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Review

Oscillations and the basal ganglia: Motor control and beyond

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ABSTRACT

Oscillations form a ubiquitous feature of the central nervous system. Evidence is accruing from cortical and sub-cortical recordings that these rhythms may be functionally important, although the precise details of their roles remain unclear. The basal ganglia share this predilection for rhythmic activity which, as we see in Parkinson's disease, becomes further enhanced in the dopamine depleted state. While certain cortical rhythms appear to penetrate the basal ganglia, others are transformed or blocked. Here, we discuss the functional association of oscillations in the basal ganglia and their relationship with cortical activity. We further explore the neural underpinnings of such oscillatory activity, including the important balance to be struck between facilitating information transmission and limiting information coding capacity. Finally, we introduce the notion that synchronised oscillatory activity can be broadly categorised as immutability promoting rhythms that reinforce incumbent processes, and mutability promoting rhythms that favour novel processing.

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Introduction

Oscillations form a ubiquitous feature of the central nervous system. Evidence is accruing from cortical and sub-cortical recordings that these rhythms may be functionally important, although the precise details of their roles remain unclear. The basal ganglia share this predilection for rhythmic activity which, as we see in Parkinson's disease, becomes further enhanced in the dopamine depleted state. While certain cortical rhythms appear to penetrate the basal ganglia, others are transformed or blocked. Here, we discuss the functional association of oscillations in the basal ganglia and their relationship with cortical activity.

Anatomical substrate

The basal ganglia consist of several parallel, homologous but functionally distinct loops that connect cortical limbic, oculomotor, prefrontal and motor territories (Nambu, 2008). We will focus predominantly on the motor loops — a series of circuits evolved for the control of voluntary

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movements (Fig. 1A). Convergence of motor projections from cortical territories occurs at the striatal level, with segregated circuits projecting through globus pallidus and substantia nigra to thalamic and brainstem (reticular) nuclei (Kaneda et al., 2002; Nambu, 2008). By far the most dominant source of synaptic inputs to the striatum comes from the corticostriatal pathways (Ingham et al., 1998; Mathai and Smith, 2011; Raju et al., 2008), where cortical afferents directly innervate the output cells of striatum — the medium spiny neurons (MSNs). A major ascending input onto the MSNs is dopaminergic and arises from the substantia nigra pars compacta. MSNs can be divided into those which express dopamine D1-class receptors and project to the globus pallidus pars interna (GPi), and those which express dopamine D2-class receptors and project to the globus pallidus pars externa (GPe). Dopamine release in the striatum leads to excitation of the direct pathway via the excitatory D1-receptors, while simultaneously inhibiting the indirect pathway via inhibitory D2-receptor activation. These pathways form the basis of the classic direct and indirect model of basal ganglia function as proposed by Albin et al. (1989) and DeLong (1990). The subthalamic nucleus (STN), the sole excitatory (glutaminergic) nucleus of the basal ganglia network also receives direct cortical afferents through a cortico-subthalamic projection (the hyperdirect pathway), of which relatively little is known (Mathai and Smith, 2011).

Oscillations — from single units to network activity

Rhythmic activity is a ubiquitous feature of the cerebro-basal ganglia network, having been observed at every level from single-units to extracranial magnetic fields. However, the origin and functional interpretation of such activity and how it relates to neuronal spiking are complex. Single-units can display highly regimented patterns of repetitive firing, with oscillatory dynamics emerging in the background local field potential (LFP). While LFPs undoubtedly result from a complex interaction of synaptic and cellular mechanisms (Logothetis et al., 2001), the major driving influence appears to originate from slow subthreshold currents, primarily post-synaptic potentials (Eccles, 1951). Numerous studies have shown rhythmic multi-unit firing that correlates with oscillations in the LFP (e.g. Kuhn et al., 2005), however the extent to which this relationship holds when moving to macroscales remains unclear (Manning et al., 2009; Ray and Maunsell, 2010; Truccolo et al., 2011; Wyler et al., 1982). Recordings must also consider neuronal morphology and, as they move towards broader spatial realms, the anatomical arrangement of cells (Buzsáki et al., 2012). For instance, magnetoencephalography is known to be sensitive to the orientation of the extensive dendritic trees of Purkinje cells that are thought to dominate the observed field (Okada and Nicholson, 1988).

Cortical rhythms

While oscillations are commonly considered to encode feature binding across various sensory modalities (e.g. visual, auditory, olfactory), their role in motor processing appears less clear (van Wijk and Daffertshofer, 2012). Before addressing the specific role of oscillations in the basal ganglia (a recipient of massive cortical input), some knowledge of their cortical counterparts would seem informative.

