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Information Processing in Modular Circuits Linking Basal Ganglia and Cerebral Cortex

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In recent years, there has been a remarkable expansion of knowledge about the anatomical organization of the basal ganglia, the signal processing that occurs in these structures, and their many relations both to molecular mechanisms and to cognitive functions. The various findings are pointing toward an unexpected role for the basal ganglia in the contextual analysis of the environment and in the adaptive use of this information for the planning and execution of intelligent behaviors. This book is about these emerging concepts. As an introductory chapter, I provide here an overview that highlights some of the more salient findings, and I outline a simple conceptual model for their interpretation. Let me begin with a brief review of the basic anatomy, since it provides a useful foundation for the interpretation of the other findings.

ANATOMICAL PLAN OF INFORMATION FLOW

Virtually the whole cerebral cortex projects to the basal ganglia, and the outputs then funnel back to the frontal areas of cortex, or in some cases directly to motor systems in the midbrain and hindbrain. In this overview, I focus on the pathways that return to the frontal cortex. The fundamental plan of information flow is shown in figure 1.1. This diagram is based on a pivotal review in which several parallel circuits, each having the basic design shown in figure 1.1, were identified (Alexander et al., 1986). Diverse areas of cerebral cortex are shown to converge upon regions of striatum that, via pallidum and thalamus, project back to the region of frontal cortex that contributed to the striatal input. There is also a less direct pathway from striatum to pallidum via the external pallidum and subthalamus, and there is a shorter route from thalamus to striatum that bypasses the cerebral cortex. The thin arrowheads in figure 1.1 represent predominantly excitatory connections whereas the solid arrowheads signify inhibition.

The impressive topographic specificity within these pathways, as described in chapters 4 through 7 of this book and reviewed elsewhere (Goldman-Rakic, 1984; Graybiel, 1991), led Houk and Wise (1993) to go

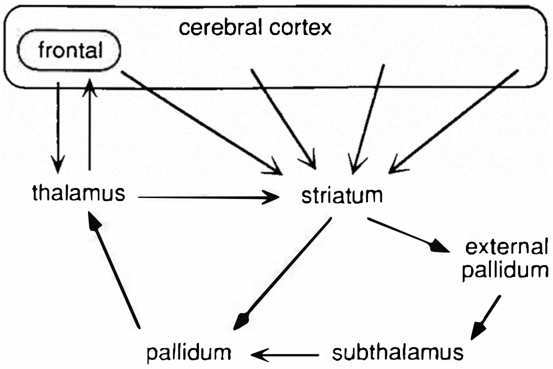

Figure 1.1 Schema of information flow between the cerebral cortex and several divisions of the basal ganglia.

one step further. We postulated that each of the segregated circuits identified by Alexander et al. (1986) is in turn comprised of a large array of modules, each module being organized according to the same plan as shown in figure 1.1 (Wise and Houk, 1994). This hypothesis fits well with the general observation that each area of frontal cortex contains a population of units with response properties that are similar to one another in some generic sense, whereas one or several parametric features of the responses differ among units (see Goldman-Rakic, 1991, and chapter 7). The parametric differences might result from slight variations in the inputs to modules that have the same structure and essentially the same information-processing capability. An hypothesis concerning the generic processing function of individual cortical-basal ganglionic modules was advanced by Houk and Wise (1993), based on the cellular properties of striatal spiny neurons discussed in the next section.

POTENTIAL FOR PATTERN RECOGNITION BY STRIATAL SPINY NEURONS

The input stage of the basal ganglia is the striatum, and the principal neurons of the striatum are called spiny neurons because of the great density of synaptic spines on their long dendrites, as discussed in chapters 3 and 4 (see also Wilson, 1990). Each spiny neuron receives input from about 10,000 different afferent fibers, a remarkable degree of convergence that is second only to that for Purkinje cells in the cerebellar cortex. This type of cellular architecture is analogous to the network architecture used in perceptrons, a pattern-recognizing network that was extensively studied by theorists a few decades ago (Rosenblatt 1962; Albus, 1971; Minsky and Papert, 1969 but see 1987). A perceptron requires a substantial convergence of different kinds of information onto individual units, analogous to the convergence of cortical inputs onto striatal spiny neurons. In addition, a perceptron requires a special input that adjusts the synaptic weights of the convergent inputs along lines discussed in chapters 4 and 10 through 13 of this book. This adjustment mechanism trains individual units to recognize particular patterns of input. There is growing evidence, summarized in chapters 4, 10, and 12, that dopamine fibers provide a reinforcement input to striatal spiny neurons that trains them to recognize patterns in their cerebral cortical input (also see Ljungberg et al., 1989; Wickens, 1990). Finally, a perceptron utilizes an abrupt activation threshold in the response properties of the unit, which forms a sharp decision line for pattern recognition. Spiny neurons also have abrupt thresholds between "up" and "down" states owing to the highly nonlinear ionic properties of their membranes (see Wilson, 1990, and chapter 3). These three features—convergence of diverse inputs, specialized training signals, and dual-state behavior—suggest that spiny neurons may be particularly well suited for pattern recognition tasks.

