

Review

# Somatotopy in the basal ganglia: experimental and clinical evidence for segregated sensorimotor channels

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Accepted 7 September 2004

Available online 23 November 2004

## Abstract

Growing experimental and clinical evidence supports the notion that the cortico-basal ganglia–thalamo-cortical loops proceed along parallel circuits linking cortical and subcortical regions subserving the processing of sensorimotor, associative and affective tasks. In particular, there is evidence that a strict topographic segregation is maintained during the processing of sensorimotor information flowing from cortical motor areas to the sensorimotor areas of the basal ganglia. The output from the basal ganglia to the motor thalamus, which projects back to neocortical motor areas, is also organized into topographically segregated channels. This high degree of topographic segregation is demonstrated by the presence of a well-defined somatotopic organization in the sensorimotor areas of the basal ganglia. The presence of body maps in the basal ganglia has become clinically relevant with the increasing use of surgical procedures, such as lesioning or deep brain stimulation, which are selectively aimed at restricted subcortical targets in the sensorimotor loop such as the subthalamic nucleus (STN) or the globus pallidus pars interna (GPi). The ability to ameliorate the motor control dysfunction without producing side effects related to interference with non-motor circuits subserving associative or affective processing requires the ability to target subcortical areas particularly involved in sensorimotor processing (currently achieved only by careful intraoperative microelectrode mapping). The goal of this article is to review current knowledge about the somatotopic segregation of basal ganglia sensorimotor areas and outline in detail what is known about their body maps.

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*Theme:* Motor systems and sensorimotor integration

*Topic:* Basal ganglia

*Keywords:* Basal ganglia; Body map; Human; Parkinson’s disease; Primate; Somatotopy

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*Abbreviations:* MPTP, 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine; CMAc, caudal cingulate motor area; CMA, cingulate motor areas; DBS, deep brain stimulation; PMd, dorsal premotor cortex; GPe, globus pallidus pars externa; GPi, globus pallidus pars interna; PD, Parkinson’s disease; PMC, premotor cortex; MI, primary motor cortex; CMAR, rostral cingulate motor area; SNr, substantia nigra pars reticulata; STN, subthalamic nucleus; SMA, supplementary motor area; PMv, ventral premotor cortex

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## 1. Introduction

The processing of motor information flows through a segregated sensorimotor loop connecting the primary motor cortex (MI), the supplementary motor area (SMA), the premotor cortex (PMC), and cingulate motor areas (CMA) with the sensorimotor areas of the basal ganglia and the thalamus [3,6,108,114]. The striking therapeutic effect of stereotactic lesioning or high-frequency stimulation of sensorimotor areas in the globus pallidus pars interna (GPi) or subthalamic nucleus (STN) of patients affected by Parkinson's disease (PD) [11,31,120] supports the notion that discrete regions of the basal ganglia exert a powerful influence on sensorimotor processing and the control of movement execution. An ordered somatotopic distribution of motor inputs along the sensorimotor areas of the basal ganglia and thalamus has been consistently described in primates [19,81,113,114,118,123]. This segregated somatosensory loop is characterized by individual channels subserving the representation of specific body parts in the context of a well-organized body map. Evidence of movement-related neurons spatially segregated in a somatotopic fashion has been described in the sensorimotor areas of the monkey striatum [113], internal and external segments of the globus pallidus (GPi and GPe; [18,20]), thalamus [118] and red nucleus [59]. Thus, a segregated body map is found not only in the somatosensory areas of the input nuclei of the basal ganglia, striatum, and STN, which receive somatotopically organized fibers from the frontal motor areas, but also in intermediate areas, such as the GPe. Finally, the main output station for sensorimotor processing, the GPi, has been shown to preserve a precise body map [76,119], and projects to the motor thalamus, an area which is again somatotopically organized [118]. The preservation of a body map in the GPi strongly suggests that sensorimotor processing along the cortico-basal ganglia-thalamo-

cortical loop is based on segregated subloops related to specific body parts and joined together in a coherent body map. Interestingly, the other main output station of the basal ganglia, the substantia nigra pars reticulata (SNr), which is involved mostly in the processing of information running along the oculomotor, associative and affective loops, is characterized by the absence of a body map, suggesting convergence of information instead of segregated processing [48]. The preservation of segregated body maps along the input and output areas of the basal ganglia is probably an essential feature of physiologic sensorimotor processing in the basal ganglia, and in pathological conditions there is enlargement of the receptive fields and consequent loss of specificity [23,96,120].

The increasing use of stereotactic lesioning and, more recently, deep brain stimulation (DBS) for the treatment of movement disorders such as PD, dystonia and essential tremor has revived clinical and experimental interest in the somatotopic organization of the basal ganglia. Microelectrode mapping during stereotactic procedures has helped to delineate somatotopic maps of the GPi [119], STN [96] and motor thalamus [50]. At the same time, experimental evidence is accumulating about the somatotopic organization of other structures in the basal ganglia, which have not been widely explored in humans, such as the striatum and the GPe. Much of this information, both clinical and basic, has only recently been published, and their mutual implications have not been thoroughly addressed. The purpose of this paper, therefore, is to review experimental and clinical findings concerning the functional organization of the sensorimotor areas of the basal ganglia, with special emphasis on assessing the evidence for segregated, somatotopically organized maps. Because from a clinical/surgical perspective the significance of body maps depends in part on whether they are preserved under pathologic conditions such as PD, we will also review data obtained from normal

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