

SENSORY CONTROL OF LOCOMOTION: REFLEXES VERSUS HIGHER-LEVEL CONTROL

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ABSTRACT

In the absence of sensory input, the central nervous system can generate a rhythmical pattern of coordinated activation of limb muscles. Contracting muscles have spring-like properties. If synergistic muscles are co-activated in the right way, sustained locomotion can occur. What is the role of sensory input in this scheme? In this chapter we first discuss the implications of positive force feedback control in hindlimb extensor reflexes in the cat. We then raise the question of whether the sensory-evoked responses, which are modest in size and quite delayed in the stance phase, contribute to any significant extent. A locomotor model is used to show that when centrally generated activation levels are low, stretch reflexes can be crucial. However, when these levels are higher, stretch reflexes have a less dramatic role. The more important role for sensory input is probably in mediating higher level control decisions.

1. INTRODUCTION

Muscles differ from most man-made robotic actuators in that they are essentially springs whose stiffness and viscosity varies with activation level (Hogan 1985). Furthermore, the stretch reflex pathways providing feedback control of individual muscles differ from those in most man-made robotic control systems in that they incorporate positive feedback loops interlaced with negative feedback loops (Prochazka and Yakovenko 2001). Finally, the overall control of rhythmical movements such as locomotion appears to combine prediction,

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central rhythm generation, proportional feedback control and finite state control. It is only recently that some of these unusual features of sensorimotor control have been recognized, partly because they have only recently been found to be effective in the control of “biomimetic” robots. In this chapter we will discuss some of the implications of these new ways of looking at sensorimotor control. First, we will identify the positive feedback loops in stretch reflex pathways and discuss how they remain stable by interacting with the negative feedback loops. Second, we will ask the more important question, do these reflexes contribute significantly to locomotor load compensation? Third, we will use biomechanical models to test some of the control schemes that have been suggested for animal locomotion. The models reveal a surprising ability of the intrinsic properties of the skeletomuscular machinery, driven by an invariant centrally generated pattern of muscle activation profiles, to adapt to speed, slope and small irregularities in terrain without sensory feedback. However they also show that although the stretch reflex contribution to load compensation in the stance phase can play an important role when the amplitudes of the centrally generated activation profiles are close to threshold for generating stable locomotion, their effects are more modest at higher central activation amplitudes. Finally, they reveal the overriding importance of prediction and finite-state control (IF-THEN rules for phase-switching) when the terrain and cadence are variable.

2. POSITIVE FEEDBACK LOOPS

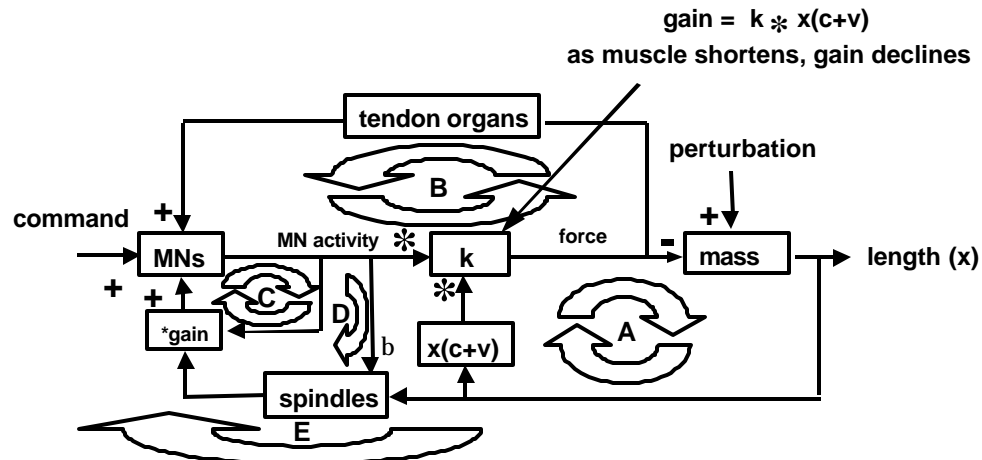


Figure 1 Reflex model of load-moving muscle. Loop A represents intrinsic muscle stiffness. Pathways B and E represent tendon organ and spindle feedback. Loop C represents automatic gain control due to motoneuron recruitment and pathway D represents β -skeletal-fusimotor action. Loops B, C and D are positive feedback loops.

