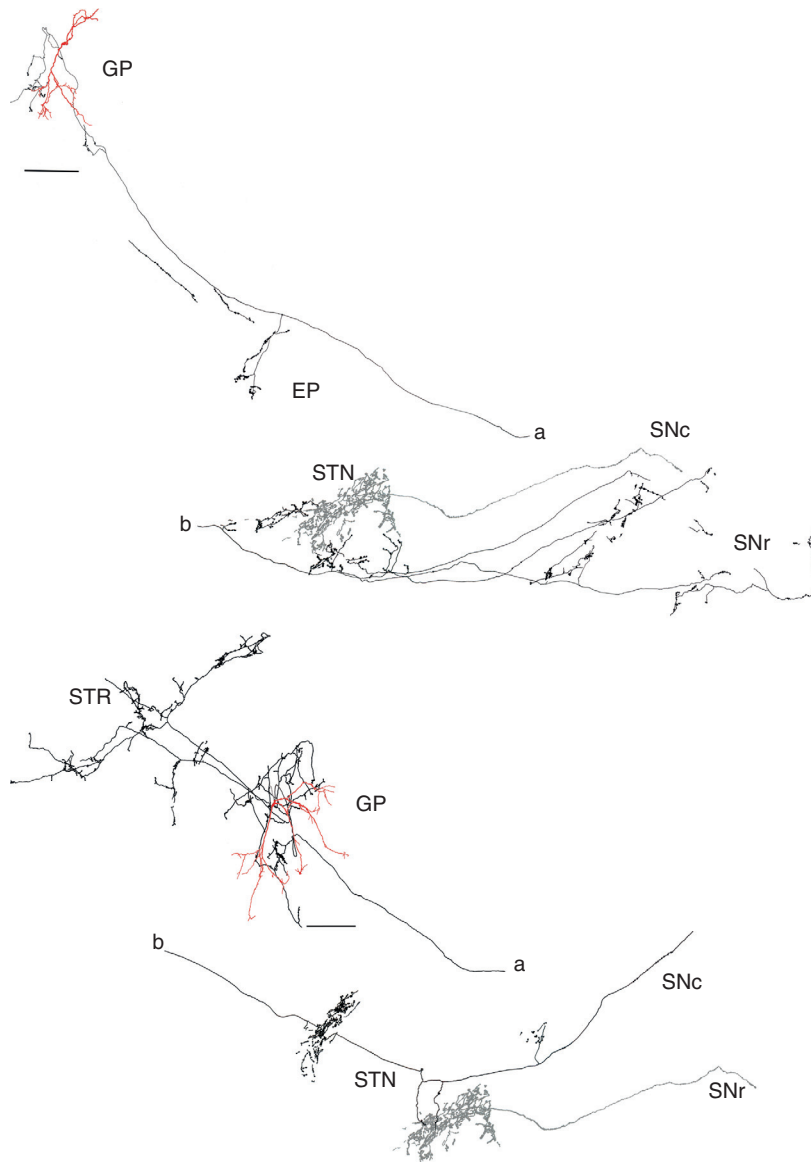
Figure 5   Individual neurons of the rat globus pallidus (GP) innervate multiple regions of the basal ganglia. Partial reconstructions of individual neurons from the rat GP that were labeled with neurobiotin *in vivo* by the juxtacellular method following electrophysiological characterization. These neurons were reconstructed from serial sections using a camera lucida drawing tube. The cell bodies and dendrites are shown in red, and the axon in black. In both cases the drawing of the axon has been cut in two; the ends of the axons marked 'a' connect with the ends marked 'b'. The upper neuron gave rise to local axon collaterals within the GP, and the main axon traveled through the internal capsule to the entopeduncular nucleus (EP), subthalamic nucleus (STN), and substantia nigra pars compacta (SNc) and pars reticulata (SNr). In addition to local axon collaterals and clear projections to the STN, SNc, and SNr, the lower neuron gives rise to two collaterals that innervate the striatum (STR). About a quarter of labeled GP neurons gave rise to collaterals that innervated the STR. Observations similar to these have been made in the external segment of the primate GP. The neuron of origin of those structures shown in gray could not be distinguished beween the two neurons. Scale bar = 300 μm. From Bevan M, Booth P, and Bolam JP (unpublished neurons).

