

Contribution of stretch reflexes to locomotor control: a modeling study

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Abstract. It is known that the springlike properties of muscles provide automatic load compensation during weight bearing. How crucial is sensory control of the motor output given these basic properties of the locomotor system? To address this question, a neuromuscular model was used to test two hypotheses. (1) Stretch reflexes are too weak and too delayed to contribute significantly to weight-bearing. (2) The important contributions of sensory input involve state-dependent processing. We constructed a two-legged planar locomotor model with 9 segments, driven by 12 musculotendon actuators with Hill-type force-velocity and monotonic force-length properties. Electromyographic (EMG) profiles of the simulated muscle groups during slow level walking served as actuator activation functions. Spindle Ia and tendon organ Ib sensory inputs were represented by transfer functions with a latency of 35 ms, contributing 30% to the net EMG profile and gated to be active only when the receptor-bearing muscles were contracting. Locomotor stability was assessed by parametric variations of actuator maximum forces during locomotion in open-loop (“deafferented”) trials and in trials with feedback control based on either sensory-evoked stretch reflexes or finite-state rules. We arrived at the following conclusions. (1) In the absence of sensory control, the intrinsic stiffness of limb muscles driven by a stereotyped rhythmical pattern can produce surprisingly stable gait. (2) When the level of central activity is low, the contribution of stretch reflexes to load compensation can be crucial. However, when central activity provides adequate load compensation, the contribution of stretch reflexes is less significant. (3) Finite-state control can greatly extend the adaptive capability of the locomotor system.

1 Introduction

At an international symposium on movement and sensation held in Cairns, Australia in 2001 we made the provocative suggestion that stretch reflexes do not contribute substantially to load compensation in mammalian locomotion (Prochazka et al. 2002). We made this suggestion on the basis of the relatively small size and long latency of electromyogram (EMG) responses that occur after ground contact in the stance phase of the locomotor step cycle. Some initial biomechanical modeling we had done indicated that these responses may only have a modest effect on the kinematics of quadrupedal gait.

Classical studies demonstrated many years ago the ability of the spinal cord to produce the basic locomotor rhythm in the absence of sensory feedback (Brown 1911). Brown coined the term “intrinsic factor” to describe the underlying neural mechanism, and more recently Grillner renamed this the “central pattern generator” (CPG) (Grillner and Zangger 1974). The fact that under some circumstances rudimentary weight-bearing locomotion can occur in the absence of sensory input indicates that the biomechanical properties of the limbs provide some flexibility in load compensation (Pearson et al. 2003). However, studies on animal and human subjects have also shown that after sensory loss gait is far less coordinated and less able to adapt to changes in terrain and body posture (Bickel 1897; Lajoie et al. 1996; Bloem et al. 2002). Thus two main roles are usually attributed to sensory feedback: it provides control of the stiffness of individual muscles and it allows higher-level control of balance, stability, and coordination.

Stretch reflexes associated with locomotion, on which we will concentrate in the following discussion, have been extensively studied with a variety of physiological techniques for over a century. Most of the studies have dwelt on the electrical responses of muscles to electrically evoked sensory inputs or to imposed muscle stretching and shortening. The amplitude of sensory-evoked EMG responses is modulated throughout the

step cycle (Akazawa et al. 1982; Capaday and Stein 1986; Dietz et al. 1990; Stein et al. 2000), so that the contribution of stretch reflexes has been posited to be highest when the receptor-bearing muscle is active. Estimates of the relative contribution of stretch reflexes to overall muscle EMG during locomotion are in the range 25%–35% (Yang et al. 1991; Bennett et al. 1996; Stein et al. 2000). But if the sensory input due to ground contact is removed at the onset of the stance phase of cat locomotion (“foot-in-hole” experiments), changes in EMG appear surprisingly late (30–40ms) (Gorassini et al. 1994). In another set of experiments, stretch of the ankle extensors after ground contact was artificially exaggerated (Gritsenko et al. 2001). This confirmed the timing of the stretch reflexes and further emphasized the modest size of the reflex components in unperturbed steps.

So what is the functional role of the stretch reflexes during locomotion? After recovery, deafferented animals show little change in yield of the limb during the stance phase of level overground locomotion, though in more demanding tasks abnormally large yielding can occur (Abelew et al. 2000). However, in experiments of this type it could be that compensatory changes in central drive learned over a period of time may replace the missing stretch reflex components and thereby mask the role of these reflexes under normal conditions. The ideal experiment would be to study locomotor performance when sensory input is suddenly abolished. It is hard to see how this manipulation could be done in real animals, but it is certainly possible in biomechanical simulations. We have used these in this study to test the following two hypotheses: (1) Stretch reflexes are too weak and too delayed to contribute significantly to weight-bearing and (2) the important contributions of sensory input involve state-dependent processing.

2 Methods

2.1 Structure of the locomotor model

We developed a planar locomotor model of two hindlimbs attached to a horizontal torso supported at the front by a frictionless wheel (Fig. 1). Each hindlimb comprised four rigid-body segments (thigh, shank, foot, and toes) that were driven by six musculotendon actuators. All joints were modeled as frictionless revolute. The model was developed using Matlab version 6.1 software (The MathWorks, USA) coupled to Working Model 2D version 5 software (Knowledge Revolution, USA). The foot interactions with the ground were modeled with the use of Working Model software. The following parameters were chosen to minimize slipping: the coefficient of restitution was set to 0.1 and the coefficient of Coulomb friction to 10. The results were computed using the Kutta-Merson numerical integration method with 0.1-ms fixed steps and 1/100 mm error tolerance.

