Positive force feedback in bouncing gaits?

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During bouncing gaits (running, hopping, trotting), passive compliant structures (e.g. tendons, ligaments) store and release part of the stride energy. Here, active muscles must provide the required force to withstand the developing tendon strain and to compensate for the inevitable energy losses. This requires an appropriate control of muscle activation. In this study, for hopping, the potential involvement of afferent information from muscle receptors (muscle spindles, Golgi tendon organs) is investigated using a two-segment leg model with one extensor muscle. It is found that: (i) positive feedbacks of muscle-fibre length and muscle force can result in periodic bouncing; (ii) positive force feedback (F+) stabilizes bouncing patterns within a large range of stride energies (maximum hopping height of 16.3 cm, almost twofold higher than the length feedback); and (iii) when employing this reflex scheme, for moderate hopping heights (up to 8.8 cm), an overall elastic leg behaviour is predicted (hopping frequency of 1.4–3 Hz, leg stiffness of 9–27 kN m^{-1}). Furthermore, F+ could stabilize running. It is suggested that, during the stance phase of bouncing tasks, the reflex-generated motor control based on feedbacks might be an efficient and reliable alternative to central motor commands.

Keywords: biomechanics; leg stiffness; motor control; muscle reflex; robust running; self-stability

1. INTRODUCTION

In bouncing gaits, animals and humans use a spring-like leg behaviour during stance (Cavagna *et al.* 1964, 1977). In this phase, passive compliant structures such as muscle tissue, tendons and ligaments store and release elastic energy, reducing the metabolic costs of locomotion (Cavagna *et al.* 1977; Alexander 1988). For instance, in some animals tendons preserve up to 70% of the stride energy (Alexander & Vernon 1975; Biewener 1998). The exploitation of passive elasticities is, however, compromised by the viscous properties of the muscle–skeleton system. For example, in humans only 40–50% of the stride energy can be stored elastically (Cavagna *et al.* 1964). To maintain a cyclic motion (e.g. running at constant speed), the energy losses resulting from dissipation must be 'refilled' during the rebound, requiring positive muscle work. But how do biological systems organize the proper muscle activation? Besides the necessity of muscle-force regulation to withstand the tendon strain, the energetic refill requires an adequate control mechanism. Such control schemes should be scalable, for instance, to achieve a higher running speed (increased stride energy). Although this could be realized using central motor commands (e.g. higher centres), a control based on afferent information of the muscle state may relax the supervisory effort.

On the muscular level, for instance, it could be demonstrated that the stretch-reflex amplifying muscle force during lengthening can control muscle stiffness (Nichols & Houk 1976; Hoffer & Andreassen 1981). However, it is not clear whether this particular reflex modulation could generate the observed bouncing leg behaviour. Here,

alternative reflex schemes might even more appropriately shape the muscle activation. In a hopping simulation, Gerritsen & Nagano (1999) investigated vestibulospinal and long-latency stretch reflexes. They found that the afferent modulation of the extensor activity yielded slow periodic knee-bending movements. Although flight phases were not considered and the movement patterns were unstable, they demonstrated the potential contribution of reflex mechanisms to the generation of cyclic locomotion.

In this study, we investigate whether continuous afferent inputs based on single-loop muscle reflexes could generate an appropriate extensor-muscle activity during bouncing tasks. Therefore, we employ a two-segment leg model with one extensor muscle and focus on human hopping in place. The sensory information used is motivated by signals from muscle spindles and Golgi tendon organs (GTOs). The bouncing capacity is assessed using three movement criteria: hopping performance (maximum hopping height, i.e. stride energy) and the stability and elasticity of the hopping pattern.

2. MODEL

(a) *Mechanical system*

Running is considered a planar (figure 1*a*) and hopping a vertical (not shown in figure 1*a*) movement. Both are characterized by alternating stance and flight phases. The body is idealized to a point mass m at the centre of mass (COM). The COM trajectory ($\ddot{r}$) is determined by the gravitational force $F_G = mg$ and, during stance, additionally by the leg force F_{Leg}

$$m\ddot{r} = F_G + [F_{Leg}]_{stance}. \tag{2.1}$$

The leg is modelled as a two-segment system with one Hill-type extensor muscle acting on the intersegmental joint (stance phase; figure 1*a*). The segments (equal

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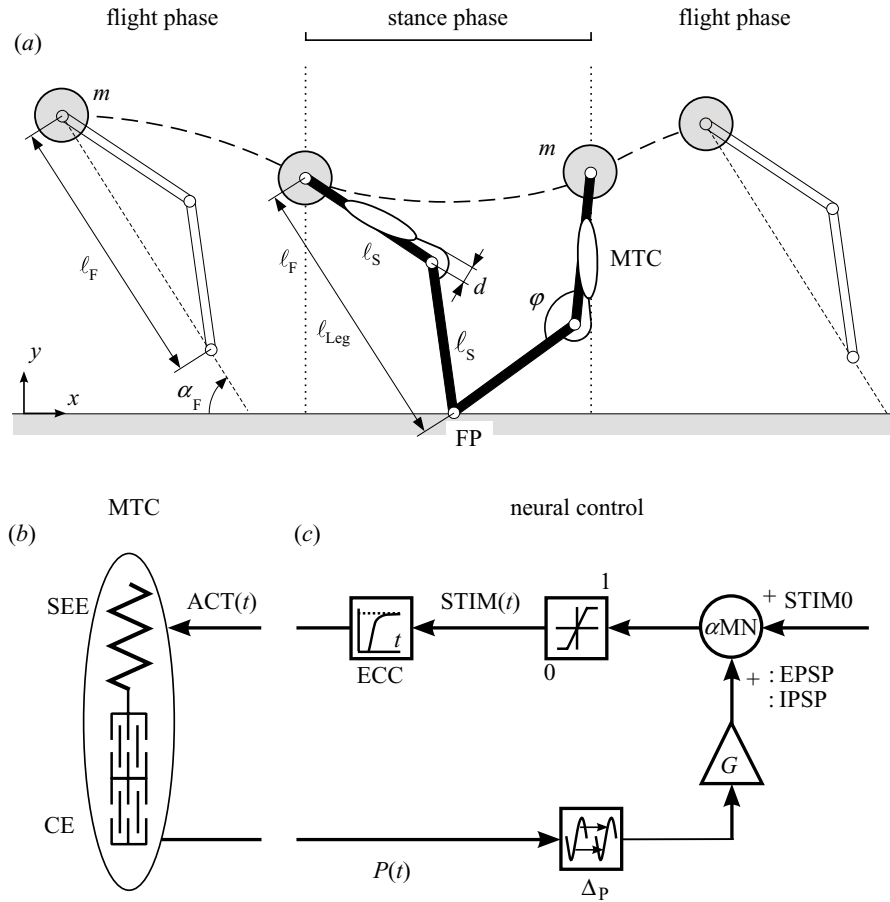*Author for correspondence (hartmut@ai.mit.edu).

