Modeling Neural Control of Locomotion: Integration of Reflex Circuits with CPG

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Abstract. A model of the spinal cord neural circuitry for control of cat hindlimb movements during locomotion was developed. The neural circuitry in the spinal cord was modeled as a network of interacting neuronal modules (NMs). All neurons were modeled in Hodgkin-Huxley style. Each NM included an α-motoneuron, Renshaw, Ia and Ib interneurons, and two interneurons associated with the central pattern generator (CPG). The CPG was integrated with reflex circuits. Each three-joint hindlimb was actuated by nine one- and two-joint muscles. Our simulation allowed us to find (and hence to suggest) an architecture of network connections within and between the NMs and a schematic of feedback connections to the spinal cord neural circuitry from muscles (Ia and Ib types) and touch sensors that provided a stable locomotion with different gaits, realistic patterns of muscle activation, and kinematics of limb movements.

1 Introduction

The central nervous system controls locomotion and other automatic movements in a hierarchical fashion. The lower-level controller in the spinal cord generates the motor program for the neuromuscular apparatus. This low-level controller interacts with proprioceptive feedback and receives descending signals from the higher-level (supra-spinal) centers. The higher centers, in turn, select and initiate the appropriate motor program from the repertoire of the low-level controller (spinal cord). The descending commands from supra-spinal centers to spinal interneurons are automatically integrated into the current state of proprioceptive and exteroceptive information [6].

The neuronal circuits in the mammalian spinal cord can generate rhythmic motor patterns that drive locomotor movements even in the absence of descending inputs from higher brain centers and sensory feedback [2], [5]. This supports the concept of

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the *central pattern generator* (CPG), which presumably is located in the spinal cord and generates a basic locomotor rhythm (for review see [4]). According to the contemporary biological view, the CPG is a complex, distributed network of interneurons in the spinal cord integrated into the system of multiple reflex circuits [6]. The basic locomotor pattern, generated by the CPG, provides a coordinated activation of functionally different muscles, which in turn control and coordinate joint movement within and between the limbs. Therefore, locomotion results from a complex interplay between the CPG, reflex circuits and multiple feedback and feedforward modulatory signals. The proprioceptive signals strongly influence the locomotor rhythm by providing necessary correction of the locomotor rhythm and pattern to maintain the walking animal in a proper relationship to the environment [12]. They regulate the timing of phase transitions and reinforce the generation of motoneuronal activity during ongoing phases of locomotion [9]. Previous modeling studies have demonstrated that a stable and adaptive locomotion involves a global entrainment between the CPGs and musculoskeletal system [7], [14]. The objective of this work was to develop and analyze a comprehensive model of neural control of locomotion at the spinal cord level using realistic models of the network of neurons (in the Hodgkin-Huxley style), muscles, and limb biomechanics.

2 Model

The neural model of the locomotory CPG was constructed using the hypothesis that each limb is controlled by one complex CPG, which in turn is connected with the other CPGs via a coordinating neural network [8]. The CPG was incorporated into the spinal cord neural circuitry and integrated with the circuits of spinal reflexes via direct synaptic interconnections and through multiple proprioceptive feedbacks. The schematic of reflex circuits was modified from the previous models, [1] and [3], and applied to each antagonistic group of muscles. Each hindlimb was modeled as a system of three rigid segments interconnected by three joints: hip, knee and ankle. Two hindlimbs were connected to the common segment (pelvis) (Fig. 1A). A trunk segment was connected with the pelvis. The distal end of the trunk was held at the necessary distance from the ground to compensate for the lack of forelimbs. Each hindlimb was controlled by nine one- and two-joint muscles. The dynamics of muscle contraction was described by a Hill-type model that incorporates the muscle force-length-velocity properties, muscle geometry, and the properties of the tendon.

The exact network of interneurons in the mammalian spinal cord responsible for the generation of the basic locomotor rhythm has not been identified yet. Therefore, in addition to the existing data on the spinal cord neural architecture, we used the suggestion that the mechanism for the locomotor pattern generation in the spinal cord is functionally similar to the brainstem mechanisms providing generation and control of the respiratory motor pattern [8]. Specifically, we assumed that some general architectural principles and particular neural schematics discovered in studies of therespiratory CPG (e.g. those for phase transitions) might be useful and applicable for the construction of the locomotory CPG (see also [8], [12]). In respect to the respiratory CPG, both experimental [11] and modeling [13] studies have demonstrated that, in addition to the "principal" CPG elements (whose activity explicitly defines each phase of the cycle), the CPG may contain special "switching" neural elements that fire during phase transitions and, in fact, produce these transitions via inhibition of the corresponding principal CPG elements. Moreover, it appears that the switching interneurons operate (fire) under control of various proprioceptive and descending control signals and hence significantly contribute to the shaping of the locomotor pattern (timing of phase transitions, shaping motoneuronal firing busts, etc.).