In the model to be presented, the dimensions, masses of the segments, and moment arms of the actuators were

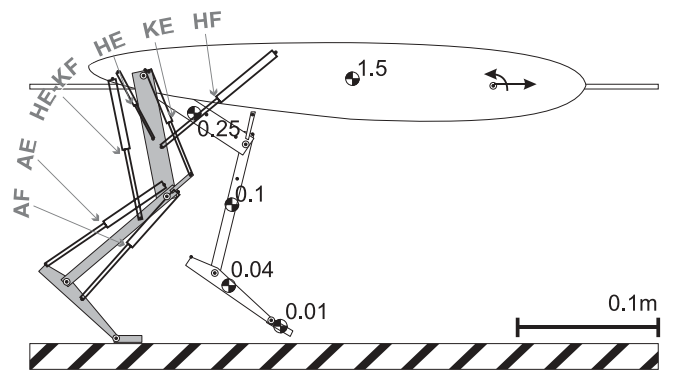


Fig. 1. Structure of neuromuscular locomotor model. A musculo-skeletal model with segment lengths and weights (indicated next to segment centers of mass) based loosely on the hindlimbs of cat. Muscle groups and their origins and insertions are represented by the following musculotendon actuators: HF (hip flexors), HE (hip extensors), KF-HE (bifunctional muscle with knee flexor and hip extensor function), KE (knee extensors), AF (ankle flexors), and AE (ankle extensors). Shoulder joint is constrained to 2 degrees of freedom, horizontal translation and rotation

chosen approximately to mimic those of a cat. All simulations were started just prior to foot contact, with initial velocity of the trunk and leading leg segments set to 0.7 m/s. We intentionally did not strive for a rigorously accurate model as we were seeking conclusions that would generalize across a large range of parametric variation (see Discussion). Internal properties of the individual actuators were modeled by Hill-type force-velocity (Hill 1938) and linear force-length (Gillard et al. 2000) relationships. Muscle force was calculated as

$$F = F_{\max} \cdot f_v \cdot f_l \cdot a_t + F_{\max}^{\text{passive}} \cdot f_l^{\text{passive}}, \quad (1)$$

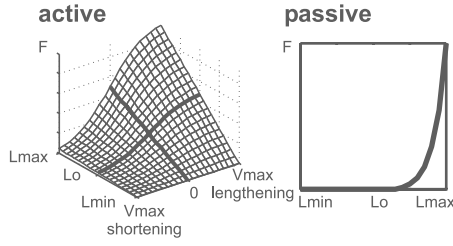
where F is muscle force, F_{\max} is the maximum isometric force, f_v and f_l are the force-velocity and the force-length relations respectively, $F_{\max}^{\text{passive}}$ is the maximum passive force, f_l^{passive} is the normalized passive force-length relation (Fig. 2a), and a_t is muscle activation, whose dynamics were described by the He-Zajac-Levine excitation-contraction coupling equation (He et al. 1991):

$$\dot{a}_t + \frac{1}{\tau_{\text{act}}} \cdot \left(\frac{\tau_{\text{act}}}{\tau_{\text{deact}}} + \left[1 - \frac{\tau_{\text{act}}}{\tau_{\text{deact}}} \right] \cdot u_t \right) \cdot a_t = \frac{1}{\tau_{\text{act}}} \cdot u_t, \quad (2)$$

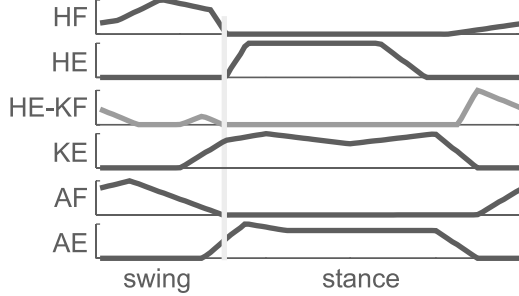
where τ_{act} , τ_{deact} are activation and deactivation time constants (20 ms and 40 ms, respectively) and u_t is motoneuron excitation described by Eq. 6.

Electromyographic (EMG) profiles of the simulated muscle groups during slow level walking (Fig. 2b) served as CPG outputs to the musculotendon actuators. Swing and stance durations were set to 30% and 70% of the step cycle period, respectively, which is an appropriate phase relationship for slow gait with a cycle period of 600 ms (Goslow et al. 1973; Halbertsma 1983). The activation profiles were based on a large number of locomotor studies and have been described elsewhere (Yakovenko et al. 2002).

A muscle properties



B activation profiles



C control system schematic

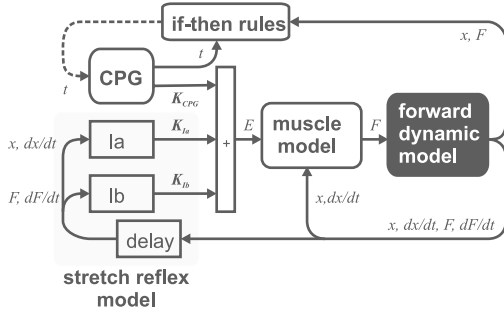


Fig. 2 **a** Active and passive force-length-velocity relationships used to model muscle properties of actuators. **b** EMG profiles used as CPG outputs to the corresponding musculotendon actuators. **c** Schematic of the organization of control system in our model

2.2 Parametric testing

A direct dynamic approach was applied to compute kinematics and to study the contribution of different types of sensory feedback to motor control of the musculoskeletal system. Instead of using dynamic optimization methods with set performance goals for certain types of locomotion, we chose to study performance of the model in parametric space, constructed from combinations of stiffnesses of the musculotendon actuators (F_{\max} in Eq. 1). A random search method was used to determine “stable” regions of parametric space, defined as the ability of the model to locomote for at least 12 s (equivalent to about 20 steps). Principal component analysis (PCA) was further performed on the “stable” sets. To quantify locomotor stability, we computed the moment of inertia for the “stable” volume defined by the

sets of force parameters in Fig. 4 using the following formula:

$$I = \sum_i^n \frac{r_i^2}{n}, \quad (3)$$

where r_i is the vector magnitude defining distance from the center of the “stable” volume to each individual parameter set and n is the total number of parameter sets (100 “stable” simulations). Locomotor performance was analyzed in the plane formed by the two principal component vectors that accounted for most of the variability in the data.