dendrites. In the GPi at least, they are similar to GPe neurons in that their dendrites are arranged in such a way as to expose their maximum surface to the incoming striatal afferents. Their major input is from the MSNs of the striatum that give rise to the direct pathway; thus dendrites and perikarya are ensheathed in afferent terminals, most of which are derived from the striatum (**Figure 4(a)**). They also receive a prominent afferent input on their perikarya and proximal dendrites from the GABAergic neurons
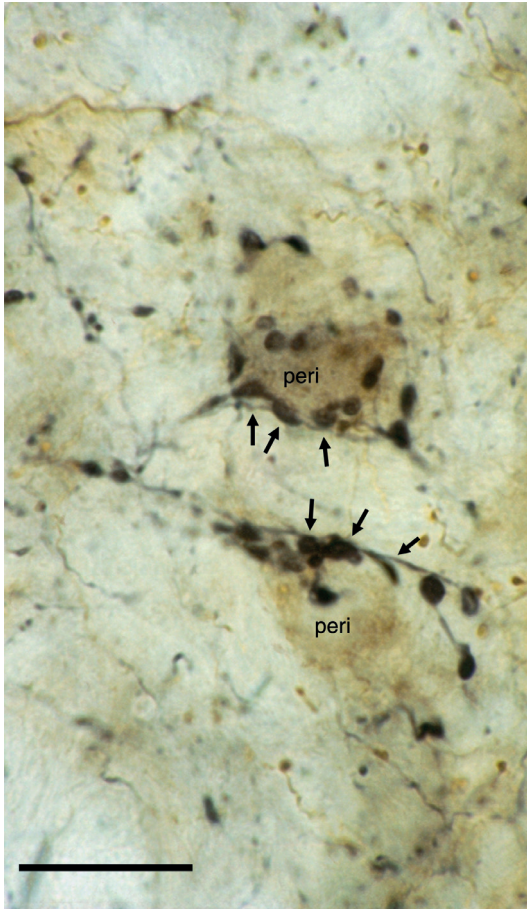
Figure 6 Globus pallidus (GP) neurons form multiple contacts with the proximal regions of their target neurons. Light micrograph of the substantia nigra pars reticulata (SNr) of a rat, in which anterograde tracer was deposited in the GP and revealed by a peroxidase method. The perikarya of two SNr neurons are present in the center of the field (peri) and are apposed by many anterogradely labeled large axonal boutons (some indicated by small arrows) derived from the GP. This 'basket-like' innervation is typical of the manner in which GP neurons innervate their target neurons. Note that this section was taken from an animal that also received an injection of anterograde tracer in the striatum; the brown-labeled structures are thus of striatal origin. Scale bar = ~20 μm. From Smith Y and Bolam JP (unpublished).
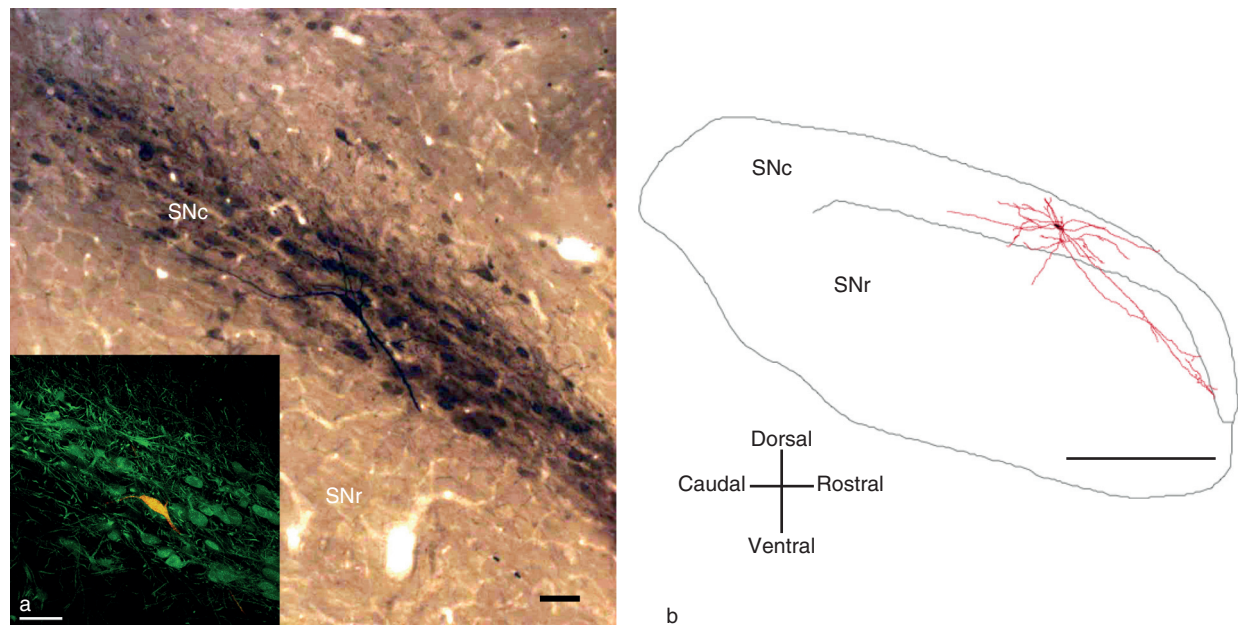
reduced inhibition (i.e., disinhibition) of the targets of the basal ganglia. This disinhibition is considered to be a key factor in the way the basal ganglia influence behavior.