Figure 1. Hopping and running model. (*a*) The body is reduced to a point mass *m*. In stance, the leg is modelled by a two-segment system with one Hill-type extensor muscle. In flight, a fixed leg length ℓ_F and angle of attack α_F are assumed. (*b*) The MTC consists of a CE and an SEE. (*c*) The single sensory signal $P(t) \geqslant 0$ is time delayed (Δ_P) and gained ($G > 0$), before being added to or subtracted from a constant stimulation bias STIM0 at the α-motor neuron (αMN) corresponding to a positive excitatory postsynaptic potential (EPSP) or a negative-feedback inhibitory postsynaptic potential (IPSP). The resulting muscle stimulation STIM(*t*) is restricted to be between 0 and 1. The excitation–contraction coupling (ECC) delays the muscle activation ACT(*t*) about 30–40 ms. ℓ_{Leg}: leg length in stance; φ: joint angle; ℓ_S: segment length; *d*: moment arm of the extensor muscle.

length ℓ_S) and the muscle are massless. The muscle length ℓ_{MTC} (where MTC is muscle tendon complex) is related to the joint angle φ:

$$\ell_{MTC} = \ell_{ref} - d(\varphi - \varphi_{ref}), \tag{2.2}$$

where φ_{ref} is the joint angle at which the muscle reaches the reference length ℓ_{ref}, and *d* is the constant moment arm of the muscle. The leg force $\boldsymbol{F}_{Leg}$ acting parallel to the leg axis (foot point (FP) to COM) is linked to the muscle force F_{MTC} by

$$|\boldsymbol{F}_{Leg}| = \frac{d}{\sqrt{\ell_S^2 - \left(\dfrac{\ell_{Leg}}{2}\right)^2}} F_{MTC}, \tag{2.3}$$

where ℓ_{Leg} is the instantaneous leg length, defined as the actual distance between FP and COM.

The touch-down occurs if the COM reaches a certain landing height corresponding to an assumed fixed leg length ℓ_F in flight. For running, additionally, a constant angle of attack α_F defines a leg orientation during flight (flight phase; figure 1*a*). The take-off occurs when the leg force vanishes, at the latest when the initial landing length of the leg is reached during leg extension.

(b) Muscle–tendon complex

The MTC consists of a contractile element (CE) and a series elastic element (SEE) (figure 1*b*). The generated CE force depends on the muscle activation state $0 \leqslant$ ACT $\leqslant 1$, the maximum isometric force F_{max}, and the force–length ($f_\ell(\ell_{CE})$) and force–velocity ($f_v(v_{CE})$) relationships (based on Aubert (1956)):

$$F_{CE}(ACT, \ell_{CE}, v_{CE}) = ACT F_{max} f_l(\ell_{CE}) f_v(v_{CE}), \tag{2.4}$$

with

$$f_l(\ell_{CE}) = \exp\left[c\left|\frac{\ell_{CE} - \ell_{opt}}{\ell_{opt} w}\right|^3\right] \tag{2.5}$$

and

$$f_v(v_{CE}) = \begin{cases} \dfrac{v_{max} - v_{CE}}{v_{max} + K v_{CE}}, & \text{if } v_{CE} < 0 \\[3mm] N + (N-1)\dfrac{v_{max} + v_{CE}}{7.56 K v_{CE} - v_{max}}, & \text{if } v_{CE} \geqslant 0 \end{cases} \tag{2.6}$$

In the force–length relationship, ℓ_{opt} is the optimum CE

length (for maximum force production), w describes the width of the bell-shaped $f_l(\ell_{CE})$ curve and c is $\ln(0.05)$, fulfilling $f_l(\ell_{opt}(1 \pm w)) = 0.05$. The force–velocity relationship follows the Hill equation (Hill 1938) for muscle shortening ($v_{CE} < 0$), where $v_{max} < 0$ is the maximum contraction velocity and K is a curvature constant. Muscle lengthening ($v_{CE} \geqslant 0$) is characterized by an equation based on Aubert (1956), where N is the dimensionless amount of force F_{MTC}/F_{max} reached at a lengthening velocity $v_{CE} = -v_{max}$.

The SEE is characterized by a nonlinear elastic force–length relationship (Van Ingen Schenau 1984)

$$f_{SEE}(\varepsilon) = \begin{cases} (\varepsilon/\varepsilon_{ref})^2, & \text{if } \varepsilon > 0 \\ 0, & \text{if } \varepsilon \leqslant 0 \end{cases}, \tag{2.7}$$

using the tendon strain $\varepsilon = (\ell_{SEE} - \ell_{rest})/\ell_{rest}$, where ℓ_{rest} is the tendon's resting length and ε_{ref} is the reference strain with $f_{SEE}(\varepsilon_{ref}) = 1$.

Because CE and SEE are arranged in series, they have equal forces matching the MTC force F_{MTC}. Using this equilibrium, $F_{MTC}(t)$ is uniquely determined for a given MTC length $\ell_{MTC}(t)$ and activation state $ACT(t)$ (e.g. Van Soest & Bobbert 1993).

(c) Neural reflex pathway

The activation state $ACT(t)$ relates to a neural input $STIM(t)$ with a first-order differential equation describing the excitation–contraction coupling

$$\tau \, dACT(t)/dt = STIM(t) - ACT(t), \tag{2.8}$$

where τ is a time constant. The neural input $STIM(t)$ consists of a constant stimulation bias STIM0 and a feedback component $\pm GP(t - \Delta_P)$:

$$STIM(t) = \begin{cases} STIM0 & t < \Delta_P \\ STIM0 \pm GP(t - \Delta_P) & t \geqslant \Delta_P \end{cases}, \, 0 \leqslant STIM(t) \leqslant 1, \tag{2.9}$$

where P is the sensory information, $G > 0$ is the gain factor and Δ_P is the signal-propagation time delay (figure 1c). Three possible sensory signals P are investigated separately: CE length ℓ_{CE} and velocity v_{CE}, and MTC force F_{MTC}. Signal combinations are not considered.

The signals are physiologically motivated by afferent information from muscle spindles and GTOs. To account for a γ-adjustment of muscle-spindle activity, the length and velocity signals are biased with a constant offset value ($P = \ell_{CE} - \ell_{off}$ and $P = v_{CE} - v_{off}$, respectively). The '$\pm$' sign indicates a positive or negative feedback with an excitatory or inhibitory postsynaptic potential at the α-motor neuron. Although this definition may deviate from other approaches in the literature, it provides a uniform assignment among the investigated feedbacks. Corresponding to the mechanism of signal transduction in neurons, the sensory signal is restricted to positive values $P(t) \geqslant 0$: varying spike rates can alter the magnitude of the postsynaptic potentials. However, the quality (excitatory or inhibitory) remains constant.