The analysis was repeated in the model where the length of the ankle was increased to match the relative segment lengths of a horse. The reason for repeating the analysis in the “horse” model was to test whether our basic conclusions held in the face of large changes in limb geometry (Fig. 1). The length of the ankle relative to the femur and tibia in the horse is double that in most other mammals.

2.3 Stretch reflex model

The stretch reflex model comprised simulated feedback from spindle Ia and tendon organ Ib afferents onto homonymous motor pools. Heterogeneous excitation and reciprocal inhibition components of afferent feedback, described by Lundberg (Engberg and Lundberg 1969), were neglected for the sake of simplicity. The contributions of Ia and Ib afferents to the output of homonymous motoneuron pools were represented by the following formulae derived from the literature (Prochazka 1999):

Ia model:

$$f_{Ia}(l, v) = K_{Ia} \cdot (21 \cdot v^{0.5} + 200 \cdot l + 60); \quad (4)$$

Ib model:

$$f_{Ib}(s, F) = K_{Ib} \cdot \frac{(s + 0.15) \cdot (s + 1.5) \cdot (s + 16)}{(s + 0.2) \cdot (s + 2) \cdot (s + 37)} \cdot F, \quad (5)$$

where f_{Ia} is a time function of the Ia afferent firing rate response to changes of muscle length and velocity, l is the muscle length in rest length units, v is the muscle velocity expressed in rest length per second, f_{Ib} is the tendon organ response in the frequency domain, s is a frequency domain operator, and K_{Ia} and K_{Ib} are gain coefficients. The middle of the range of motion of each musculotendon actuator was chosen as its rest length. Note that the above equations are in the time and frequency domains, respectively. Though Eq. 3 can be written as a differential equation in the time domain, its filtering properties are then very difficult to infer. Inspection of Eq. 3 indicates that tendon organs act as high-pass filters, with 20 dB/decade increases in transmission occurring between the following pairs of frequencies: 0.15–0.2, 1.5–2, 16–37 rad/s (i.e., ~ 0.02 – 0.03 , 0.2 – 0.3 , and 2.6 – 5.9 Hz). Matlab Simulink allows a mixture of time and frequency domain transfer functions within the same model.