SNc

The SNc consists principally of dopamine neurons although some evidence suggests it also has a population, albeit small, of GABAegic neurons. The dopamine neurons lie in a densely packed band with the majority of dendrites following the plane of the compacta (Figure 7). Some dendrites, particularly of those neurons located in the ventral part of the compacta, also descend into the SNr (Figure 7). Dopamine neurons receive a dense innervation from GABAergic terminals derived from the striatum and the GPe and also receive glutamatergic input from the STN, cholinergic terminals from the PPN, and serotonergic terminals from the dorsal raphé. The axon emerges from the cell body or primary dendrite (and, rarely, a secondary dendrite). Dopamine neurons do not give rise to local axon collaterals within the SN, although it is evident that the dendrites can release dopamine and thus influence neighboring neurons. The main target of the axon is the striatum, but the GPe and the STN also receive a significant dopaminergic input via collaterals of the main axon. Individual dopamine neurons give rise to a remarkable number of synapses. Estimates vary between about 250 000 and 330 000 synapses at the level of the striatum, plus any additional synapses arising from collaterals in the GP and STN. The axon terminals of dopamine neurons give rise to symmetric synapses. The major targets in the striatum are the spines, dendritic shafts, and perikarya of MSNs (Figure 2). Synaptic contact on spines generally occurs at the neck, and the spine invariably receives a glutamatergic terminal derived from the cortex or thalamus, forming an asymmetric synapse (Figure 2). This spatial relationship underlies the modulatory role of dopamine on the excitatory influence from cortex and thalamus.

Concluding Remarks

For the sake of clarity, this description of the internal organization of the basal ganglia has been simplified, omitting many of the less well understood (but probably still important) synaptic connections. Furthermore, the description relies heavily on data derived from the dorsal division of the basal ganglia. Nevertheless, the basic principles of the connections

of the GPe (Figure 4(b)) and glutamatergic neurons of the STN (b3 in Figures 4(a) and the labeled boutons in Figures 4(d)–(4f)). Individual basal ganglia output neurons thus receive synaptic input from both the direct pathway and the indirect pathway. The high resting discharge rate of neurons in the GPi and SNr underlies a tonic inhibition of neurons in the target regions of the basal ganglia under resting conditions. Increased activity of striatal afferents to these neurons leads to a reduction in their firing rate and hence

Figure 7 Micrographs and a digital reconstruction of an individual dopamine neuron in the rat substantia nigra pars compacta (SNc), recorded *in vivo* and then labeled with neurobiotin by the juxtacellular method. The neurobiotin, together with immunoreactivity for tyrosine hydroxylase (TH), were revealed by fluorescence methods ((a), inset). In this section the TH immunoreactive elements were revealed by a green fluorescent marker and the double labeling for TH and the neurobiotin by the yellow fluorescence. The labeled neuron was thus confirmed to be dopaminergic by the presence of immunoreactivity for TH. After neurochemical characterization, the neurobiotin and immunoreactivity for TH were localized by peroxidase reaction products, and the main panel in (a) shows the labeled neuron in the dense layer of TH-positive neurons in the SNc. The digital reconstruction in (b) shows the typical arrangement of the majority of dendrites of dopamine neurons that follow the plane of the SNc, with some dendrites descending into the SN pars reticulata (SNr). The axon of this neuron was followed to the globus pallidus, where is gave rise to a cluster of boutons, and then to the striatum. Scale bar = 25 μm; (a, inset) 500 μm (b). From Brown MTC, Bolam JP, and Magill PJ (unpublished).

described here also apply to the ventral division of the basal ganglia. One can thus conclude from the study of the functional organization of the basal ganglia that the complex functions of the basal ganglia are underpinned by an equally complex cellular and synaptic architecture.

See also: Basal Ganglia: Functional Models of Normal and Disease States; Basal Ganglia: Motor Functions; Basal Ganglia: Acetylcholine Interactions and Behavior; Basal Ganglia: Physiological Circuits; MPTP Parkinsonism Model; Procedural Learning: Striatum; Striatum: Internal Physiology.

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