The upper part of figure 1.2 incorporates these features into a schematic diagram of a cortical-basal ganglionic information-processing module as defined by Houk and Wise (1993). The diagram shows convergent excitatory input onto a spiny neuron (*SP*) from five (out of 10,000) cortical neurons (the *C*'s and the *F*) originating from diverse regions of the cerebral cortex; *F* is a neuron from the frontal cortex. The more diffuse dopamine input is assumed to function as a training signal that reinforces the synaptic weights of C and F inputs to guide the pattern recognition process. Since reinforcement guides learning, the pattern that is eventually learned should reflect a context that is behav-

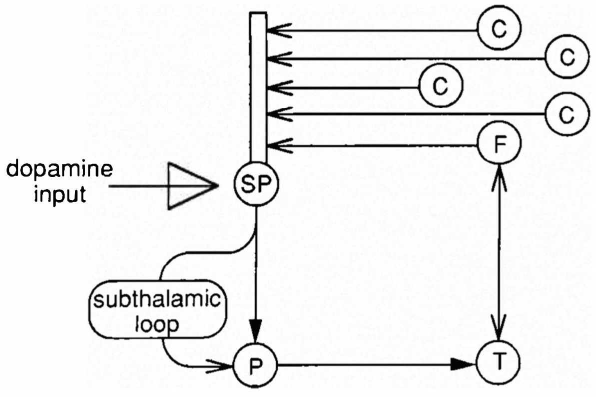

Figure 1.2 Schematic diagram of a cortical-basal ganglionic module. Thin arrowheads signify net excitation; the solid black arrowheads in the direct SP to P projection and in the P to T projection signify net inhibition; the triangular arrowhead for the dopamine input signifies neuromodulation. C, cerebral cortical neuron; F, neuron in frontal cortex; SP, spiny neuron of the striatum; P, pallidal neuron; T, thalamic neuron.

iorally significant, as discussed in chapters 10 through 13. Later, when the spiny neuron is exposed to the same or a similar contextual pattern, the resultant excitation would cause a transition to the up state of the neuron, whereupon it would fire a burst of action potentials and then return to its down state. In chapter 2 Schultz and colleagues describe how the burst discharges of spiny neurons relate to a variety of contextual situations that the animal confronts in performing behavioral tasks. Assuming that a burst generated by a spiny neuron signifies the detection of a behaviorally significant context, the remainder of the circuit in figure 1.2 could then serve to refine this computation and deposit it in working memory for use in planning subsequent behavioral actions, as discussed in the next section.

CORTICOTHALAMIC LOOPS AND WORKING MEMORY

Single-unit studies have shown patterns of persistent discharge in frontal cortical neurons that appear to represent transitory, working memories of behaviorally significant stimuli or events (Goldman-Rakic, 1991). In chapter 7 Goldman-Rakic describes how these signals provide distributed representations of contextual information consisting of stimulus features or internal states that need to be saved for a short duration so that they can be used in controlling an ongoing behavioral action. After the action is completed, this information is no longer needed, and the sustained discharge in frontal neurons correspondingly ceases.

Houk and Wise (1993) suggested a mechanism whereby cortical-basal ganglionic modules might serve to detect these contexts and register them in working memory. Bursts of spiny neurons are known to produce a pause in the sustained inhibitory output from pallidal neurons (Chevalier and Deniau, 1990), as illustrated by the solid traces in figure 1.3. This pause in inhibitory input to the thalamic neurons would be expected to initiate a brief burst of thalamic discharge, due to the inhibitory rebound properties of these neurons (Wang et al., 1991). We postulated that the rebound burst would then initiate positive feedback in the reciprocal corticothalamic loop shown in figure 1.2. This could mediate the sustained discharge of working memory. The sustained activity is a property of both thalamic and cortical neurons (Fuster and Alexander, 1973; Goldman-Rakic and Friedman, 1991).