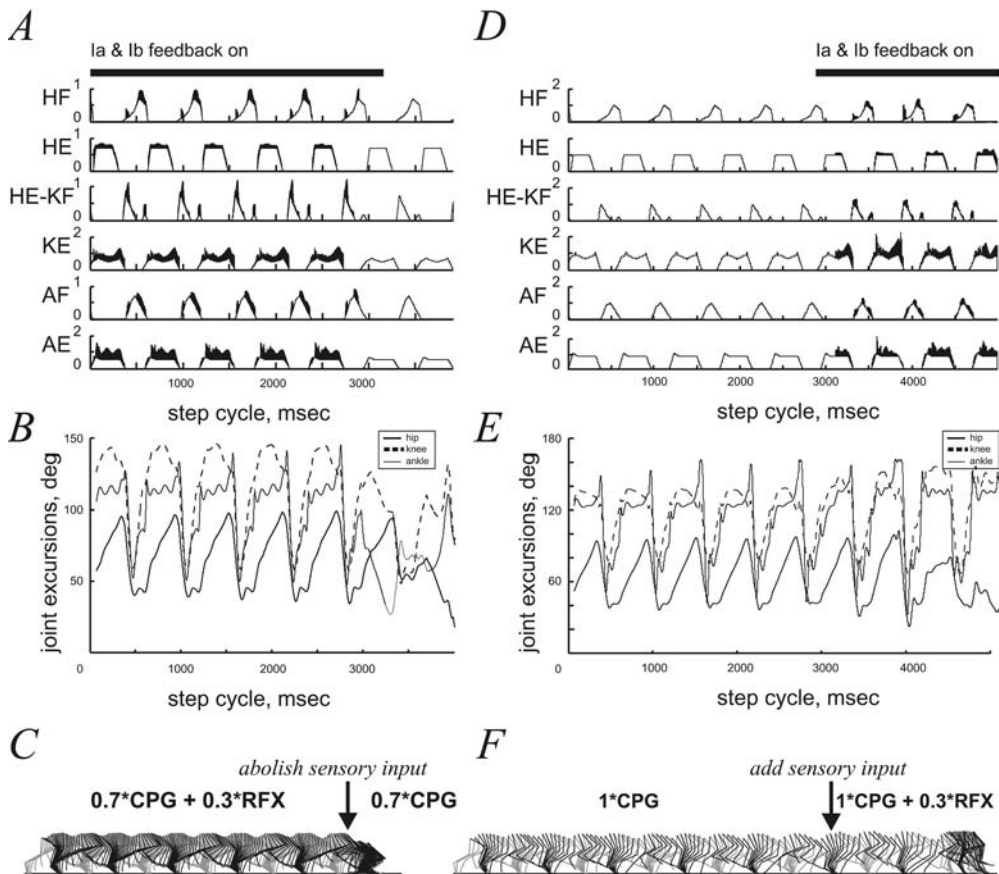


Fig. 3a-f. Contribution of stretch reflexes during locomotion. Two simulation results are shown in the *left* and *right* panels. **a-c** Centrally generated levels of muscle activation were not quite high enough to support stable locomotion. Stretch reflex contributions comprising 30% of the total activation (black portions of the activation profiles) were initially present and then suddenly removed. **d-f** Centrally generated levels of muscle activation were sufficient to support stable locomotion; stretch reflex contributions (black portions of profiles) were initially absent and then suddenly added. Stick figures of **c** indicate that the stretch reflexes are crucial to maintaining stable locomotion when CPG activation alone is insufficient to support load bearing. However, in a trial with sufficient CPG activity (**f**), the addition of stretch reflexes only had the effect of slightly increasing gait velocity, which eventually led to collapse (see supplementary material)

The Ia and Ib reflex feedback contributed to the muscle contractile force with a latency of 35 ms (Gorassini et al. 1994; Gritsenko et al. 2001). This feedback was active only when the CPG EMG profile for the receptor-bearing muscle was nonzero to satisfy the known modulation of the stretch reflex within the step cycle (Capaday and Stein 1986). 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 component throughout a full locomotor cycle. Thus, together both signals contributed 30% to the CPG EMG profiles, which is in accordance with the suggested reflex contribution to the EMG during walking (Bennett et al. 1996; Stein et al. 2000). When the stretch reflex component was present, the excitation function in Eq. 2 was of the form

$$u_t = CPG_t + f_{Ia} + f_{Ib} \quad (6)$$

2.4 Finite-state rules

The following IF-THEN rules were used to model higher-level control of phase switching in the step cycle (Granat et al. 1993; Prochazka 1993):

1. Stance to swing transition: IF stance AND ipsilateral hip is extended AND ipsilateral leg is unloaded, THEN swing.
2. Swing to stance transition: IF swing AND ipsilateral hip is flexed AND ipsilateral knee is extended, THEN stance.

The thresholds for the firing of these rules were determined on a trial-and-error basis. The schematic of all control systems implemented in the model are shown in Fig. 2c.

3 Results

3.1 Simulation of “deafferentation” experiment

Figure 3 illustrates two examples of the type of experiment mentioned in the introduction, where a sudden change in sensory feedback occurs during locomotion. In the left panels (Fig. 3a-c) sensory feedback was suddenly withdrawn, whereas in the right panels (Fig. 3d-f) sensory feedback was suddenly added. In both cases the sensory inputs contributed about 30% to the overall muscle activation profiles as described above. In the example on the left the amplitudes of the centrally generated components were deliberately chosen to produce forces that alone would be insufficient for weight bearing, whereas in the example on the right the CPG activation levels were chosen to be sufficient to produce stable locomotion. In the first case, withdrawal of the stretch reflex contribution led to a collapse of the model, from which one would conclude that stretch reflexes are crucial to maintaining stable locomotion. This would refute the suggestion we made in Cairns (hypothesis 1 above) that stretch reflexes are too weak and too delayed to contribute significantly to weight

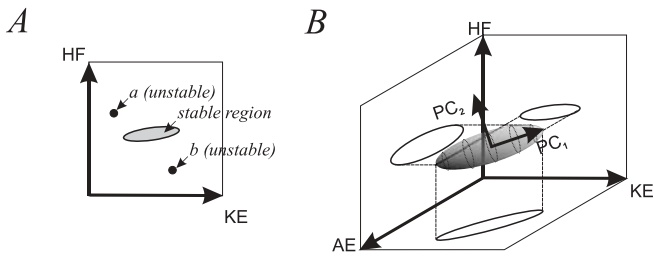


Fig. 4a,b. Schematic explaining how principal component analysis (PCA) was used to evaluate locomotor stability over a wide range of parameter variations. **a** Hip and knee forces must lie within the ellipse for stable locomotion to occur. The larger the ellipse, the greater the range of parameters for which locomotion is stable. **b** When another parameter is added (in this case ankle extensor force), the stable region lies within a three-dimensional volume. The larger the volume, the greater the range of stability. Orthogonal axes can be identified mathematically that point in the directions of largest variations of the coordinates within the volume. Unit vectors along these axes are called principal components. PCA may be extended to any number of parameters, in our case six, corresponding to the six actuators in our model. PCA allowed us to compare the sizes of six-dimensional stability “volumes” for different types of control. Since the first and second principal components described on average 90% of all variability in the stable parameters, the two-dimensional plots of Fig. 4 provide nearly all of the information required to compare stability between control schemes over a large range of parameter variation

bearing. But in the second case, when the levels of the CPG muscle activation profiles were 30% higher, i.e., enough to support body weight, the sudden addition of the stretch reflexes caused only a modest increase in the rate of locomotion and often decreased stability of the model. From this we would conclude that stretch reflexes had a rather minor role, which supports hypothesis 1. Thus it seems that the importance of stretch reflexes depends on whether central drive is well matched to the anticipated loads or not.