Most research into event-related brain oscillations focuses on changes in power that likely reflect the degree, and in the case of extracranial fields the spatial extent, of synchronisation in the neuronal population. Early

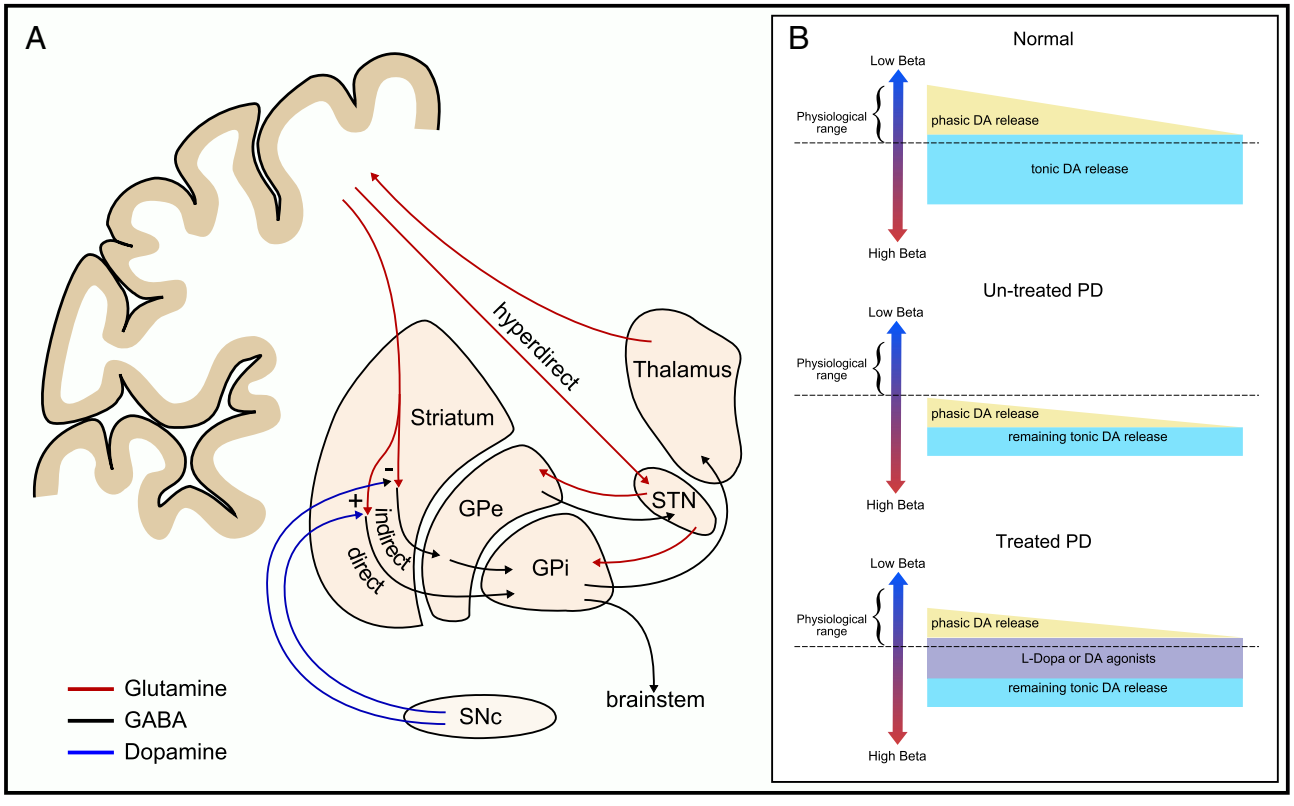

Fig. 1. Anatomy of the basal ganglia and dopaminergic modulation of basal ganglia oscillations in Parkinson's disease. [A] Major anatomical connections within and between the basal ganglia and cortex. [B] Schematic of the relationship between dopaminergic activity in the basal ganglia, and beta activity in health and in PD. Upper panel; normal state associated with low levels of beta. Middle panel; untreated PD. Due to the loss of nigral dopaminergic neurones there is less presynaptic dopamine for release in the striatum and STN. Net dopamine, the sum of tonic and phasic release modes, is low and the dynamic range of dopamine variation begins from a lower threshold than in the healthy state. Lower panel; treatment of PD patients with levodopa or dopamine agonists is thought to change the set-point of the system, driving the dynamic range into normal limits.
[B] Adapted with permission, Jenkinson and Brown (2011).

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