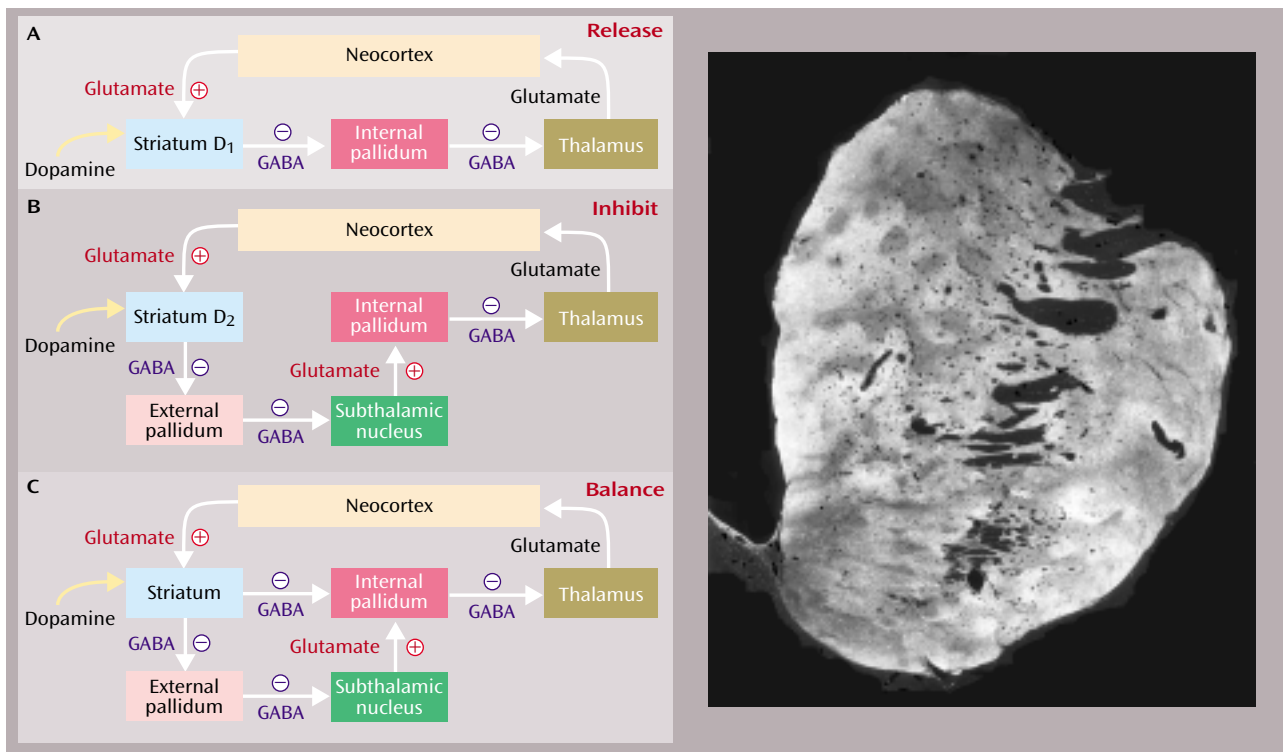


Neural Networks



Left, part A: the direct basal ganglia–thalamocortical pathway consists of two successive connections involving  $\gamma$ -aminobutyric acid (GABA), from the striatum to the internal pallidum and from the internal pallidum to the thalamus; this component of the circuit would disinhibit the thalamus and release movement. Left, part B: the indirect pathway includes an extra excitatory path from the subthalamic nucleus to the internal pallidum; this part of the circuit would inhibit movement. Left, part C: balance is achieved when these antagonistic circuits are dynamically combined under circumstances of use. Right: thin coronal section through the striatum of the human brain, stained for the enzyme acetylcholinesterase (AChE). The AChE-poor striosomes are lightly stained; the AChE-rich extra-striosomal matrix is more darkly stained.

Neural Systems V: Basal Ganglia

Activity in neuronal populations in the frontal cortex is influenced by the basal ganglia and thalamus through basal ganglia–thalamocortical feedback pathways. Neuronal circuits course from the cortex to the caudate-putamen, on to the basal ganglia output nuclei through the indirect or direct pathways, and then to nuclei in the thalamus that project back to the cortex (figure, left). Some of the circuits remain segregated through this course, with axons returning to the same region of the cortex from which their signal originated. What could be the function of these kinds of cortical-subcortical neuronal circuits? The answer to this question must be reflected in the physiologic and biochemical characteristics of the regions. The basal ganglia contain neurotransmitter-specific compartments that bring the different cortical inputs under multiple neurochemical controls. The great diversity of neurotransmitters in the basal ganglia, especially the striatum, may function to complexly modulate behaviors on the basis of sensorimotor, memory-related, or conditional cues derived from the neocortex and limbic systems. Cortical projections to the striatum segregate into two different striatal compart-

ments: striosomes and matrix (figure, right). These are two structurally similar but histochemically distinct compartments within the striatum. The striosomes are acetylcholine-poor, while the matrix is acetylcholine-rich. Moreover, the striosome-matrix compartmentalization, first recognized by transmitter histochemistry, turns out to be an architecture that largely defines the input-output connections of the striatum. The distinct histochemistry combined with the different connections of striosomes and matrix make functional differences between these striatal compartments likely. Already it is known that the matrix receives the striatal afferents most directly related to sensorimotor processing. By contrast, striosomes (including the entire ventral striatum) tend to receive inputs from neural structures affiliated with the limbic system, particularly the amygdala. Their segregated projections, intimately associated within the striatum, could subservise communication between these functionally distinct pathways.

ANN M. GRAYBIEL, PH.D.  
Cambridge, Mass.

Address reprint requests to Dr. Tamminga, Maryland Psychiatric Research Center, University of Maryland, P.O. Box 21247, Baltimore, MD 21228. The image on the left is reprinted from *Current Biology*, vol. 10, A.M. Graybiel, "The basal ganglia," pp. R509–R511, 2000, with permission from Elsevier Science; the image on the right is courtesy of Dr. Graybiel.