To gain a better understanding of the range of central drive over which stretch reflexes would have a major vs. a minor role, and also to test the validity of our conclusions in the face of parametric variations in both muscle stiffness parameters and limb geometry, we examined changes in the parametric space defined by forces of musculotendon actuators in the two models. Because six actuators were used in each limb in the models, parametric space was six-dimensional and therefore hard to represent with conventional Cartesian plots. However, it is possible to simplify this representation by grouping variations in the six force parameters into “principal components”. This is illustrated schematically in Fig. 4. First, let us consider the effect on locomotion of changes in the peak forces of just two of the six actuators (hip flexors and knee extensors, Fig. 4a). Clearly if hip flexion is too forceful (point “a”), the leg will overshoot and locomotion will be destabilized. If there is too little hip flexion coupled with forceful knee extension (point “b”), locomotion will also be unstable. Only certain combinations of the two parameters will be compatible with stable gait. Suppose that these are contained within the shaded ellipse. Now let us add ankle extensors (Fig. 4b).

Again there will be a restricted range of peak ankle extensor force compatible with stable locomotion. When combined with the stable combinations of the other two variables, the stable region may now be represented by the shaded volume in the three-dimensional plot. By calculating eigenvectors and eigenvalues for the data autocorrelation matrix it is possible to define orthogonal axes along which the parameter combinations making up the volume are the most spread out. These axes thus “account for” the largest amount of variation in the data and are called the “principal components” (PC). Principal component analysis (PCA) can be extended to all six parameters.

3.2 Locomotor performance in the absence of sensory feedback

Locomotor performance was explored in six-dimensional parameter space of musculotendon actuator forces using a gradient-descent method with random initial position. Figure 5 shows sets of parameters associated with stable locomotor performance of the model driven by the CPG alone (gray circles) and the CPG with the addition of stretch reflexes (black upward triangles). Figure 5a–c show the projections of six-dimensional data on the planes formed by the three extensor actuators, whereas Fig. 5 d–f show the projections of the same data on the planes formed by the remaining predominantly flexor actuators. The origin of the plots corresponds to zero force in all actuators. It is clear from Fig. 5 that stable locomotion can emerge over a fairly large range of force parameter variation, even in the absence of sensory feedback. Similar results were previously obtained using inverse dynamics or neural networks to optimize activation patterns (Taga et al. 1991; Taga 1998; Neptune et al. 2001; Ogihara and Yamazaki 2001).

3.3 Effect of stretch reflexes on locomotor performance

Figure 5 shows a stability plot for the cat model where stretch reflexes contributed about 30% of the overall activity (see Eq. 6). In Fig. 5a–c the volume of stability associated with the model with sensory feedback (upward triangles) extends much closer to the origin than in the “deafferented” model (gray circles). This was also the case for the “horse” model (not illustrated). This indicates that stretch reflexes are capable of increasing extensor muscle stiffness when central drive is low and thus provide the necessary load compensation. Despite the long latency of the reflexes and their dynamic nature, their 30% mean contribution essentially takes the place of the missing 30% of central activation. This explains the destabilizing effect of a sudden removal of the stretch reflex contribution in Fig. 3a–c where the central activation levels were low. A contribution of stretch reflexes to flexor activity does not seem essential judging by the

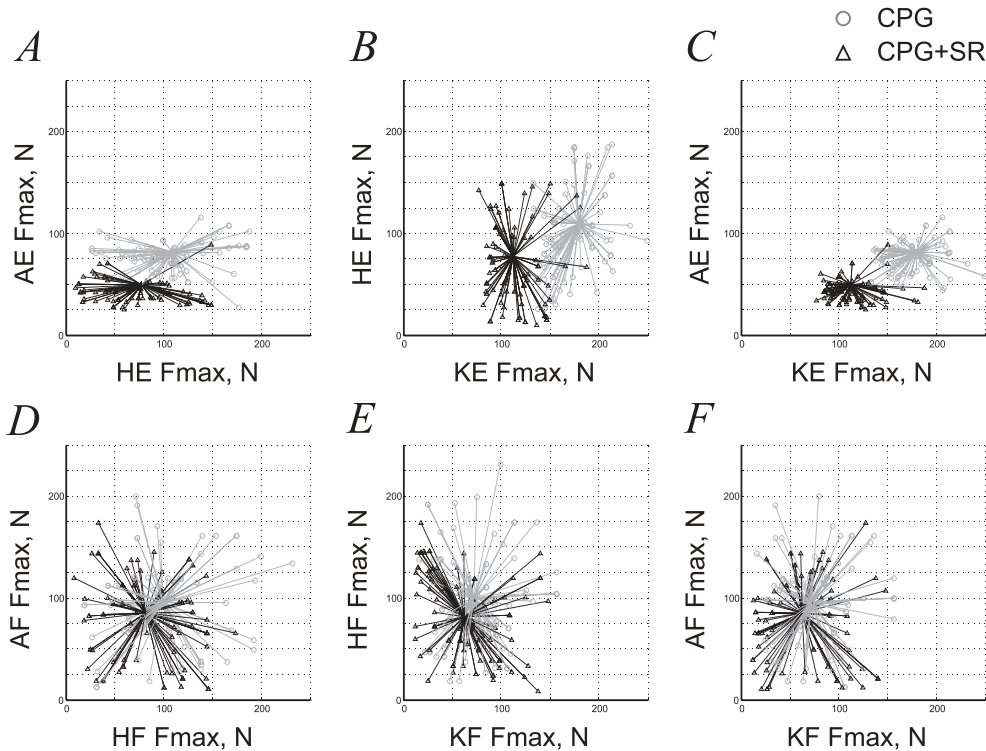


Fig. 5a-f. Locomotor performance plots of stable trials of models without sensory feedback (*gray circles*) and with stretch reflex (*black upward triangles*) are plotted as projections on the planes of three extensor (**a-c**) and three mainly flexor (**d-f**) musculotendon actuators. Horizontal and vertical axes represent maximum isometric force at muscle rest length (F_{\max} in Eq. 1) of the corresponding musculotendon actuator. The large region of stability of the model without sensory feedback indicates that the intrinsic stiffness of the muscles sufficed to compensate for kinetic and kinematic variations over a fairly large parametric range. Since the origins of the coordinate systems

