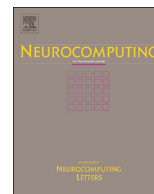




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The rhythms of steady posture: Motor commands as spatially organized oscillation patterns



Stewart Heitmann^{a,b,*}, Tjeerd Boonstra^{c,d,e}, Pulin Gong^{f,g}, Michael Breakspear^{c,d,h,i}, Bard Ermentrout^{a,b}

^a Department of Mathematics, University of Pittsburgh, USA

^b Center for the Neural Basis of Cognition, Pittsburgh, USA

^c School of Psychiatry, The University of New South Wales, Sydney, Australia

^d The Black Dog Institute, Sydney, Australia

^e Research Institute MOVE, VU University, Amsterdam, The Netherlands

^f School of Physics, The University of Sydney, Australia

^g Faculty of Medicine, The University of Sydney, Australia

^h Queensland Institute of Medical Research, Brisbane, Australia

ⁱ Royal Brisbane and Women's Hospital, Brisbane, Australia

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ABSTRACT

Beta-band (15–30 Hz) oscillations in motor cortex have been implicated in voluntary movement and postural control. Yet the mechanisms linking those oscillations to function remains elusive. Recently, spatial waves of synchronized beta oscillations have been observed in primary and pre-motor cortex during delayed-reaching movements. Here we propose that the motor cortex may exploit differences in the morphological properties of spatial oscillation patterns to encode motor commands. Furthermore, we argue that the descending motor pathways spatially filter those patterns to selectively shape the motor drive to the muscles. The ensuing motor drive need not be overtly rhythmic despite the oscillatory nature of the neural coding scheme. We demonstrate this principle using a model of the descending motor system in which oscillatory cortical patterns govern steady postures in a simulated biomechanical joint. The cortex was represented by a sheet of coupled oscillators operating in the beta-band. Lateral inhibition between the oscillators induced spatially synchronized beta waves. The spatial orientation of those waves was governed by the dominant direction of lateral inhibition, which we manipulated. The descending motor tracts that emanated from the cortex were tuned such that specific muscles responded selectively to cortical waves with a given orientation. A range of steady joint postures could thus be achieved by manipulating the dominant direction of the lateral coupling. The model thereby demonstrates the proposed mechanism by which oscillatory patterns in cortex are translated into steady motor postures. The model also reproduces some oscillatory aspects of motor physiology. In particular, it replicates the general reduction of cortical beta power at the onset of movement and the weak but significant levels of corticospinal coherence observed during steady motor output.

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1. Introduction

Neural oscillations in the beta band (15–30 Hz) have long been implicated in the planning and execution of voluntary movement [1,2], but how those oscillations relate to specific muscle movements is unknown. We present a theoretical model of the descending motor system which proposes a neural mechanism by which spatial patterns of beta band oscillations in motor cortex may be translated into muscle activity. We argue that specific

patterns of beta oscillations in cortex are spatially filtered by the pyramidal tract neurons of the descending motor tract to selectively shape the motor drive to the muscles (Fig. 1). The proposed mechanism suggests a functional role for neural oscillations in which the ensuing movements need not be rhythmic. This decoupling of the cortical rhythm from the movement rhythm distinguishes the proposed model from central pattern generator models where oscillations in the spinal cord are typically translated directly into rhythmic muscle movements (see [3,4] for reviews). We demonstrate this principle by modeling propagating waves of cortical beta oscillations controlling steady postures in a simulated biomechanical limb joint. The aim is to explore a putative role for motor rhythms [5,6] that goes beyond the

* Corresponding author.

E-mail address: heitmann@pitt.edu (S. Heitmann).