The developed model of the spinal cord neural circuitry has a modular structure. The schematic of a single Neuronal Module (NM) is shown in Fig. 2A. This schematic is considered as a minimal network structure necessary for integration of basic reflexes with the CPG. The NM contains a part of the reflex circuitry and two CPG elements. Each NM controls one muscle. Specifically, the NM includes the output α-motoneuron (α-MN), that actuates the controlled muscle, and several interneurons, including the Renshaw cell (R-In), Ia interneuron (Ia-In) receiving Ia proprioceptive feedback, Ib interneuron (Ib-In) receiving force-dependent Ib proprioceptive feedback, and two interneurons associated with the locomotory CPG. The CPG elements within the NM include the principal CPG neuron (CPG-N) providing activation to the α-MN and the switching interneuron (CPG-In) controlling the principal CPG neuron. The entire neural circuitry for control of locomotion comprises a network of NMs (interconnected directly and via mutual proprioceptive afferents). The CPG, in turn, is formed as a network of all CPG elements located in all participating NMs. Fig. 2B shows an example of two interconnected NMs, controlling a pair of antagonistic flexor and extensor muscles actuating the same joint. The synaptic connections within and between the NMs and the structure of Ia and Ib proprioceptive afferents provide for the classical flexor and extensor stretch reflexes.

The locomotor movement (see Fig. 1B) could be initiated by applying the “descending” drive to all principal CPG neurons (CPG-Ns). Switching the locomotor phases was performed by the firing of the corresponding “switching” CPG interneuron (CPG-In). The timing of phase transitions was controlled by multiple control signals (Ia, Ib, touch sensors) to the “switching” CPG-Ins. These signals provided a necessary adjustment of the duration of each locomotor phase. Interestingly, during the extension phase of locomotion (“stance”), the active extensor CPG-N neuron inhibited the extensor Ib neuron (Ib-In) and hence broke the “classical” negative feedback loop of Ib fibers to the extensor α-motoneurons (α-Mn) (see left side of Fig. 2B). At the same time, the same extensor CPG-N neuron received input from Ib fibers and provided excitation of the extensor α-Mn. Therefore during locomotion the Ib feedback loop to the extensor α-Mn changed from negative to the positive, which is consistent with the experimental data [9], [10].

The developed model was able to provide control of stable locomotor movements (see Fig. 1B). The model demonstrated the flexibility necessary for the adaptive adjustment of locomotor movements to characteristics of the environment.

The above modeling studies allowed us to hypothesize the possible structure of the locomotory CPG, the architecture of network connections within the spinal cord circuitry, and the schematic of feedback connections, which may be tested in further experimental studies.