Fig. 1 shows a simple model of the neural feedback loops controlling muscles at the spinal segmental level. The first thing to notice is that the intrinsic properties of the muscle

actuator are represented by a negative feedback loop involving length and velocity (loop A in the figure). This merely describes the fact that as a muscle is stretched, the force it develops is basically a product of muscle length, velocity and activation level. The fact that this can be represented in terms of a feedback loop was recognized many years ago (Partridge 1966).

The second thing to notice is that the excitatory action of the tendon organ pathway on the motoneuron element represents positive force feedback (loop B in Fig. 1). Until fairly recently, tendon organ feedback to homonymous motoneurons was assumed to be inhibitory (negative feedback), but in 1987 it was shown that in the cat locomotor system, when locomotion starts, there is a switch from inhibition of extensors by their tendon organ afferents to excitation and this has been confirmed by other groups (Conway *et al.* 1987; Pearson and Collins 1993; Guertin *et al.* 1995; Prochazka *et al.* 1997b). Normally one would expect that a positive feedback loop would become unstable when the open loop gain in the loop exceeded unity, however in digital simulations of the operation of the system in Fig. 1, stability was maintained even though the open loop gain of loop B was set to start at values greater than unity. The reason turned out to be that even though the loop gain exceeded unity at a given initial muscle length, provided the muscle was free to shorten, the gain in this loop rapidly declined to unity as the muscle shortened. This is because muscles produce less force for a given neural input the shorter they become. In the model in Figure 1, shortening is represented by a decline in the length variable in loop A. Because forward gain in loop B depends on the product of motoneuron activation level and muscle length, this gain therefore declines and when it reaches unity, stability is restored. Negative feedback loop A thus stabilizes the interlaced positive feedback loop B. Spindle afferent feedback (pathway E) excites homonymous motoneurons, which causes the receptor-bearing muscle to resist lengthening, i.e. negative feedback. Positive feedback loops are never included intentionally in linear control systems by control engineers, so the above explanation of how stability is maintained in the presence of positive feedback, though simple, was not obvious from the perspective of linear control theory.

The final thing to notice is that as more motoneurons are recruited, the response to a given synaptic input increases. This is represented by positive feedback loop C. Yet another positive feedback loop can also be identified (D), representing β -skeletofusimotor drive to muscle spindles. Evidently because the gains in all the positive feedback loops involved (B, C and D) are held in check by the operation of the interlaced negative feedback loops A and E (the spindle stretch reflex loop), the system as a whole is surprisingly stable.

3. ARE STRETCH REFLEXES IMPORTANT IN LOCOMOTOR CONTROL?

Having said all of this, we will now argue that in locomotion in the cat at least, the gains of the stretch reflex loops appear to be rather low and reflex action is surprisingly delayed during load compensation in the stance phase. Some years ago, we designed the so-called "foot-in-hole" experiment to separate the reflex and centrally-generated components of ankle extensor muscle activation in cat locomotion (Gorassini *et al.* 1994). Many skin and muscle afferents of the foot and lower leg generate high frequency bursts when the paw touches the ground. We reasoned that if ground contact were absent, the sensory bursts and the responses to them would be absent, leaving just the centrally-generated components of