corresponds to a simulation with zero muscle stiffnesses, the minimum vector to the stable region corresponds to the minimum muscle stiffnesses required for locomotion. The region of stability of the model with stretch reflexes extends closer to the origin compared to the one without sensory contribution (**a-c**), i.e., when stretch reflexes contribute 30% of overall extensor muscle excitation, less central activation is required to maintain stable locomotion. However, largely overlapping stability regions of flexors (**d-f**) indicate that stretch reflexes are not essential for flexor activity without additional kinematic constraint

largely overlapping stable parameter spaces of both models in Fig. 3d-f.

In the example in Fig. 3d-f the addition of stretch reflexes when central activation was adequate to provide stable locomotion has a destabilizing effect. However, if we consider all the stable simulations obtained, the calculated moment of inertia (see Eq. 3) of the model with stretch reflexes was 1.9 times larger than that without ($I_{\text{CPG+SR}} = 5.6 \times 10^4 \text{N}^2$, $I_{\text{CPG}} = 3.0 \times 10^4 \text{N}^2$). This indicates that stretch reflexes can contribute significantly to load compensation and, taken over the entire parameter space, may even stabilize locomotion in many cases.

3.4 Contribution of state-dependent control to locomotor stability

In the stretch reflex modeling above, the cycle frequency of the CPG pattern was invariant. This placed constraints on the range of gait velocities consistent with stability. Adaptive control of cadence based on sensory information about actual biomechanical states might therefore be expected to increase stability. To test this hypothesis we implemented simple sensory rules to

trigger the transitions between flexion and extension phases of the centrally generated pattern of muscle activation profiles. Figure 6 shows the extent to which IF-THEN sensory rules controlling step transitions (see Methods) stabilized the simulations in the cat model with CPG and stretch reflexes active. Figure 6a and c shows locomotor performance plots in the plane of two first principal components of the stable sets of parameters associated with the model with stretch reflexes in Fig. 5. The stability region is further defined by a contour plot, which shows the amount of time that elapsed in simulations before the model collapsed. In Fig. 6c the stable region was enlarged by about 30% compared with that in Fig. 6a. Note that the main increase of stability coincides with the direction of the increasing force of hip extensor actuator, which regularly leads to an increase of forward velocity.

An analysis of the velocities of gait corresponding to the stable and unstable regions showed that stability was associated with a fairly narrow band of gait velocities. Figure 6b shows that gait velocity was closely related to stride length for all of the stable simulations. This is not surprising given that the frequency of the CPG rhythm in all of these simulations was constant. If stride length increases at a constant step cycle frequency, velocity

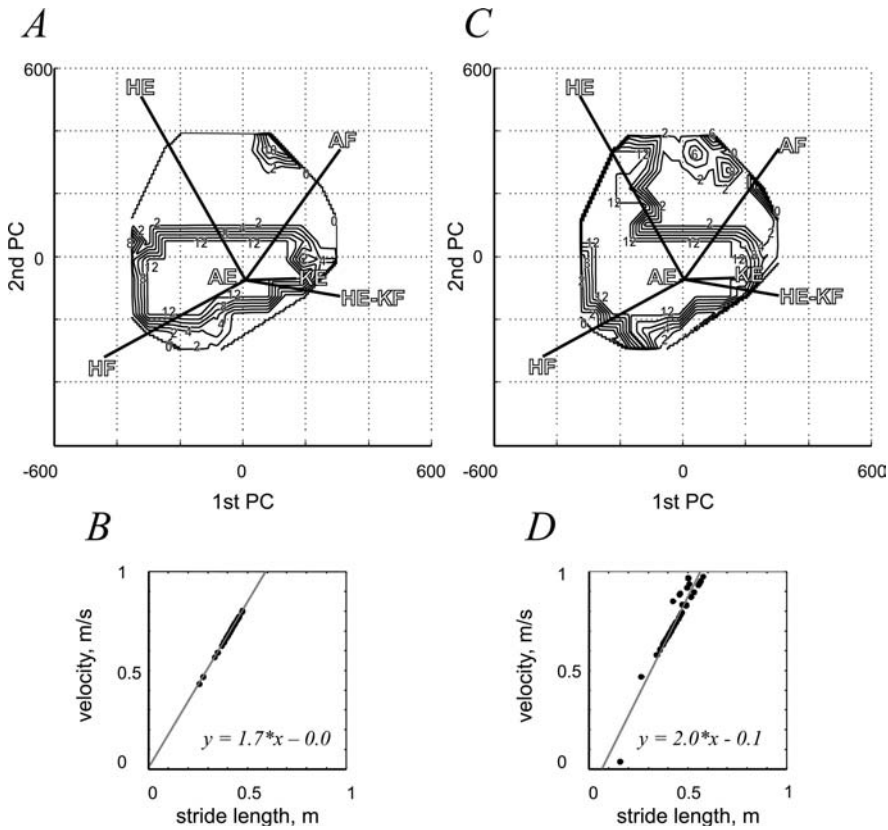


Fig. 6a–d. PCA locomotor performance plots and plots of mean gait velocity vs. stride length of stable trials of models with CPG and stretch reflexes (**a, b**) and with CPG, stretch reflexes, and IF-THEN rules (**c, d**). The *contour lines* connect points of equal stability measured in seconds of stable gait. The region of stability in the model with IF-THEN rules is about 30% bigger, particularly in the direction of increase of hip extensor force. Labeled *straight lines* in **a** and **c** represent projections of the six-dimensional force axes (axis vector magnitude is 250 N) on the plane of the first two principal components. **b** Velocity was proportional to stride length in stable locomotion because the cycle frequency of the centrally generated pattern was constant in these trials. Stability was confined to a fairly narrow band of velocities. **d** Addition of IF-THEN rules to the control system shown in **a** and **b** increased the range of stable gait velocities