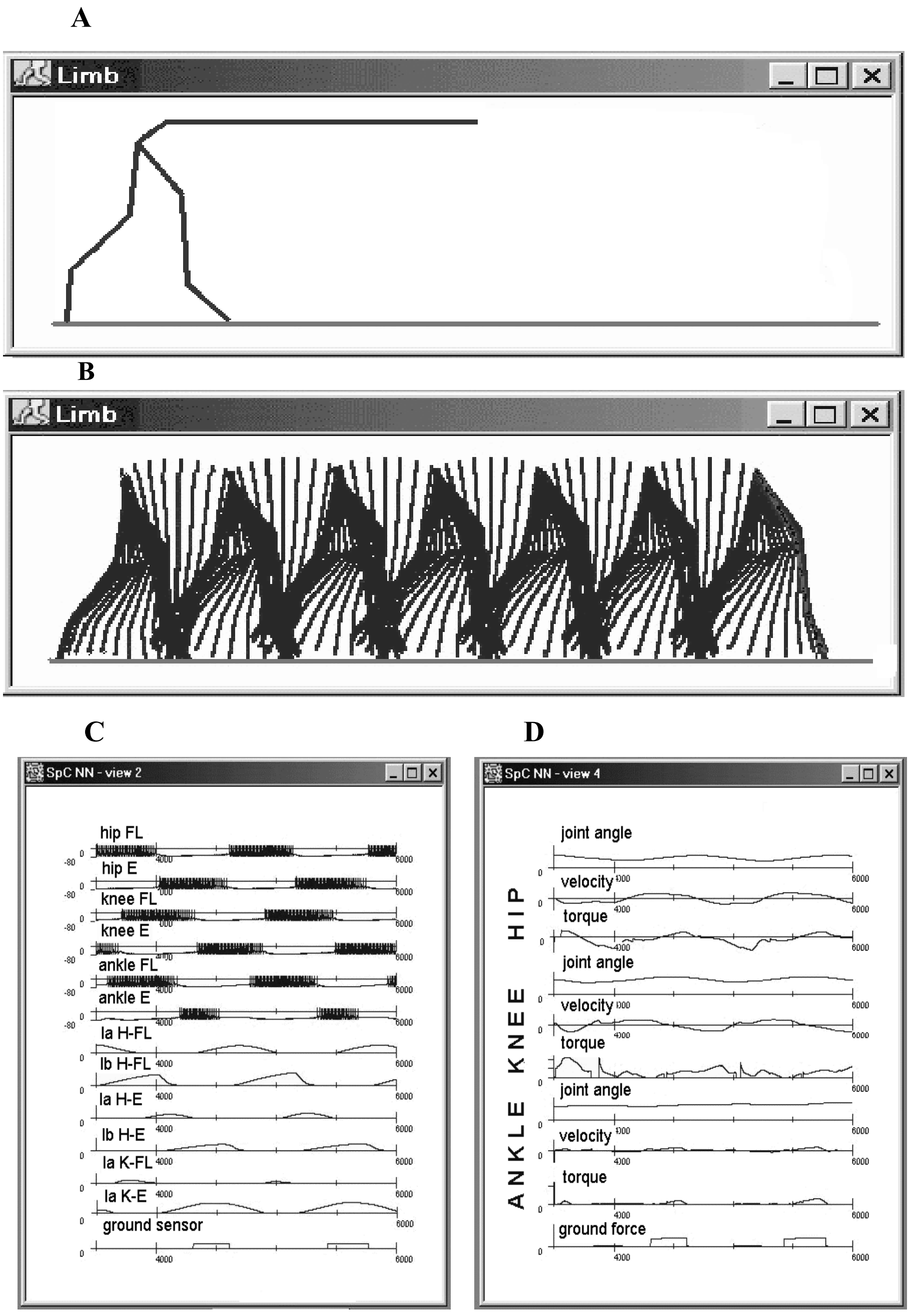

Fig. 1. A. The model of two hindlimbs with the trunk. **B**. Stick diagram of movement of one hindlimb. C. Activity of selected motoneurons and proprioceptive feedbacks. D. Dynamics of some key biomechanical variables.

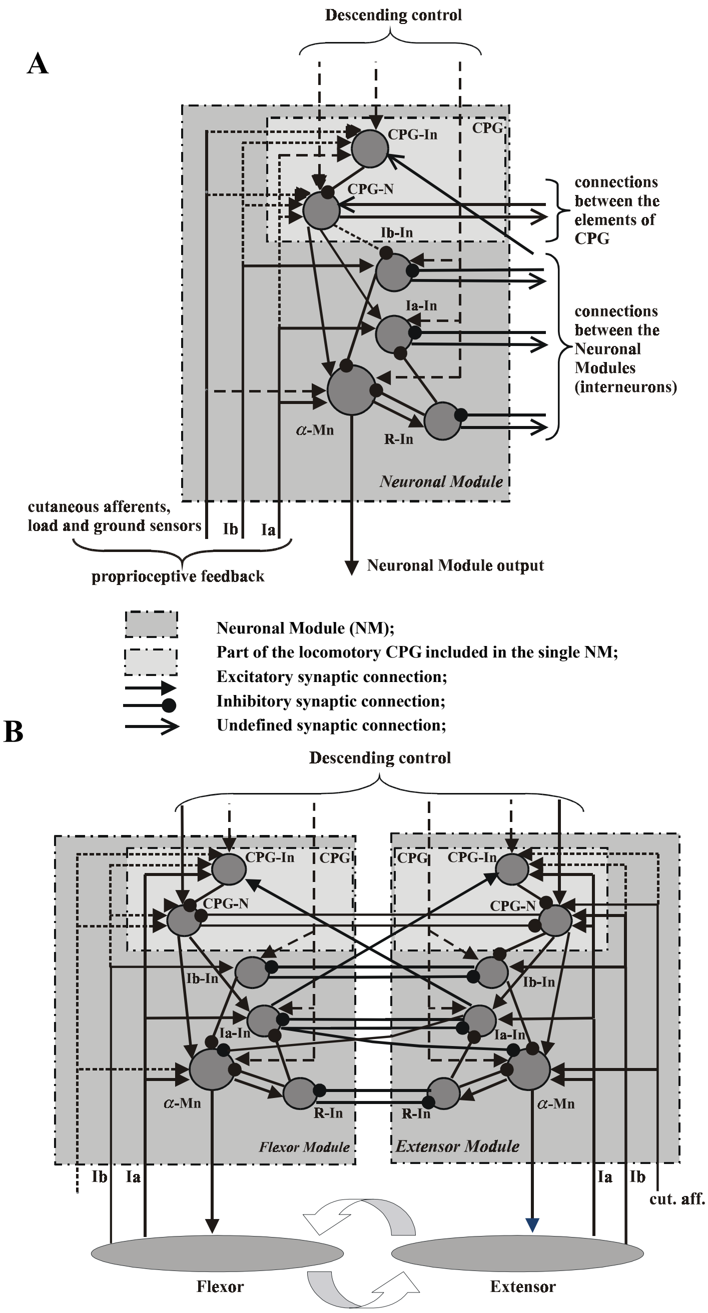

Fig. 2. A. Neuronal Module (NM) of CPG-based neural sub-system. **B**. Two NMs controlling a pair of antagonistic muscles.

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