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Single body parts are processed by individual neurons in the mouse dorsolateral striatum

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ABSTRACT

Interest in the dorsolateral striatum (DLS) has generated numerous scientific studies of its neuropathologies, as well as its roles in normal sensorimotor integration and learning. Studies are informed by knowledge of DLS functional organization, the guiding principle being its somatotopic afferent projections from primary somatosensory (S1) and motor (M1) cortices. The potential to connect behaviorally relevant function to detailed structure is elevated by mouse models, which have access to extensive genetic neuroscience tool kits. Remaining to be demonstrated, however, is whether the correspondence between S1/M1 corticostriatal terminal distributions and the physiological properties of DLS neurons demonstrated in rats and non-human primates exists in mice. Given that the terminal distribution of S1/M1 projections to the DLS in mice is similar to that in rats, we studied whether firing rates (FRs) of DLS neurons in awake, behaving mice are related to activity of individual body parts. MSNs exhibited robust, selective increases in FR during movement or somatosensory stimulation of single body parts. Properties of MSNs, including baseline FRs, locations, responsiveness to stimulation, and proportions of responsive neurons were similar to properties observed in rats. Future studies can be informed by the present demonstration that the mouse lateral striatum functions as a somatic sensorimotor sector of the striatum and appears to be a homolog of the primate putamen, as demonstrated in rats (Carelli and West, 1991).

1. Introduction

The dorsolateral or sensorimotor striatum (DLS) (Flaherty and Graybiel, 1994) figures prominently in research on control of voluntary movement, sensorimotor integration, and neuroplasticity involved in procedural learning and habit formation. Also heavily researched are dorsal striatal dysfunctions in Tourette syndrome, obsessive compulsive disorder, psychomotor stimulant addiction, Parkinson's disease, and Huntington's disease. The DLS role in these processes is enlightened by knowing its anatomical-functional organization. Seminal neuroanatomical studies using then new tract tracing tools began to elucidate the long-sought topography of corticostriatal projections from primary somatosensory (S1) and motor (M1) cortices (Kunzle, 1975, 1977). These anatomical findings played a

Abbreviations: DLS, dorsolateral striatum; MSNs, medium spiny neurons; FR, firing rate

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pivotal role in informing subsequent studies clarifying striatal function. For example, the findings were soon corroborated by physiological studies (Liles, 1979; Crutcher and Delong, 1984a; Alexander and Delong, (1985); Lyles and Updyke, 1985) that revealed clusters of medium spiny neurons (MSNs) whose activity is related to sensorimotor activity of individual body parts and that project into pallidothalamocortical reentrant loops (Alexander et al., 1986). Hence, the functional organization of the sensorimotor striatum became known as a patchy somatotopy (Flaherty and Graybiel, 1993). A sequence similar to these studies in monkeys soon followed in rats. Anatomical projections indicating a sensorimotor sector in the DLS (Cospito and Kultas-Ilinsky, 1981; McGeorge and Faull, 1989) were corroborated by physiological studies demonstrating a patchy somatotopic functional organization in rats similar to that in primates (West et al., 1990; Carelli and West, 1991; Cho and West, 1997; West, 1998). In monkeys and rats, knowledge of DLS functional organization has facilitated both design and interpretation of detailed studies of striatal function, including single cell relations to movement parameters (Crutcher and DeLong, 1984b; Liles, 1985; Kimura, 1992), mechanisms by which psychomotor stimulants activate movement (Pederson et al., 1997; Tang et al., 2008; Pawlak et al., 2010; Ma et al., 2013), effects of reduced dopamine transmission on somatosensory responsiveness of single neurons (Prokopenko et al., 2004), effects of dopamine deafferentation on the functional organization (Cho et al., 2004), corticostriatal plasticity during motor learning (Carelli et al., 1997; Tang et al., 2007, 2009), and the differential roles of dorsal striatal regions in habitual vs. goal-directed behavior (Yin et al., 2008; Thorn et al., 2010).