must increase, or stability is lost. Consider the case where hip flexor forces are large but body velocity is low. The leg swings far forward and at ground contact the ground reaction force points back, decelerating the body. If velocity drops to zero before the center of mass moves over the point of support, further forward motion becomes impossible and the model collapses backward. As we shall see, stretch reflexes do not fundamentally change this effect because in essence they just augment the inherent load compensation mechanism provided by muscle stiffness and viscosity (Partridge 1966). On the other hand, conditional control can increase the range of stable velocities by adapting the cadence (cycle frequency) to the actual kinematics of the limb. The range of velocities of the stable simulations shown in the plot of Fig. 6d was greatly increased, showing that adaptive control of cadence granted by IF-THEN rules was associated with the increased range of stability.

3.5 Closed-loop gain of stretch reflex during locomotion

Figure 7 shows the dependence of the response of the system on the amplitude of the feedforward commands in our model. It is clear that increases in the central command are associated with decreases of the contribution of the stretch reflex loops. This cannot be attributed to changes in the generalized forces because these changes are quite small (Fig. 7b). Rather, Fig. 7c demonstrates that higher activation levels drive the extensor muscles to operate at substantially shorter

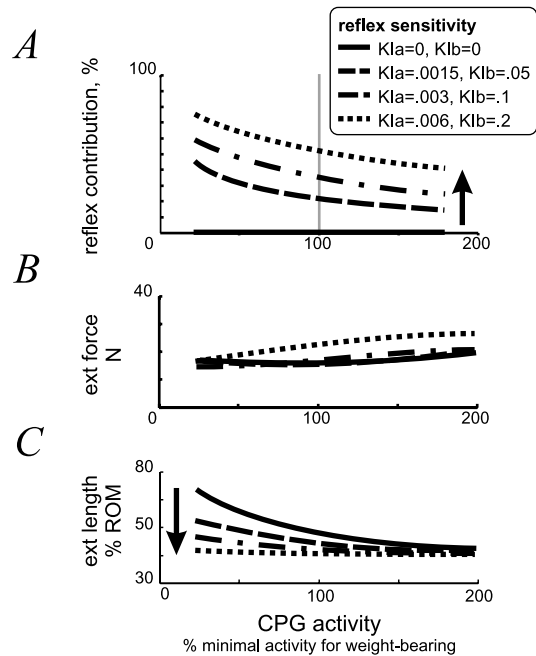


Fig. 7a–c. Strength of stretch reflexes is modulated by muscle length. **a** Relationship between CPG amplitudes and relative reflex contribution for four sets of reflex gains. Both parameters are normalized to the minimal activity level required to produce stable locomotion in the “deafferented” model. Notice the decrease in the reflex component with the increasing CPG amplitude. **b** Mean extensor force did not change significantly with CPG amplitude except at the highest reflex gains. **c** Mean muscle length decreases with increasing CPG amplitudes. This effectively decreases stretch reflex loop gains (see text)

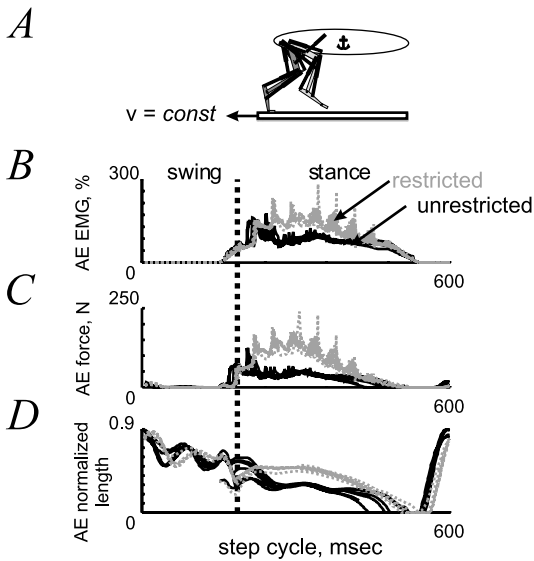


Fig. 8a-d. Effect of abolishing vertical hip motion on EMG, force, and length. Restriction of vertical hip movement during walking increases activation levels of extensor muscles (a), increases extensor muscle forces (b), and increases extensor muscle lengths (c) during stance. This restriction, which is used in many decerebrated locomotor experiments, may lead to overestimations of the level of reflex contribution during locomotion

lengths, which attenuates the closed-loop gains of the length and force feedback loops, thus reducing the relative contribution of reflexes. As was shown previously (Prochazka et al. 1997), when muscles are short, they respond with a smaller force output to a given motoneuronal input, and this in turn attenuates the gains of the feedback loops of which they are a part. Thus the relative force contribution of proprioceptive reflexes is attenuated.

