Abstract
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Organization of mammalian locomotor rhythm and pattern generation.

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We have developed a simplified computational model that includes the locomotor central pattern generator (CPG) integrated with spinal reflex circuits. In this model, the CPG has a two-level organization with separate networks for the rhythm generator (RG) and for motoneuron activation (pattern formation, PF). The model describes interacting populations of interneurons and motoneurons modelled in the Hodgkin-Huxley style with 20-50 neurons per population. Locomotor oscillations result from a combination of intrinsic rhythmogenic properties (based on persistent sodium currents in excitatory interneurons), mutual excitatory connections and reciprocal inhibition between flexor and extensor-controlling circuits at both the PF and RG levels. The model reproduces realistic firing patterns in two antagonist motoneuron populations and the full range of locomotor cycle periods and phase duration observed during cat locomotion.

During fictive locomotion in cats, spontaneous deletions (omissions) of rhythmic motoneuron activity occur in multiple agonist motoneuron pools. In the majority of these deletions, the spinal locomotor network can maintain step cycle timing and the phase of locomotor oscillations. The model reproduces these non-resetting deletions based on the assumption that an unknown perturbation changes neuron excitability within the PF network without affecting the RG. With the separation of RG and PF networks, the CPG can "remember" the step cycle period at the RG level and maintain the phase of post-deletion oscillations when motoneuron activation is disrupted by disturbances at the PF level.

The two-level CPG model also provides explanations for phenomena observed during proprioceptive control of cat fictive locomotion. Depending on stimulus intensity, timing and the nerve stimulated, activation of sensory afferents can either delay or advance phase switching without changing the ongoing step cycle period. In such cases the sensory-induced prolongation or shortening of one phase is compensated by a complementary change in the duration of the following phase. In the two-level CPG model this is achieved when the effects of sensory stimulation are mediated by the PF network without involvement of the RG. Accordingly, moderate levels of sensory input affect the duration of motoneuron bursts (locomotor phase duration) without changing the ongoing step cycle period. More intense sensory drive will affect the RG network and hence step cycle period.

Spontaneous reflex reversals occur during fictive locomotion in which for example, stimulation of certain flexor afferents initiates a premature switching to extension instead of the usual action of prolonging the ongoing flexion phase. According to our model, such reflex reversals are possible when group I flexor afferents activate flexor-controlling CPG circuits (at both the PF and RG levels) and spindle secondary afferents activate extensor-controlling CPG circuits. We postulate that central mechanisms can control the relative weighting of primary and secondary afferent inputs to the RG and PF networks and thereby select the appropriate reflex response.

In summary, our model demonstrates that a simple two-level CPG organization with separate rhythm generator and pattern formation networks can provide a plausible explanation for a number of features of real CPG network operation. These features would be difficult if not impossible to achieve using a classical half-centre CPG organization in which a single network is responsible for both rhythm generation and motoneuron activation.
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