(d) Model parameter identification

The model parameter values used in the simulation are summarized in table 1. They reflect data from the literature (Winters 1990; Van Soest 1992; Van Leeuwen 1992;

Table 1. Model parameters.

parameter	value
body weight m	80 kg
gravitational constant g	9.81 m s^{-2}
assumed flight leg length ℓ_F	0.99 m
segment length ℓ_S	0.5 m
moment arm d	0.04 m
MTC reference length ℓ_{ref}	0.5 m
corresponding reference joint angle φ_{ref}	110°
maximum isometric force F_{max}	22 kN
optimum length ℓ_{opt}	0.1 m
width w	0.4 ℓ_{opt}
maximum shortening velocity v_{max}	$-12 \, \ell_{opt}$ s^{-1}
eccentric force enhancement N	1.5
curvature constant K	5
rest length ℓ_{rest}	0.4 m
reference strain ε_{ref}	0.04 ℓ_{rest}
excitation–contraction coupling constant τ	0.01 s
feedback time delay Δ_P	0.015 s

Herzog 1999), yet are partially compromised by the simplified leg representation: (i) the maximum isometric force $F_{max} = 22$ kN assumes that both knee and ankle extensor muscles provide proper thrusting; (ii) the constant moment arm d of the extensor muscle would lead to exaggerated leg forces at erect leg positions (equation (2.3)) for muscle activations of $ACT > 0$ (equation (2.4)) (this is compensated for by the reduced width $w = 0.4$ of the force–length relationship (values from the literature include $w = 0.56$; Winters 1990); and (iii) the signal propagation delay $\Delta_P = 15$ ms can be approximated by the time shift between M- and H-waves in H-reflex experiments. For the triceps surae this difference is *ca.* 20–25 ms (e.g. Stein & Capaday 1988; Knikou & Rymer 2002). For the quadriceps femoris, a smaller delay occurs owing to shorter afferent pathways (estimated as 5–10 ms from the signal transduction difference to the spinal cord between the deep peroneal and femoral nerves; Meunier *et al.* 1990). Taking these deviations and uncertainties into account, the robustness of the model results to changes in MTC parameters (w, N, v_{max} and ε_{ref}) and feedback time delay (Δ_P) is checked.

(e) Simulation environment

The model is implemented in MATLAB 6 using the SIMULINK 4 toolbox (Mathworks Inc., Natick, MA, USA). The forward dynamic simulation is performed with the embedded ode45 integrator with a maximum step size of 10^{-3} (absolute and relative error tolerances of 10^{-8}). The results of the numerical integration are checked using a tenfold higher accuracy.

(f) Movement criteria

Three movement criteria are addressed to evaluate the model's bouncing behaviour.

(i) The hopping *performance*, defined as maximum hopping height h_{max}, is investigated with genetic algorithm optimization exploring the feedback parameter space (population of 500 individuals, 150 generations, recombination probability of 'fitter' individ-

uals of 75%, mutation rate of 0.5%, single-point crossover rate of 75%; results checked by three repetitions; Goldberg 1989).

(ii) For given feedback set-ups, the *stability* of the hopping pattern is investigated with the apex return map $y_{i+1}(y_i)$. At apex, the system state is uniquely determined by the apex height y_{apex} as $\dot{y}_{apex} = 0$, and the neuro–muscle–skeleton dynamics are re-initiated at each touch-down. The system's periodic behaviour can therefore be addressed by analysing the relationship $y_{i+1}(y_i)$ of two consecutive apices i and $i + 1$ (index 'apex' omitted here). Fixed points $y_{i+1}(y_i) = y_i$ represent periodic solutions. Stable periodic solutions require a slope of $-1 < dy_{i+1}/dy_i < 1$ in the neighbourhood of fixed points.

(iii) For stable hopping patterns, the *elasticity* of the leg force–length relationship is evaluated by introducing the elasticity coefficient C_{EL}

$$C_{EL} = \left(1 - \frac{A}{A_{max}}\right)^2, \qquad (2.10)$$

which describes the ratio between the area A enclosed by the force–length trace of the leg and the area $A_{max} = F_{max}\Delta\ell_{max}$ given by the maximum leg force $F_{max} = \max(F_{Leg})$ and leg displacement $\Delta\ell_{max} = \max(\ell_F - y)$ in stance. In contrast to the calculation of the total work done during contact (work loop equals zero in steady-state movements), for the calculation of A the absolute values of the difference of positive and negative work are added. The coefficient C_{EL} provides a measure of how closely the leg approximates perfectly elastic behaviour ($C_{EL} = 1$), independent of nonlinearities in the actual spring law. The corresponding spring stiffness is approximated by $k = F_{max}/\Delta\ell_{max}$.

To elucidate the elasticity coefficient required for spring-like human hopping, an experimental study was conducted with 12 healthy subjects (mean ± s.d. of body mass = 72 ± 10 kg; age = 32 ± 6 years). C_{EL} was measured for each contact during hopping on a force plate over a total time period of 60 s at a frequency of 2 Hz. The leg displacement was calculated by twice integrating the vertical acceleration (H. Geyer, A. Seyfarth and R. Blickhan, unpublished data). The preliminary results yielded $C_{EL} = 0.92 \pm 0.03$. The mean value is defined as a reference value.

3. RESULTS

(a) *Hopping performance: optimal stimulation versus reflexes*

First, the maximum hopping performance of the model is assessed by optimizing the muscle stimulation STIM(t). Hereto, the population of the genetic algorithm consists of individuals with 36 values determining the interpolated stimulation pattern STIM(t) at every 20 ms following touch-down (total duration 700 ms). These patterns are applied to single-step simulations (figure 2a). Starting at an initial apex height y_0, the simulation stops at the subsequent apex y_1. To ensure an optimization towards periodic hopping patterns, the individuals are judged by: (i)
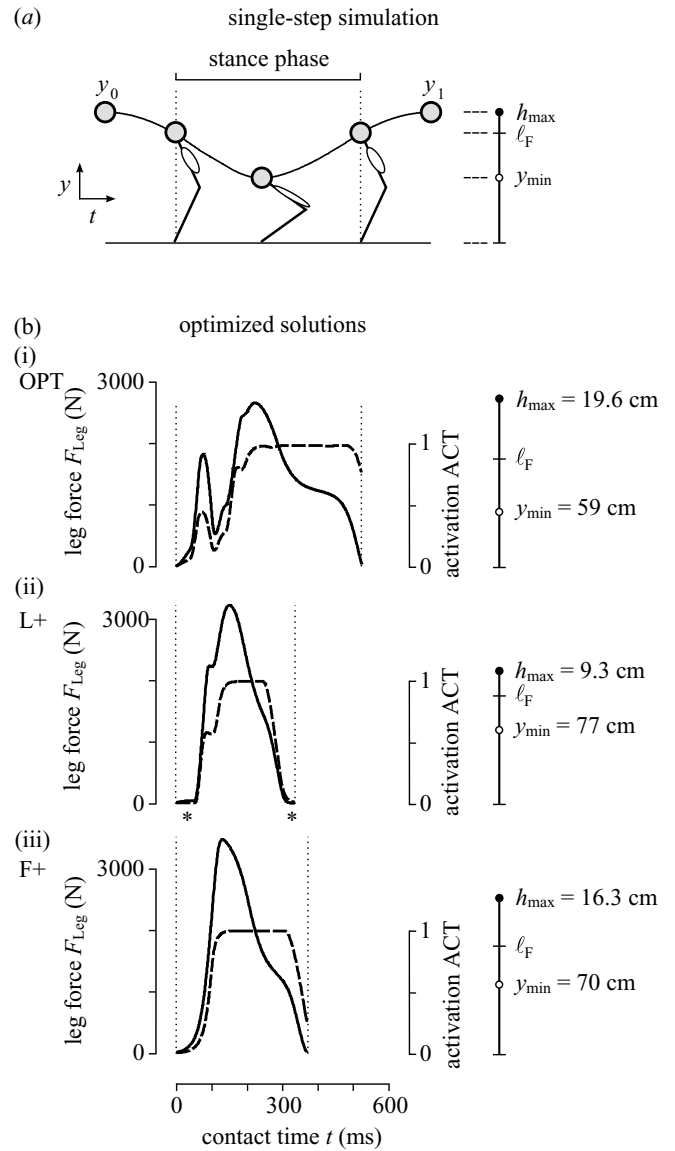