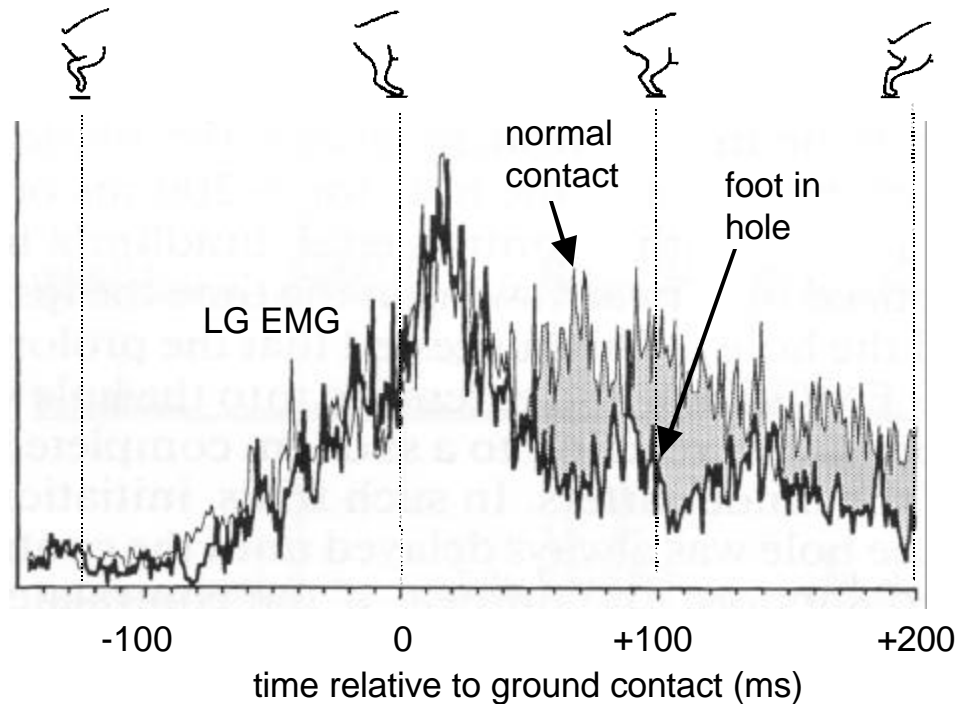


Figure 2 Mean EMG of lateral gastrocnemius (LG) muscle in 29 steps with normal ground contact (thin trace) and 29 steps in the absence of ground contact (thick trace). Data from 9 cats. Grey area represents the component of EMG attributable to sensory input to CNS signalling ground contact and stretch of ankle extensor muscles.

activity. A walkway was built with a hidden spring-loaded trapdoor that could be triggered to descend a few milliseconds before footpad contact, i.e. at precisely the time the sensory guard hairs between the toes of the hind paw would have signaled first contact to the spinal cord. The foot then continued on into the hole, usually for at least 40 to 50 ms before an adaptive flexion response occurred. We compared averaged electromyograms (EMGs) of ankle extensor muscles in trials in which the trapdoor remained locked in place, providing normal ground contact and support, with trials in which the trapdoor was triggered (foot-in-hole trials). The result was surprising. The averaged EMG signals were virtually identical for the first 40 ms or so after the trigger signal (Fig. 2). We had expected to see a clear difference commencing at about 9-10 ms, the latency of the monosynaptic reflex arc in cat extensor muscles and we had posited that the peak of stance-phase EMG at around 20 ms after ground contact was reflexive in origin (Prochazka *et al.* 1976; Trend 1987). In retrospect, we should probably have anticipated the long latency, because in a previous study of EMG responses in ankle extensors to landing from falls, even though the ankle extensors are stretched at velocities up to 500 mm/s, there is a delay in this occurring, that we attributed to an initial dorsiflexion of the toes (Prochazka *et al.* 1977).