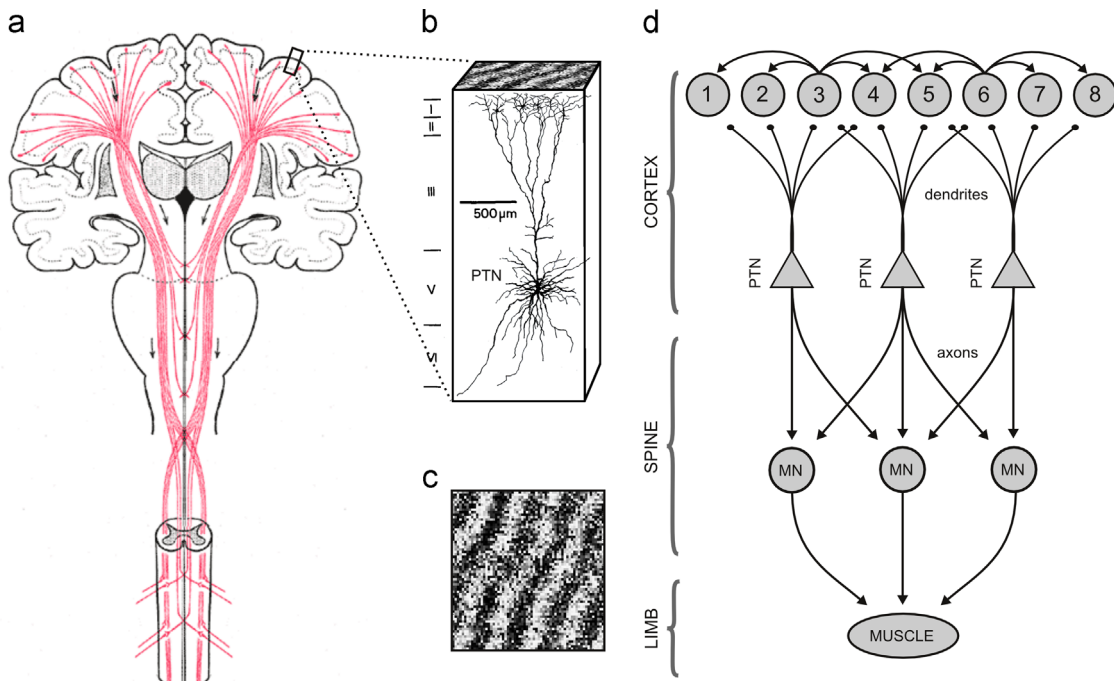


Fig. 1. Modeling the descending motor system (adapted from [8]). (a) Major fiber tracts of the descending motor system, redrawn from Fig. 764 Gray's Anatomy of the Human Body [9]. Axons of the pyramidal tract neurons descend from layer 5 of motor cortex to innervate motor neurons in the spine. (b) The apical dendrites of pyramidal tract neurons project widely throughout the superficial layers of motor and so are ideally placed to detect spatial activity patterns. A typical dendritic receptor field spans a horizontal distance of approximately 600 μm . (c) Example of a spatial synchronization pattern in our cortical model. Gray scale indicates the phases of 200 \times 200 oscillators arranged on a spatial grid. The morphology of the synchronization pattern is governed by the topology of the lateral connections between oscillators. (d) Schematic of the descending motor model. Cortical oscillators are represented by circles (1–8). The synchronization patterns formed by these oscillators are spatially filtered by the dendritic receptors of the pyramidal tract neurons (PTN). Spikes initiated by the pyramidal tract neurons are then distributed among a pool of motor neurons (MN) located in the spine. Each motor neuron within the pool integrates the incoming spikes to produce a motor drive signal innervating the muscle. The full model has two such descending motor tracts that independently drive antagonist muscles in a simulated biomechanical limb joint.

generation of rhythmic locomotion and tackles the problem of translating cortical activity into motor output (see [7] for a recent discussion).

The neurophysiology of beta oscillations in the descending motor system is complex. In primary and pre-motor cortex, the spectral power of the beta rhythm is most pronounced during the maintenance of steady motor output and rapidly attenuates at the onset of movement to rebound strongly after movement termination [10]. These event-related fluctuations in power are thought to reflect dynamic reorganization of the phases of oscillatory activity at the neuronal scale [11]. Task-specific beta oscillations are also observed in the pyramidal tract neurons [12], which form the major output of primary motor cortex and directly innervate the motor neurons in the spine. These descending beta oscillations are weakly coherent with the activity of spinal motor neurons and can also be observed non-invasively as corticomuscular coherence between electromyograph (EMG) activity and electroencephalograph (EEG) or magnetoencephalograph (MEG) activity [13,14]. Corticomuscular coherence may have a functional role by enabling more efficient recruitment of spinal motor neurons [15] or effective corticospinal interaction [16]. It is thought that beta-band oscillations favor the stationary motor state [17–19] since the presence of beta oscillations is inversely proportional to the likelihood that a new voluntary action will need to be processed and performed [20].

Cortical beta oscillations are not necessarily spatially uniform. Propagating waves of beta oscillations have recently been observed in the primary and pre-motor cortices of primates and humans during delayed-reaching tasks [21–23]. These waves are most prominent during states of motor readiness and are attenuated during movement concomitant with the general reduction of beta power. The phase of the propagating wave is reset at the

onset of the instruction cue, suggesting a role for information transfer from pre-frontal decision-making areas [21]. On average, the direction of wave propagation tends to follow the direction of the underlying cytoarchitecture but there is substantial variation between individual waves. It has been suggested that the propagating wave corresponds to the proximal-to-distal sequencing of muscle recruitment in the reaching task [24]. In the present paper, we speculate that the morphological properties of waves may serve as the neural basis for encoding motor commands.

Propagating waves contain potential information in their wavelength, orientation, amplitude, phase and speed. For simplicity, we consider only wavelength and orientation since those properties are known to be governed by the topology of lateral inhibitory connections in neural field models [25–27]. Previous numerical studies have shown that manipulating the strength of lateral inhibition induces transitions between waves and coherent synchrony among coupled oscillators [28]. Introducing anisotropy into the inhibitory coupling permits control over the spatial orientation of waves to encode motor commands [29]. The orientation of those waves can be discriminated (decoded) by the extensive dendritic arbors of the pyramidal tract neurons to selectively drive motor unit activity [8]. That motor unit activity can in turn drive muscle movement in a simulated biomechanical limb [30].

The present study combines the previous findings [28–30,8] into a combined set of simulations that demonstrate the entire chain of events from cortex to limb. The full model comprises two parallel motor tracts that each descend from the cortex to independently drive antagonist muscles in a single biomechanical joint which is restricted to planar movements with one degree of freedom. Waves and synchrony are elicited in the cortical model by manipulating the lateral inhibitory connectivity. The descending motor tracts are each

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