Sensorimotor interactions during locomotion: some neurobiological principles that would help improving the design of walking bio-inspired robots

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Earlier studies demonstrated that a neural network located in the spinal cord (central pattern generator: CPG) can produce the basic pattern of muscle contractions underlying locomotion without receiving any rhythmic descending or sensory input [21].

During the last decades, the use of different vertebrate models, novel neurobiological techniques and modelling has enabled considerable progress to be made in our understanding on the design and operating mode of the CPG for locomotion [18].

Other studies revealed that the CPG for locomotion is strongly influenced by various descending and sensory signals. Indeed, descending signals can trigger, stop or steer locomotion [4, 17, 21]. Importantly, the strength of some of these signals determines the locomotor speed, the gait (e.g. walk/trot/gallop in cat) and the locomotor mode (e.g. stepping and swimming in salamander) [7, 29]. On the other hand, the sensory signals originating from muscles and skin afferents as well as those from special senses (vision, audition, vestibular) dynamically adapt the limb/body movements to the requirements of the environment [8, 24]. Furthermore, the body mechanics, the muscle dynamics and the environment properties importantly contribute to the production of the locomotor movements generated by the nervous system [3, 13].

The complex dynamic interactions between these elements (Figure 1) make difficult to design accurate computer simulations of the locomotor system as well as robots emulating animal locomotion.

However, some general principles extracted from neurobiological studies of locomotion can help in addressing these issues. We will focus here on the main rules that govern the sensorimotor interactions that take place during locomotion in limbed vertebrates.

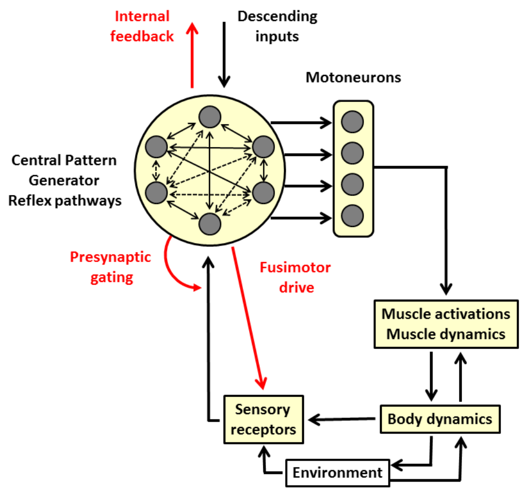

Figure 1. Interactions of components of the locomotor system. Central neuronal elements (central pattern generator (CPG) and reflex pathways) are influenced by descending inputs and by feedback from sensory receptors which are affected by muscle dynamics and body dynamics. The internal feedback from the CPG, the presynaptic gating of the sensory inputs and the fusimotor modulation of the sensitivity of muscle spindles by the CPG are indicated.

1. During the step cycle some limb muscles ("uni-functional muscles") are activated simply as flexors or extensors with one single contraction per step cycle, while other muscles ("**bi-functional muscles**") display more complex and versatile activations during each locomotor cycle, depending on the form of locomotion (e.g. walk/gallop; forward/backward) and environment [30]. Bi-functional limb muscles are the main targets of peripheral and supraspinal inputs in adapting limb movements according to the demand [24].

2. **Proprioceptive inputs** from the limbs (e.g. sensory signals signaling hip or shoulder position, extensor load) play a crucial role in controlling the ongoing locomotor rhythm (i.e. speed of walking), the transition from one phase of the locomotor cycle to another, and the magnitude of the muscle forces in load-bearing muscles [23]. Proprioceptive inputs from the trunk determine the pattern of activation of the axial musculature (i.e. the intersegmental coordination pattern) [27]. **Cutaneous inputs** from the limbs shape the locomotor command (mainly by modifying the discharge pattern of bi-functional muscles) to allow stepping over obstacles and accurate foot placing on uneven terrain [5, 11].

3. The tight interactions between the limb CPGs and the sensory signals induce an adjustment of reflex responses to the ongoing locomotor movement: i.e. the reflexes have different effects, depending on their timing within the cycle ("**phase-dependent modulation**") [21, 24]. Similarly, the descending signals affect the locomotor pattern in only certain phases of the step cycle [24].

4. Numerous **gating mechanisms**, at the cellular and network levels in the spinal cord, contribute to the phase-dependent modulation of sensory and descending effects [24]. Importantly, the sensory modulation can occur early in the reflex pathways, at the level of the afferent terminals

within the spinal cord (**"presynaptic modulation"**) in order increase efficiency of synaptic transmission in those pathways at two transition (swing-stance and stance-swing) phases of the step cycle, i.e. at times bi-functional muscles are activated [1, 9, 15].

5. The **sensitivity of sensory receptors** can be modulated by the locomotor command itself. For instance, the stretch sensitivity of muscle spindles is both tonically and rhythmically modulated by the **fusimotor drive** in accordance with the functional role of the muscles and the environmental conditions [2, 10]. Furthermore, the mechanisms underlying spike generation in muscle stretch receptors can be altered by **antidromic discharges** induced by the activity of spinal locomotor networks on afferent terminals [14].
6. Specific spinal circuits and sensory inputs from the moving limbs govern gait changes [12, 18, 22, 26]. Importantly, these sensory inputs are efficient only when they occur during critical points (e.g. at time of weight transfer) in the locomotor cycle ("**phase-dependent motor coordination**") [25]. Moreover, the direction of stepping (i.e. forward/backward/sideward) is determined by sensory inputs coming from the limbs during stance [20].
7. In tailed quadrupeds, the axial musculoskeletal system operates as a three **functionally independent modules** (neck/trunk/tail) that can be coupled or uncoupled by sensory inputs and descending signals according to the locomotor mode (e.g. stepping/swimming), the gait (e.g. turning) and the environment (e.g. slipperiness of the subtrate) [6, 28].
8. Stepping over obstacles is produced by **feedforward motor commands** planned several steps in advance by using information concerning the obstacle, obtained from vision, together with an estimation of body and limb state [19].

Using the aforementioned neurobiological principles to design bio-inspired walking robots will help to increase their skills during navigation in complex and changing environments. Conversely, experimenting on bio-inspired walking robots will provide new information on the complex mechanisms of sensorimotor integration during locomotion. Finally, the assumption that sensory feedback plays a relatively minor role when animals move quickly, while it plays a major role, not only for determining foot placement in a complex environment, but also for coordinating limbs, when animals move slowly can be tested [16].

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