To shed light on the elusive reflex component, we did the opposite experiment. A

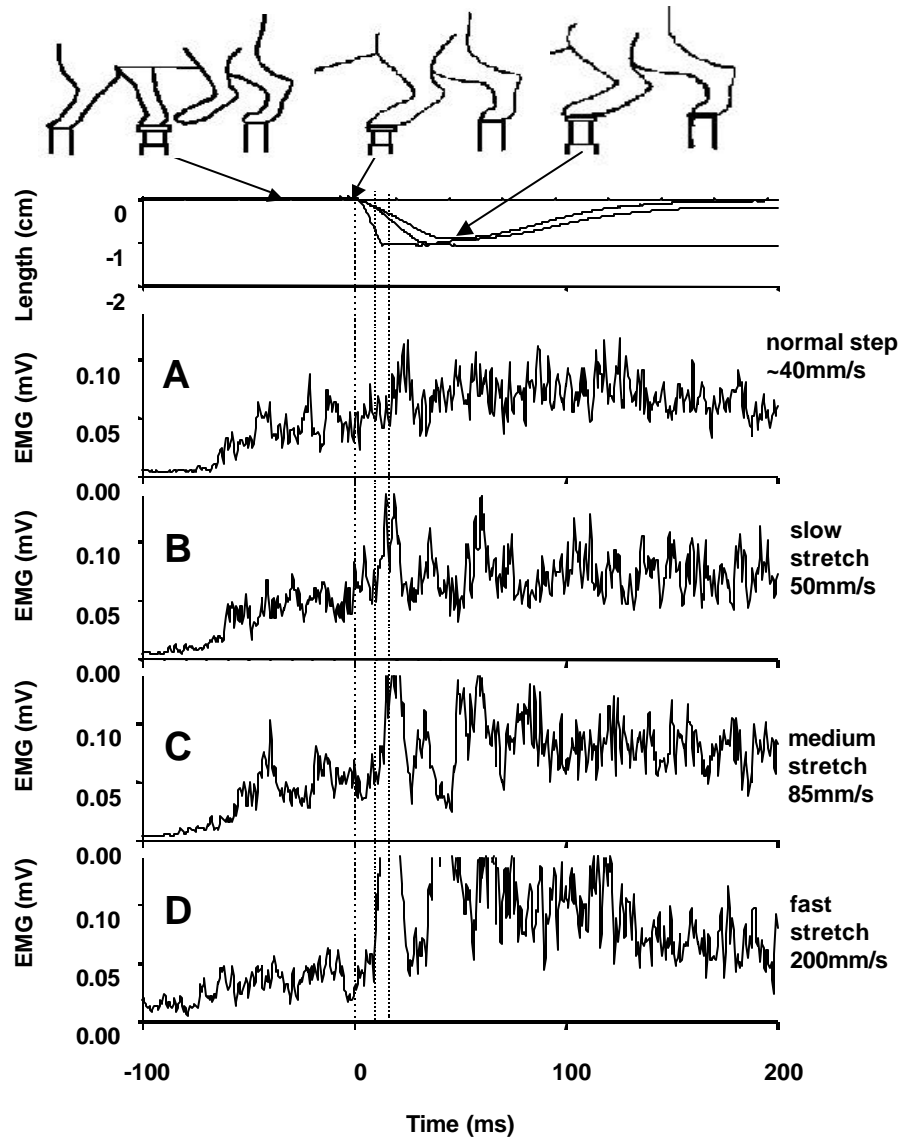


Figure 3 Rapid upward displacement of ground support pegs triggered at the moment of contact of left hindlimb. LG EMG responses for four peg velocities. Estimated stretch velocities of triceps surae are shown on right. A: normal ground contact (no peg displacement). B-D increasing rates of stretch (corresponding displacements of pegs shown in top panel).

walkway was built which consisted of a row of pegs, some of which were spring-loaded. These could be triggered to pop up, dorsiflexing the ankle (stretching the ankle extensor muscles) at the moment the cat's hind paw made contact. Fig. 3 shows the averaged ankle