Figure 2. Maximum hopping performance. (*a*) Single-step simulation applied to each individual of the genetic algorithm optimization (see § 3a). (*b*) Leg force F_{Leg} (solid line) and muscle activation ACT (dashed line) during stance for maximum hopping performance h_{max} employing (i) the OPT, (ii) L+ (STIM0 = 0.01, G = 125, ℓ_{off} = 0.08) and (iii) F+ (STIM0 = 0.01, G = 2.64/F_{max}). The asterisks indicate suppressed signal output resulting from the offset value (see § 4).

the hopping height achieved $h = y_1 - \ell_F$; and (ii) the increase in height $\Delta y = y_1 - y_0$ (optimization function $f = 0.9h + 0.1\Delta y$). Hereto, y_1 is reused as the initial apex height y_0 in the subsequent generation. The leg force $F_{Leg}(t)$ and muscle activation ACT(t) corresponding to the optimized stimulation pattern (OPT) STIM(t) are shown in figure 2b, yielding a maximum hopping performance of $h_{max} = 19.6$ cm.

Second, the influence of the different reflex pathways on the hopping performance is investigated using the same single-step simulation and optimization goals. Instead of stimulation patterns, the population now consists of different feedback parameter combinations (stimulation bias STIM0, gain G, and—for length and velocity feedback—offset value ℓ_{off} or v_{off}). The stimulation pattern STIM(t)
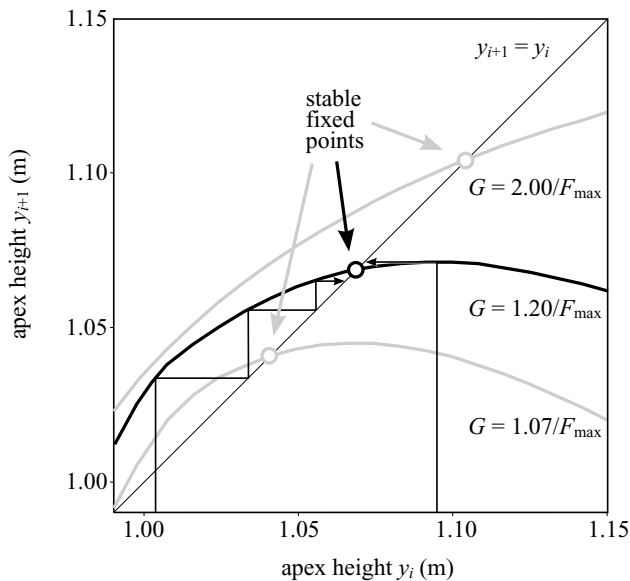
Figure 3. Stabilization of periodic hopping. The apex height return maps $y_{i+1}(y_i)$ for three different force feedback gains G are shown (stimulation bias STIM0 = 0.05). The intersections of the return maps with the diagonal $y_{i+1} = y_i$ represent periodic solutions (fixed points, denoted by small circles). The slope $-1 < \mathrm{d}y_{i+1}/\mathrm{d}y_i < 1$ within the neighbourhood of the fixed points guarantees stable hopping. Starting from disturbed initial apex heights y_i the system converges to the steady-state height after a few hops (indicated by the arrow tracings for the return map with feedback gain $G = 1.20/F_{\max}$).

is generated by the acting reflex pathway. All three afferent signals can stabilize the model in the stance phase, but only positive length feedback (L+) and positive force feedback (F+) generate an appropriate muscle-activation pattern ACT(t) resulting in aerial phases ('L+' and 'F+' in figure 2b). In terms of maximum hopping height, F+ ($h_{\max} = 16.3$ cm) clearly outperforms L+ ($h_{\max} = 9.3$ cm) reaching almost 85% of the model's maximum hopping performance.

(b) Stabilization of the movement pattern

The performance results suggest F+ as the most appropriate reflex scheme for extensor muscles in bouncing tasks. However, functional relevance of this feedback during cyclic locomotion further requires the stabilization of the movement pattern. Therefore, the return map $y_{i+1}(y_i)$ of the apex height is analysed. For a given stimulation bias (STIM0 = 0.05), the apex return maps for three feedback gains ($G = 1.07/F_{\max}$, $G = 1.2/F_{\max}$ and $G = 2/F_{\max}$ are depicted in figure 3. In all three cases stable solutions exist (denoted by the small circles in figure 3). With increasing gain the movement pattern stabilizes at increasing hopping heights ($h = 5$, 7.9 and 11.4 cm, respectively). After a disturbance the system returns to the steady-state condition within a few steps (arrow tracings in figure 3).

(c) Elastic leg operation

In experiments on human hopping, spring-like leg operation with varying leg stiffness k is observed. To investigate the elasticity of stable hopping patterns achieved with F+, the model behaviour is mapped throughout the feed-

back parameter space (STIM0, G; figure 4). For feedback adjustments leading to stable hopping (shaded area in figure 4a), the elasticity coefficient C_{EL} is calculated (equation (2.10)). Different parameter combinations result in stable hopping (STIM0 < 0.2, $G > 1/F_{\max}$) with largely varying elasticities ($0.7 < C_{EL} < 0.97$). Only within a smaller region (STIM0 < 0.2, $1/F_{\max} < G < 3.5/F_{\max}$) does the elasticity coefficient exceed the reference value of $C_{EL} = 0.92$ ('reference region' in figure 4a).