The solid traces in figure 1.3 spell out the proposed relationships between these neural signals. The burst in spiny neuron discharge (trace *SP*), signifying the detection of a behaviorally significant context, produces a pause in pallidal neuron discharge (trace *P*), which through disinhibition initiates sustained positive feedback in reciprocally connected thalamic and frontal cortical neurons (trace *T-F*). The suggested mechanism can be thought of as a registration of the context detected by a spiny neuron into working memory, so that this information can

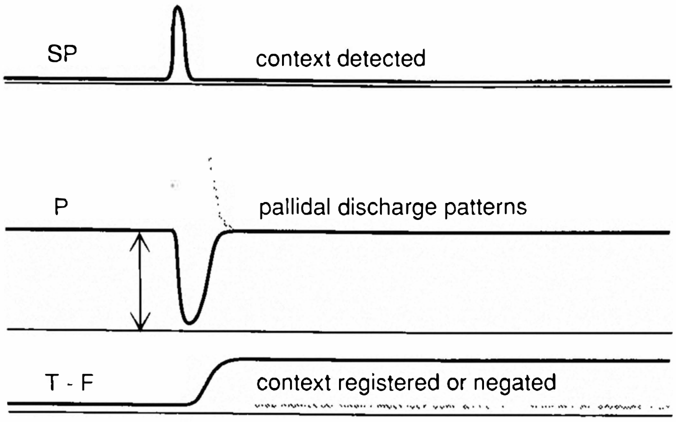

Figure 1.3 Postulated relationship between basal ganglia signals and the sustained discharge of thalamic and frontal cortical neurons (T-F). Solid traces show responses that would be mediated by the direct pathway in figure 1.2 and stippled traces show those mediated via the subthalamic sideloop. SP, spiny neuron discharge; P, pallidal neuron discharge.

be used later in the control of behavior. The stippled traces in figure 1.3 indicate how transmission that was specifically directed through the subthalamic sideloop (see figure 1.2) might serve to cancel a previously registered context. Concurrent activity in both the direct inhibitory and the excitatory sideloop pathways could control the competitive selection processes that are discussed in chapter 17 of this book.

USE OF REGISTERED CONTEXTS IN THE CONTROL OF BEHAVIOR

How might the working memories in the frontal cortex be used to control behavior? Three anatomical pathways for the use of this information were considered by Houk and Wise (1993, 1994). One is through the extensive corticocortical pathways that lead, by many routes, to the primary motor cortex, as discussed in chapter 7. These connections might be an effective way of initiating activity in the recurrent network that interconnects cerebellum, red nucleus, and motor cortex; positive feedback in this network has been suggested as the main driving force for generating the motor commands that control limb movement (Houk et al., 1993). A second major output pathway is via the pons to the cerebellum. This pathway might help to program the cerebellum to control an action (Berthier et al., 1993). A third pathway would be through corticostriatal inputs to different basal ganglionic modules, and this might permit the detection of one context, in the first module, to contribute to the detection of a subsequent context, in another module. This recursive process could be a very powerful mechanism for generating complex properties that might be useful in the high-level planning of actions (Houk and Wise, 1994).

CONCLUSION

In this introductory chapter, I have given an overview of the salient anatomy and physiology of basal ganglia circuits, and I have attempted to integrate these findings into a simple conceptual model of the essential information-processing operations performed in cortical-basal ganglionic modules. At the input stage of the basal ganglia, spiny neurons in the striatum receive a diversity of convergent signals from widespread areas of the cerebral cortex. The spiny neurons are postulated to function as pattern classifiers that learn, under the training influence of their dopamine fiber input, to recognize patterns of activity in their cortical inputs that signify occurrences of behaviorally significant contexts. When such a context is detected, the resultant burst of spiny neuron discharge is thought to disinhibit thalamocortical loops to initiate sustained activity in clusters of frontal cortical neurons. In this manner, detected contexts would be registered as working memories, whereupon this information would become available for subsequent use in the planning and control of motor behavior.

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