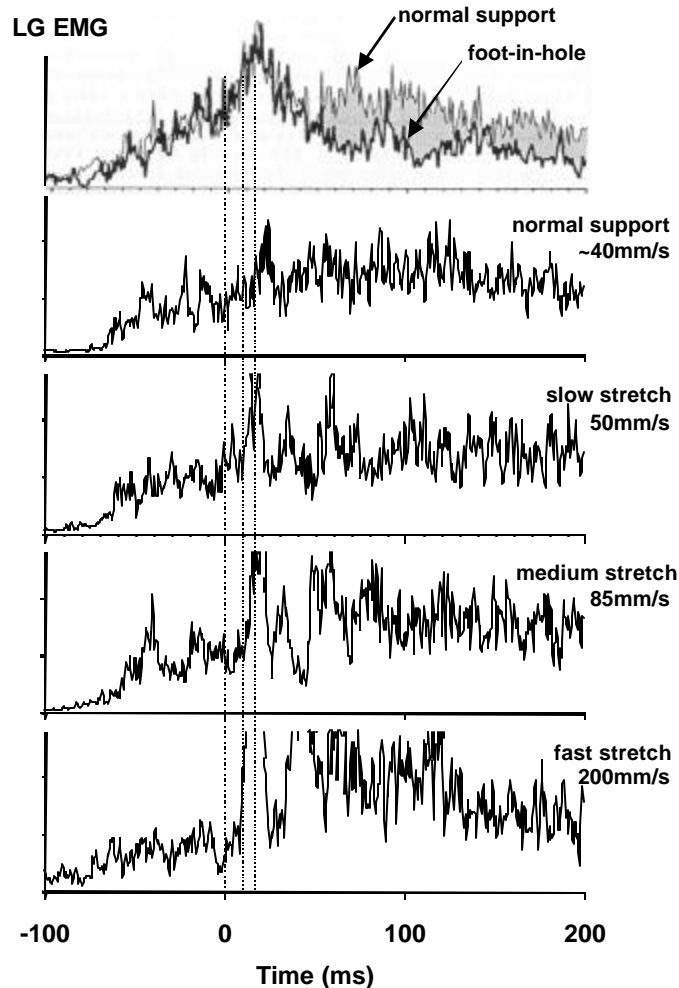


Figure 4 Data of Figs. 2 and 3 superimposed, to highlight timing of presumed stretch reflex components of EMG.

extensor EMGs for trials with normal ground support (A) and with stretch at three rates (B, C and D). As the stretch rate increased, the reflex response emerged clearly. In D it had a latency of about 10 ms, as expected of the monosynaptic response. In the slower stretch responses of B and C the latency was 15 to 20 ms and in the normal contact trials, it is arguable whether there was a clear stretch reflex at all, given the existence of an EMG peak at about 20 ms latency in the foot-in-hole trials of Fig. 2 (where no reflex could have been elicited). To make the comparison easier we have re-scaled and combined the traces of Fig. 2 and 3 in Fig. 4.

Not only was the activity attributable to sensory responses of unexpectedly long latency, it was also a rather modest component of the overall time course of extensor EMG in the step cycle. From time to time, researchers have tried to estimate the percentage

contribution of stretch reflexes to overall muscle EMG and force in locomotion and other motortasks (Allum *et al.* 1982; Bennett *et al.* 1994; Bennett *et al.* 1996; Stein *et al.* 2000). The estimates were in the range 25% (Bennett *et al.* 1996) to 35% (Stein *et al.* 2000). However, as we have seen above, a clear reflexive contribution only emerges 30 to 40 ms after ground contact, about 110 ms after commences, and after peak EMG has been reached. Most if not all of the load compensation in the first third of the stance phase is therefore attributable to EMG of non-stretch-reflex origin that commences about 70 ms before foot contact and the onset of load-bearing.

The activation of EMG prior to expected load-bearing is a well-known feature in the control of postural muscles of the trunk (Massion 1994), leg muscles in locomotion (Engberg and Lundberg 1968), arm and hand muscles in tasks such as catching a ball (Lacquaniti *et al.* 1991). Our laboratory has previously compared the yield at the human elbow caused by impact of a heavy ball with three types of compensation: intrinsic stiffness of the steadily activated flexors), intrinsic stiffness modulated by stretch reflexes, intrinsic stiffness plus reflexes plus predictive activation (Bennett *et al.* 1994). Net yield was less when reflexes modulated the intrinsic stiffness and it became near-zero when prediction was allowed (Lang and Bastian 1999). The crucial factor for such an effective compensation was that biceps EMG started 100 ms prior to first loading.

If extensor stretch reflexes including the positive force feedback responses mediated by tendon organs were absent, would this make a big difference to the kinematics of the limb during cat locomotion? De-afferentation experiments have been equivocal on this issue. In the first days and weeks after de-afferentation there is usually a greatly increased yield of the limb in the stance phase, which manifests as a pronounced limp. But this may be because extensor EMG activity, including pre-ground-contact EMG, is generally reduced. After some weeks, little difference is noticed between de-afferented and normal limbs (Wetzel *et al.* 1976; Goldberger 1977; Rasmussen *et al.* 1986; Giuliani and Smith 1987) unless specialized tasks are performed (Abelew *et al.* 2000). The ideal experiment would be somehow to abolish sensory input suddenly in single step cycles with normal ground support, but it is hard to see how this could be done. However, it can certainly be simulated in models.