In the reference region, with increasing stimulation bias and feedback gain the leg stiffness k and the hopping frequency f shift from 9 to 27 kN (figure 4b) and from 1.4 to 3 Hz (figure 4c), respectively. The range of hopping height, from 0 to 8.8 cm (figure 4d), allows different control strategies. For instance, starting from the parameter set of the largest height (STIM0 = 0.065, $G = 1.32/F_{\max}$, indicated by the arrow in figure 4d), the hopping height decreases and the leg stiffens if bias and gain are increased. Alternatively, the hopping height decreases with little change in the leg stiffness if merely the gain is decreased.

To test the reliability of the elastic leg regime ($C_{EL} \geqslant 0.92$), a sensitivity analysis is performed for STIM0 = 0.145 and $G = 1.84/F_{\max}$, guaranteeing the largest feedback parameter tolerance within the reference region (intersection of dashed lines in figure 4a; leg force and muscle activation during contact as well as leg force–length relation shown in figure 5). The tolerance range fulfilling $C_{EL} \geqslant 0.92$ covers a considerable range of physiologically supported values for the investigated muscle parameters reference strain ε (1–6.5%), eccentric force enhancement N (1.4–1.6), maximum shortening velocity $v_{\max}$ (-10.6 to -13.4 l_{opt} s^{-1}) and width of the force–length relationship w (0.33–0.45 l_{opt}). Similarly, the model behaviour is robust to changes in the signal propagation delay Δ_P (tolerance range of 13–18 ms).

4. DISCUSSION

In this study, we investigated the potential role of single-loop muscle reflexes in periodic bouncing tasks. Although a rather simple approach to addressing human reflex pathways is applied, a surprisingly successful strategy could be identified: positive muscle force feedback can generate and stabilize hopping patterns over a large range of hopping heights ($h_{\max} = 16.3$ cm, up to 85% of the model's maximum hopping height). Moreover, for moderate hopping heights (up to 8.8 cm) spring-like leg behaviour is achieved with a leg stiffness of between 9 kN m^{-1} and 27 kN m^{-1}.

The identified feedback is probably the simplest decentralized control strategy for bouncing tasks. Replacing a predefined ('voluntary') stimulation pattern with adaptive control based on the actual muscle–skeleton dynamics could serve as an efficient and reliable alternative to central motor control. Out of the investigated reflex pathways, L+ could also generate periodic hopping, but its hopping performance was clearly limited ($h_{\max} = 9.3$ cm). However, owing to our simplified approach, we cannot exclude the possibility that other feedback signals (e.g. joint position), signal combinations (e.g. fibre length and velocity) or reflex structures may also succeed in bouncing tasks.
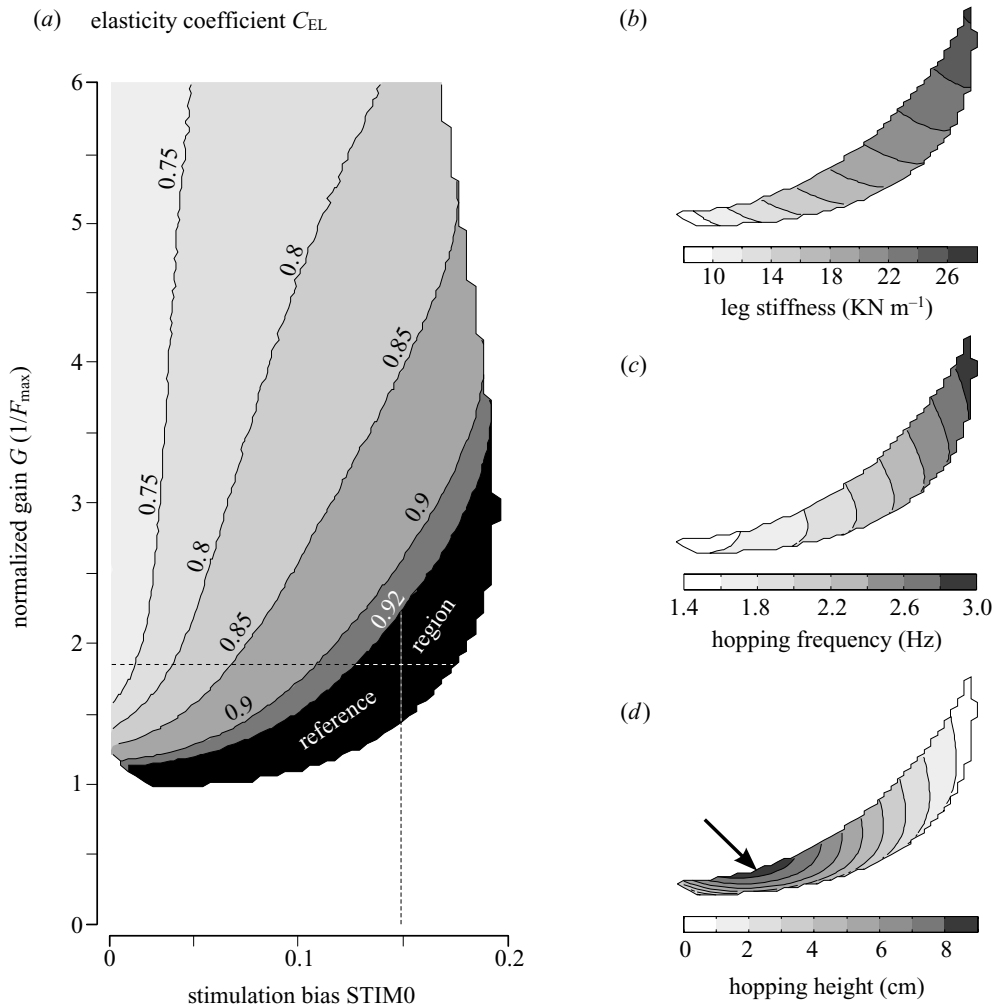
(a)   elasticity coefficient C_{EL}

(b)

leg stiffness (KN m^{-1})

(c)

hopping frequency (Hz)

(d)

hopping height (cm)