Anatomical studies in mice (White and DeAmicis, 1977; Jinno and Kosaka, 2004; Hattox and Nelson, 2007; Tai and Kromer, 2014) have demonstrated a pattern of corticostriatal terminal distribution similar to that in rats, confirming that S1 and M1 cortices project selectively to the DLS. However, whether neurons in the DLS of awake, behaving mice exhibit selective responses to sensorimotor activity of individual body parts is unknown. Although such activity might be predicted because it follows logically from the above evidence, it cannot be presumed. Moreover, the importance of establishing the anatomical-functional organization of the mouse DLS is underscored because of the utility of mouse models in neuroscience research. Transgenic mice enable selective manipulation of genetically or anatomically defined specific cell types during behavior in a temporally precise manner, e.g., using optogenetic stimulation to study synaptic connectivity and circuit function (Ting and Feng, 2013; Warden et al., 2014; Marton and Sohal, 2015). Coupling the characterization of sensorimotor responsiveness of a recorded DLS neuron with specific information gained using optogenetic stimulation would enable an exciting synergy of both types of information, making the study of striatal SBP neurons particularly attractive. The present study aimed to establish evidence regarding DLS neuron responsiveness in the awake, freely moving mouse, toward achieving the goal of enhancing the ability of

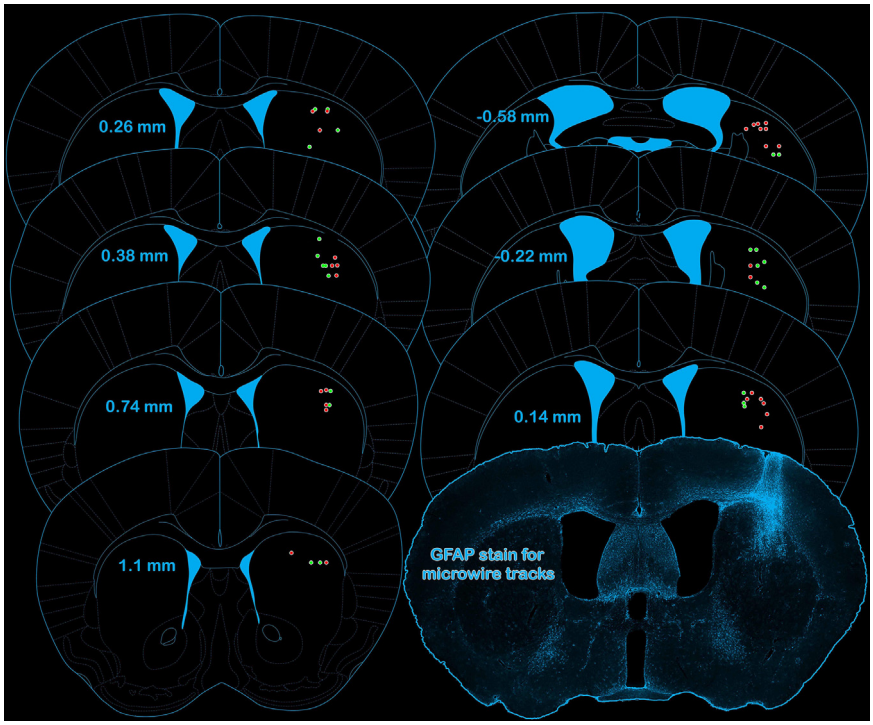

Fig. 1 – *Histology:* Atlas Plates (Paxinos and Franklin, 2004) showing the approximate locations of all wire tips exhibiting an isolated neuronal waveform. Green/white dots: wire tips which recorded a Single Body Part Neuron (SBP); red dots/open: wire tips which recorded an Uncategorized Neuron. The actual histology slice (lower right) shows histochemical staining for activated astrocytes (GFAP), which surround wires. Wires can easily be tracked from their entrance into cortex until their tips in striatum.