Figs. 5 and 6 show the results of this experiment performed with a biomechanical locomotor model (Prochazka and Yakovenko 2001). A full description of the model and analytical methods will be published elsewhere. Briefly, the model comprises a simplified skeletal structure with a representative set of leg muscles (Fig. 5C) characterized by Hill-type length-force-velocity relationships. The model is based on the anatomy of the cat but as it is intended as a test bed for general hypotheses of locomotion across species we did not strive for an exact parametric representation. A point near the front of the body is supported on a frictionless rail. The model was constructed and simulated using Matlab version 5.3 software coupled to 2D Model version 5 software.

Locomotion was driven by a set of “EMG” activation patterns of the muscles of the model. These were based on known EMG profiles (Yakovenko *et al.* 2000). After some trial and error adjustments of these profiles we were able to optimize them to produce stable locomotion on a flat surface in the absence of sensory input. The EMG patterns may therefore be viewed as the centrally generated, or “default” output of the central pattern generator (CPG) in the spinal cord in the absence of sensory input. Each step was kinematically unique, indicating that the intrinsic muscle properties compensated for small

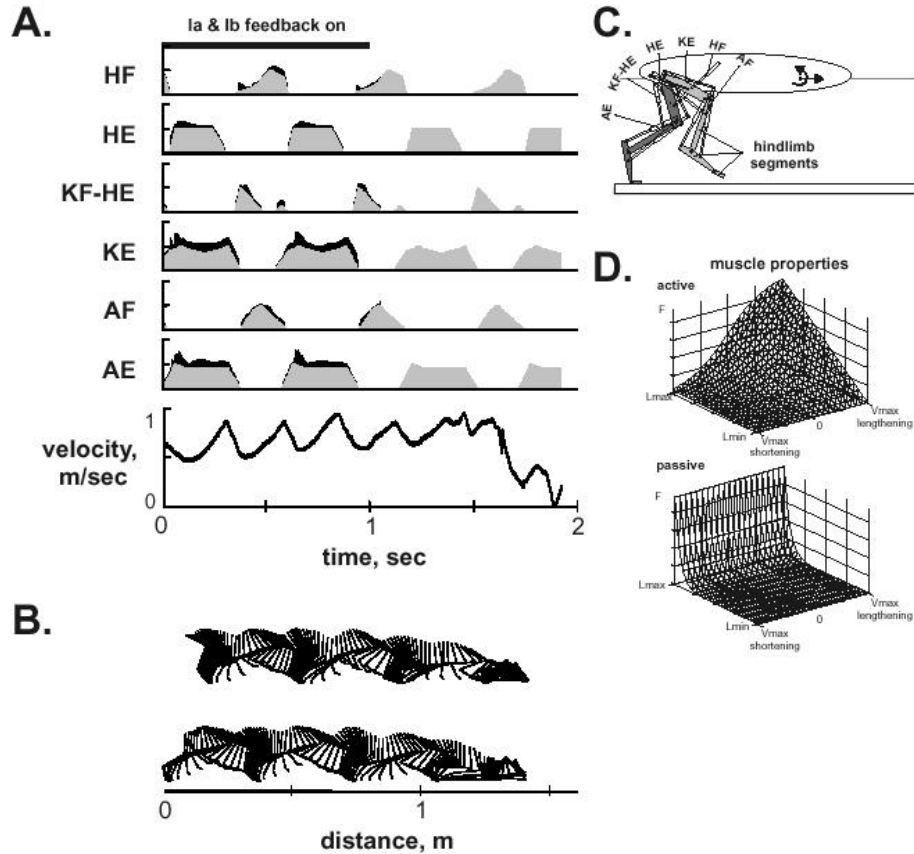


Figure 5 Model of control of quadruped hindlimbs during locomotion with and then without stretch reflexes mediated by muscle spindle Ia and tendon organ Ib afferents. A) top: black bar indicates reflexes present. Basic EMG profiles due to central pattern generator (CPG) shown in grey, additional reflex components in black: hip flexors (HF), hip extensors (HE), knee flexors (KF), knee extensors (KE), ankle flexors (AF), ankle extensors (AE). Bottom trace shows velocity. B) stick figures of left and right legs. C: Physical structure of model. D: muscle properties: length-force and velocity-force.

variations in the kinematic and kinetic variables involved. Similar results have been obtained before using inverse dynamics or neural networks to optimize activation patterns (Taga *et al.* 1991; Taga 1995b; Taga 1995a; Yamazaki *et al.* 1996; Neptune *et al.* 2001; Ogiwara and Yamazaki 2001).