Figure 4. Elastic leg behaviour. The model behaviour using F+ is mapped throughout the feedback parameter space (STIM0, G). (a) The elasticity coefficient C_{EL} for stable hopping patterns (shaded area) is shown. The intersection of the dashed lines refers to the parameters used for sensitivity analysis (STIM0 = 0.145, G = 1.84/F_{max}; see figure 5). (b–d) In the reference region the elasticity coefficient exceeds the reference value of C_{EL} = 0.92 (see (a)). Here, the corresponding (b) leg stiffness, (c) hopping frequency and (d) hopping height are shown. The arrow indicates the maximum hopping height within the reference region (STIM0 = 0.065, G = 1.32/F_{max}).
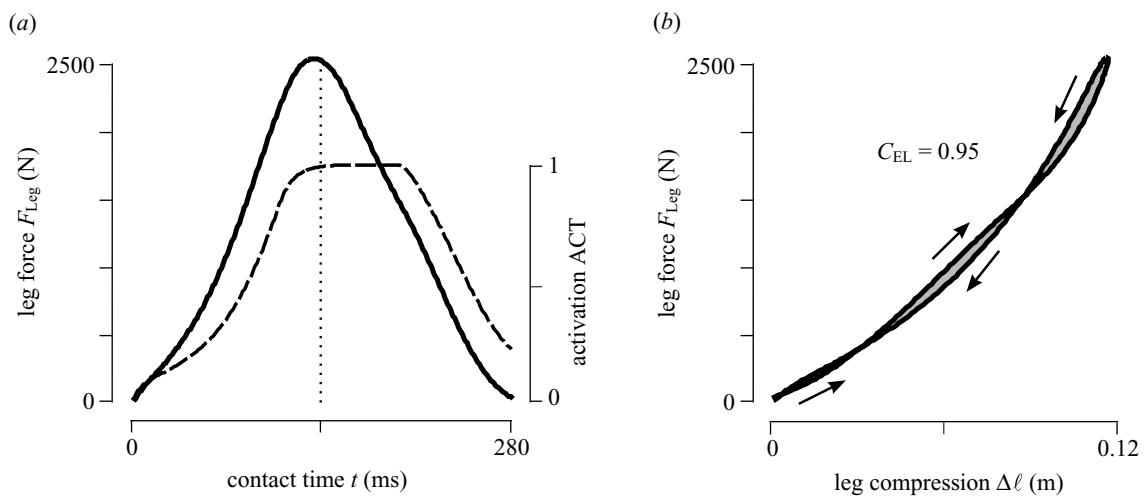
(a)

(b)

Figure 5. Example of the hopping pattern using F+. (a) The leg force (solid line) and muscle activation (dashed line), and (b) the leg force–length curve ($\Delta \ell = \ell_{F-y}$) of the steady-state hopping pattern used for the sensitivity analysis are shown (STIM0 = 0.145, G = 1.84/F_{max}). The shaded area enclosed by the force–length curve depicts the area A used for the calculation of the elasticity coefficient C_{EL} (equation (2.10)).

(a) Comparison of optimal stimulation and reflexes

If subjects are asked to jump as high as possible, a counter-movement jump is observed. Starting in stance, the subjects bent their legs prior to an extension with fully activated extensor muscles providing maximum thrust (e.g. Bobbert & Van Ingen Schenau 1988). This implies that the minimum leg position achieved y_{min} strongly influences the maximum hopping performance h_{max}, which indeed is observed among the applied control schemes (see figure 2b). However, complete leg flexion would exceed the ascending limb of the extensor force–length relationship (equation (2.5)), and the system would fall down owing to insufficient force generation. Because large hopping heights result in high impact velocities, proper braking forces have to be applied in the early stance phase. Here, the eccentric operation of the extensor force–velocity relationship (equation (2.6)) provides adequate force to solve this issue. For instance, the OPT is characterized by an initial activation (force) peak sufficient to redirect the movement at the minimum position $y_{min} = 59$ cm. Similar force peaks are known from drop jump experiments (e.g. Voigt *et al.* 1995). Hereafter, full muscle activation is required to reach the maximum steady-state hopping height $h_{max} = 19.6$ cm.

But how closely can the considered feedbacks imitate this control strategy? The shapes of the feedback-based activation patterns are largely constrained by the available sensory information. For instance, the stretch-shortening cycle of the extensor muscle during the rebound leads to a negative slope of the CE–velocity time-series. To achieve increasing muscle activation during leg flexion ($P = v_{CE} - v_{off}$), *velocity feedback* requires a *negative* feedback scheme (V−). Although applicable at first glance, this feedback inherently destabilizes periodic hopping patterns. For instance, an increased hopping height leads to larger eccentric velocities v_{CE} (increased impact). Instead of damping, the negative feedback delays the development of increasing muscle activation. Initially, this results in a larger hopping height (as muscle activity is shifted towards the concentric phase). However, a self-amplifying cascade is induced, further increasing the impact velocity and delaying the muscle-activation growth. Inevitably exceeding a critical impact velocity, the leg collapses during stance.

Both the length ($P = l_{CE} - l_{off}$) and the force signal ($P = F_{MTC}$) increase during leg bending. Here, positive-feedback schemes with a small initial stimulation bias result in an increasing muscle activation during stance. L+ is characterized by a rapid increase of $P(t)$, which still produces considerable breaking forces. To delay this fast build-up and, therefore, to reach a lower position y_{min} during stance, the offset value ℓ_{off} is used. The length of the CE at touch-down is $\ell_{CE,TD}$. During leg compression the muscle lengthens and an offset value $\ell_{off} > \ell_{CE,TD}$ suppresses any signal output until ℓ_{CE} reaches ℓ_{off} (left asterisk in figure 2b). However, as the ℓ_{CE} signal is almost symmetric about the midstance, the suppression is equally present during late stance (right asterisk in figure 2b). Consequently, the amount of positive work is limited and only moderate maximum hopping heights are achieved ($h_{max} = 9.3$ cm).

F+ has no sensory offset. Here, a different mechanism prolongs the activation build-up. The proprioceptive signal $P = F_{MTC}(t)$ depends on the instantaneous muscle activation $ACT(t)$, the normalized force–length $f_l(t)$ and force–velocity $f_v(t)$ relationships, and the maximum isometric force F_{max} (equation (2.4)). The activation itself depends on the stimulation history, according to the excitation–contraction coupling (equation (2.8)), which has a characteristic delay Δ_{ECC}. Thus, the contribution of the gained and time-delayed feedback signal $P(t - \Delta_P)$ to the muscle stimulation $STIM(t)$ is proportional to the preceding stimulation signal $STIM(t - \Delta_P - \Delta_{ECC})$ and to the muscle state $M(t - \Delta_P) = f_l(t - \Delta_P)f_v(t - \Delta_P)$. Assuming that M is constant, the activation development is characterized by exponential growth (see Appendix A). Although it is modulated by the muscle dynamics $M(t)$, the initial slope of the activation build-up can be adjusted using different feedback gains G, and the maximum activation can be delayed until leg extension. As a result, F+ yields an almost twofold better hopping performance than L+. The exponential growth of muscle activation is an appropriate response to the breaking in the eccentric phase of periodic bouncing.

An initial suppression of the sensory signal, to a certain extent, improves the hopping performance for positive feedbacks. For each reflex, the suppression can be tuned with the signal propagation delay Δ_P. As a result, the maximum hopping height can almost be reached using either positive length or force feedback. The required 'optimal' delay is larger for length ($\Delta_P \sim 60$ ms) than for force feedback ($\Delta_P \sim 25$ ms). This suggests that length feedback could control hopping tasks using longer latency reflex loops. However, the longer the signal delay is, the more sensitive the system gets with respect to external disturbances. Here, additional control effort would be required. By contrast, F+ is an autonomous rapidly adapting control scheme well suited for the short contact periods in bouncing gaits.