This mechanism may play a particularly important role when changes in muscle length are restricted, e.g., by experimental design. For example, numerous studies have been conducted to investigate control of treadmill locomotion in decerebrate cats where the hips are firmly clamped or pinned to a strong metal frame over the treadmill. This constraint abolishes vertical motion of the hips, which is normally present in locomotion, and confines extensor muscle operation to longer lengths during the stance phase of gait. One would predict that extensor muscles would therefore operate further up the force-length curves, thus increasing the loop gain of the stretch reflex pathways. Estimation of the reflex contribution under these conditions would result in overestimates compared to normal unrestrained locomotion.

Figure 8 shows simulation results of “unrestrained” and treadmill locomotion with “fixed hips”. The moderate increases of the operating length of extensors due to hip fixation resulted in a dramatic increase of the activation level and generated force. This indicates that experiments of this type, where hip motion is prevented, may distort the neural control of locomotion significantly.

4 Discussion

The purpose of this study was to gain insight into the contribution of sensory input to the control of locomotion. Though many experiments have been done on locomotor stretch reflexes, most of these have been limited to EMG measurements (Capaday and Stein 1986; Gorassini et al. 1994; Gritsenko et al. 2001) rather than kinetic or kinematic changes of the whole limb (Sinkjaer et al. 1988; Pearson et al. 1999). The amount of EMG activation attributable to reflexes elicited by muscle length and force changes during the step cycle is generally less than 35% of the total (Stein et al. 2000). Furthermore, the reflex components have rather long latencies (Gorassini et al. 1994; Gritsenko et al. 2001). Finally, bursts of sensory input from stretch receptors elicited by electrical stimulation (Whelan and Pearson 1997) or by muscle vibration (Ivanenko et al. 2000) have surprisingly little impact on the kinematics of locomotion. All of these findings led us to propose that the biomechanical consequences of stretch reflexes elicited in the course of unperturbed gait did not contribute significantly to load compensation during weight-bearing locomotion.

The biomechanical modeling described in this paper was done to test the following hypotheses: (1) Stretch reflexes are too weak and too delayed to contribute significantly to weight bearing and (2) the important contributions of sensory input involve state-dependent processing. The results did not support hypothesis 1, but they did support hypothesis 2.

Hypothesis 1 was not supported because stretch reflexes could rescue stable locomotion in cases where the amplitudes of the CPG activation profiles were insufficient to support locomotion. On the other hand, adding stretch reflex components to CPG activation profiles that were adequate to support stable locomotion tended to increase body height, propulsion, and speed. When these increases were inappropriately scaled between muscles, locomotion became unstable. Thus, although hypothesis 1 was not supported, stretch reflexes nonetheless only seem to contribute significantly when central activation levels are low.

Regarding hypothesis 2, the incorporation of IF-THEN rules increased stability and in particular greatly increased the range of cadences and velocities of stable locomotion, even though the time course of the actual muscle activation profiles did not change. How could gait velocity vary without the activation profiles changing? The answer is that the triggering of, say, the stance-swing transition terminates the reading out of the extensor muscle activation profiles, even if they are only half completed, and initiates the reading out of the flexor activation profiles. Similarly, flexor profiles are terminated earlier in the next half cycle. The interesting point here is that cadence and gait velocity can be varied over a wide range without changing the time course or amplitude of the activation profiles but merely by skipping parts of these profiles and resetting to a new part of the step cycle. To our knowledge, this possibility has not been recognized until now.

It is important to mention some of the restrictions and limitations of the modeling performed. A general criticism of modeling of this type is that when the model contains many parameters, there is scope for choosing sets of parameters that fit one's favored hypothesis. To safeguard against this, we deliberately avoided making the models represent faithfully the anatomy of a particular "animal". Furthermore, our approach to the exploration of parameter space using an observer-independent stability search algorithm and PCA allowed for an unbiased representation of stability over several hundred sets of parameters in two models that represented extremes of limb geometry. The conclusions we drew regarding the two hypotheses were therefore broad based and not model specific, i.e. they remained valid in the face of a large range of parameter variations.

This is not to say that we were able to explore all types of parameter variations that could influence the conclusions. For example, the muscle models did not take into account the hysteretic property of short-range stiffness (Rack and Westbury 1973). We intend to add this characteristic in future modeling work. We did not explore all possible muscle spindle and tendon organ models (Prochazka and Gorassini 1998), nor did we vary the latency of the stretch reflex or try to represent separate short-, medium-, and long-latency reflex components or heterogeneous reflex connections. There is in any case considerable uncertainty in the literature regarding the relative sizes of such components. In previous modeling, we found that varying reflex latencies within reasonable limits did not substantially change muscle kinetic responses (Prochazka et al. 1997). By varying the level of the stretch reflex contribution during locomotion we found that closed-loop gain of the sensory evoked responses depended strongly on muscle length and velocity. This dependence was previously implicated in stabilizing positive force feedback (Prochazka et al. 1997). Since estimation of the gain of the closed-loop reflex system during various tasks poses a considerable experimental challenge, the relative level of contribution of the stretch reflex to muscle excitation remains a contentious issue. Models such as ours may greatly clarify and assist in evaluation of components of feedforward and feedback systems of motor control.

To conclude, our model provided insight into the interplay between neural commands and biomechanical properties of the musculoskeletal actuators of the locomotor system. The main conclusion was that homonymous stretch reflexes are capable of adjusting muscle forces at several joints to achieve weight bearing during gait, and this is particularly significant when central activation is low. Simple finite state rules provide dramatic improvements in flexibility and stability of level overground locomotion in our model. Cadence is constantly adjusted to kinematic state. This also raises the possibility that gait velocity could be controlled by changing the firing thresholds of sensory rules in a state-dependent controller. Our method of testing stability by exploring parametric space using PCA is novel and provides a systematic measure of the generality of the conclusions.

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