Spindle Ia and tendon organ Ib response properties are represented by the following equations derived from the literature (Prochazka 1999).

$$\begin{aligned} \text{Ia model} \quad & \text{Ia}(t) = K_{\text{Ia}} * (65 * \text{velocity}^{0.5} + 200 * \text{length} + 50) \\ \text{Ib model:} \quad & \text{Ib}(s) = K_{\text{Ib}} * \text{force} * (s+0.15)(s+1.5)(s+16) / (s+0.2)(s+2)(s+37) \end{aligned}$$

where $\text{Ia}(t)$ is the time function of the Ia signal and $\text{Ib}(s)$ is the tendon organ response in the frequency domain, s = frequency domain operator. K_{Ia} and K_{Ib} represent gain coefficients.

The Ia and Ib reflex signals were set to have a latency (delay) of 35 ms, in accordance with the latency of the EMG components attributable to reflexes in Fig. 3, top panel. They were active only when the receptor-bearing muscles were active, i.e. only when the CPG EMG profile of the corresponding muscle was non-zero. The gain coefficients K_{Ia} and K_{Ib} were adjusted so that the Ia and Ib signals each added a mean of 15% to the CPG EMG profile. The value of 15% was chosen because the sum, 30%, corresponded to the proportion of net EMG attributable to reflexes in Fig. 3.

At the meeting in Cairns, Prochazka predicted from Figs. 2 and 3 above that the size and timing of the reflexes were such that they could have little kinematic effect on the step cycle. This prediction has since been tested as illustrated in Figs. 5 and 6. In Fig. 5, the amplitudes of the CPG patterns were scaled down to about 90% of the level required to just produce stable locomotion. The net reflexive components of EMG are shown as black caps on top of each EMG profile in the first two step cycles of Fig. 5A. Locomotion was stable in the presence of the reflex contributions. Reflex transmission was suddenly reduced to zero after the second cycle. The resulting reduction in weight support and forward thrust were such that the hindquarters collapsed over the next two cycles (Fig. 5). This was of course expected, because the CPG pattern had been deliberately set at 90% of the level needed to sustain locomotion. The surprise was that in the first two steps, the stretch reflexes clearly provided enough extra activation to make gait possible.

The next question was, if the basic CPG profiles were adequate to sustain gait, would the addition of the reflexes make any significant difference? In Cairns, Prochazka had suggested they would not. Fig. 6 shows that adding the stretch reflexes after the first few cycles, again set to add about 30% to the underlying CPG activation profiles, caused a modest but significant increase in the velocity of gait.

We conclude that even though the reflex contributions are delayed in the cycle and add only about 30% to the centrally generated extensor EMGs, they can play a role in sustaining and controlling the speed of gait. This outcome was not obvious from qualitative judgements, though the modulation of locomotor speed by gain control of positive force feedback had been proposed from a simpler single-muscle analysis (Prochazka *et al.* 1997a).

4. HIGHER LEVEL CONTROL

The modulation of load compensation and speed described above, though significant, still seems a rather modest role for sensory input to the CNS given that muscle afferents are the fastest-conducting axons in the body and that axons involved in proprioception and sensation far outnumber motor axons innervating extrafusal muscle (Matthews 1972). Another crucial role for sensory input is to allow for higher-level decisions, for example those based on conditional logic in which IF-THEN rules determine state transitions such as phase-switching in the step cycle and the prediction of global EMG levels required for future movements “one-step-ahead” control (Granat *et al.* 1993; Prochazka 1993).