(b) Task variability of positive force feedback

F+ has been investigated previously in an experimental study. By converting the measured ground reaction force into extensor-muscle stimulation, Prochazka *et al.* (1997b) showed that this reflex successfully operates in load-compensation tasks. In a simulation study they further demonstrated that the muscle's force–length relationship provides an inherent feedback gain adaptation (Prochazka *et al.* 1997a), which—if opposing forces are present (e.g. antagonistic muscle forces, gravity)—prevents the traditionally observed destabilizing effect of F+ (Van Helm & Rozendaal 2000).

In our study we observe a similar behaviour. For small gains ($0 < G < 1/F_{max}$) hopping does not occur (figure 4a), but the system stabilizes in stance at a leg position characterized by the equilibrium of muscle and gravitational forces (not shown in figure 4a). Any further leg extension reduces the muscle force (owing to the force–length relationship of the shortening extensor muscle) and the resulting net force restores the equilibrium position. The opposite holds for leg bending.

With increasing gain ($G > 1/F_{max}$), F+ leads to periodic hopping at different steady-state apex heights (examples shown in figure 3). Although the same reflex is applied,

the stabilization here is based on a different mechanism. Instead of the muscle's force–length relationship, the force–velocity relationship becomes crucial. For instance, an increased apex height results in a larger landing velocity. Owing to the amplified muscle response (force–velocity relationship), the force builds up more rapidly. Since the feedback gain remains constant, the muscle force production is inherently shifted towards the eccentric phase. The system compensates for the disturbance through damping until the steady-state apex height is restored within the next few ground contacts (the opposite holds for decreased apex heights). Consequently, the stability of hopping is unaffected even if no force–length dependency $f_l(\ell_{CE}) = 1$ is assumed.

This suggests that the proposed muscle-reflex system is an adjustable biological actuator suited to more than a single movement task. The flexibility ranges from load compensation over elastic leg operation to maximum-performance hopping, and clearly benefits from the muscle properties; thereby elucidating these properties from an integrative perspective, which may help to design technical actuators adapted to legged locomotion.

(c) Leg stiffness as an emergent property

Since the observation that, during bouncing gaits, the legs of animals and humans behave in a spring-like manner, 'leg stiffness' has become a key parameter in investigating these gaits. For instance, it has been demonstrated that leg stiffness is hardly affected by running speed (He *et al.* 1991; Farley *et al.* 1993), indicating passive elastic elements (e.g. tendons, ligaments) as the likely origin of spring-like leg operation. However, humans adapt their leg stiffness if subjected to constraints (e.g. hopping frequencies or height (Farley *et al.* 1991; Seyfarth *et al.* 2001); running stride frequencies (Farley & Gonzalez 1996)) or environmental changes (e.g. surface stiffness (Ferris & Farley 1997; Ferris *et al.* 1998; Kerdok *et al.* 2002)). Consequently, this posed the question of how leg stiffness is controlled at the muscle–skeleton level. Experimental and simulation studies suggested that ankle-joint moment generation plays an important role (Farley & Morgenroth 1999). Although this indicated the participation of neural control in the adjustment of leg stiffness, evidence of what the appropriate control resulting in bouncing gaits could actually be remained elusive.

In this study, F+ of the extensor muscle(s) is suggested as an appropriate control scheme. For certain feedback parameters ('reference region', figure 4*a*), it enables elastic leg operation within a considerable range of leg stiffness (between 9 and 27 kN m^{-1}; figure 4*b*), hopping frequency (from 1.4 to 3 Hz; figure 4*c*) and hopping height (up to 8.8 cm; figure 4*d*). Experimental studies on human hopping at different frequencies (1.5–3 Hz) report a similar correspondence to the leg stiffness (10–30 kN m^{-1}; Farley *et al.* 1991; Seyfarth *et al.* 2001).

The change of hopping height within the reference region reveals a simple control strategy for the stride energy. If the feedback stimulation bias is fixed at STIM0 = 0.065, an increased gain leads to an increased steady-state stride energy (hopping height) while the leg stiffness remains almost constant. Reconsidering the experimental results showing that leg stiffness is hardly affected by speed (i.e. system energies) (He *et al.* 1991;

Farley *et al.* 1993), this might indicate that the stride energy is the parameter that should be controlled in animal and human locomotion. Here, leg stiffness itself emerges from the muscle-reflex dynamics adapting external constraints.

(d) From hopping to running

In a previous study, we identified a movement criterion for running with elastically operating legs: a proper adjustment of the landing angle of attack to the leg stiffness results in self-stabilized and robust running (Seyfarth *et al.* 2002). Using this criterion, only two conditions have to be fulfilled for running based on a muscle–skeleton system: (i) elastic leg operation and (ii) stabilization of the stride energy. Positive muscle force feedback meets both requirements. Hence, the movement criterion can be successfully applied by selecting an angle of attack appropriate to the emergent leg stiffness (figure 6). This suggests that the identified muscle-reflex mechanism might also be an efficient and powerful concept for running. To our knowledge, it is the first model describing running within such a framework.

(e) Reflex-generated motor control

The control of locomotion can be divided into (central) feed-forward commands and (decentralized) feedback responses. It is assumed that the feed-forward component generates a time-varying cyclic muscle-activation pattern (referred to as 'background activity') resulting in basic locomotor functions (e.g. as found in partially deafferented cats; Goldberger 1977). The identification of central pattern generators (CPGs) in animals as diverse as invertebrates and mammals supports this hypothesis (for a review see Orlovsky *et al.* 1999). Reflex responses can modulate this feed-forward activation pattern. However, the functional relevance of this modulation in undisturbed locomotion remains largely unclear (Zehr & Stein 1999).

For instance, experimental studies addressing extensor-muscle activities in human hopping and running have identified a short-latency (35–45 ms) stretch-reflex response following touch-down (Melvill Jones & Watt 1971; Dietz *et al.* 1979; Voigt *et al.* 1998). This reflex is mainly attributed to proprioceptive information from muscle spindles (Ia-afferents), although contributions from GTOs (Ib-afferents) cannot be ruled out. Such rapid responses are likely to reduce extensor lengthening ('muscle yield') after landing and, consequently, could enhance the loading of the corresponding tendons. Hence, it is suggested that the observed stretch reflex is of functional importance for the generation of leg stiffness during bouncing gaits. However, further contributions of this reflex (e.g. at longer latencies) to the stance phase (*ca.* 200–400 ms) are not observed. It is supposed that here the overlap with the (centrally initiated) background activity may conceal the direct observation (Voigt *et al.* 1998; Funase *et al.* 2001).