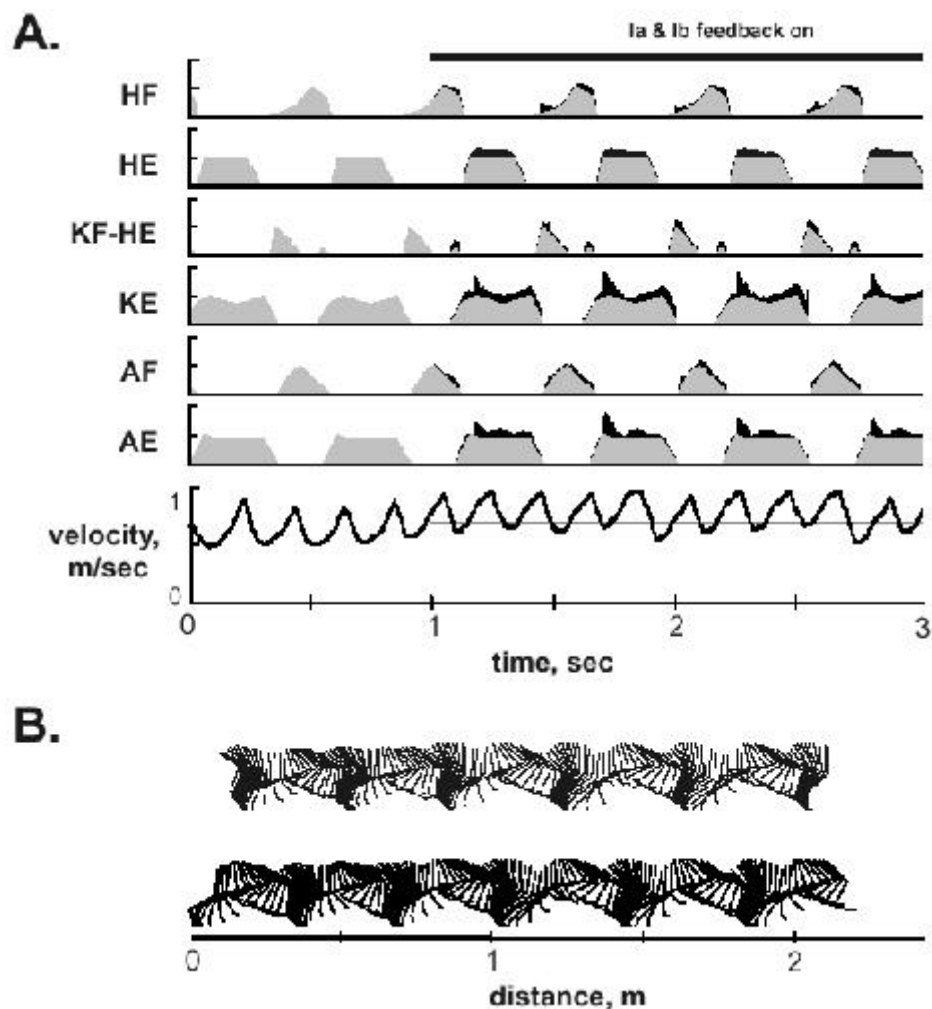


Figure 6 Adding stretch reflexes to a stable locomotor pattern. Similar simulation to that in Fig. 5, except that amplitude of CPG EMG patterns was sufficient to sustain locomotion without reflexes. A) Reflexes added as shown by black bar. The result was a small increase in velocity. B) stick figures of left and right legs.

The biomechanical modeling described above, and also the accelerating effort being put into the design of control systems for biomimetic robots (Quinn and Ritzmann 1998; Nelson and Quinn 1999) has led to a number of general conclusions about the overall roles of sensory feedback that are in line with the concepts presented in this article and will serve as a fitting conclusion:

1. The intrinsic stiffnesses of limb muscles, when activated with optimized cyclical patterns can generate stable locomotion in the face of small variations in speed and terrain. Stretch

reflexes contribute to load compensation within a given phase of the step cycle, and provide a limited means of changing gait speed and posture.

2. Larger adjustments in speed and terrains require higher-level control strategies such as finite-state logic.
3. Global rules that use multisensory input are required for movement selection, predictions about upcoming movements and overall balance.

5. ACKNOWLEDGMENTS

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