Further information about potential reflex contributions can be obtained by evoking the H-reflex (the electrically elicited analogue to the stretch reflex). Comparing standing with the stance phases of walking and running, such experiments indicate a progressive inhibition of the stretch-reflex activity from standing to walking to running (Capaday & Stein 1987; Ferris *et al.* 2001). Sinkjaer *et al.*
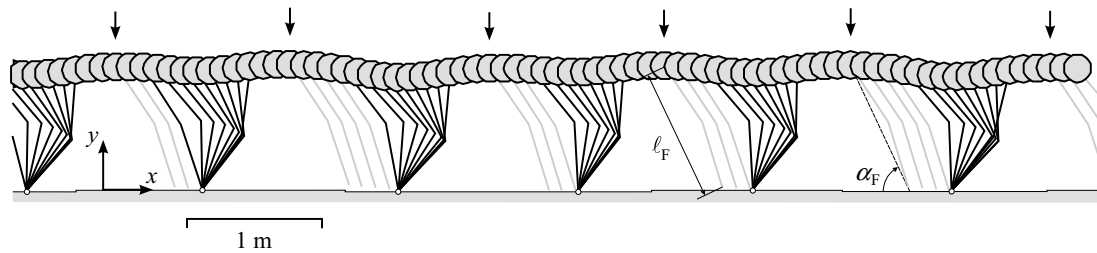
Figure 6. Robust running (ground irregularities ± 0.5 cm) using F+ (STIM0 = 0.185, $G = 1.4/F_{\max}$). The stick figures correspond to time intervals of 20 ms. The arrows denote the apices, at which the virtual leg with a length $\ell_F = 0.99$ m and an angle of attack $\alpha_F = 65°$ (mean leg stiffness of 16.5 kN m^{-1}) is introduced during flight.

(2000) suggested that this reflex could have little or no contribution to the muscle activity during normal walking, although compensatory reflex responses to large disturbances may still occur (Morita *et al.* 1998). For hopping and running, this could explain the extensor stretch-reflex response following touch-down (a large disturbance) without the observation of later contributions, suggesting that, for the remaining stance phase, the centrally thought background activity would be essential. Experiments where extensor muscles fatigue further support this hypothesis. For instance, during marathon running the stretch-reflex response significantly decreases (Avela & Komi 1998). However, the subjects can still run.

The present study predicts that the muscle activity usually associated with the background activity is not just a central contribution, but is largely shaped by F+. In contrast to the role of feedbacks as mechanisms for reacting to disturbances, here the reflex organizes the muscle activation pattern. The result is a task-specific uniform leg force pattern as observed across species and individual morphologies. This reflex-based force generation is, however, restricted to the stance phase and may depend on other structures such as CPGs triggering the phases of the gait cycle. In fact, load receptor reflexes themselves may be involved in the initiation of phase transitions (Pearson 1995). Although we did not address a possible influence of reflex schemes on the flight phase, it seems that the self-organizing dynamics of the neuromechanical system may significantly contribute to the coordination of legged locomotion. Synchronized and supervised by central commands including CPGs, this self-organization could largely simplify the required control effort.

But how far is a positive feedback pathway supported by experimental observations? Although traditionally associated with negative feedback schemes, experimental studies on leg extensor muscles have shown a reflex reversal to F+ in quadruped standing and during the stance phase of quadruped walking (Pearson & Collins 1993; Gossard *et al.* 1994; Pratt 1995). Subsequent investigations suggested a similar reflex reversal during the stance phase of human walking (Stephens & Yang 1996). Although there is increasing experimental evidence for F+ as homonymous reflex, its functional contribution to the stance phase of the locomotor cycle remains controversial. Some studies suggest that this reflex might appropriately modify the extensor-muscle force during stance depending on the carried load (Pearson & Collins 1993; Pratt 1995; Prochazka *et al.* 1997*b*). However, it is still unclear whether afferent information from GTOs serves this function (Fouad & Pearson 1997; Sinkjaer *et al.* 2000). Experimental investi-

gations of this reflex pathway in bouncing gaits are lacking and should be the subject of future research.

(f) Summary

In our understanding, biological locomotor systems are highly redundant systems, which probably have various control strategies at their disposal to manage a distinct movement objective. In the final instance, central motor commands will resolve the issue. However, the more a movement task becomes routine, the more the evolution of decentralized largely autonomous solutions embodied in morphology seems plausible. F+ represents such a local control strategy. Whether it can be verified in experiments or not, we feel that the consideration of muscle reflexes, not only as disturbance responses but also as an integrated part of biological actuation, is important to understanding the control of locomotion in animals and humans.

APPENDIX A

The comparison of the proprioceptive signals $P = \ell_{CE} - \ell_{off}$, $P = v_{CE} - v_{off}$, $P = F_{MTC}$ (see § 2c) indicates that they are all influenced by the muscle dynamics (time-series of force–length and/or force–velocity relationships, owing to equations (2.4), (2.5) and (2.6)). In contrast to the muscle fibre length and velocity feedbacks, the muscle force signal is further influenced by the dynamics of the muscle activation ACT, which itself is related to the history of the stimulation signal STIM (equation (2.8)).

Assuming that: (i) the stimulation does not exceed the saturation level (STIM$(t) \leqslant 1$); and (ii) the muscle activation instantaneously follows the stimulation ($A \equiv$ STIM), for positive muscle force feedback the time-series of the stimulation signal (2.9) simplifies to

$$\text{STIM}(t) = \begin{cases} \text{STIM0} & t < \Delta_P, \\ \text{STIM0} + G_F M(t - \Delta_P)\text{STIM}(t - \Delta_P) & t \geqslant \Delta_P, \end{cases}$$
(A 1)

with $M(t - \Delta_P) = f_1(l_{CE}(t - \Delta_P))f_v(v_{CE}(t - \Delta_P))$ describing the muscle dynamics and $G_F = G F_{\max}$ representing the normalized gain factor.

Using equation (A 1), the stimulation STIM(t) at time t can be calculated by dividing the time-scale into equal intervals of the feedback delay Δ_P. Beginning at the last interval, which includes t, the actual stimulation is iterat-

ively substituted with the corresponding stimulation from the preceding interval. This procedure yields the expression

$$\text{STIM}(t) = \text{STIM0}\left[1 + \sum_{k=1}^{n}\left\{G_F^k \prod_{l=1}^{k} M(t - l\Delta_P)\right\}\right], \ n \geqslant 0$$
$$n\Delta_P \leqslant t < (n + 1)\Delta_P, \tag{A 2}$$

for the time-series $\text{STIM}(t)$. From this equation, the change in muscle stimulation between two consecutive intervals is found to be

$$\begin{aligned}\Delta\text{STIM} &= \text{STIM}(t) - \text{STIM}(t - \Delta_P)\\ &= \text{STIM0} + [G_F M(t - \Delta_P) - 1]\\ &\quad \times \text{STIM}(t - \Delta_P).\end{aligned} \tag{A 3}$$

As shown in equation (A 3), the development of the muscle stimulation $\text{STIM}(t)$ follows a modulated natural growth or decay function. Provided that $G_F M(t - \Delta_P) > 1$, the stimulation rises exponentially with each interval Δ_P. But, as soon as the muscle dynamics enforces a negative value on the right side of equation (A 3), the stimulation decreases.

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